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Highlights

1. Evidence shows animal water balance driving top-down effects in food webs.
2. Traits may help predict ecological responses to moisture.
3. Smaller animals, like arthropods, are particularly likely to be water-limited.
4. Water-limitation may interact with predation or demand for energy or nutrients.
5. Ecological effects of animal water balance may be widespread and common.

Implications of animal water balance for terrestrial food webs

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Abstract

Recent research has documented shifts in *per capita* trophic interactions and food webs in response to changes in environmental moisture, from the top-down (consumers to plants), rather than solely bottom-up (plants to consumers). These responses may be predictable from effects of physiological, behavioral, and ecological traits on animal water balance, although predictions could be modified by energy or nutrient requirements, the risk of predation, population-level responses, and bottom-up effects. Relatively little work has explicitly explored food web effects of changes in animal water balance, despite the likelihood of widespread relevance, including during periodic droughts in mesic locations, where taxa may lack adaptations for water

conservation. More research is needed, particularly in light of climate change and hydrological alteration.

Introduction

Maintaining water balance is a key challenge to the evolution of terrestrial organisms. Dehydration can have severe and immediate consequences, including declines in growth [1], reproduction [2-5], and survival [6, 7]. Varied adaptations to meet this challenge have long fascinated biologists, who have developed methods of measuring fluxes of water into and out of organisms, generating animal water budgets (Figure 1A) [8-14]. Physiological ecologists use these approaches to quantify effects of adaptations and climate on water balance [11, 15-20]. But how does variation in animal water balance alter species interactions and food webs? Until recently, this topic had received relatively little attention (but see [21]). Instead, food web ecologists often focused on effects of variable moisture from the bottom-up, via effects on plants, with energy or nutrients driving food web responses (e.g. [22-28]). For instance, Banfield-Zanin and Leather [24] recently found increased per capita consumption of aphids by lady beetles when aphids were reared on drought-stressed spruce trees, which led to smaller aphids. Other studies have documented significant bottom-up effects from precipitation associated with ENSO cycles [26, 29-31]. While bottom-up effects are likely to be important, top-down effects, where variation in animal water balance affects lower trophic levels, also deserve attention.

Recent evidence suggests that water can greatly influence food webs from the top-down [32, 33], altering the strength of species interactions [33-36] and trophic cascades [37]. McCluney and Sabo [37] found that under dry conditions, large spiders in a semi-arid floodplain suppressed populations of crickets and reduced herbivory (a trophic cascade), but with added

water, large spiders had no effect on crickets and an almost neutral effect on herbivory. In another study, Deguines *et al.* [32] found that direct effects of precipitation on animals were commonly stronger than indirect, plant-mediated, bottom-up effects in a semi-arid grassland over 7 years of variable precipitation. Moreover, Hagan *et al.* [36] found potential human health implications, because dehydrated mosquitoes increased blood-meal feeding. Careful consideration of water balance models can help identify mechanisms of these effects (Figure 1A). Because metabolic water production and atmospheric uptake are generally (but not always, see [20, 38-40]) small fluxes [11, 38, 39], to prevent dehydration, declines in drinking water must often be met by either A) declines in water loss rates (with associated energetic or reproductive costs), or B) increases in consumption of moist food (Figure 1B, 1C, [33]; if food is dry, declines in water often result in decreases in consumption [41, 42]). Thus, with variable environmental moisture (precipitation, moist soils, waterbodies), terrestrial animals should experience periods of heightened demand for moist food, which often is found in the form of other living organisms, thus resulting in stronger per capita trophic interactions (Figure 1B). This mechanism linking moisture to trophic interactions may be complicated by intra- and interspecific variation in water loss rates, optimal and minimum hydration states, behavior (e.g. ability to wait for better conditions), food nutrient and water content and density, trade-offs with other constraints (e.g. predator avoidance; Figure 1B, 1C), population-level responses, and bottom-up effects. Here I review recent advances in our understanding of the drivers, frequency, and consequences of variation in animal water balance and propose conceptual models for understanding food web implications.

Variation with Physiological, Behavioral, and Ecological Traits

Physiological traits can greatly influence organismal water loss rates and ability to tolerate dehydration [11, 16, 19]. One key trait is body size. Smaller organisms, like terrestrial arthropods, have greater surface area to volume ratios and this should result in greater relative water loss rates, due to the importance of cutaneous water loss as a key water efflux [16]. Moreover, smaller organisms, including most insects ($< \sim 70$ g), have higher rates of water loss relative to metabolic rate (Figure 2), suggesting greater likelihood of water limitation than energy limitation. This result emerges from re-analysis of data from Woods and Smith [43], who published a universal model linking gas exchange (a proxy for metabolic rate in animals) and water loss rates. The data suggest there is a difference in scaling of body size with metabolic rate versus body size with water loss rate. Thus, water loss rates tend to surpass metabolic rates in smaller organisms.

Evidence of greater water loss rates for smaller animals has consequences. For instance, smaller ants may die from dehydration more quickly than larger (e.g. [6, 7]). In general, dehydration should present a more time-sensitive constraint in smaller animals (although these animals may be better able to seek out moist microenvironments). What are the potential food web consequences? One might expect a greater propensity of smaller organisms to display greater increases in moist food consumption, and thus stronger trophic interactions under periodic declines in environmental water sources. This suggests that terrestrial arthropod food webs may often be driven by water more than energy (i.e. water webs, *sensu* [34]).

Could physiological traits other than body size influence food webs through water balance mechanisms? Very little work has investigated this question. But it seems likely that variation in excretory systems, cuticular hydrocarbons, critical water content (lower limits), and

other physiological traits could mediate responses of consumption behavior, species interactions, and food webs to variation in environmental moisture.

Behavioral traits can also greatly influence how animals respond to variability in water sources. For example, Davis and DeNardo [44] found that water supplementation stimulated above-ground Gila monster activity, potentially allowing for greater rates of predation. This finding differs from the earlier general expectation and the findings of others [34, 37] that water supplementation should lower per capita predation due to decreased demand for moist food. The explanation could lie in the fact that taxa that have greater ability to seek shelter, greatly lower rates of water loss, and wait for better conditions, may choose to reduce activity in response to substantially reduced environmental moisture rather than increase consumption of moist food (shifting the left side of the curve in Figure 1C to the right). Thus, water supplementation would lead to increases in consumption for taxa that are “dormant” during periods of low moisture. This behavior is probably more common in long-lived, large-bodied animals with an ability to burrow deep belowground; however, some animals (e.g. tardigrades, nematodes, Antarctic midges, spider beetles, bed bugs) have the ability to substantially lower water loss rates, tolerate extreme desiccation, and/or enter resistant life stages—but these capabilities appear mostly restricted to extremely small, desert, or blood-feeding taxa [11, 19, 45-48].

Excluding groups that are able to wait for better conditions, most small, and especially short-lived species (most terrestrial arthropods), should be particularly constrained in their behavioral responses to periodic reductions in environmental moisture, because of short windows for reproduction. Reproductive periods generally occur in spring and summer growing seasons, which can be impacted by drought events with low predictability. The ability to maintain activity during these periodic growing season droughts should have substantial reproductive benefits,

115 especially for taxa that live only one or two years, like many arthropods. Increasing consumption
116 of moist food may allow arthropods and other animals to maintain activity and reproductive
117 effort during periodic environmental water declines.

118 Variation in ecological traits may also be fundamentally important in mediating effects of
119 periodic reductions in environmental moisture on trophic interactions. Expected shifts in trophic
120 interactions to meet water demands depend on the degree to which an animal is capable of
121 switching to alternative food sources. Generalists may be able to switch to food items of higher
122 water content under reduced environmental moisture. For example, field crickets are generalist
123 consumers and have been shown to consume moist vegetation when environmental water sources
124 are limited [34, 37]. Specialists, on the other hand, may be unable to switch to alternative food
125 sources of higher moisture content, instead being forced to consume greater amounts of existing
126 lower moisture food (compensatory feeding), or suffer dehydration. Moreover, herbivores or
127 omnivores capable of eating plant materials may have generally greater access to moist food
128 sources than strictly carnivorous species (e.g. most spiders). Thus, differences in ecological traits
129 could influence consumption behavior in ways that could have important implications for food
130 webs (discussed more below).

131 In general, there is a stark contrast between substantial existing research documenting
132 how physiological traits influence animal water balance and the dearth of studies linking
133 physiological, behavioral, or ecological traits to food web dynamics via water balance
134 mechanisms. However, I suggest that a trait-based approach, examining water-balance relevant
135 traits, could be a powerful method for predicting food web responses to variation in
136 environmental moisture.

137

Tradeoffs with Other Constraints

Water balance may be a strong driver of consumption behavior, especially for small animals like arthropods, but it is likely that these behaviors are simultaneously modified by tradeoffs with other constraints (Figure 1B). For instance, risk of predation may modify how an organism responds to changes in water balance (Figure 1C). Hochman and Kotler [41] found that risk of predation lowers dry food consumption (increases giving up density, the density of food at which the animal no longer forages) and water availability increases dry food consumption (lowers giving up density) for Nubian ibex. Similarly, Valeix *et al.* [49] found that African herbivores were more likely to drink from water holes under drier conditions or with less perceived predation risk. McCluney and Sabo [37] found suggestive evidence for an interaction between predation risk and water availability on consumption. Large spiders reduced rates of herbivory by crickets under dry conditions, with added moist leaves, despite a lack of direct effect of spiders on cricket abundance. This suggests that fear of predation reduced the time crickets spent consuming moist food under dry conditions with abundant moist food. With moderate addition of drinking water, this effect disappeared (and slightly reversed, with large spiders slightly increasing rates of herbivory by crickets, possibly due to crickets avoiding water resource patches being used by spiders in preference for moist vegetation without spiders). More research is needed to better explore the tradeoffs between dehydration and predator avoidance behavior in influencing consumption (Figure 1C).

Recent efforts in nutritional physiology and ecology that view limitation through a lens of ratios of potentially limiting nutrients have led to substantial scientific progress [50-52]. Optimal growth or reproduction is likely achieved by a balance of intake of various nutrients and energy containing molecules. Imbalances between requirements and ratios in food items may alter

species interactions by stimulating compensatory feeding (*sensu* [53]). As outlined here, water may be another key factor influencing the growth, reproduction, and species interactions of animals. Integrating water into these nutritional frameworks, comparing demand for water relative to energy or nutrients, and ratios of these dietary factors within food, could be a strong approach to predicting species interactions (Figure 1B, 1C, suggested by [52]). For instance, McCluney and Sabo [37] found that the effect of large spiders on small spiders versus crickets changed with water—large spiders reduced crickets under dry conditions, but not wet, and the effect of large spiders on small spiders also varied with water (lack of post-hoc difference reduced interpretability). Together these results caused the authors to suggest that large spiders may have switched from consuming water-laden crickets to consuming energy- or nutrient-rich small spiders with added water availability. Similarly, in another study, Frizzi *et al.* [54] found that water supplemented ants subsequently consumed the most of a high-sucrose concentration liquid diet. Thus, with increased environmental water, generalists may tend to consume more energy- or nutrient-rich food sources of lower water content (Figure 1C).

Water availability could also interact with behavior and food quality in other ways to influence consumption. One might expect that omnivorous predators (e.g. many beetles and ants) could increase herbivory when moisture declines. If an omnivorous predator is an active hunter, increased herbivory could lead to decreased activity by the omnivorous predator (with further water balance benefits for the predator), which could decrease perception of predation risk by herbivores, which could in turn increase their rates of herbivory (Figure 1C). Thus, there could be multiple pathways by which decreased water availability could increase herbivory. However, if predators are strictly carnivorous, they would be expected to inhibit herbivory under periodic declines in environmental moisture, or if omnivorous predators are not active hunters, perception

of predation risk may go unchanged. Again, behavioral and ecological traits may be important in predicting responses.

Decreased water availability could also potentially reduce decomposition due to dietary trade-offs. Omnivorous detritivores (e.g. crickets), might decrease consumption of dry detrital materials in favor of increasing consumption of moist foods (leaves, other animals) in response to a dry period or conditions [55]. Thus, increased water limitation could make food webs more “green” rather than “brown,” with potential reductions in food web stability [56, 57]. More research is needed to better test for these potential effects.

Short-term vs Long-term

Most of the research and ideas described thus far have focused on the effects of animal water balance on short-term changes in *per capita* consumption. These ideas should be quite relevant under realistic scenarios of periodic fluctuations in moisture availability. And per capita interactions can influence food web dynamics on their own [58]. However, continuous and prolonged changes in water availability may have population-level effects that could differ from per capita effects. Drought may lead to increases in *per capita* consumption of moist food as described above, but over the long-term, may lead to decreases in abundance of consumers [59], via reductions in growth [1], reproduction [2-5], and survival [6, 7]. Thus, prolonged drought may initially increase the strength of population-level trophic effects, as per capita consumption increases without significant population changes, but then could decrease the strength of these population-level interactions as populations of consumers decline, even if per capita effects are still strong. The relative degree to which populations of different taxa decline with prolonged drought could again be dependent on many of the same physiological, behavioral, and ecological

traits outlined above. Systematic variation in these traits could help predict changes in populations as well as changes in per capita effects. For instance, if generalists are more sensitive to changes in environmental moisture than specialists, the frequency of omnivory might first increase, but then decrease with drought duration.

Interacting top-down and bottom-up effects

Although this review focuses on top-down effects of variation in moisture, mediated by animal water balance, bottom-up effects are likely to interact with top-down [33]. The relative importance of each likely varies among systems and over time (e.g. with ENSO events [60]), but it is important to point out that direct effects of environmental moisture on animals can potentially exceed bottom-up in real-world scenarios, over relatively long time frames [32]. Thus, both top-down and bottom-up effects likely contribute substantially to observed responses [32, 33, 60].

A number of studies have specifically focused on bottom-up effects of plant water balance, sufficiently that Huberty and Denno [27] synthesized existing studies and posed the “pulsed-stress hypothesis,” suggesting that continuous plant water stress reduces herbivory by phloem-feeding taxa, but that periodic pulses of plant water stress can increase herbivory by this group (they hypothesize due to increases in N). Patterns for chewing insects were less clear. On the other hand, multiple studies of pulsed rainfall inputs to arid or semi-arid areas, often associated with ENSO cycles, suggest that bottom up stimulation of plant productivity can stimulate production of rodents and other herbivores, then predators, often leading to delayed top-down effects [22, 25, 26, 29, 30, 60-62]. These studies generally assume that the top-down

effects following precipitation pulses are driven by increasing numbers of predators, but I suggest that increasing demand for moist food with drying may also contribute.

Many unanswered questions remain about how plant and animal water balance interact to influence food webs. For instance, do drought pulses lead to reduced food web stability and thus diversity due to the combination of higher per capita trophic interactions and reduced plant growth [33]? Or do drought pulses lead to greater coexistence and diversity (temporal β -diversity) by selectively reducing abundance of those plant and animal taxa that would be dominant under moist conditions, but are highly sensitive to drought? In light of climate change, urbanization, and hydrologic alteration, there is great need for a more thorough consideration of the interaction between top-down and bottom-up effects of moisture over both the short and long-term.

Spatiotemporal Variation in the Frequency of Water-mediated Trophic Interactions

How commonly does animal water balance influence food webs? One would expect animal water balance to be infrequently important in perennial wetlands, given high and consistent water availability (Figure 3; in these locations, lower water content, nutrient-rich food may be preferred, Figure 1C, [54]). Some might expect animal water balance to be most important for food webs in very dry, desert locations, but the limited taxa able to persist in extreme deserts may have physiological, behavioral, or ecological adaptations that allow them to conserve water or remain dormant during droughts (bottom-up effects of environmental moisture, on the other hand, may be strongest in the most arid areas, [21, 25, 26, 63]). Thus, the food webs most frequently and intensely affected by variation in animal water balance may be those which experience intermediate levels of environmental moisture. These environments

should allow the persistence of many taxa that are not strongly adapted to arid conditions and thus may respond very strongly to periodic reductions in moisture. For example, Lensing and Wise [64] found that effects of water on the effect of spiders on decomposition (via top-down effects) were stronger at a wetter site than a drier site.

How widely distributed are locations of intermediate water availability that might promote animal water-balance-mediated trophic effects? McCluney and Sabo [37] used relationships between soil moisture and rates of herbivory (by crickets) in a floodplain forest in a semi-arid region of Arizona to predict the frequency of similar observations of water-balance associated herbivory across the continental US (Figure 4). They found that these crickets would be expected to exhibit water-balance-driven herbivory at 49% of all soil moisture measurement stations in the US, including mesic locations, at some point in time. I suggest that this likely underestimates the frequency with which animal water balance has important ecological effects. The soil moisture-herbivory relationships were determined in a dryland floodplain, an environment of intermediate aridity [55]. More mesic locations may have taxa less adapted to desiccating environmental conditions, and thus showing stronger ecological responses to reductions in environmental moisture. Along these lines, McCluney *et al.* [65] found that mean hydration (water content) of arthropods responded to changes in desiccating environmental conditions (e.g. lower soil moisture, higher temperature) across three US metropolitan areas, including those located in mesic regions (Raleigh, NC, Orlando, FL, and Phoenix, AZ), suggesting sub-optimal hydration can occur across a broad range of US climates. If many arthropod taxa respond to sub-optimal hydration via changes to per capita consumption of moist food, as described above, this data suggests a common role for water balance in food web dynamics.

Conclusion

Animal water balance may play key roles in mediating species interactions, altering food webs in diverse terrestrial environments. Differences in physiological, behavioral, and ecological traits likely underpin how animals respond to changes in environmental moisture. Moreover, demand and availability of energy and nutrients, as well as differences in predation pressure, likely further modify these responses, and long-term consequences may be altered by population-level responses and bottom-up effects. The interplay between these factors results in intriguing unanswered questions, important for understanding how species interactions and food webs change with variation in environmental moisture. For instance, how does variation in water balance of arboreal vs understory ants [6, 7] influence rates of predation and herbivory during heatwaves? Questions like this are particularly important in light of global climate change and land modification, which can have potentially large effects on animal water balance, with relatively unknown food web consequences.

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Annotations of References

6. Bujan J, Yanoviak SP, Kaspari M: **Desiccation resistance in tropical insects: causes and mechanisms underlying variability in a Panama ant community.** *Ecology and Evolution* 2016, **6**: 6282-6291.

Special interest: This article finds that larger ants and those in the canopy of tropical forests (a more desiccating environment) take longer to die under dessicating laboratory conditions.

24. Banfield-Zanin J, Leather S: **Prey-Mediated Effects of Drought on the Consumption Rates of Coccinellid Predators of *Elatobium abietinum***. *Insects* 2016, **7**: 49.

Special interest: This article reports findings that lady beetles increase consumption of aphids that have been reared on severely drought stressed spruce trees, which they hypothesize is due to a need for greater consumption of smaller aphids to meet dietary requirements.

32. Deguines N, Brashares JS, Prugh LR: **Precipitation alters interactions in a grassland ecological community**. *Journal of Animal Ecology* 2017, **86**: 262-272.

Outstanding interest: This article found that direct effects of variation in precipitation on animals often outweighed plant-mediated effects in a semi-arid food web and changes in precipitation were capable of altering the sign and strength of speices interactions.

36. Hagan R, Szuter E, Rosselot A, Holmes C, Siler S, Rosendale A, Hendershot J, Elliott K, Jennings E, Rizlallah A: **Dehydration Bouts Prompt Increased Activity And Blood Feeding By Mosquitoes**. *bioRxiv* 2017, 120741.

Special interest: This article demonstrates that dehydrated mosquitoes increase blood-meal feeding, suggesting that animal water balance may have consequences for disease transmission.

37. McCluney KE, Sabo JL: **Animal water balance drives top-down effects in a riparian forest—implications for terrestrial trophic cascades.** *Proceedings of the Royal Society B: Biological Sciences* 2016, **283**: 20160881.

Outstanding interest: This article finds that trophic cascades from spiders, to crickets, to leaves that occur under dry conditions can disappear with water supplementation and that effects can be either direct via consumption of crickets by spiders or behaviorally-mediated responses of crickets to the presence of spiders.

52. Rosenblatt AE, Schmitz OJ: **Climate Change, Nutrition, and Bottom-Up and Top-Down Food Web Processes.** *Trends in Ecology & Evolution* 2016, **31**: 965-975.

Special interest: This article discusses a general approach for connecting variation in the nutritional quality (including water) of resources to food web dynamics, reviewing recent advances.

54. Frizzi F, Rispoli A, Chelazzi G, Santini G: **Effect of water and resource availability on ant feeding preferences: a field experiment on the Mediterranean ant *Crematogaster scutellaris*.** *Insectes Sociaux* 2016, **63**: 565-574.

Special interest: this article found that hotter summer conditions reduced preferential demand for higher sucrose (energy-rich) foods (accepted all liquid sucrose diets equally) by ants and that supplemental water increased demand for high sucrose (energy-rich) foods, highlighting the tradeoffs between water and nutrient demand vs availability in influencing consumption.

65. McCluney KE, Burdine JD, Frank SD: **Variation in arthropod hydration across US cities with distinct climate.** *Journal of Urban Ecology* 2017, **3**: 1-9.

Special interest: This article found that arthropod water content varied with urbanization and environmental conditions in three different US cities, with urbanization decreasing hydration in a region with a mild climate, but increasing hydration in regions with hot climates.

Figure Captions

Figure 1. A) A typical water budget for an animal (here, a cricket), showing fluxes into and out of the animal. If effluxes exceed influxes, dehydration can result, with potentially severe negative consequences for the animal. B) Hypothesized pathways mediating effects of animal water balance on food webs. Multiple factors interact to influence water balance and then water balance, combined with predation risk and energy and nutrient demand and food content interact to influence consumption of moist food, altering trophic interactions when moist food is living. C) Generalized predicted rates of consumption of water-laden and nutrient-rich (dry) food with variable environmental moisture and risk of predation. At extremely low soil moisture, food consumption is low due to limited activity of animals. With increased moisture availability, consumption of moist food at first rapidly increases to help meet water balance requirements, but then declines as environmental moisture becomes sufficient to meet water demand and animals switch to consuming more high nutrient content food. Consumption of both types of food is decreased by increasing predation risk. For more details, see “Tradeoffs with Other Constraints.”

Figure 2. Body mass as a predictor of the relative demand for water versus energy, based on data in Woods and Smith [43]. Smaller organisms tend to have higher water fluxes relative to gas fluxes, which suggests a greater likelihood of being water-limited than energy-limited.

Figure 3. Prediction of the frequency with which animal water balance influences food webs with increasing environmental moisture availability. Environments with intermediate levels of moisture may have food webs most frequently and strongly affected by animal water balance due to the abundance of large numbers of taxa with high rates of water loss and few adaptations to resist dehydration. Note: classification scheme is similar to the xeric, mesic, and hygric designations of Hadley [11].

Figure 4. The frequency with which the field cricket *Gryllus alogus* would be expected to show high rates of herbivory, around the US, based on extrapolation from experimental measurements in a semi-arid floodplain [37] to observations in the COSMOS soil moisture network [66]. Coloration represents the frequency of observations, shallower than 35 cm, that fall below the maximum cut-off for water-limited herbivory observed in experimental work (6.8% volumetric soil moisture). 49% of all stations in the US and 63% of all stations in the sunbelt (below dashed line) have experienced soil moistures that could promote herbivory by this omnivorous cricket. Reprinted with permission, from McCluney and Sabo [37].

A **C** **B**