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Implications of animal water balance for terrestrial food webs

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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.

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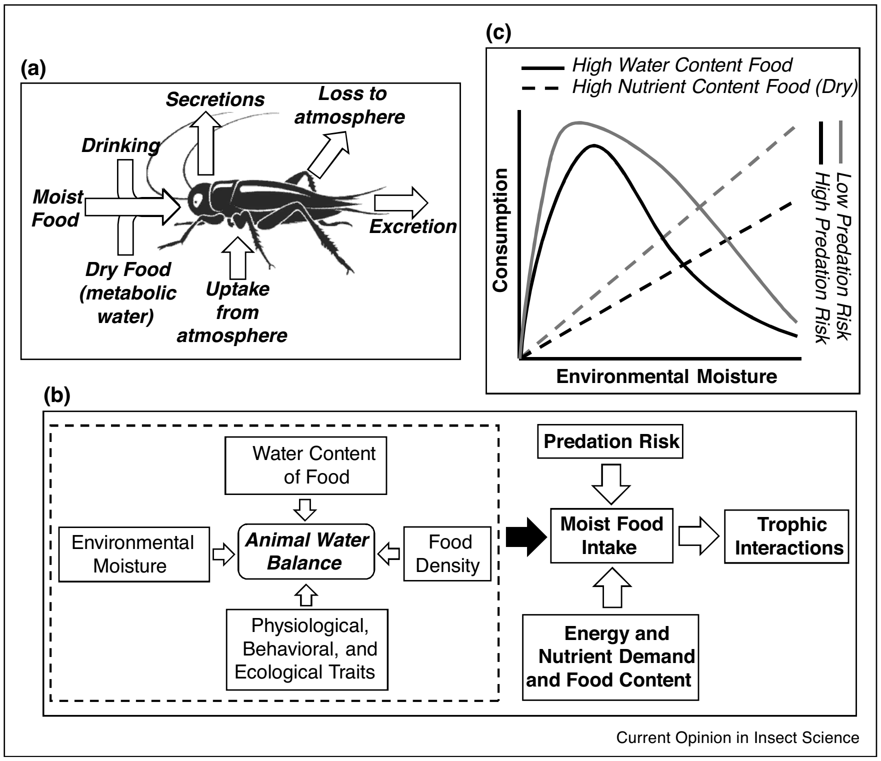
Introduction

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 [33–35,36•] 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,c [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 intraspecific 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,c), 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

Figure 1



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(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.’

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 (<∼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