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## Implications of animal water balance for terrestrial food webs

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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.

1                   **Implications of animal water balance for terrestrial food webs**

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14  
15   **Abstract**

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

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

26

## 27 **Introduction**

28         Maintaining water balance is a key challenge to the evolution of terrestrial organisms.  
29 Dehydration can have severe and immediate consequences, including declines in growth [1],  
30 reproduction [2-5], and survival [6, 7]. Varied adaptations to meet this challenge have long  
31 fascinated biologists, who have developed methods of measuring fluxes of water into and out of  
32 organisms, generating animal water budgets (Figure 1A) [8-14]. Physiological ecologists use  
33 these approaches to quantify effects of adaptations and climate on water balance [11, 15-20]. But  
34 how does variation in animal water balance alter species interactions and food webs? Until  
35 recently, this topic had received relatively little attention (but see [21]). Instead, food web  
36 ecologists often focused on effects of variable moisture from the bottom-up, via effects on plants,  
37 with energy or nutrients driving food web responses (e.g. [22-28]). For instance, Banfield-Zanin  
38 and Leather [24] recently found increased per capita consumption of aphids by lady beetles when  
39 aphids were reared on drought-stressed spruce trees, which led to smaller aphids. Other studies  
40 have documented significant bottom-up effects from precipitation associated with ENSO cycles  
41 [26, 29-31]. While bottom-up effects are likely to be important, top-down effects, where  
42 variation in animal water balance affects lower trophic levels, also deserve attention.

43         Recent evidence suggests that water can greatly influence food webs from the top-down  
44 [32, 33], altering the strength of species interactions [33-36] and trophic cascades [37].  
45 McCluney and Sabo [37] found that under dry conditions, large spiders in a semi-arid floodplain  
46 suppressed populations of crickets and reduced herbivory (a trophic cascade), but with added

47 water, large spiders had no effect on crickets and an almost neutral effect on herbivory. In  
48 another study, Deguines *et al.* [32] found that direct effects of precipitation on animals were  
49 commonly stronger than indirect, plant-mediated, bottom-up effects in a semi-arid grassland over  
50 7 years of variable precipitation. Moreover, Hagan *et al.* [36] found potential human health  
51 implications, because dehydrated mosquitoes increased blood-meal feeding. Careful  
52 consideration of water balance models can help identify mechanisms of these effects (Figure  
53 1A). Because metabolic water production and atmospheric uptake are generally (but not always,  
54 see [20, 38-40]) small fluxes [11, 38, 39], to prevent dehydration, declines in drinking water  
55 must often be met by either A) declines in water loss rates (with associated energetic or  
56 reproductive costs), or B) increases in consumption of moist food (Figure 1B, 1C, [33]; if food  
57 is dry, declines in water often result in decreases in consumption [41, 42]). Thus, with variable  
58 environmental moisture (precipitation, moist soils, waterbodies), terrestrial animals should  
59 experience periods of heightened demand for moist food, which often is found in the form of  
60 other living organisms, thus resulting in stronger per capita trophic interactions (Figure 1B). This  
61 mechanism linking moisture to trophic interactions may be complicated by intra- and  
62 interspecific variation in water loss rates, optimal and minimum hydration states, behavior (e.g.  
63 ability to wait for better conditions), food nutrient and water content and density, trade-offs with  
64 other constraints (e.g. predator avoidance; Figure 1B, 1C), population-level responses, and  
65 bottom-up effects. Here I review recent advances in our understanding of the drivers, frequency,  
66 and consequences of variation in animal water balance and propose conceptual models for  
67 understanding food web implications.

68

69 **Variation with Physiological, Behavioral, and Ecological Traits**

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

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

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

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

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

109 Excluding groups that are able to wait for better conditions, most small, and especially  
110 short-lived species (most terrestrial arthropods), should be particularly constrained in their  
111 behavioral responses to periodic reductions in environmental moisture, because of short windows  
112 for reproduction. Reproductive periods generally occur in spring and summer growing seasons,  
113 which can be impacted by drought events with low predictability. The ability to maintain activity  
114 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



## 138 Tradeoffs with Other Constraints

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

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

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

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

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

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

192

### 193 **Short-term vs Long-term**

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

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

211

### 212 **Interacting top-down and bottom-up effects**

213         Although this review focuses on top-down effects of variation in moisture, mediated by  
214 animal water balance, bottom-up effects are likely to interact with top-down [33]. The relative  
215 importance of each likely varies among systems and over time (e.g. with ENSO events [60]), but  
216 it is important to point out that direct effects of environmental moisture on animals can  
217 potentially exceed bottom-up in real-world scenarios, over relatively long time frames [32].  
218 Thus, both top-down and bottom-up effects likely contribute substantially to observed responses  
219 [32, 33, 60].

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

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

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

240

#### 241 **Spatiotemporal Variation in the Frequency of Water-mediated Trophic Interactions**

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

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

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

275

276 **Conclusion**

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

289

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#### 464 **Annotations of References**

465

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470 more desiccating environment) take longer to die under desiccating laboratory conditions.

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472 24. Banfield-Zanin J, Leather S: **Prey-Mediated Effects of Drought on the Consumption**  
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474 Special interest: This article reports findings that lady beetles increase consumption of aphids  
475 that have been reared on severely drought stressed spruce trees, which they hypothesize is due to  
476 a need for greater consumption of smaller aphids to meet dietary requirements.

477

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

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

483

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

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

489

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

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

497

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

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

503

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

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

511

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

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

517

518

### 519 **Figure Captions**

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

533

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

537

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

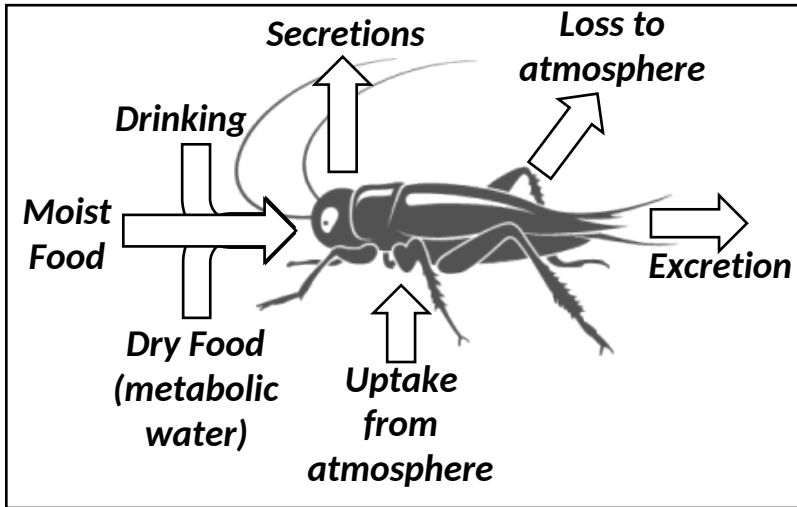
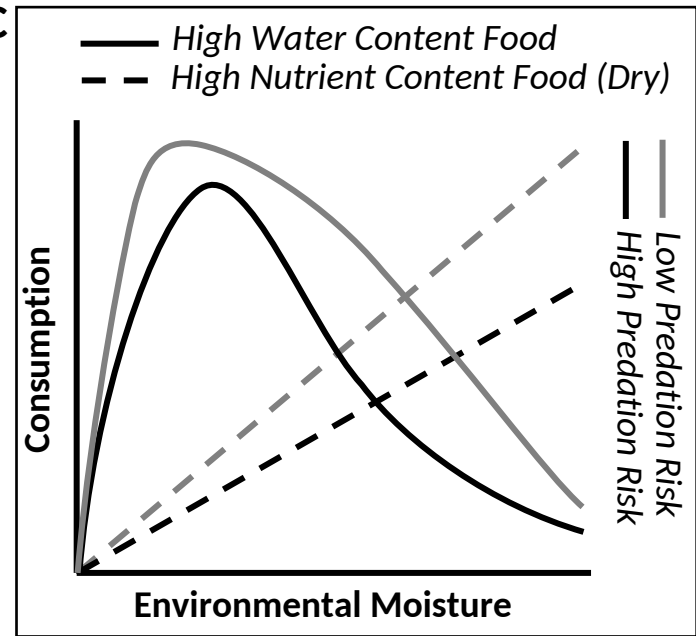
544

545 Figure 4. The frequency with which the field cricket *Gryllus alogus* would be expected to show  
546 high rates of herbivory, around the US, based on extrapolation from experimental measurements  
547 in a semi-arid floodplain [37] to observations in the COSMOS soil moisture network [66].

548 Coloration represents the frequency of observations, shallower than 35 cm, that fall below the  
549 maximum cut-off for water-limited herbivory observed in experimental work (6.8% volumetric  
550 soil moisture). 49% of all stations in the US and 63% of all stations in the sunbelt (below dashed  
551 line) have experienced soil moistures that could promote herbivory by this omnivorous cricket.

552 Reprinted with permission, from McCluney and Sabo [37].

553

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