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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 β -
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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295

296

297

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464 **Annotations of References**

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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*
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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.

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501 nutritional quality (including water) of resources to food web dynamics, reviewing recent
502 advances.

503

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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].

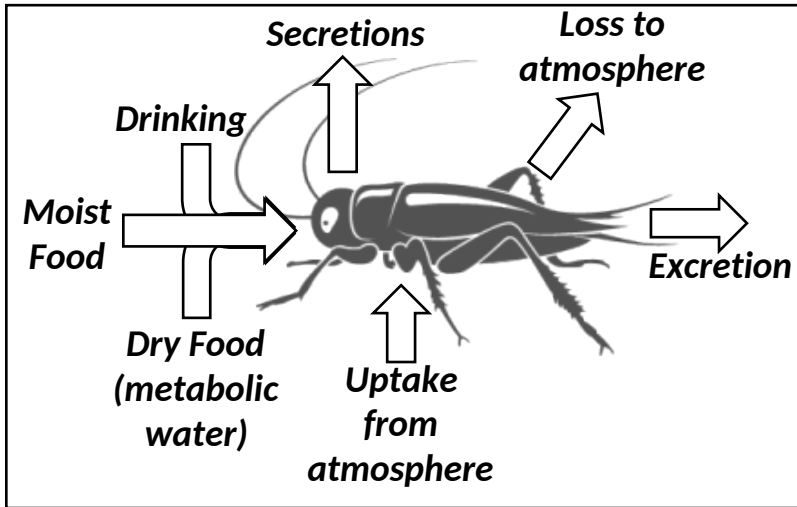
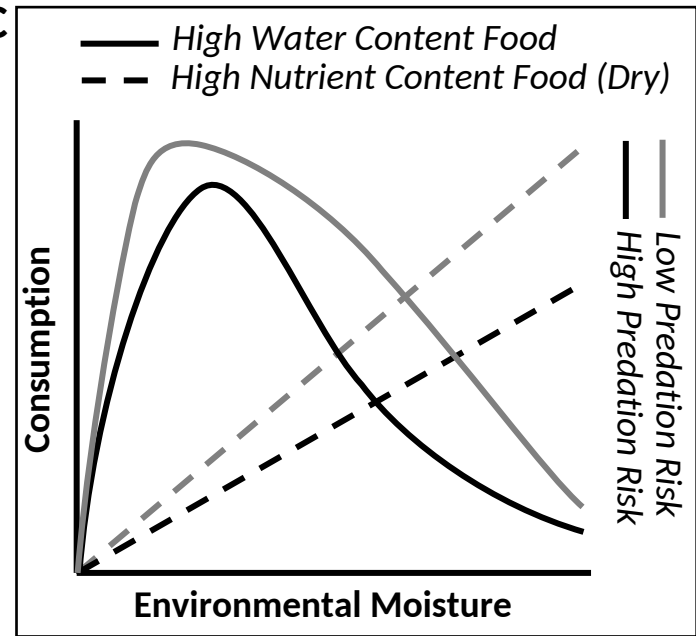
544

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].

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