ANNUAL REVIEWS

Annual Review of Entomology

Dehydration Dynamics in Terrestrial Arthropods: From Water Sensing to Trophic Interactions

Joshua B. Benoit,[1,*] Kevin E. McCluney,[2]
Matthew J. DeGennaro,[3] and Julian A.T. Dow[4]

[1]Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio, USA;
email: joshua.benoit@uc.edu

[2]Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio, USA; email: kmcclun@bgsu.edu

[3]Department of Biological Sciences, Florida International University and Biomolecular Sciences Institute, Miami, Florida, USA; email: matthew.degennaro@fiu.edu

[4]Institute of Molecular, Cell and Systems Biology, University of Glasgow, United Kingdom;
email: julian.dow@glasgow.ac.uk

Annu. Rev. Entomol. 2023. 68:129–49

First published as a Review in Advance on
October 21, 2022

The *Annual Review of Entomology* is online at
ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-120120-091609

*Corresponding author

Keywords

dehydration, climate change, water balance, humidity sensing, drought

Abstract

Since the transition from water to land, maintaining water balance has been a key challenge for terrestrial arthropods. We explore factors that allow terrestrial arthropods to survive within a variably dry world and how they shape ecological interactions. Detection of water and hydration is critical for maintaining water content. Efficient regulation of internal water content is accomplished by excretory and osmoregulatory systems that balance water intake and loss. Biochemical and physiological responses are necessary as water content declines to prevent and repair the damage that occurs during dehydration. Desiccation avoidance can occur seasonally or daily via a move to more favorable areas. Dehydration and its avoidance have ecological impacts that extend beyond a single species to alter trophic interactions. As climate changes, evolutionary and ecological processes will be critical to species survival during drought.

1. INTRODUCTION

As arthropods made the transition from water to land, they went from living in a surplus of water to the frequent pressure of preventing the negative effects of dehydration (**Figure 1**). While arthropods that reside in water sources with a high salt content (i.e., higher osmolarity) also experience challenges in maintaining water balance, terrestrial environments typically pose more severe challenges than aquatic ones.

The terrestrialization of arthropods did not occur as a single transition; instead, multiple lineages transitioned from water to land starting at the Cambrian–Ordovician boundary (ca. 488 Ma), with direct evidence of chelicerates in the Silurian (ca. 416–443 Ma) and hexapods in the Devonian (ca. 398–416 Ma) (41, 82). The process of moving to the terrestrial environment was accompanied by physiological changes including altered gas exchange, reproduction, and osmoregulation; increased responses to ultraviolet radiation exposure without the protection of water; body changes to tolerate gravity pressure; and modifications of sensory organs to function in a dry environment (41, 82, 122). Details of these adaptations have been previously reviewed (41, 82). Following the transition to land, terrestrial arthropod species were able to diversify; there are now likely over 7 million extant species, representing a major component of the biodiversity of Earth. This review focuses on water homeostasis in terrestrial arthropods, ranging from how individuals detect water sources to how organisms respond to varying internal levels of water and the impact of drought on ecological interactions.

A great deal of research is devoted to how insects locate food sources or mates, but these activities are less urgent than maintaining water balance. During hot and arid periods, a terrestrial arthropod can die in as little as an hour if water stores cannot be replenished (12). Arthropods have particularly high water loss rates because they are small, and smaller organisms have higher surface area to volume ratios that promote water loss across a surface (142). Oxygen is the only factor that is more critical to survival; in its absence, death can occur within minutes. However, oxygen consumption and gas exchange also result in water loss, and this too scales with body size: Smaller animals have higher water loss rates relative to gas flux (metabolic) rates (89). Water can be acquired from imbibing liquid water, ingestion of food, or the metabolic breakdown of specific nutrients. Metabolic water production likely occurs in all organisms but is typically only a major water source for those with extremely suppressed water loss (10, 18). A few taxa can also obtain water directly from subsaturated air through uptake systems (4, 8, 15).

As water is not always available, the prevention of water loss represents a critical factor for survival. In general, species that reside in wet environments tend to have higher water loss rates

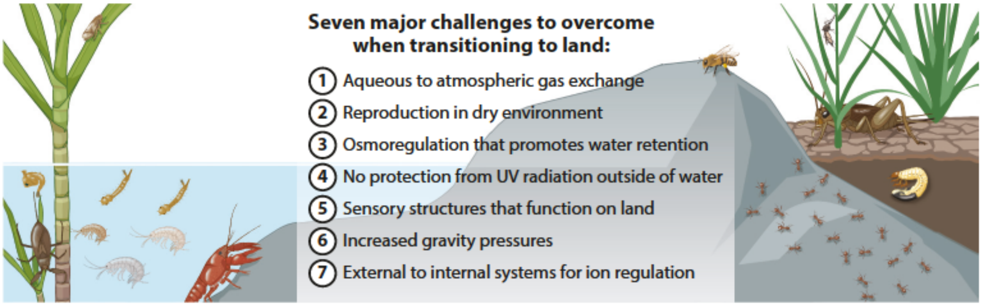

Figure 1

Summary of the transition from water to land. As arthropods move from living within water, a variety of factors must be overcome, most involving losing the protection and support present within an aqueous environment. A summary of factors that underlie the transition from water to land has been provided in reviews by Little (82) and Dunlop et al. (41). Figure adapted from images created with BioRender.com.

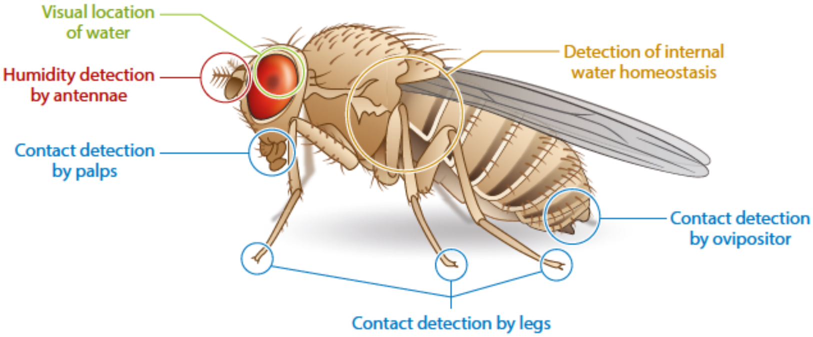

Figure 2

Humidity detection localization on terrestrial arthropods. A combination of vision, humidity, and contact detection allows insects to visualize large bodies of water, locate water or moist substrate for water ingestion, and make contact with liquid water based on osmolarity levels. Lastly, an internal detection system allows for the regulation of water content within the individual arthropod. A combination of these factors allows terrestrial arthropods to maintain water balance.

compared to those that reside in drier habitats (12, 71, 149). The reduction of water loss is predominantly accomplished through behavioral shifts, direct changes in the cuticle, shifts in cuticular hydrocarbon types or abundance, altered cuticle proteins, smaller spiracle size (12), or a reduction in breathing. These mechanisms suppress transpiration through the cuticle and/or respiratory water loss (28). A balance between obtaining water and preventing water loss allows terrestrial arthropods to maintain water homeostasis and survive. As climate change progresses, drought is expected to increase in duration, frequency, and intensity, (34); thus, establishing how terrestrial arthropods respond to potential or actual dehydration will be critical for understanding changes in populations of these species and their impacts on humans.

2. HOW ARTHROPODS SENSE WATER AND WATER VAPOR

The ability to locate water relies on a combination of visual and chemosensation cues to find water or wet materials (**Figure 2**). Visual cues rely on light polarization to distinguish large bodies of water, which are mostly associated with aquatic insects and those that deposit eggs in bodies of water (20, 62, 63). Humidity detection and contact with a moist surface represent the critical methods for the location of water (12, 44). This is accomplished through two distinct mechanisms: (*a*) contact chemosensation, which likely operates through sensory structures on the mouthparts, legs, and ovipositor, and (*b*) detection of varying humidity levels in the air by the olfactory system.

2.1. Humidity Detection

Extensive humidity and water detection studies have been limited to *Drosophila* and mosquitoes (29, 44, 77, 78, 87); however, electrophysiological surveys have identified humidity-sensitive sensilla in other arthropods (129, 130). Ionotropic receptors (IRs) have been identified as the major humidity detectors in insects. IRs have been linked to the detection of temperature, taste, and humidity; specific IRs even have overlapping roles in detecting multiple cues (19, 135). Multiple IRs have been identified in the sacculus of *Drosophila* antenna, which is directly linked to water sensing in flies. The IRs found in *Drosophila* have closely related orthologs in other species, indicating that IR-based humidity detection likely occurs in most insect systems and in related arthropods such as mites (19, 66, 128). The coexpression of *IR21a*, *IR25a*, and *IR93a* is involved in the detection of water and cool temperatures (77). For mosquitoes, IR21a is involved in heat sensing (53), further highlighting the dynamics between thermal and humidity sensing in insects, and IR8a has been linked to altered water detection (106). The association between IRs that sense thermal changes and humidity suggest that there is neural integration of these cues. This is not surprising given that vapor pressure deficits directly link humidity and temperature to water loss (60).

Along with IRs, odorant-binding proteins (OBPs; low-molecular-weight soluble proteins that may act as carriers for specific chemicals) have been tied to humidity detection. As with IRs, this role has only been examined in *Drosophila*. One specific OBP, Obp59a, is highly conserved and is necessary for hygroreception in *Drosophila* (123). Mutants for Obp59a have an impaired ability to detect water but, paradoxically, increased survival during desiccation (123). The specific mechanism by which this OBP is involved in humidity detection is unknown, but the abundance of OBPs in arthropod systems suggests that other members of this gene family may have roles in humidity detection (128, 137).

2.2. Contact Detection of Water and Drinking

Liquid water not only exists in water pools, but can also be accessed from saturated soil or other moist materials; thus, contact detection of moisture is necessary for arthropods. This specifically involves channel proteins that respond to the osmolarity levels of the water. The *pickpocket* (*ppk*) gene has been tied to the cellular and behavioral responses to osmolality in mosquitoes and *Drosophila* (26, 27, 87). In *Drosophila*, *ppk28* has been linked to response to osmotic changes and potentially plays a role in gustatory water detection (27). In mosquitoes, *ppk301* is expressed in legs and acts in the mechanical response to water and salt (87), likely playing a critical role in the decision of where oviposition should occur.

Insects and other arthropods need to know when to drink water, and determining this likely involves the integration of both external cues like humidity and internal cues such as osmolality. Nanchung, a transient receptor channel, acts to restrict water consumption in *Drosophila* (67), which helps to regulate sugar and water consumption. Nanchung-expressing interoceptive SEZ neurons (ISNs) in the taste center of the brain work to regulate both water and sugar consumption, responding to cues from the hemolymph. Specifically, the activity of ISN-expressing nanchung will increase when low blood osmolality is detected extracellularly, promoting sugar consumption. When the blood osmolality is high, the same ISNs have reduced activity, leading to the consumption of water to lower internal osmolality (67). Mechanosensation of water and osmolarity detection need further investigation to establish the mechanisms used to identify external water sources and maintain internal hydration states in arthropods. Studies in genetically accessible insects such as *Drosophila* and the yellow fever mosquito, *Aedes aegypti*, may point the way to common mechanisms across taxa.

3. BEHAVIORAL DYNAMICS OF ARTHROPODS IN HUMID AND DRY ENVIRONMENTS

3.1. How Does Humidity Alter Arthropod Behavior?

Most terrestrial arthropods are more active during more humid periods. There are a few exceptions, such as bed bugs and spider beetles, that prefer dry conditions; for these species, extended periods of water levels near saturation can yield overhydration and increase the likelihood of fungal growth (18, 147). During periods of rest, such as during the night and hot periods during the day, most species will search for or move into the microhabitat with the highest relative humidity (74). This ability to move between areas with varying relative humidity is likely possible because most terrestrial arthropods can sense humidity gradients with variations as low as 20% relative humidity (RH) (44). Movement into reprieves during periods of low humidity; movement within these reprieves into the most favorable location; and subsequent emergence when conditions are more positive, such as during the night or following precipitation, are critical for survival in dry areas. Emergence from reprieves is likely triggered by detection of weather factors, such as barometric pressure changes, or sensing of a humid gradient where the higher concentration is outside the protected microhabitat.

3.2. How Does Hydration Status Impact Behavioral Changes Across Daily and Seasonal Cycles?

There are distinct changes in terrestrial arthropod behavior and distribution associated with daily and seasonal cycles. Many species undergo periods of inactivity in refugia that occur both in the winter, to avoid cold and dryness, and as aestivation during hot and arid periods (8). Most species have decreased water loss rates in their diapause stage, usually due to a combination of reduced respiration and increased cuticle waterproofing, along with retreating into protected areas (8, 11). An alternative is movement to more favorable regions, from movements of short distances (e.g., to permanent water bodies or within hibernacula) to migrations across hundreds of kilometers (36, 65). Long-distance movement was previously thought to be limited to a few species, but wind-borne migration at higher altitudes has been demonstrated to move insects long distances (64, 65).

Daily variation in the potential for dehydration is common. In general, warm dry periods during midday represent the period when most species are most susceptible to desiccation, due to the highest vapor pressure deficit. As such, few terrestrial arthropods are active during this time, with most active at dusk, night, and dawn, but some taxa, such as bees, are most active during the peak of photophase (17, 132). Factors such as humidity may directly impact daily activity, but this has not been well established. Humidity cues would be unreliable for setting circadian changes, as precipitation could supersede daily humidity changes.

3.3. Food versus Water: Eat to Rehydrate

A few organisms do not directly drink water, but rather have unique mechanisms to obtain water from the air (discussed below in Section 5.3) or maintain their water budget from food sources (13, 76). When hydration is limited to feeding, most species consume water-rich foods, such as blood and plant-based fluids or other wet food sources. To survive this lifestyle, an organism will need to ensure that feeding occurs regularly [e.g., tsetse flies, which feed every two to three days (9)] or have the ability to withstand long periods without water [common in beds bugs and other members of Cimicidae (10)]. In environments that are extremely dry, such as sub-Saharan Africa or many human dwellings (86), obtaining water from a large bag of fluid (e.g., human or livestock) may be more likely than obtaining free water. Most arthropods obtain water by drinking liquid water and by eating. In these situations, changes in water availability may lead to changes in consumption of moist food (89) or altered intake of macronutrients (5, 23, 47) to maintain water balance through dietary intake of water or metabolic water production, respectively.

4. MOLECULAR AND BIOCHEMICAL RESPONSES TO DEHYDRATION

4.1. Transcriptional Shifts and Genomic Changes Prevent Dehydration-Induced Damage

Molecular and biochemical responses to dehydration stress have been studied in multiple systems, and research on this topic has expanded with new technologies that allow for the assessment

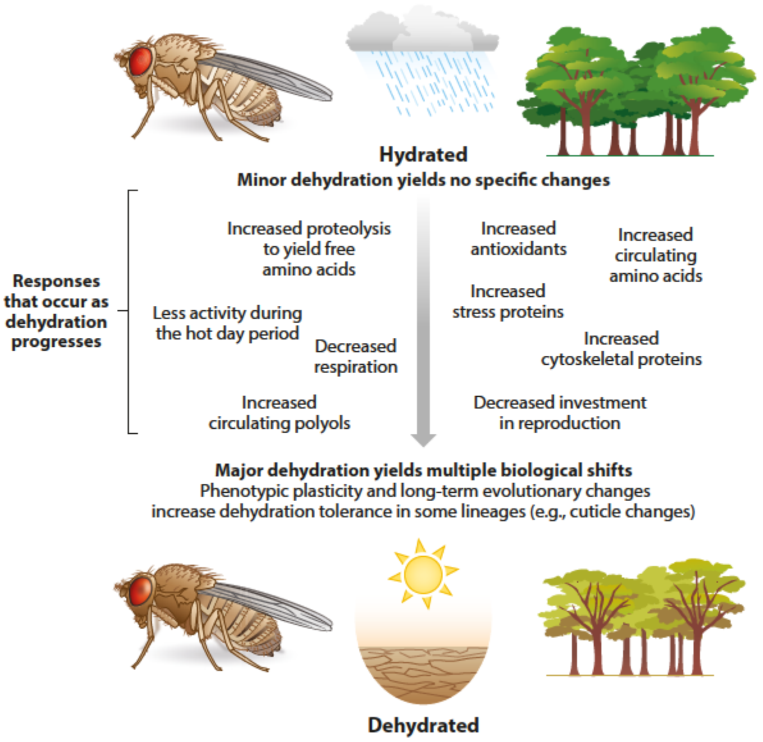

Figure 3

Molecular and biochemical factors that occur when terrestrial arthropods are exposed to dehydration.

of complete transcriptional, metabolite, and proteomic shifts (57, 113, 141) (**Figure 3**). Changes include increases in ubiquitin-dependent proteolysis, heat shock proteins, and oxidative stress proteins (12, 126, 127). These changes are most likely to prevent and repair cellular damage during dehydration. Expressional changes in aquaporins or other transmembrane genes do not usually occur during dehydration stress in most terrestrial arthropods (12, 126, 127), even though they are critical to water homeostasis. Specifically, these proteins do play critical roles in water and ion regulation, but only if they are already present and active in the specific cells before water stress. A reduction in metabolism commonly occurs during dehydration and lowers water loss through respiration, as has been shown by RNA sequencing (RNA-seq) and functional studies in several systems (12, 126, 127). Cytoskeletal changes have been noted in both transcriptional and proteomic levels (80, 83) to support cell structure as the insect encounters conditions that would threaten internal homeostasis. Lastly, transcriptional changes involved in amino acid and carbohydrate metabolism have been associated with dehydration in multiple systems (57, 127), where the increase in these metabolites plays a critical role during dehydration stress in providing energy and acting as a buffer (discussed in Section 4.2) and could also be involved in the production of metabolic water. Additional lineage-specific differences also occur, such as increased levels of expression of autophagic-associated genes during extreme dehydration in the Antarctic midge (125) and changes that allow for postdehydration responses, such as increased water vapor uptake, in ticks when humidity increases (113). These specific changes have allowed some insects to tolerate a near complete loss of water (see the sidebar titled Extreme Dehydration—Anhydrobiosis).

EXTREME DEHYDRATION—ANHYDROBIOSIS

A few terrestrial arthropods, mainly midges and collembolans, can lose nearly all of their water content. A model for this process is the sleeping chironomid, *Polypedilum vanderplanki*, which resides in dry regions of Africa. The larvae live at the bottom of temporary water pools that commonly dry. To survive, larval stages will lose 97% of their water content and resume activity following subsequent hydration, even after 17 years in the dehydrated state. While in this dehydrated state, these larvae can tolerate extreme heat, cold, and even exposure to the vacuum of space (59). Importantly, many of the mechanisms that are utilized by this system to prevent dehydration damage are similar to those of other insects but are more extensive (12, 14, 127). Metabolome and transcriptome studies have revealed that there is a massive increase of trehalose, accumulation of components of the citric acid cycle, and mechanisms to accumulate stable waste products (114). Genomics studies have revealed that distinct paralogous stress-associated gene clusters are highly expressed in desiccating larvae (55, 114).

Specific genomic changes have been linked to dehydration resistance (51, 69, 108, 110). For example, chromosomal inversions have been found to be associated with increased dehydration resistance in mosquitoes (51, 110, 141). Other changes have been identified through genome sequencing following prolonged selection for increased dehydration resistance in *Drosophila* (69). Specific genes with positive selection following artificial selection include those involved in cuticle structure and development (cuticle proteins), along with a multitude of other specific genes (69). Importantly, many of the genomic factors that underlie the increased dehydration resistance following selection are not factors typically known to increase during dehydration, suggesting that the potential evolutionary changes that increase dehydration resistance may be different than those that are directly critical for survival during acute exposure to dry periods.

4.2. Metabolite Shifts Prevent Dehydration-Induced Damage

A suite of metabolite shifts is critical to allowing for rapid survival and recovery from desiccation stress. Importantly, many of the processes to increase metabolites are not without cost: Each bout of dehydration and rehydration will result in a metabolic breakdown of nutrient reserves (16, 111). If the life stage feeds, then replenishing nutrient reserves is relatively easy, but for species or life stages that rarely feed (ticks or diapausing adults) or life stages incapable of feeding (pupae), these bouts of dehydration can eventually exhaust nutrient reserves. Glycerol represents one of the most common metabolites to be increased and acts to protect unwanted biochemical interactions, such as deleterious protein–protein interactions (7, 148). Trehalose, which likely acts similarly to glycerol and protects cells from potentially damaging biochemical interactions or serves in osmolyte balance, is commonly noted to be increased during dehydration stress in multiple systems (114). Increased trehalose and other sugars within the hemolymph likely act as an immediate energy source to restart metabolic processes to repair the damage. Multiple amino acids are increased during dehydration stress, with proline and alanine being most common (57, 85, 113, 143). These metabolites are not likely to be only colligative and fully interchangeable during dehydration stress (133); instead, there may be overlapping and specific roles for each metabolite.

4.3. Population Differences in the Response to Dehydration

Dehydration resistance varies both between species and among populations of the same species (31, 71, 107). Most studies of differences among populations have focused on insect eggs or adults, with most projects conducted on *Aedes* and *Drosophila* (31, 71, 72, 108). In *Drosophila*, species with the strongest basal desiccation resistance sometimes show the least plasticity, and basal resistance is higher in drier locations (71) but does not vary with latitude, unlike thermal tolerance (2). A variety of differences between populations related to desiccation resistance have been identified, including distinct genomic variation, shifts in gene expression profiles, altered structural aspects (e.g., cuticle changes), and distinct variation in survival under dry conditions (31, 71, 72, 108). In general, populations collected from drier environments display increased dehydration resistance. This suggests that inferences related to drought tolerance for a species as a whole should be made only after examining the dehydration response in multiple populations of that species, but also that species-level basal desiccation resistance may be important for understanding sensitivity to climate change (72).

5. PHYSIOLOGICAL RESPONSES TO DEHYDRATION

5.1. Malpighian Tubules and Hindgut in Water Regulation

Internal water regulation is predominantly accomplished by generation of primary urine by the Malpighian tubules (MT) and selective reabsorption by the hindgut. The MT open into the gut at the junction of midgut and hindgut. The main function of the hindgut is to allow water and other key ions and compounds to be reabsorbed, allowing defecation of dry waste such as nontoxic uric acid and other products.

The mechanisms underlying the MT's role as the kidney equivalent have been extensively examined, and studies have begun to elucidate cellular differences that may underly functional differences among cell types in this organ (25, 81, 97, 101, 116, 146). A general synopsis of MT factors that underlie the function of this organ in relation to water balance can be found in **Figure 4**. For *Drosophila*, and likely other systems, filtration nephrocytes (garland cell nephrocytes and pericardial nephrocytes) occur outside of the renal process involving the MT, but these are mainly involved in filtration rather than osmoregulation (97) and as such are not discussed in this review. The adult MT are functionally analogous to renal tubular systems and, in *Drosophila*, develop from the ectodermal hindgut primordium and visceral mesoderm (68). The MT directly attaches to the hindgut at the posterior midgut and consists of a varying number of epithelial tubes depending on the lineages (21, 40, 116). Single-cell RNA-seq studies in *Drosophila* have established that there are nine distinct cell types associated with the MT, consisting of two types of stellate cells, six types of principal cells, and stem cells (81, 146). The differences in the cell types suggest that principal cells and stellate cells likely have functional differences depending on their location in the MT, specifically whether they exist in the upper, main, or lower tubules or as part of the ureter. Similar cell type differences based on transcript-level variation are likely to occur in other terrestrial arthropods as cell shapes vary throughout the length of the MT (42, 139).

The function of the MT relies on a combination of specific proteins that transport water and other small molecules from the hemolymph into the MT lumen for diuresis (**Figure 4**). A particular combination of aquaporins is critical to the transport of water, glycerol, and urea in both the principal cells and the stellate cells. A combination of ion channels allows for the movement of factors such as chloride and potassium, and specific pumps act in the movement of hydrogen, potassium, and sodium ions (25, 81, 97, 101, 116, 146). The activity of the components of the MT relies on the dynamics between the relative abundance of the specific channels and pumps along with factors that regulate their activity, such as hormonal cues discussed below.

5.2. Internal Control of Water Homeostasis—Diuretic and Antidiuretic Hormones

The factors that regulate the internal water content consist of a suite of hormones that regulate water release (diuretic) and retention (antidiuretic) (100). The specific hormones that underlie the

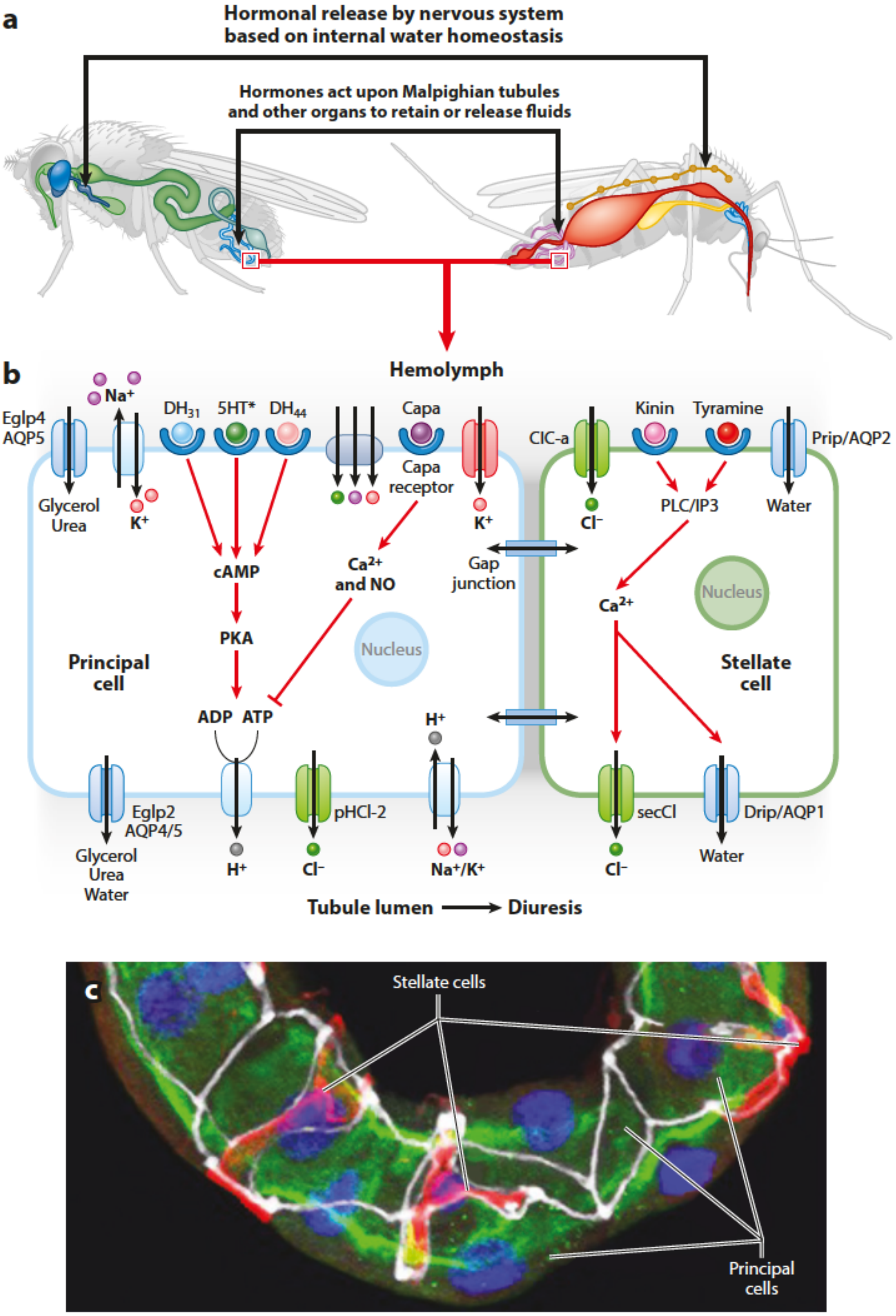

Figure 4

Function of the Malpighian tubules in relation to hormonal control during dehydration based on mosquito and *Drosophila* studies. (*a*) Location of the Malpighian tubules. (*b*) Specific factors in the principal (*left*) and stellate (*right*) cells that are involved in the movement of water and ions from the hemolymph to the tubule lumen for removal within the urine (25, 97, 116). Colored arrows indicate signaling cascades, and black arrows indicate ion or water movement. * indicates factors occurring only in mosquitoes. In general, there is a decrease in water movement into the urine when insects are dehydrated, allowing the retention of more water (61). (*c*) An image of the Malpighian tubules from *Drosophila* showing the principal and stellate cells. Tubule photomicrograph courtesy of Dr. Anthony Dornan.

processes of water regulation have been examined extensively in *Drosophila*, due to the genetic tools available for that species, and in mosquito and kissing bug systems, as blood gluttony yields unique water balance requirements (25, 101, 116). Outside of insect systems, there is some focus on factors that act in the regulation of diuresis in ticks (145), but little is known about this process in other terrestrial arthropods. In *Drosophila*, active cation transport is stimulated by three peptides: DH_{31} and DH_{44} (acting through cAMP) and CAPA (acting though calcium/cGMP). In *Rhodnius*, DH_{31} acts as a natriuretic agent, prompting sodium release and diuresis; 5-hydroxytryptamine serves as a kaliuretic, prompting the release of potassium and diuresis; and DH_{44} serves as a general diuretic factor (24, 25, 73, 101, 116). Kinin-like peptides serve as diuretic factors on the stellate cells, acting though calcium to stimulate chloride conductance, and the biogenic amine tyramine acts similarly (40, 73, 116).

5.3. Alternative Mechanisms for Hydration—Water Vapor Uptake

Hydration can occur via routes other than the ingestion of liquid water and food. One of the most unique of these processes is the ability to utilize water from subsaturated air (water vapor absorption), which occurs in at least 60 species and has evolved independently at least eight times (99). The specific site where this occurs varies between species and include oral routes, which have been found in ticks and some cockroaches; rectal-based mechanisms, which have been noted in fleas, thysanurans, and select beetles and lice; and routes passing directly through the cuticle or some specific cuticle-associated structure (4, 99). Some mechanisms are extremely efficient and allow replenishment of water near 40% RH, and others can only accomplish this process near saturation between 98% and 99% RH. What allows this to occur is the presence of hygroscopic material or fluid in or on a specific tissue or organ, which allows water to be drawn from the air and moved into the arthropod. The properties of these materials vary, but most are made up of a variety of salts, carbohydrates, amino acids, and polyhydric alcohols (e.g., glycerol) that promote water absorption (4, 99). Water vapor absorption is an active process that is energy depleting. This has been demonstrated in ticks, where the process of generating hygroscopic materials and hydration will drastically reduce survival between the rare blood meals (75, 111). More details on this process are given by O'Donnell & Machin (99), but little is still known about the molecular mechanism except that gamma-aminobutyric acid likely drives secretion by tick salivary glands to promote water uptake (113).

5.4. Impact of Dehydration on Reproduction and Cross-Tolerance to Other Stresses

Cross-tolerance between dehydration and other stress types has been documented in multiple terrestrial arthropod systems (112, 120, 121). In the most common type of cross-tolerance, slight bouts of dehydration increase the cold tolerance in many species (14, 120). This most likely occurs because cellular dehydration is a common component associated with cold stress (96, 103, 120). Dehydration in the presence of ice (cryoprotective dehydration) occurs in many terrestrial arthropods, specifically, small species that reside within the soil that have higher water loss rates (30, 43, 70). The impact of short bouts of dehydration on other stress types is not as conclusive.

Bouts of dehydration seem to lead to decreased growth rates (58) and a general reduction in reproductive output (1, 16, 46), which is likely due to issues with metabolism and stress. Prolonged selection for dehydration yields a general reduction in reproductive output in *Drosophila* (1). The specific role of dehydration in relation to immune responses in terrestrial arthropod systems has been understudied; dehydration may increase or suppress immune responses (147, 150).

6. ROLE OF DEHYDRATION IN ECOLOGICAL INTERACTIONS

6.1. Connecting Behavioral Responses to Dehydration and Trophic Interactions

Insects and other arthropods employ a variety of behavioral approaches to avoid or cope with dehydration, and these activities have profound impacts on trophic interactions. Under desiccating conditions, arthropods may either seek out additional water sources (e.g., 6, 45, 92, 140) or seek refugia that lower water loss rates (32, 89). When terrestrial arthropods seek water sources, in some cases, the only available water is within food, resulting in increases in consumption of vegetation by herbivores or prey by predators (89). For instance, studies have documented increases in consumption of moist leaves by crickets (*Gryllus alogus*) and increases in consumption of crickets by spiders (*Hogna antelucana*) in response to limited drinking water (79, 93). Other studies show similar patterns for parasites and plant–arthropod interactions (see Sections 6.2 and 6.3). In contrast, although arthropod-based examples of this behavior are lacking, when animals seek refugia to prevent water loss, their rates of consumption should decline, reducing the strength of species interactions (for vertebrate examples, see, e.g., 37, 52). A complex set of trade-offs likely influences whether dehydration results in increased consumption and stronger trophic interactions versus increased time in refugia and weakened trophic interactions.

6.2. Impact of Dehydration on Parasite–Host Interactions

Dehydration has been demonstrated to impact arthropod disease vector interactions with their host and dynamics between parasitoid wasps and their fly hosts (22, 57, 113) (**Figure 5**). Dehydration increases host landing and blood feeding in many mosquito species, which is likely to have a significant impact on disease transmission (57). Importantly, this only occurs during actual dehydration, and not during exposure to merely dry conditions. Similarly, dry periods have been demonstrated to both increase and decrease tick activity, suggesting that questing for hosts and subsequent tick-borne disease transmission are impacted by dry periods (15, 107). Along with increased vertebrate–disease vector interactions, dehydration drives increased parasitism by wasps on their invertebrate hosts (22).

6.3. Plant–Arthropod Interactions Under Dry Conditions

The effects of plant water deficits on the interactions between plants and arthropod pests have been examined, with most studies focusing on pestiferous insects and mites (49, 88, 90, 124). These effects are inconsistent across studies, possibly because water-stressed plants may have higher nutrient levels, likely due to increased foliar nitrogen in relation to total mass, but other factors, such as leaf water potential, may limit feeding in specific species (49, 117). These effects may differ with the duration or periodicity of drought (49). Hydration of plant-feeding arthropods can also impact plant–arthropod interactions, altering feeding rates and the ability of arthropods to reduce the toxicity of plant defensive compounds (109). In general, specialist pests seem to be more negatively impacted by severe drought, while benefiting under mild or moderate stress, and generalist pests may proliferate better under more severe dehydration stress (35, 49) (**Figure 5**). Importantly, few studies have addressed the impact of variable drought stress (mild to severe) on both plants and arthropods during their interactions (49), suggesting that the full extent of plant–arthropod interactions under drought conditions is not yet understood.

6.4. Dehydration, Food Webs, and Ecosystems: How Do Changes in Species Interactions Alter Entire Food Webs and Ecosystems?

The responses of entire food webs and ecosystems to desiccating conditions often depend on trophic interactions, with arthropods frequently playing an important role (98). For example, in

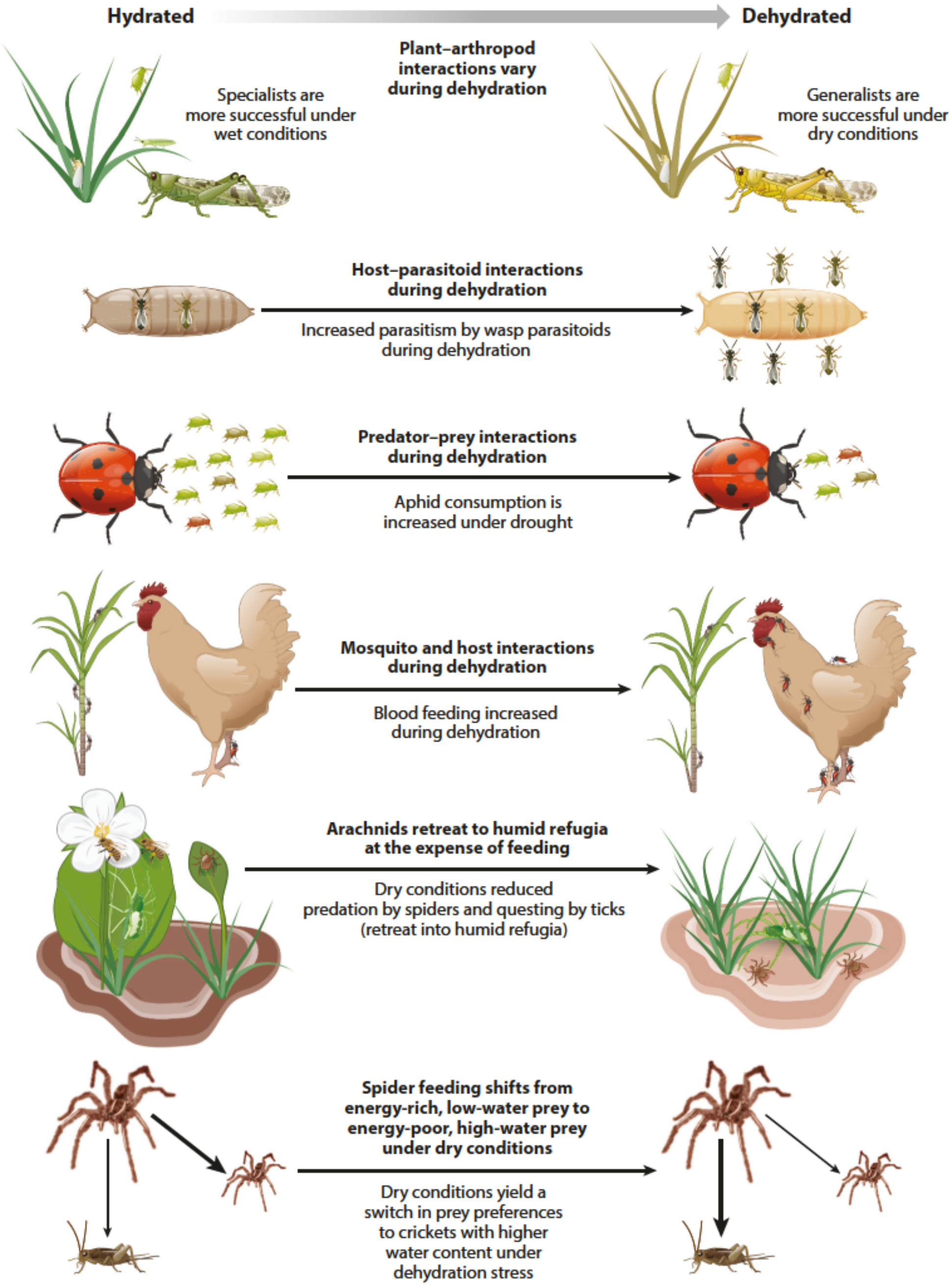

Figure 5

Specific interactions between species in relation to dehydration stress based on studies that have assessed the impact of dehydration on ecological interactions of terrestrial arthropods. In order from top to bottom: plant–arthropod pest interactions (49, 88, 90, 124), parasitoid–host dynamics (22), predation of aphids by beetles (2), impacts of drought on blood feeding by mosquitos on hosts (57, 60), arachnid predation or questing suppressed by arid periods (16, 89, 113), and wolf spider predation shifted from small conspecifics to crickets when water is not available (93). Figure adapted from images created with BioRender.com.

experimental mesocosms, large wolf spiders (*H. antelucana*) have been shown to switch between consuming energy-rich small spiders (*Pardosa* spp.) under wetter conditions and consuming water-laden crickets (*G. alogus*) under drier conditions (79). Similar patterns have been seen in large open-air manipulations, with large spiders causing trophic cascades under dry conditions (large spiders suppress crickets, reducing their effect on leaf material) but not causing these trophic cascades under wetter conditions (94).

Although in some cases trophic interactions dominate ecosystem responses to drought, in other cases, bottom-up effects of water on plants may dominate or at least complicate predictions (3, 90, 95). Animals may experience water stress when plants do not, e.g., when plants can access groundwater (115); plants may experience water stress when animals do not, e.g., when herbivores can still obtain enough water from water-stressed plants or locate surface water sources (84); or both plants and animals may simultaneously experience water stress (although explicit examinations of this possibility have yet to be conducted). In situations where animals experience water stress, but plants do not, arthropod trophic interactions likely play a key role in understanding the dynamics of the system (top-down effects are important; see, e.g., 94). Alternatively, when plants experience water stress, but animals do not, food web and ecosystem dynamics may be governed by the responses of the plants themselves, whether mediated by changes in plant nutrient content (49), changes in plant defensive compounds, or simply changes in primary productivity (95). When both plants and animals experience water stress, predictions are complicated. Although arthropod examples are limited, some studies suggest that bottom-up effects on primary productivity may predominate in these situations (3), while other studies suggest that direct effects on trophic interactions are most important (38). It may be that whether effects are bottom up or top down depends on traits of the specific members of the food web, or that systems oscillate between bottom-up and top-down effects over time (95). Continued research on the effects of altered plant and animal water balance on food webs and ecosystems is needed, especially in light of climate change.

7. LONG-TERM ADAPTATIONS AND RECENT EVOLUTION TO SURVIVE IN DRY ENVIRONMENTS

7.1. Wet and Dry Environments Shape Arthropod Diversity

Terrestrial arthropods occur in nearly all environments. Although exceptions exist (e.g., bees, which are most diverse in temperate regions; 102), the general trend is that species diversity and abundance of terrestrial arthropods are higher in wet, warm tropical habitats (33). Temperate regions usually represent a middle ground, with temperate dry regions generally having fewer species (131, 144). Elevational changes in tropical areas can lead to similar patterns, where higher elevations are usually drier and colder, leading to reduced terrestrial arthropod diversity and abundance (33). Desert regions are sometimes limited to a few species (e.g., ants, specific beetles, firebrats, and spiders) with extremely low water loss rates and other traits that enable their survival in these inhospitable environments (32, 56). Similarly, polar regions are limited to specific species, which can be locally abundant, that can tolerate the extreme cold and dryness of these regions (105). The stability of water availability (and the environment in general) leads to larger and more diverse terrestrial arthropod communities in complex environments (33, 118, 144). Regions with extended and severe dry seasons (or dry winter periods) will be dominated by species that can decline and rebound during growing seasons following dormancy or migration to survive the inhospitable periods (39).

7.2. Climate Change, Drought, and Terrestrial Arthropod Distribution

Climate predictions suggest that the duration and periodicity of extreme weather, including droughts, will increase (34, 134). These climate changes, along with urbanization (see

Section 7.3) and other factors, have led to significant reductions in terrestrial arthropod numbers during the Anthropocene (136, 138). The effects of climatic shifts in water availability and vapor pressure deficit on insects and other arthropods have been understudied relative to those of thermal shifts, which is surprising given the direct relationship between relative humidity and temperature in relation to water vapor deficits (60). Moreover, dry periods impact, and even increase, arbovirus transmission by mosquitoes; alter tick questing; and impact the survival and proliferation of many critical pests (57, 89, 113, 117, 119).

Directly assessing the impact of drought is much more difficult than assessing the impact of thermal stress, as exposure to dehydrating conditions does not always yield actual dehydration. Additionally, experimental dehydration is sometimes hard to achieve when food must be provided and is burdensome to monitor, as individuals need to be killed to establish their true water content. Thus, careful studies of the effects of dehydration have rarely been conducted (57). Selection-based studies to determine how species may respond to an increasing period of drought have been limited to *Drosophila* (48, 50), which limits our predictions of how terrestrial arthropods might adapt to increasing drought prevalence. Importantly, future studies will need to examine population differences (dry-adapted versus wet-adapted lines) or focus on prolonged selection in response to both thermal and dehydration stresses to determine how specific species may adapt to climate change.

7.3. Cities and Indoor Habitats Are Dry or Wet Islands

Human development has created substantial changes to the environment, and nowhere is that more apparent than in cities and within buildings. Cities and indoor locations have unique biophysical characteristics, and the impact of humans in creating these environments varies based on the natural local environment and social systems (86). Residential parts of cities and indoor environments tend to be drier in mesic regions and wetter in xeric regions (54, 86). Urbanization has been shown to influence the hydration of arthropods (91). Arthropods' hydration in cities can influence their demand for macronutrients (5) and the relative abundance of arboreal species (92). The numerous potential impacts of these human-created dry or wet islands on insects and mites need further study, particularly given the direct effects of arthropods on humans living in these environments.

8. CONCLUSIONS AND FUTURE DIRECTIONS

Dehydration has been a continual pressure on arthropods since their movement into the terrestrial environment. The ability to resist dehydration has been critical to the proliferation of terrestrial arthropods, especially insects and mites, which has allowed them to dominate in most, if not all, biomes. Climate change is leading to rapid changes in water availability (34) and increases in temperature that create increasing vapor pressure deficits that desiccate terrestrial arthropods. Human development can also alter water availability and vapor pressure deficits across cities and within buildings (86, 104). These factors will have a major impact on the proliferation of both beneficial and pestiferous species. To fully understand these impacts, more in-depth studies will be needed to measure how drought and dehydration directly alter terrestrial arthropods, how drought impacts interactions between terrestrial arthropods and their food sources, and how climate change and urbanization interact with water deficits to impact the proliferation of terrestrial arthropods.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The development of this review was partially supported by the National Institute of Allergy and Infectious Diseases of the National Institutes of Health award R01AI148551 (to J.B.B. and M.J.D.), National Science Foundation award DEB-1654417 (to J.B.B.), US Department of Agriculture National Institute of Food and Agriculture awards 2019–06138 (to K.E.M.) and 2018–67013 (to J.B.B.), and UK BBSRC grants BB/P024297/1 and BB/V011154/1 (to J.A.T.D.). We apologize for references that have been omitted due to space limitations.

LITERATURE CITED

1. Albers MA, Bradley TJ. 2006. Fecundity in *Drosophila* following desiccation is dependent on nutrition and selection regime. *Physiol. Biochem. Zool.* 79:857–65
2. Arthur AL, Weeks AR, Sgrò CM. 2008. Investigating latitudinal clines for life history and stress resistance traits in *Drosophila simulans* from eastern Australia. *J. Evol. Biol.* 21:1470–79
3. Báez S, Collins SL, Lightfoot D, Koontz TL. 2006. Bottom-up regulation of plant community structure in an aridland ecosystem. *Ecology* 87:2746–54
4. Bayley M, Holmstrup M. 1999. Water vapor absorption in arthropods by accumulation of myoinositol and glucose. *Science* 285:1909–11
5. Becker JE, McCluney KE. 2021. Urbanization-driven climate change increases invertebrate lipid demand, relative to protein—a response to dehydration. *Funct. Ecol.* 35:411–19
6. Becker JE, Mirochnitchenko NA, Ingram H, Everett A, McCluney KE. 2021. Water-seeking behavior among terrestrial arthropods and mollusks in a cool mesic region: spatial and temporal patterns. *PLOS ONE* 16:e0260070
7. Benaroudj N, Lee DH, Goldberg AL. 2001. Trehalose accumulation during cellular stress protects cells and cellular proteins from damage by oxygen radicals. *J. Biol. Chem.* 276:24261–67
8. Benoit JB. 2010. Water management by dormant insects: comparisons between dehydration resistance during summer aestivation and winter diapause. *Prog. Mol. Subcell. Biol.* 49:209–29
9. Benoit JB, Attardo GM, Baumann AA, Michalkova V, Aksoy S. 2015. Adenotrophic viviparity in tsetse flies: potential for population control and as an insect model for lactation. *Annu. Rev. Entomol.* 60:351–71
10. Benoit JB, Del Grosso NA, Yoder JA, Denlinger DL. 2007. Resistance to dehydration between bouts of blood feeding in the bed bug, *Cimex lectularius*, is enhanced by water conservation, aggregation, and quiescence. *Am. J. Trop. Med. Hyg.* 76:987–93
11. Benoit JB, Denlinger DL. 2007. Suppression of water loss during adult diapause in the northern house mosquito, *Culex pipiens*. *J. Exp. Biol.* 210:217–26
12. Benoit JB, Denlinger DL. 2010. Meeting the challenges of on-host and off-host water balance in blood-feeding arthropods. *J. Insect Physiol.* 56:1366–76
13. Benoit JB, Hansen IA, Attardo GM, Michalková V, Mireji PO, et al. 2014. Aquaporins are critical for provision of water during lactation and intrauterine progeny hydration to maintain tsetse fly reproductive success. *PLOS Negl. Trop. Dis.* 8:e2517
14. Benoit JB, Lopez-Martinez G, Elnitsky MA, Lee RE Jr., Denlinger DL. 2009. Dehydration-induced cross tolerance of *Belgica antarctica* larvae to cold and heat is facilitated by trehalose accumulation. *Comp. Biochem. Physiol. A* 152:518–23
15. Benoit JB, Oyen KJ. 2021. Drought and tick dynamics during climate change. In *Climate, Ticks and Disease*, ed. P Nuttall, pp. 67–73. Wallingford, UK: CAB Int.
16. Benoit JB, Patrick KR, Desai K, Hardesty JJ, Krause TB, Denlinger DL. 2010. Repeated bouts of dehydration deplete nutrient reserves and reduce egg production in the mosquito *Culex pipiens*. *J. Exp. Biol.* 213:2763–69
17. Benoit JB, Vinauger C. 2022. Chronobiology of blood feeding arthropods: influences of their role as disease vectors. In *Sensory Ecology of Disease Vectors*, ed. S Hill, R Ignell, C Lazzari, M Lorenzo. Wageningen, Neth.: Wageningen Acad. Publ. In press

18. Benoit JB, Yoder JA, Rellinger EJ, Ark JT, Keeney GD. 2005. Prolonged maintenance of water balance by adult females of the American spider beetle, *Mezium affine* Boieldieu, in the absence of food and water resources. *J. Insect Physiol.* 51:565–73
19. Benton R, Vannice KS, Gomez-Diaz C, Vosshall LB. 2009. Variant ionotropic glutamate receptors as chemosensory receptors in *Drosophila*. *Cell* 136:149–62
20. Bernáth B, Horváth G, Meyer-Rochow VB. 2012. Polarotaxis in egg-laying yellow fever mosquitoes *Aedes* (*Stegomyia*) *aegypti* is masked due to infochemicals. *J. Insect Physiol.* 58:1000–6
21. Beyenbach KW, Skaer H, Dow JAT. 2010. The developmental, molecular, and transport biology of Malpighian tubules. *Annu. Rev. Entomol.* 55:351–74
22. Bezerra Da Silva CS, Price BE, Walton VM. 2019. Water-deprived parasitic wasps (*Pachycrepoideus vindemmiae*) kill more pupae of a pest (*Drosophila suzukii*) as a water-intake strategy. *Sci. Rep.* 9:3592
23. Bong L-J, Wang C-Y, Shiodera S, Haraguchi TF, Itoh M, Neoh K-B. 2021. Effect of body lipid content is linked to nutritional adaptation in the acclimation responses of mesic-adapted *Paederus* to seasonal variations in desiccation stress. *J. Insect Physiol.* 131:104226
24. Cabrero P, Radford JC, Broderick KE, Costes L, Veenstra JA, et al. 2002. The Dh gene of *Drosophila melanogaster* encodes a diuretic peptide that acts through cyclic AMP. *J. Exp. Biol.* 205:3799–807
25. Cabrero P, Terhzaz S, Dornan AJ, Ghimire S, Holmes HL, et al. 2020. Specialized stellate cells offer a privileged route for rapid water flux in *Drosophila* renal tubule. *PNAS* 117:1779–87
26. Cameron P, Hiroi M, Ngai J, Scott K. 2010. The molecular basis for water taste in *Drosophila*. *Nature* 465:91–95
27. Chen Z, Wang Q, Wang Z. 2010. The amiloride-sensitive epithelial Na^+ channel PPK28 is essential for *Drosophila* gustatory water reception. *J. Neurosci.* 30:6247–52
28. Chown SL, Nicolson SW. 2004. Water balance physiology. In *Insect Physiological Ecology: Mechanisms and Patterns*, pp. 87–114. Oxford, UK: Oxford Univ. Press
29. Chu E, Chakraborty S, Benoit JB, DeGennaro M. Water homeostasis and hygrosensation in mosquitoes. In *Sensory Ecology of Disease Vectors*, ed. S Hill, R Ignell, C Lazzari, M Lorenzo. Wageningen, Neth.: Wageningen Acad. Publ. In press
30. Clark MS, Thorne MA, Purać J, Burns G, Hillyard G, et al. 2009. Surviving the cold: molecular analyses of insect cryoprotective dehydration in the Arctic springtail *Megaphorura arctica* (Tullberg). *BMC Genom.* 10:328
31. Clemson AS, Sgrò CM, Telonis-Scott M. 2018. Transcriptional profiles of plasticity for desiccation stress in *Drosophila*. *Comp. Biochem. Physiol. B* 216:1–9
32. Cloudsley-Thompson JL. 2001. Thermal and water relations of desert beetles. *Naturwissenschaften* 88:447–60
33. Crespo-Pérez V, Kazakou E, Roubik DW, Cárdenas RE. 2020. The importance of insects on land and in water: a tropical view. *Curr. Opin. Insect Sci.* 40:31–38
34. Dai A. 2012. Increasing drought under global warming in observations and models. *Nat. Clim. Change* 3:52–58
35. Dale AG, Frank SD. 2017. Warming and drought combine to increase pest insect fitness on urban trees. *PLOS ONE* 12:e0173844
36. Dao A, Yaro AS, Diallo M, Timbiné S, Huestis DL, et al. 2014. Signatures of aestivation and migration in Sahelian malaria mosquito populations. *Nature* 516:387–90
37. Davis JR, DeNardo DF. 2009. Water supplementation affects the behavioral and physiological ecology of Gila monsters (*Heloderma suspectum*) in the Sonoran Desert. *Physiol. Biochem. Zool.* 82:739–48
38. Deguines N, Brashares JS, Prugh LR. 2017. Precipitation alters interactions in a grassland ecological community. *J. Anim. Ecol.* 86:262–72
39. Denlinger DL. 2022. *Insect Diapause*. Cambridge, UK: Cambridge Univ. Press
40. Dow JAT, Krause SA, Herzyk P. 2021. Updates on ion and water transport by the Malpighian tubule. *Curr. Opin. Insect Sci.* 47:31–37
41. Dunlop JA, Scholtz G, Selden PA. 2013. Water-to-land transitions. In *Arthropod Biology and Evolution: Molecules, Development, Morphology*, ed. A Minelli, G Boxshall, G Fusco, pp. 417–39. Berlin: Springer
42. el Shoura SM. 1988. Fine structure of larval malpighian tubules and rectal sac in the tick *Ornithodoros* (Pavlovskyella) *erraticus* (Ixodoidea: Argasidae). *J. Morphol.* 196:187–93

43. Elnitsky MA, Hayward SAL, Rinehart JP, Denlinger DL, Lee RE Jr. 2008. Cryoprotective dehydration and the resistance to inoculative freezing in the Antarctic midge, *Belgica antarctica*. *J. Exp. Biol.* 211:524–30
44. Enjin A, Zaharieva EE, Frank DD, Mansourian S, Suh GSB, et al. 2016. Humidity sensing in *Drosophila*. *Curr. Biol.* 26:1352–58
45. Ferry C, Corbet SA. 1996. Water collection by bumble bees. *J. Apic. Res.* 35:120–22
46. Finch G, Nandyal S, Perretta C, Davies B, Rosendale AJ, et al. 2020. Multi-level analysis of reproduction in an Antarctic midge identifies female and male accessory gland products that are altered by larval stress and impact progeny viability. *Sci. Rep.* 10:19791
47. Frizzi F, Rispoli A, Chelazzi G, Santini G. 2016. Effect of water and resource availability on ant feeding preferences: a field experiment on the Mediterranean ant *Crematogaster scutellaris*. *Insect. Soc.* 63:565–74
48. Gefen E, Marlon AJ, Gibbs AG. 2006. Selection for desiccation resistance in adult *Drosophila melanogaster* affects larval development and metabolite accumulation. *J. Exp. Biol.* 209:3293–300
49. Gely C, Laurance SGW, Stork NE. 2020. How do herbivorous insects respond to drought stress in trees? *Biol. Rev. Camb. Philos. Soc.* 95:434–48
50. Gibbs AG, Chippindale AK, Rose MR. 1997. Physiological mechanisms of evolved desiccation resistance in *Drosophila melanogaster*. *J. Exp. Biol.* 200:1821–32
51. Gray EM, Rocca KAC, Costantini C, Besansky NJ. 2009. Inversion 2La is associated with enhanced desiccation resistance in *Anopheles gambiae*. *Malar. J.* 8:215
52. Grenot C. 2001. Adaptation of small Saharan vertebrates to arid conditions. *Bull. Soc. Zool. Fr.* 126:129–67
53. Greppi C, Laursen WJ, Budelli G, Chang EC, Daniels AM, et al. 2020. Mosquito heat seeking is driven by an ancestral cooling receptor. *Science* 367:681–84
54. Groffman PM, Cavender-Bares J, Bettez ND, Grove JM, Hall SJ, et al. 2014. Ecological homogenization of urban USA. *Front. Ecol. Environ.* 12:74–81
55. Gusev O, Suetsugu Y, Cornette R, Kawashima T, Logacheva MD, et al. 2014. Comparative genome sequencing reveals genomic signature of extreme desiccation tolerance in the anhydrobiotic midge. *Nat. Commun.* 5:4784
56. Hadley NF. 1994. *Water Relations of Terrestrial Arthropods*. Cambridge, MA: Academic
57. Hagan RW, Didion EM, Rosselot AE, Holmes CJ, Siler SC, et al. 2018. Dehydration prompts increased activity and blood feeding by mosquitoes. *Sci. Rep.* 8:6804
58. Hera I, Reichert MS. 2021. Water content in diet affects growth and timing of female first mating, but not coloration, in the admirable grasshopper (*Syrbula admirabilis*). *Invertebr. Biol.* 140:e12356
59. Hinton HE. 1960. A fly larva that tolerates dehydration and temperatures of −270° to +102°C. *Nature* 188:336–37
60. Holmes CJ, Benoit JB. 2019. Biological adaptations associated with dehydration in mosquitoes. *Insects* 10:375
61. Holmes CJ, Brown ES, Sharma D, Nguyen Q, Spangler AA, et al. 2022. Bloodmeal regulation in mosquitoes curtails dehydration-induced mortality, altering vectorial capacity. *J. Insect Physiol.* 137:104363
62. Horváth G, Csabai Z. 2014. Polarization vision of aquatic insects. In *Polarized Light and Polarization Vision in Animal Sciences*, ed. G Horváth, pp. 113–45. Berlin: Springer
63. Horváth G, Móra A, Bernáth B, Kriska G. 2011. Polarotaxis in non-biting midges: female chironomids are attracted to horizontally polarized light. *Physiol. Behav.* 104:1010–15
64. Hu G, Lim KS, Horvitz N, Clark SJ, Reynolds DR, et al. 2016. Mass seasonal bioflows of high-flying insect migrants. *Science* 354:1584–87
65. Huestis DL, Dao A, Diallo M, Sanogo ZL, Samake D, et al. 2019. Windborne long-distance migration of malaria mosquitoes in the Sahel. *Nature* 574:404–8
66. Jia N, Wang J, Shi W, Du L, Sun Y, et al. 2020. Large-scale comparative analyses of tick genomes elucidate their genetic diversity and vector capacities. *Cell* 182:1328–40.e13
67. Jourjine N, Mullaney BC, Mann K, Scott K. 2016. Coupled sensing of hunger and thirst signals balances sugar and water consumption. *Cell* 166:855–66
68. Jung AC, Denholm B, Skaer H, Affolter M. 2005. Renal tubule development in *Drosophila*: a closer look at the cellular level. *J. Am. Soc. Nephrol.* 16:322–28

69. Kang L, Aggarwal DD, Rashkovetsky E, Korol AB, Michalak P. 2016. Rapid genomic changes in *Drosophila melanogaster* adapting to desiccation stress in an experimental evolution system. *BMC Genom.* 17:233
70. Kawarasaki Y, Teets NM, Denlinger DL, Lee RE. 2014. Alternative overwintering strategies in an Antarctic midge: freezing versus cryoprotective dehydration. *Funct. Ecol.* 28:933–43
71. Kellermann V, Hoffmann AA, Overgaard J, Loeschcke V, Sgrò CM. 2018. Plasticity for desiccation tolerance across *Drosophila species* is affected by phylogeny and climate in complex ways. *Proc. Biol. Sci.* 285:20180048
72. Kellermann V, McEvey SF, Sgrò CM, Hoffmann AA. 2020. Phenotypic plasticity for desiccation resistance, climate change, and future species distributions: Will plasticity have much impact? *Am. Nat.* 196:306–15
73. Kerr M, Davies SA, Dow JAT. 2004. Cell-specific manipulation of second messengers; a toolbox for integrative physiology in *Drosophila*. *Curr. Biol.* 14:1468–74
74. Kessler S, Guerin PM. 2008. Responses of *Anopheles gambiae*, *Anopheles stephensi*, *Aedes aegypti*, and *Culex pipiens* mosquitoes (Diptera: Culicidae) to cool and humid refugium conditions. *J. Vector Ecol.* 33:145–49
75. Kim D, Maldonado-Ruiz P, Zurek L, Park Y. 2017. Water absorption through salivary gland type I acini in the blacklegged tick, *Ixodes scapularis*. *PeerJ*. 5:e3984
76. Kleynhans E, Terblanche JS. 2011. Complex interactions between temperature and relative humidity on water balance of adult tsetse (Glossinidae, Diptera): implications for climate change. *Front. Physiol.* 2:74
77. Knecht ZA, Silbering AF, Cruz J, Yang L, Croset V, et al. 2017. Ionotropic receptor-dependent moist and dry cells control hygrosensation in *Drosophila*. *eLife* 6:e26654
78. Knecht ZA, Silbering AF, Ni L, Klein M, Budelli G, et al. 2016. Distinct combinations of variant ionotropic glutamate 1 receptors mediate thermosensation and hygrosensation in *Drosophila*. *eLife* 5:e17879
79. Leinbach IL, McCluney KE, Sabo JL. 2019. Predator water balance alters intraguild predation in a streamside food web. *Ecology* 100:e02635
80. Li A, Benoit JB, Lopez-Martinez G, Elnitsky MA, Lee RE Jr., Denlinger DL. 2009. Distinct contractile and cytoskeletal protein patterns in the Antarctic midge are elicited by desiccation and rehydration. *Proteomics* 9:2788–98
81. Li H, Janssens J, De Waegeneer M, Kolluru SS. 2021. Fly Cell Atlas: a single-cell transcriptomic atlas of the adult fruit fly. bioRxiv 2021.07.04.451050. **https://doi.org/10.1101/2021.07.04.451050**
82. Little C. 1990. *The Terrestrial Invasion: An Ecophysiological Approach to the Origins of Land Animals*. Cambridge, UK: Cambridge Univ. Press
83. Lopez-Martinez G, Benoit JB, Rinehart JP, Elnitsky MA, Lee RE Jr., Denlinger DL. 2009. Dehydration, rehydration, and overhydration alter patterns of gene expression in the Antarctic midge, *Belgica antarctica*. *J. Comp. Physiol. B* 179:481–91
84. Lundgren EJ, Ramp D, Stromberg JC, Wu J, Nieto NC, et al. 2021. Equids engineer desert water availability. *Science* 372:491–95
85. Mamai W, Mouline K, Blais C, Larvor V, Dabiré KR, et al. 2014. Metabolomic and ecdysteroid variations in *Anopheles gambiae* s.l. mosquitoes exposed to the stressful conditions of the dry season in Burkina Faso, West Africa. *Physiol. Biochem. Zool.* 87:486–97
86. Martin LJ, Adams RI, Bateman A, Bik HM, Hawks J, et al. 2015. Evolution of the indoor biome. *Trends Ecol. Evol.* 30:223–32
87. Matthews BJ, Younger MA, Vosshall LB. 2019. The ion channel ppk301 controls freshwater egg-laying in the mosquito *Aedes aegypti*. *eLife* 8:e43963
88. Mattson WJ, Haack RA. 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience* 37:110–18
89. McCluney KE. 2017. Implications of animal water balance for terrestrial food webs. *Curr. Opin. Insect Sci.* 23:13–21
90. McCluney KE, Belnap J, Collins SL, González AL, Hagen EM, et al. 2012. Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biol. Rev. Camb. Philos. Soc.* 87:563–82

91. McCluney KE, Burdine JD, Frank SD. 2017. Variation in arthropod hydration across US cities with distinct climate. *J. Urban Ecol.* 3:jux003
92. McCluney KE, George T, Frank SD. 2018. Water availability influences arthropod water demand, hydration and community composition on urban trees. *J. Urban Ecol.* 4:juy003
93. McCluney KE, Sabo JL. 2009. Water availability directly determines per capita consumption at two trophic levels. *Ecology* 90:1463–69
94. McCluney KE, Sabo JL. 2016. Animal water balance drives top-down effects in a riparian forest—implications for terrestrial trophic cascades. *Proc. R. Soc. B* 283:20160881
95. Meserve PL, Kelt DA, Milstead WB, Gutiérrez JR. 2003. Thirteen years of shifting top-down and bottom-up control. *Bioscience* 53:633–46
96. Michaud RM, Benoit JB, Lopez-Martinez G, Elnitsky MA, Lee RE, Denlinger DL. 2008. Metabolomics reveals unique and shared metabolic changes in response to heat shock, freezing and desiccation in the Antarctic midge, *Belgica antarctica*. *J. Insect Physiol.* 54:645–55
97. Miller J, Chi T, Kapahi P, Kahn AJ, Kim MS, et al. 2013. *Drosophila melanogaster* as an emerging translational model of human nephrolithiasis. *J. Urol.* 190(5):1648–56
98. Noy-Meir I. 1974. Desert ecosystems: higher trophic levels. *Annu. Rev. Ecol. Syst.* 5:195–214
99. O'Donnell MJ, Machin J. 1988. Water vapor absorption by terrestrial organisms. In *Advances in Comparative and Environmental Physiology*, ed. SH Wright, pp. 47–90. Berlin: Springer
100. Orchard I, Lange AB. 2020. Hormonal control of diuresis in insects. In *Advances in Invertebrate (Neuro)Endocrinology*, ed. S Saleuddin, I Orchard, AB Lange, pp. 225–82. Palm Bay, FL: Apple Acad.
101. Orchard I, Paluzzi J-P. 2009. Diuretic and antidiuretic hormones in the blood-gorging bug *Rhodnius prolixus*. *Ann. N. Y. Acad. Sci.* 1163:501–3
102. Orr MC, Hughes AC, Chesters D, Pickering J, Zhu C-D, Ascher JS. 2021. Global patterns and drivers of bee distribution. *Curr. Biol.* 31:451–58
103. Overgaard J, Gerber L, Andersen MK. 2021. Osmoregulatory capacity at low temperature is critical for insect cold tolerance. *Curr. Opin. Insect Sci.* 47:38–45
104. Pincetl S. 2015. Cities as novel biomes: recognizing urban ecosystem services as anthropogenic. *Front. Ecol. Evol.* 3:140
105. Potts LJ, Gantz JD, Kawarasaki Y, Philip BN, Gonthier DJ, et al. 2020. Environmental factors influencing fine-scale distribution of Antarctica's only endemic insect. *Oecologia* 194:529–39
106. Raji JI, Gonzalez S, DeGennaro M. 2019. *Aedes aegypti* Ir8a mutant female mosquitoes show increased attraction to standing water. *Commun. Integr. Biol.* 12:181–86
107. Randolph SE, Storey K. 1999. Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. *J. Med. Entomol.* 36:741–48
108. Rane RV, Pearce SL, Li F, Coppin C, Schiffer M, et al. 2019. Genomic changes associated with adaptation to arid environments in cactophilic *Drosophila* species. *BMC Genom.* 20:52
109. Reid ML, Ahn S. 2020. Realised toxicity of plant defences to an insect herbivore depends more on insect dehydration than on energy reserves. *Ecol. Entomol.* 45:771–82
110. Reidenbach KR, Cheng C, Liu F, Liu C, Besansky NJ, Syed Z. 2014. Cuticular differences associated with aridity acclimation in African malaria vectors carrying alternative arrangements of inversion 2La. *Parasit. Vectors* 7:176
111. Rosendale AJ, Dunlevy ME, Fieler AM, Farrow DW, Davies B, Benoit JB. 2017. Dehydration and starvation yield energetic consequences that affect survival of the American dog tick. *J. Insect Physiol.* 101:39–46
112. Rosendale AJ, Farrow DW, Dunlevy ME, Fieler AM, Benoit JB. 2016. Cold hardiness and influences of hibernaculum conditions on overwintering survival of American dog tick larvae. *Ticks Tick Borne Dis.* 7:1155–61
113. Rosendale AJ, Romick-Rosendale LE, Watanabe M, Dunlevy ME, Benoit JB. 2016. Mechanistic underpinnings of dehydration stress in the American dog tick revealed through RNA-seq and metabolomics. *J. Exp. Biol.* 219:1808–19
114. Ryabova A, Cornette R, Cherkasov A, Watanabe M, Okuda T, et al. 2020. Combined metabolome and transcriptome analysis reveals key components of complete desiccation tolerance in an anhydrobiotic insect. *PNAS* 117:19209–20

115. Sabo JL, McCluney KE, Marusenko Y, Keller A, Soykan CU. 2008. Greenfall links groundwater to aboveground food webs in desert river floodplains. *Ecol. Monogr.* 78:615–31
116. Sajadi F, Paluzzi J-PV. 2021. Hormonal regulation and functional role of the "renal" tubules in the disease vector, *Aedes aegypti*. *Vitam. Horm.* 117:189–225
117. Sconiers WB, Eubanks MD. 2017. Not all droughts are created equal? The effects of stress severity on insect herbivore abundance. *Arthropod Plant Interact.* 11:45–60
118. Senapathi D, Fründ J, Albrecht M, Garratt MPD, Kleijn D, et al. 2021. Wild insect diversity increases inter-annual stability in global crop pollinator communities. *Proc. Biol. Sci.* 288:20210212
119. Shaman J, Day JF, Stieglitz M. 2005. Drought-induced amplification and epidemic transmission of West Nile virus in southern Florida. *J. Med. Entomol.* 42:134–41
120. Sinclair BJ, Ferguson LV, Salehipour-shirazi G, MacMillan HA. 2013. Cross-tolerance and cross-talk in the cold: relating low temperatures to desiccation and immune stress in insects. *Integr. Comp. Biol.* 53(4):545–56
121. Sinclair BJ, Nelson S, Nilson TL, Roberts SP, Gibbs AG. 2007. The effect of selection for desiccation resistance on cold tolerance of *Drosophila melanogaster*. *Physiol. Entomol.* 32:322–27
122. Stensmyr MC, Erland S, Hallberg E, Wallén R, Greenaway P, Hansson BS. 2005. Insect-like olfactory adaptations in the terrestrial giant robber crab. *Curr. Biol.* 15:116–21
123. Sun JS, Larter NK, Chahda JS, Rioux D, Gumaste A, Carlson JR. 2018. Humidity response depends on the small soluble protein Obp59a in *Drosophila*. *eLife* 7:e39249
124. Tamburini G, van Gils S, Kos M, van der Putten W, Marini L. 2018. Drought and soil fertility modify fertilization effects on aphid performance in wheat. *Basic Appl. Ecol.* 30:23–31
125. Teets NM, Denlinger DL. 2013. Autophagy in Antarctica: combating dehydration stress in the world's southernmost insect. *Autophagy* 9:629–31
126. Teets NM, Kawarasaki Y, Lee RE Jr., Denlinger DL. 2013. Expression of genes involved in energy mobilization and osmoprotectant synthesis during thermal and dehydration stress in the Antarctic midge, *Belgica antarctica*. *J. Comp. Physiol. B* 183:189–201
127. Teets NM, Peyton JT, Colinet H, Renault D, Kelley JL, et al. 2012. Gene expression changes governing extreme dehydration tolerance in an Antarctic insect. *PNAS* 109:20744–49
128. Thomas GWC, Dohmen E, Hughes DST, Murali SC, Poelchau M, et al. 2020. Gene content evolution in the arthropods. *Genome Biol.* 21(1):15
129. Tichy H, Kallina W. 2010. Insect hygroreceptor responses to continuous changes in humidity and air pressure. *J. Neurophysiol.* 103:3274–86
130. Tichy H, Loftus R. 1996. Hygroreceptors in insects and a spider: humidity transduction models. *Naturwissenschaften* 83:255–63
131. Tigar BJ, Osborne PE. 1997. Patterns of arthropod abundance and diversity in an Arabian desert. *Ecography* 20:550–58
132. Tomioka K, Matsumoto A. 2019. The circadian system in insects: cellular, molecular, and functional organization. *Adv. Insect Phys.* 56:73–115
133. Toxopeus J, Koštál V, Sinclair BJ. 2019. Evidence for non-colligative function of small cryoprotectants in a freeze-tolerant insect. *Proc. Biol. Sci.* 286:20190050
134. Trenberth KE. 2011. Changes in precipitation with climate change. *Clim. Res.* 47(1):123–38
135. van Giesen L, Garrity PA. 2017. More than meets the IR: the expanding roles of variant ionotropic glutamate receptors in sensing odor, taste, temperature and moisture. *F1000Research* 6:1753
136. van Klink R, Bowler DE, Gongalsky KB, Swengel AB, Gentile A, Chase JM. 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* 368:417–20
137. Vieira FG, Rozas J. 2011. Comparative genomics of the odorant-binding and chemosensory protein gene families across the Arthropoda: origin and evolutionary history of the chemosensory system. *Genome Biol. Evol.* 3:476–90
138. Wagner DL. 2020. Insect declines in the Anthropocene. *Annu. Rev. Entomol.* 65:457–80
139. Wall BJ, Oschman JL, Schmidt BA. 1975. Morphology and function of Malpighian tubules and associated structures in the cockroach, *Periplaneta americana*. *J. Morphol.* 146:265–306
140. Walter A, Westphal C, Bliss P, Moritz RFA. 2011. Drinking behaviour of the orb web spider *Argiope bruennichi* (Araneae; Araneidae). *Behaviour* 148:1295–309

141. Wang M-H, Marinotti O, Vardo-Zalik A, Boparai R, Yan G. 2011. Genome-wide transcriptional analysis of genes associated with acute desiccation stress in *Anopheles gambiae*. *PLOS ONE* 6:e26011

142. Wharton GW. 1985. Water balance of insects. In *Regulation: Digestion*, *Nutrition*, *Excretion*, ed. GA Kerkut, LI Gilbert, pp. 565–601. Oxford, UK: Pergamon

143. Williams JB, Lee RE Jr. 2011. Effect of freezing and dehydration on ion and cryoprotectant distribution and hemolymph volume in the goldenrod gall fly, *Eurosta solidaginis*. *J. Insect Physiol.* 57:1163–69

144. Wolda H. 1992. Trends in abundance of tropical forest insects. *Oecologia* 89:47–52

145. Xiong C, Yang Y, Nachman RJ, Pietrantonio PV. 2021. Tick CAPA propeptide cDNAs and receptor activity of endogenous tick pyrokinins and analogs: towards discovering pyrokinin function in ticks. *Peptides* 146:170665

146. Xu J, Liu Y, Li H, Tarashansky AJ, Kalicki CH, et al. 2021. A cell atlas of the fly kidney. bioRxiv 2021.09.03.458871. **https://doi.org/10.1101/2021.09.03.458871**

147. Yoder JA, Ark JT, Benoit JB, Rellinger EJ, Tank JL. 2006. Inability of the lone star tick, *Amblyomma americanum* (L.), to resist desiccation and maintain water balance following application of the entomopathogenic fungus *Metarhizium anisopliae* var. *anisopliae* (Deuteromycota). *Int. J. Acarol.* 32:211–18

148. Yoder JA, Benoit JB, Denlinger DL, Rivers DB. 2006. Stress-induced accumulation of glycerol in the flesh fly, *Sarcophaga bullata*: evidence indicating anti-desiccant and cryoprotectant functions of this polyol and a role for the brain in coordinating the response. *J. Insect Physiol.* 52:202–14

149. Yoder JA, Hedges BZ, Benoit JB. 2012. Water balance of the American dog tick, *Dermacentor variabilis*, throughout its development with comparative observations between field-collected and laboratory-reared ticks. *Int. J. Acarol.* 38:334–43

150. Zheng W, Rus F, Hernandez A, Kang P, Goldman W, et al. 2018. Dehydration triggers ecdysone-mediated recognition-protein priming and elevated anti-bacterial immune responses in *Drosophila* Malpighian tubule renal cells. *BMC Biol.* 16:60

Annual Review
of Entomology

Volume 68, 2023

Contents

Errata

An online log of corrections to *Annual Review of Entomology* articles may be found at http://www.annualreviews.org/errata/ento

Related Articles

From the ***Annual Review of Animal Biosciences***, Volume 10 (2022)

Translating Basic Research to Animal Agriculture
George E. Seidel Jr.

Concepts and Consequences of a Core Gut Microbiota for Animal Growth and Development
Daphne Perlman, Marina Martínez-Álvaro, Sarah Moraïs, Ianina Altshuler, Live H. Hagen, Elie Jami, Rainer Roehe, Phillip B. Pope, and Itzhak Mizrahi

Host Genetic Determinants of the Microbiome Across Animals: From *Caenorhabditis elegans* to Cattle
Erica P. Ryu and Emily R. Davenport

Chagas Disease Ecology in the United States: Recent Advances in Understanding *Trypanosoma cruzi* Transmission Among Triatomines, Wildlife, and Domestic Animals and a Quantitative Synthesis of Vector–Host Interactions
Rachel E. Busselman and Sarah A. Hamer

From the ***Annual Review of Genetics***, Volume 56 (2022)

The Genetics of Autophagy in Multicellular Organisms
Hong Zhang

From the ***Annual Review of Microbiology***, Volume 76 (2022)

Division and Transmission: Malaria Parasite Development in the Mosquito
David S. Guttery, Mohammad Zeeshan, David J.P. Ferguson, Anthony A. Holder, and Rita Tewari

From the ***Annual Review of Phytopathology***, Volume 60 (2022)

Yellow Dwarf Viruses of Cereals: Taxonomy and Molecular Mechanisms
W. Allen Miller and Zachary Lozier

Future of Bacterial Disease Management in Crop Production
Anuj Sharma, Peter Abrahamian, Renato Carvalho, Manoj Choudhary, Mathews L. Paret, Gary E. Vallad, and Jeffrey B. Jones

Ecology of Yellow Dwarf Viruses in Crops and Grasslands: Interactions in the Context of Climate Change
Jasmine S. Peters, Beatriz A. Aguirre, Anna DiPaola, and Alison G. Power

From the ***Annual Review of Virology***, Volume 9 (2022)

Citrus Tristeza Virus: From Pathogen to Panacea
Svetlana Y. Folimonova and Yong-Duo Sun

Advances in Understanding Neuropathogenesis of Rift Valley Fever Virus
Kaleigh A. Connors and Amy L. Hartman