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Seeking the limits of osmoregulation: Thirst and fluid ionic balance research in non-model vertebrates

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The current understanding of osmoregulation has been largely shaped by studies in traditional laboratory models such as mice and rats. Yet, across habitats, animals have diversified the ways they seek, consume, and manage water, revealing that the mechanisms governing thirst and fluid ionic balance are more flexible than those known from traditional laboratory models. In this integrative review, we explore the insights some diverse animal models can provide to the field of osmoregulation, highlight recent discoveries, and propose new research trajectories grounded in comparative neurophysiology.

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Introduction

For many vertebrate species, drinking free-standing water (e.g., from a glass or a pond) is the primary means of osmoregulation, the process of correcting disturbances in water/mineral balance and restoring homeostasis. Other species may meet water requirements primarily through alternative, non-drinking sources (e.g., metabolic or atmospheric water). Nevertheless, research on thirst regulation in mammals has largely relied on traditional laboratory animals (i.e., mice and rats), who employ the stereotypical drinking strategy rather than relying on non-drinking alternatives. While these species have provided critical insights into the fundamental neural and molecular mechanisms of thirst (Box 1; see reviews in Refs. [1–3]), they are also constrained in important ways, and emerging work underscores the need to broaden the taxonomic scope of fluid-ionic balance and thirst research.

Historically, thirst was often thought of as a homeostatic feedback response to increased blood osmolarity or loss in fluid volume (hypovolemia). Work in mice, however, has shown how thirst can arise even if homeostatic need is absent (i.e., in anticipation of daily cycles) [4], or suppressed before homeostatic need is satisfied (i.e., through oropharyngeal and gut signals) [5], demonstrating how thirst extends beyond purely reactive mechanisms. Although these mechanisms protect mice from dehydration, their effectiveness is limited to a relatively narrow window. Species inhabiting more demanding environments may retain these mechanisms but also rely on additional, or fundamentally different, strategies to maintain hydration (Figure 1).

Some strategies are anatomical, such as hydrophilic microstructures in the integument of some lizards [6,7] or the specialized salt glands that allow seabirds to drink seawater routinely [8,9]. Sometimes, anatomical adaptations are accompanied by behavioral strategies, such as prairie rattlesnakes folding their bodies into a tea-cup shape to harvest rainfall on their scales [10] or frogs adopting a stereotyped posture to "drink" through absorption across the ventral skin [11,12]. Other strategies are physiological, such as the reduction of evaporative water losses in camels [13,14], the circannual suppression of thirst in hibernating squirrels [15,16], and the reprogramming of ionic permeability in the gills of salmon in preparation for the transition into saltwater [17]. Here, we review these strategies and discuss recent progress in related fields.

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Box 1. Mammalian thirst and fluid-ionic balance: a primer

See Zhang Y & Oka Y [1]; Grove JRC & Knight ZA [2]; D'Acierno M, Fenton RA, Hoorn EJ [3].

Homeostatic thirst arises when fluid balance deviates and is classically **osmotic** *(~1% rise in plasma osmolality)* or **hypovolemic** *(~10% decrease in volume.)* In humans and mice, these disturbances are corrected via water intake. **The lamina terminalis**—comprised of the subfornical organ (**SFO**), the organum vasculosum of the lamina terminalis (**OVLT**), and the median preoptic nucleus (**MnPO**)—integrates these peripheral cues and drives drinking. At the molecular level, a sodium-activated channel (SCN7A) in glia and a transmembrane protein (TMEM63B) in excitatory neurons have been proposed as potential osmosensors. Epithelial sodium channels (ENaC) and transient receptor potential vanilloid-1 and -4 (TRPV1/4) have also been proposed osmosensors, but their absence does not fully abolish water intake. Together, these support a complementary, multi-node detection system of osmolarity changes in the brain.

At the endocrine level, angiotensin II (**ATII**; and downstream **aldosterone**) powerfully drive hypovolemic thirst by the brain, whereas vasopressin (**AVP**) primarily directs water retention at the kidney. At the renal level, **aquaporins** mediate water transport along the nephron. Drinking is rapidly quenched by feed-forward signals: gut/liver osmolality via vagal afferents can engage **MnPO GLP1r-expressing neurons**, with hindbrain and parabrachial nucleus circuits further suppressing drinking. The circadian suprachiasmatic nucleus to OVLT vasopressin pathway adds an additional layer of predictive control (also known as **anticipatory thirst**).

Mammals

Hibernating thirteen-lined ground squirrels: circannual modulation of thirst

Thirteen-lined ground squirrels (13LGS) possess the outstanding ability to reversibly alter their physiology to adapt to ever-changing environments. Natives to the North American grasslands and prairies, they enjoy resource-abundant summers but must also withstand barren winters. Squirrels spend most of hibernation in torpor: a state characterized by drastically reduced metabolic, heart, and breathing rates alongside a drop in core body temperature (CBT) to ambient levels, often as low as 2–4 °C [18]. Every 2–3 weeks, torpor is spontaneously interrupted by interbout arousals (IBA), when animals return to active-like state, restoring most of their physiological functions for 24–48 h [18]. Importantly, thirst and hunger remain inhibited during this time [15,16,19].

In summer, when water is abundant, squirrels drink normally and maintain a plasma osmolality (P_{osm}) of ~330 mOsm [16]. During torpor, when metabolic processes undergo a massive shutdown, P_{osm} drops to 300 mOsm [16]. Under these conditions, plasma levels of the antidiuretic hormones arginine vasopressin (AVP) and oxytocin (OXT) decrease [20], and glomerular filtration in the kidney nearly halts [21]. The subsequent restoration of metabolic processes during the transition from torpor to IBA poses the risk of massive water loss due to increased perfusion and accelerated metabolic waste production. This risk is mitigated by an early onset of electrical activity in hypothalamic supraoptic nucleus (SON) neurons, which begin to release antidiuretic hormones before the body temperature reaches 10 °C, together with a concurrent acceleration in glomerular filtration [20,21].

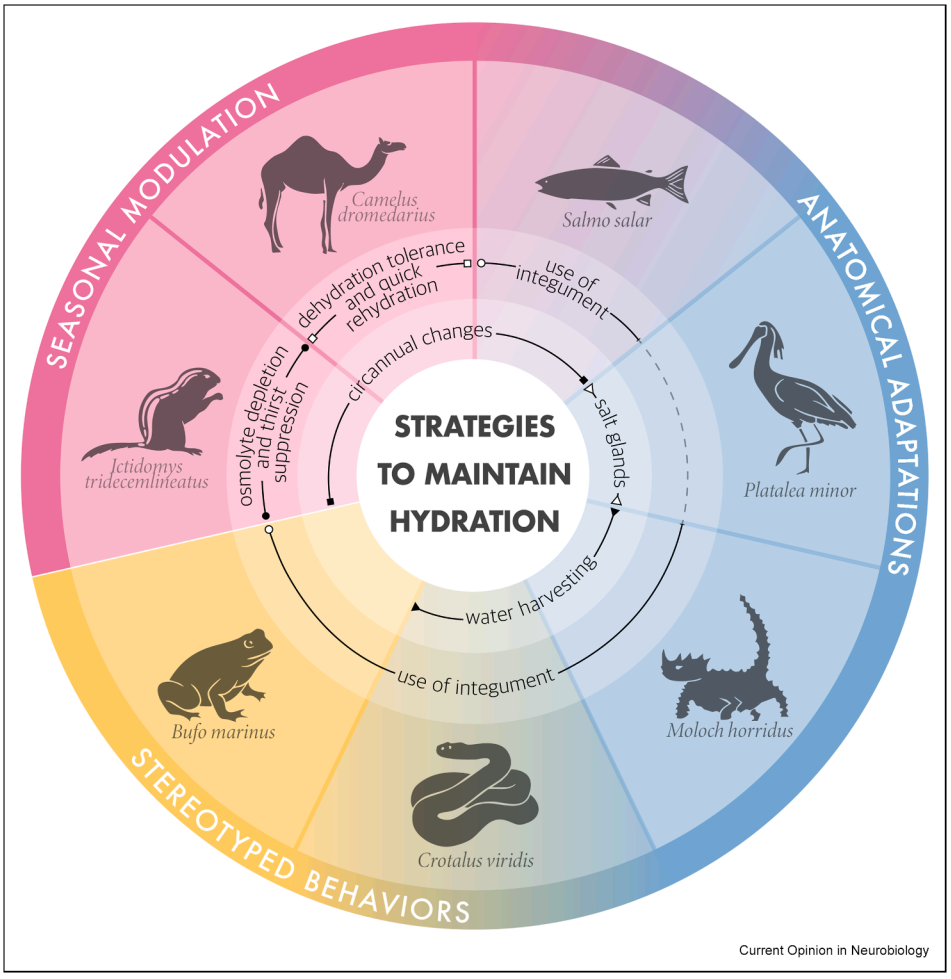
Paradoxically, even though during IBA P_{osm} is restored to ~330 mOsm [16], squirrels virtually cease to drink compared to active squirrels with the same P_{osm}. The underlying mechanism includes the suppression of activity of excitatory thirst-driving $nNOS^{+}$ neurons in the circumventricular organs (CVO) of the lamina terminalis [15]. Although CVO neurons retain sensitivity to dipsogenic hormones like angiotensin II (ATII), they become more susceptible to inhibition through increased expression of type A γ-aminobutyric acid ($GABA_A$) receptor *Gabrg1* [15]. Consistent with this, the subfornical organ neurons of IBA squirrels are intrinsically less excitable: they have a hyperpolarized resting membrane potential, reduced firing frequency and spike amplitude, and heightened sensitivity to GABA inhibition compared to those of active animals [15]—functionally raising the threshold for eliciting water-seeking behavior in hibernation. The exact trigger or source of these humoral and neuronal changes during hibernation, however, remains puzzling. Further studies into the reversible adipsia of 13LGS are needed to reveal the adaptive potential of the mammalian thirst circuit. We provide a summary of the osmoregulatory strategies used by 13LGS in Figure 2.

Camels: extreme dehydration tolerance and rapid rehydration

In most mammals, including humans, water loss corresponding to ~12% of body weight can lead to circulatory disturbances, cardiac failure, and death [22]. Yet, desert-inhabiting dromedary camels *(Camelus dromedarius)* can survive severe dehydration for up to 20 days, losing up to ~30% of their body weight in water without major harm to their vital organs [13,23,24]. To optimize water economy, dromedary camels employ multiple strategies, including producing small volumes of very concentrated urine, efficiently extracting water from food, and undergoing diurnal shifts in body temperature to reduce sweating and evaporative losses [13]. For more on the physiological adaptations of camels, see Chapter 3 in K Schmidt–Nielsen [13].

The camel's ability to generate highly concentrated urine depends on exceptional renal water reabsorption, a process regulated by AVP. AVP is released by the magnocellular neurons in the SON and paraventricular nuclei (PVN), which comprise the hypothalamo-

Figure 1

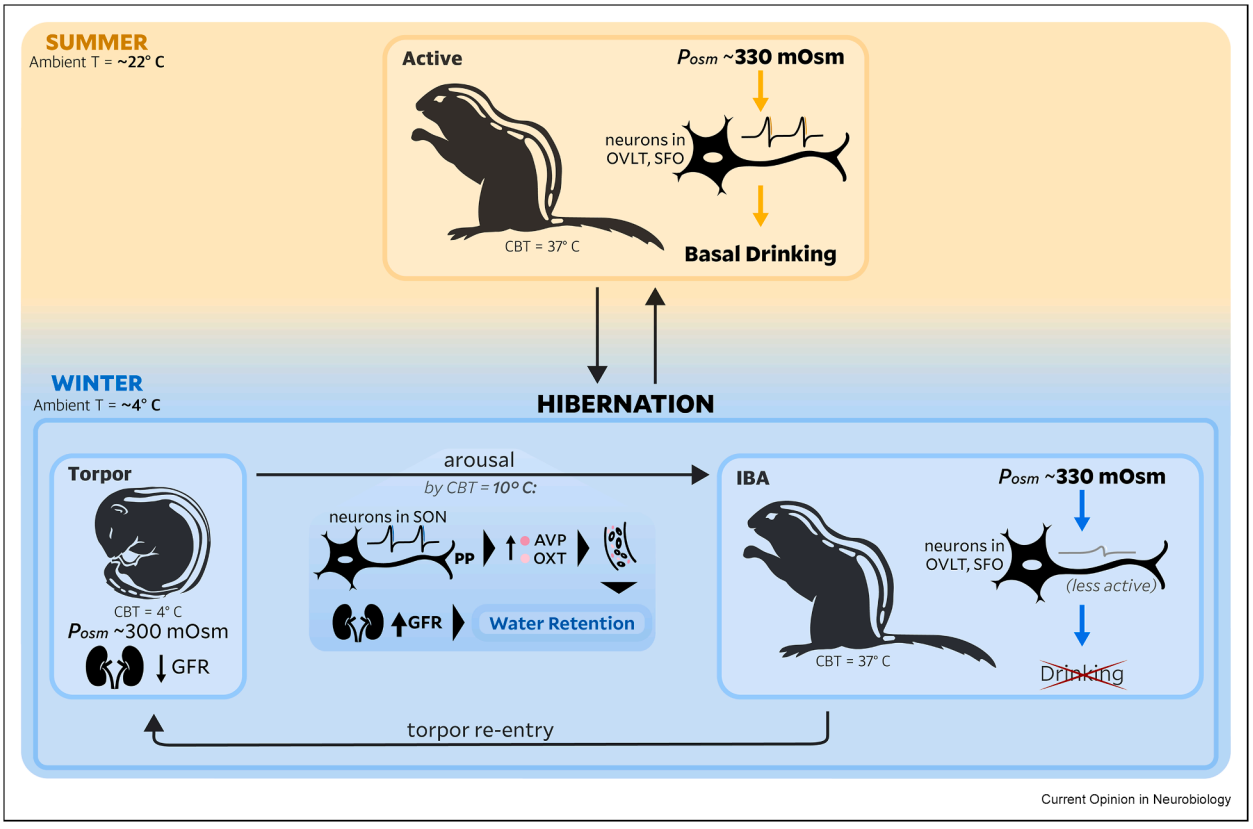


Comparative overview of strategies to maintain hydration among diverse vertebrates. Illustrated examples from Atlantic salmon (*Salmo salar*), Black-faced spoonbill (*Platalea minor*), Thorny devil lizard (*Moloch horridus*), Prairie rattlesnake (*Crotalus viridis*), Cane toad (*Bufo marinus*), Thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*), and Dromedary camel (*Camelus dromedarius*) highlight shared and specialized mechanisms for supporting fluid ionic balance. The figure summarizes strategies discussed in this review and is not intended to be exhaustive.

neurohypophyseal system (HNS). The ultrastructure of the HNS is known to be seasonally regulated in camels [25]. For example, the basal lamina of the SON is thinner in the summer compared to winter, a change that may influence endothelial barrier function and protect neurons from fluctuations in P_{osm} during the winter [23]. In addition to these seasonally-modulated structural changes, AVP gene expression in the camel SON rises significantly during the summer months [25].

At the tissue level, prolonged dehydration induces renal oxidative stress, inflammation, and apoptosis [23,24]. One of the strategies employed by dehydrated camels is to increase the levels of antioxidants in their blood, which helps protect their tissues from the oxidative stress that the long-term water scarcity induces [24]. Rehydration quickly reverses most of these adaptive changes [23]. In the kidney, F Alvira-Iraizoz et al. [26] show changes in gene expression encoding membrane proteins that may contribute to water retention during dehydration and underly functional reorganization of nephron. One of these changes is the overexpression of the potassium inwardly-rectifier KCNJ8 and Na^+/H^+ antiporter SLC9A7 in the apical membrane of epithelial cells in various locations of the nephron [26]. Dehydrated camels also exhibit upregulation of aquaporins across the renal cortex and medulla [26]. A more recent transcriptomic and immunohistochemical study from the same group compared kidney adaptations to desert life in the Arabian camel and the Egyptian jerboa [27]. Their findings suggest that suppression of cholesterol

Figure 2



Summary of osmoregulatory strategies in the thirteen-lined ground squirrel.
T = temperature, CBT = core body temperature, P_{osm}=plasma osmolarity, OVLT = organum vasculosum of the lamina terminalis, SFO = subfornical organ, GFR = glomerular filtration rate, SON = supraoptic nucleus, PP = posterior pituitary, AVP = arginine vasopressin, OXT = oxytocin.

biosynthesis pathways may play an adaptive role during chronic dehydration in both of these species [27].

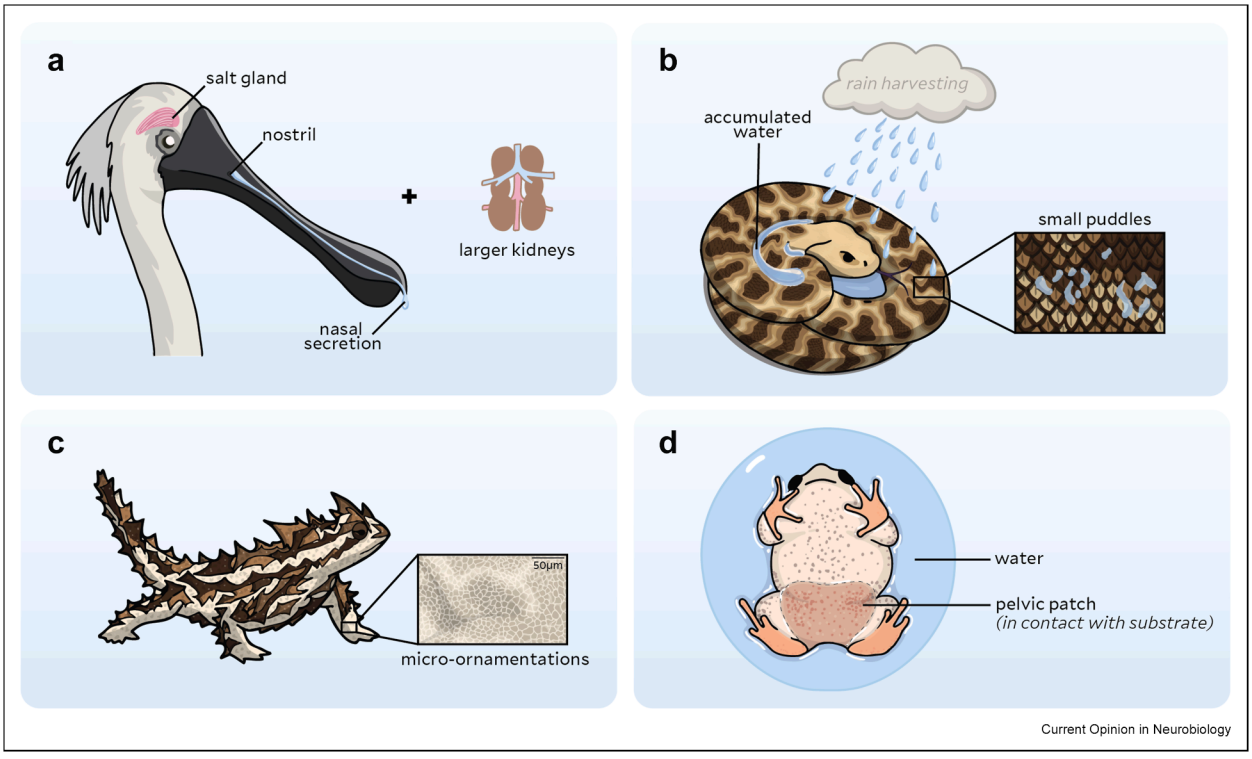
Birds

Seabirds: solutions to the osmotic burden of saltwater drinking

Birds display remarkable diversity of ecological strategies for maintaining water balance, ranging from behavioral adjustments to renal structural changes. While many of these adaptations are striking and relevant to the field of thirst and osmoregulation, many have already been covered elsewhere [28,29]. Of special interest to this review are seabirds, who possess specialized glands that enable them to stay hydrated while routinely drinking saltwater.

Because of this constant osmotic stressor, seabirds tend to possess larger kidneys compared to birds that inhabit low-salinity environments [30]. Still, the concentrating power of the kidneys is limited and, by themselves, cannot fully compensate for the magnitude of this osmotic burden. Therefore, seabirds have developed nasal salt glands. These glands are under parasympathetic control and secrete highly concentrated NaCl in response to an osmotic load [8,9]. The usual concentration of sodium in the nasal secretion varies across species due to variables like their dietary habits or life history [9]. Still, these nasal secretions reach higher concentrations than achievable by the avian kidneys, allowing the excretion of excess salts with reduced water expenditure compared to urine [8,31,32]. K Schmidt—Nielsen et al. [8] illustrate the concentrating ability of salt glands by positing that *"the rate of elimination is so high that with continuous secretion the entire sodium content of the body could be eliminated in roughly 10 h"*. Consistent with this, birds inhabiting high-salinity environments tend to not only possess larger kidneys but also functional salt glands [30] (Figure 3a), relying on the synergistic action of both structures to maintain hydration. Evolutionary analyses support the idea that habitat salinity, salt gland presence, and kidney size are linked, and that this convergent evolution enabled birds to colonize hyper-saline environments [30]. Future work integrating molecular, anatomical, and behavioral approaches to osmoregulation in bird species across

Figure 3



Example osmoregulatory adaptations in birds, non-avian reptiles, and amphibians. a) Salt glands and larger kidney sizes observed in the seabird *Platalea minor*. Adapted from Schmidt–Nielsen K (1960) and Chiu CC et al. (2024). b) Rain-harvesting position and water capture in the scales of rattlesnake *Crotalus viridis*. Adapted from McIntyre MG et al. (2025). c) Micro-ornamentations that support water harvesting through capillary action in the scales of lizard *Moloch horridus*. Adapted from Commans P et al. (2011). d) Pelvic patch and water absorption response position in toads. Adapted from Hillyard SD et al. (2007).

salinity gradients can further clarify how these mechanisms arise and allow species to thrive in osmotically harsh environments.

Non-avian reptiles

Snakes and lizards: water harvesting in arid environments to prevent desiccation

Non-avian reptiles inhabiting dry, hot environments face chronic threats of water loss due to ambient heat and the large evaporative gradient between their bodies and the arid air [33]. As ectotherms, they incur a substantial water cost when thermoregulating. For example, if an animal moves from the shade to a sunny area to raise its body temperature, the increased heat exposure will increase evaporative water loss. Therefore, ectotherms rely on behavioral and anatomical adaptations that can offset the hydric costs of thermoregulation. Some snake species utilize specialized rain-harvesting strategies to obtain water from fleeting precipitation events. For example, the prairie rattlesnake (*Crotalus viridis*) flattens its body into a coiled, teacup-like shape to capture water into its scales during rainfall [10] (Figure 3b). It subsequently drinks the captured water off its own scales, in addition to the water captured on substrates (e.g. rocks and leaves) or on the scales of other snakes [10].

Similar behaviors have been documented in many vertebrate species, including lizards such as the Australian thorny devil, *Moloch horridus* [34,35]. This species can harvest environmental moisture using micro-ornamentations that form honeycomb-like structures on its scale integument (Figure 3c), rendering its entire body surface hydrophilic [7]. The micro-ornamentations then transport the collected water to the mouth via an interscalar capillary system [7,36]. During this process, the lizards appear immobile except for periodic mouth movements [36]. Interestingly, several xeric lizard species across continents utilize this water harvesting strategy [37–40], and they appear to have developed analogous scale structures independently, through a process of convergent evolution [41].

To the best of our knowledge, the neuroendocrine control of thirst and drinking in reptiles remains understudied. While it is known that arginine vasotocin (AVT, the non-mammalian homolog of AVP) neurons exist in reptile hypothalamic/preoptic regions, there are no detailed functional characterizations of thirst-related neural circuits in the reptile brain to date. Contemporary studies have rather focused on AVT's role in reproduction and social behavior (reviews in Refs. [42,43]).

Amphibians

Frogs and toads: cutaneous water uptake

Many anurans, rather than consuming water orally, restore hydration through absorption across the skin [11]. To achieve this, they possess a specialized osmoregulatory organ, the pelvic patch of the ventral skin (Figure 3d), equipped with aquaporins regulated by AVT [44]. Anuran species differ in aquaporin expression depending on whether they are terrestrial, semiaquatic, or aquatic, as reviewed in Refs. [44,45]. To rehydrate, some anurans adopt water-absorbing postures, spreading the hindlimbs and pressing the ventral skin against moist surfaces [12]. They also avoid hypertonic solutions, suggesting the presence of finely tuned osmosensors in the skin [46,47].

From an ethological perspective, amphibians expand the definition of drinking. Rather than being tied exclusively to oral ingestion, thirst in these species is quenched by cutaneous absorption. This highlights both the diversity of effector mechanisms across vertebrates and the conservation of central endocrine regulators like AVP/AVT. Furthermore, recent advances in genetic technologies are beginning to transform amphibian research: viral vectors, including adeno-associated viruses (AAVs), have now been successfully adapted for *in vivo* use in frogs and salamanders [48,49]. The availability of genetic approaches opens the possibility of directly interrogating how molecular, endocrine, circuit and behavioral responses are coordinated in amphibians to enable cutaneous hydration. In the future, combining these methods with opto- and/or chemogenetics could allow for causal tests of hypothalamic control of thirst-like behaviors. This approach would provide experimental leverage for understanding how endocrine, neural, and in this case, cutaneous mechanisms coordinate thirst and maintain fluid homeostasis in vertebrates.

Fish

Diadromous fishes: migration and salinity transitions

Life originated in marine environments, and early fishes developed mechanisms to regulate water and ion balance across diverse aquatic habitats and osmotic landscapes. The strategies that these earliest vertebrates developed form the physiological groundwork from which terrestrial osmoregulation later emerged. Fishes are, therefore, central to any discussion of vertebrate osmoregulation. In this review, we focus on salmonids, specifically salmon and trout. Several salmonid species exhibit diadromous life histories, utilizing both freshwater and marine environments during their life cycles and undergoing discrete physiological changes prior to migration that enable their survival in a specific osmotic environment [50]. This adaptation is distinct from the capacity of most fishes to tolerate modest deviations from their typical environmental salinity, as well as from species that adapted to survive more drastic and recurring fluctuations (such as those inhabiting river mouths). The mechanisms that enable the latter to cope with dynamic salinities have been reviewed elsewhere [51].

In diadromous salmonids, the transition to freshwater includes strategies like reducing drinking, decreasing water permeability of their outer layers, and producing highly diluted urine to retain osmolytes [17]. Osmolyte loss can be further prevented by decreasing ionic permeability and increasing ion absorption through ionocytes in the gills and skin (reviewed in Refs. [52,53]). Ionocytes are mitochondria-rich epithelial cells specialized in the active transport of ions between the internal environment and the surrounding water. Some salmonid species differentially express distinct isoforms (sometimes referred to as "ion-secretory" or "ion-absorptive") of the α1 Na^+/K^+-ATPase subunit in their gills, intestines, and kidneys in order to meet their specific osmoregulatory needs [54–56]. In seawater, salmon can drink to offset the passive loss of water, excreting excess Na^+ and Cl^+ ions primarily through their gills and divalent ions through the gut and kidney [17]. This physiological flexibility is reflected at the molecular level as well, as single-cell RNA sequencing of gills from Atlantic salmon has identified cell-type specific changes associated the fresh-to sea–water transition [57].

Collectively, the pre-emptive restructuring of tissues that salmonids undergo in anticipation of migration into seawater is called smoltification [17]. Unlike many other vertebrates, where thirst circuits respond primarily to changes in P_{osm}, these fish rely on photoperiodic and endocrine cues to initiate smoltification instead [58]. The light-brain-pituitary (LBP) axis integrates these signals, conveying photoperiod information to the neuroendocrine system (for an overview of the LPB, see SO Stefansson et al. [17]). Studies on the neuroendocrine contributions of osmoregulation in these fishes have traditionally emphasized cortisol's actions at the gill; however, cortisol also modulates ion and fluid transport in the intestine, which has been increasingly recognized as a key osmoregulatory organ, particularly during smoltification [59,60]. Besides cortisol, evidence from Atlantic salmon suggests AVT neurons in the

preoptic area of the hypothalamus may also contribute to smoltification by stimulating the hypothalamic-pituitary-interrenal axis [61].

Conclusion

Osmoregulation is a fundamental physiological capacity shared by all species, yet the way different species achieve fluid ionic balance is ecologically-tuned and can vary widely (Figure 1). To keep a balanced internal environment, many mammals rely on thirst as a motivational signal that drives drinking behavior, thereby restoring balance of water and salt in the body. In this framework, thirst links our internal state to a specific behavioral output—fluid ingestion through drinking. However, environmental constraints, like those discussed in this review, render drinking by itself an insufficient solution for many species. Therefore, species-specific strategies often extend beyond this framework to include anatomical, physiological, and behavioral adaptations that efficiently serve their own osmotic needs. As demonstrated by the studies discussed here, these strategies can include cutaneous water absorption, water harvesting, possessing specialized glands, or seasonally regulated shifts in physiology that support hydration under fluctuating needs or environmental conditions. Understanding the true breadth of osmoregulatory capacity in vertebrates cannot be achieved by studying standard laboratory models alone. Instead, a comprehensive understanding of how animals maintain fluid ionic balance requires incorporating diverse animal models into research to examine the various approaches they take to meet this fundamental challenge.

Declaration of competing interest

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Data availability

No data was used for the research described in the article.

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