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REVIEW

Hormonal Effect on the Osmotic, Electrolyte and Nitrogen Balance in Terrestrial Amphibia

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ABSTRACT—Two main hormones regulate water balance in amphibian. First, mesotocin (MT) acting as a diuretic agent, and second arginine vasotocin (AVT) being an anti-diuretic hormone. In addition, prolactin (PRL), aldosterone, corticosterone, angiotensin II and atriunatriuretic hormones, play a role too in regulating water and ion balance. The hormones affect the epidermis and bladder permeability to water and ions as well as the kidney through the control of the glomerular filtration rate (GFR). The main questions concern the presence and action of these hormones during the amphibian's life history. Are they present in both larval and adult stages? Are these hormones being synthesized in both aquatic and terrestrial adult phases? Under what circumstances are they being stored or released? Would the target organs (epidermis, bladder, kidney) respond in a similar way during all periods? The problem is the fact that under most circumstances an amphibian while in an aquatic environment responds physiologically differently than when on land. Only partial information concerning hormone presence, release and control of water balance is available at the moment, and even that is fragmentary and based on only a very small number of amphibian species.

INTRODUCTION

Amphibians are unique among the vertebrates as they live part of their lives in water and part on land. The proportion of time they spend in each environment varies among the various species even within one genus. Thus, some terrestrial amphibians spend as little as 2% of their lifetime in water until they metamorphose and during their breeding season (*Salamandra* [217]), whereas others may spend up to 5% in water. Moreover, some return to water (to breed) at certain intervals and for various length of time. This requires different mechanisms for maintaining their water, electrolyte and nitrogen balance under such extremely different environments. Thus, being aquatic requires diuresis and enables ammonotelism, whereas terrestrial life requires antidiuresis and ureotelism or even uricotelism. Moreover, the hormones regulating these functions need to be available (secreted and in circulation) at all times because they are essential whenever required. On the other hand, each such hormone must not function as a regulating agent continuously all the time, only when necessary. This would also imply some preparedness on behalf of specific organs in order to respond to hormonal action only at a certain definite period. In a previous paper we have discussed the effects of hormones on ion, and water balance in the aquatic amphibians. These included larval forms as well as the aquatic phase of terrestrial amphibians, and the completely aquatic amphibians [217].

In the present paper an attempt will be made to evaluate our present knowledge about three aspects of endocrine control in terrestrial amphibians: water, ion and nitrogen balance.

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ENDOCRINE CONTROL

Various aspects of the endocrine control of water balance in amphibians were reviewed by Heller [92], Jorgensen [122], Sawyer and Sawyer [183], Sawyer [179], Heller [93, 94], Bentley [17, 18], Warburg [213], Scheer *et al.* [185], Pang [171], Alvarado [3], Goldenberg and Warburg [80], Bentely [22], Warburg [214], Warburg and Rosenberg [217], Olivereau *et al.* [170], Hourdry [104], and Hanke and Kloas [89]. It was known that neurohypophysial hormones are involved in regulating the water balance. This so called "Brunn effect" caused a weight increase due to water uptake by the animal following injections of pituitary extracts (see Belhradek and Huxley [11]). Jorgensen *et al.* [125] found that this hormone was liberated during dehydration (in *Bufo bufo*). Both the par distalis and pars nervosa seem to be involved [55]. The pre-optic neurohypophysial system is responsible for anti-diuretic reaction of the bladder of *Bufo bufo* [124]. No effect was seen in transport of ions in the larvae of *Ambystoma* [130].

Some of the data available at the present time is summarized here (see Table 1).

A. The hydrins

These peptides found recently in aquatic and terrestrial amphibians are involved specifically in water and electrolyte regulation of amphibians [177]. Hydrin 2 (vasotocinyl-Gly) is found in terrestrial species (*Bufo regularis, B. marinus* and *B. viridis*, see Acher *et al.* [1]).

They were also shown to affect the secretory action in the granulated glands of the dorsal skin of *Xenopus* [139].

Table 1. Endocrine control of water, ion and nitrogen balance in amphibia

	Water			Ions			Nitrogen		
	Tadpoles	Aquatic Adults	Terrestrial Adults	Tadpoles	Aquatic Adults	Terrestrial Adults	Tadpoles	Aquatic Adults	Terrestrial Adults
AVT	+	−	+	+/−	+/−				
MT	+	−	+						
OXY	+/−	+	+						
AVP		−	+/−			+			
PRL	+	+	+	+	+	+	+	+	
ALDOS.		−		+	+	+/−		+	
ACTH								+	
CORT.	+	+		+	+	−		+	+
T_3/T_4	+					+/−		+	+
ANP				+	+				

+: some effect
−: no effect
Cort.: corticosterone
Aldos.: aldosterone

B. Arginine vasotocin (AVT)

Presence of AVT in hypophysis

AVT was located in the neurohyphophysis of *Rana catesbeiana* [16] more precisely in the median eminence and the neural lobe of *Rana ridibunda* [167], and other anuran species [166]. AVT perikarya were localized in the nucleus preopticus of *Bufo japonicus* [118]. In the tadpole the amounts were a quarter of those found in adult frogs [24]. AVT concentration rose after dehydration due to a decrease in blood volume not because of increased osmolality [169]. Dehydration also affected the levels of AVT in the ventral preoptic brain area in the newt *Taricha granulosa* [229]. There is evidence of seasonal effect on AVT levels which appear to be higher during the breeding season of the newts in spring [230]. Perhaps because of the breeding activity of the male. Nothing is known about AVT levels in the aquatic anurans (*Xenopus, Pipa, Discoglossus*), or urodeles (*Necturus, Siren, Amphiuma*). Nor do we know about levels of AVT in amphibians from xeric habitats (*Bufo, Neobatrachus, Scaphiopus*). Finally, is there a change in AVT levels when the tadpole or larvae metamorphose and emerge onto land, or when the adult urodele (newt) returns to water to breed?

AVT effect on water balance

Weight increase (as a result of water uptake) was studied in several amphibian species following treatment with AVT. In tadpoles or larvae it was more pronounced towards metamorphic climax (*Rana catesbeiana*, [24], and *Ambystoma tigrinum*, [5]). However, the response was noticeable already in the 2-limbed tadpole of *Rana ridibunda* [79], or in the metamorphosing *Salamandra* larva [215], (see Fig. 1). No effect was noticeable in the young tadpole of *Bufo bufo* [106]. The response to AVT in *Rana ridibunda* tadpoles or juveniles was much lower than to oxytocin (OXY) [79]. In adult frogs the water uptake was about 50% of the body weight (*Hyla hyla*), or 5% in *Pelobates cultripes* [95]. In adult *Hyla arborea* water uptake following treatment with AVT was remarkable, twice as much as when treated with OXY. On the other hand, in both *Pelobates syriacus* and *Bufo viridis*, it was considerably lower than the uptake following treatment with OXY [211]. A similar pattern was observed in *Salamandra salamandra* and *Triturus vittatus* (aquatic phase). The terrestrial phase of the newt (*T.*

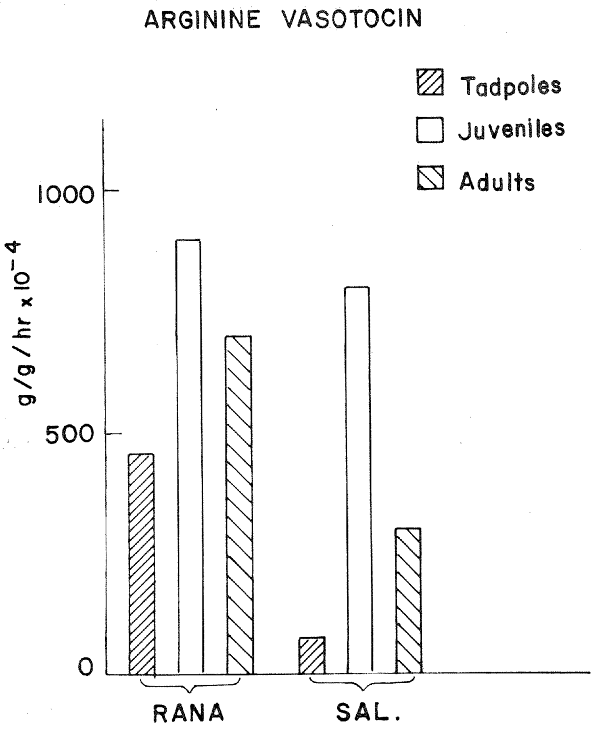

Fig. 1. Water retention response in *Rana ridibunda* and *Salamandra salamandra* tadpoles, juveniles and adults, 1hr after being treated with AVT. Note the major response in juveniles of both species. The response of *Salamandra* larvae and adults is much less apparent.

vittatus), responded to AVT in much the same way as to OXY [212]. Elliott [68], described an increase in water uptake in *Bufo melanostictus*. Similarly, Cree [59, 60] found increased water retention in two terrestrial liopelmatid frogs but not in a semi-aquatic species. On the other hand, the aquatic amphibians (*Siren, Amphiuma, Discoglossus*, see [95]), or the aquatic phase of the newt (*Notophthalmus viridescens* see Brown *et al.* [36]), did not respond to AVT by taking up water. Although some effect was noticed later in *Siren* and *Amphiuma* [19]. In the newt *Triturus cristatus*, the level of activity of alkaline phosphatase was reduced by AVT [65]. It was twice higher in the aquatic phase compared with the terrestrial phase.

"In vitro" effect of AVT on water movement across the epidermis

In the aquatic phase of the newt *Notophthalmus viridescens*, no water movement across the isolated skin was noticeable in response to AVT [33]. On the other hand, *Litoria aurea,* showed an increased cutaneous water uptake [61]. Similarly, in *Crinia georgiana*, AVT caused greater water uptake through the skin than in *Bufo marinus* [27]. The osmotic permeability through the ventral pelvic epidermis of *Bufo bufo* increased following treatment by AVT [54]. This was shown also in *Bufo boreas* by Kent [129]. AVT caused an increase in skin permeability in *Rana temporaria* and *R. esculenta*, but reduced the permeability of *Bufo viridis* [147]. No effect on water passage across the epidermis of *Scaphiopus couchi* was noticeable [98].

"In vitro" effect of AVT on water movement across the urinary bladder

In the aquatic urodele, *Necturus maculosus*, the bladder was not affected by AVT [18], nor was there any effect in *Xenopus* [20], or in *Amphiuma* or *Siren* [19]. Some effect was noticeable in the bladder of *Notophthalmus viridescens* [33]. Similarly, in *Rana cancrivora* the bladder responded to AVT [53]. In *Salamandra* an increase of 14% in body weight was noted following treatment with AVT [26]. This was not seen when the bladder was ligatured. An increased bladder resorption was noted in *Taricha* [43]. In the hylid *Litoria aurea* AVT caused a reduction in the rate of urine accumulation [61].

AVT effect on kidney function

The weight gain observed "in vivo" in larvae of *Ambystoma tigrinum* appears to be the result of an antidiuretic response due to reduced GFR [4, 193]. In the aquatic urodele, *Necturus maculosus* [71, 73, 74], there is an antidiuretic response. In *Siren* and *Amphiuma* this response is caused by a 50% decrease in GFR [19]. In the newt, *Taricha*, GFR is reduced by 84% [43], and in *Rana catesbeiana* by 80% [174].

There is evidence for increased tubular reabsorption [12, 20, 69, 70, 184], or an effect on the number of functional glomeruli in *Bufo marinus* [112]. Pang *et al.* [174], found no evidence for a tubular effect by AVT, whereas Garland *et al.* [74] found changes in the permeability of the distal tubules in response to AVT. Recently, Uchiyama [204, 205] found that the connecting and distal tubules contain V 2 type receptors to AVT. On the other hand there seems to be a decrease in GFR [182], and a glomerular antidiuresis in both *Necturus* and *Rana catesbeiana* [174]. Finally, in the spadefoot toad, *Scaphiopus couchi* [98], and in the frog *Litoria aurea* [61], evidence was found for reduced GFR when treated with AVT. There is also a lower rate of urine excretion in *Bufo marinus* [182], *Rana catesbeiana* [209], and *Rana esculenta* [115,116]. Morel and Jard [154], Jard and Morel [116], and Jard [115] found that AVT caused antidiuresis in *Rana esculenta* by stimulating Na^+ (and water) reabsorption through the renal tubules, and causing a decline in GFR.

AVT effect on ion balance

AVT caused sodium accumulation in larval *Ambystoma* [6], and caused sodium uptake in *Rana catesbeiana* tadpoles and *Ambystoma* larvae [4, 123]. AVT was not found to affect sodium influx in *Ambystoma tigrinum* larvae [23].

In the aquatic urodele *Necturus*, sodium transport was affected by AVT [10]. However in *Amphiuma* and *Siren* no effect of AVT on sodium balance was noticeable [21, 28]. Some effect on sodium transport was noticeable in *Xenopus* [14]. However, no effect was noticeable in the SCC of *Ambystoma* larvae or *Necturus* [25]. The renal output of Na^+ and K^+ increased as a result of AVT [109].

C. Arginine Vasopressin (AVP), Mesotocin (MT) and Oxytocin (OXY)

Arginine Vasopressin (AVP)

Whereas some amphibians: the aquatic *Desmognathus* [39], and littoral *Rana cancrivora* [64], did not respond to AVP, others: *Bufo melanostictus* [64], and *Notophthalmus* [33] showed an increased water uptake. In some amphibians AVP caused an increase in water uptake either through the epidermis (*Notophthalmus*, [33]), or by an increase in water reabsorbed through the bladder (*Notophthalmus*, [33] or *Aneides*, [97]). On the other hand in *Bufo marinus*, AVP caused a sodium and water transfer across the bladder [15]. No effect was observed in *Scaphiopus couchi* [99].

AVP was also reported to cause reduced urine production in *Plethodon* [39], possibly due to a decrease in GFR in *Notophthalmus*, [33].

Mesotocin (MT)

Mesotocin (MT) was found to be present in amphibians [2], and was located in the median eminence of the neural lobe [167], and in the serum of *Rana esculenta* [168]. MT caused weight gain in *Taricha* due to integumental osmosis [43].

MT caused diuresis in *Rana catesbeiana* adults [152], possibly due to increased GFR (in *Ambystoma tigrinum* larvae [192,195]). It was found to increase urine production in *Calyptocephalella* and *Necturus* [72].

Oxytocin (OXY)

Most experiments were conducted with oxytocin (OXY), a hormone not occurring naturally in Amphibia. The animals responded to this hormone by gaining weight (water), or by increasing the permeability of skin or urinary bladder to water.

OXY effect "in vivo" on water balance

The 2-limbed tadpole of *Rana ridibunda* was found to respond to OXY by weight increase. This response reached its peak in the juvenile stage but was still noticeable in the adult ([77], Fig. 2). In *Bufo viridis*, the response was significant towards metamorphic climax reaching a peak at the juvenile stage [77]. In the adult *Bufo viridis* and *Pelobates syriacus* the response to OXY was significant although less than in juveniles ([211], Fig. 2). It also caused water uptake in *Bufo melanostictus* [68], and increased the cutaneous water uptake in *Bufo marinus* [9], and in *Bufo bufo* [108].

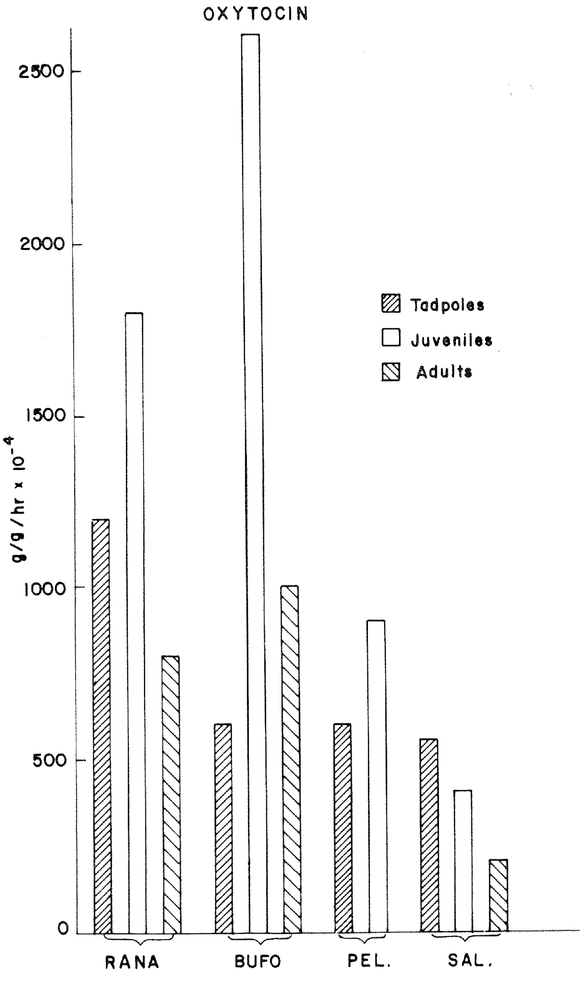

Fig. 2. Water retention response in *Rana ridibunda, Bufo viridis, Pelobates syriacus* and *Salamandra salamandra*, tadpoles, juveniles and adults 1hr after being treated with OXY. Note the extremely high response of juvenile *Rana* and *Bufo* and the comparatively high response of *Salamandra* larvae.

In *Rana ridibunda*, the response to OXY has shown a seasonal pattern: high in summer and lower in winter [77, 88]. In *Rana temporaria* and *Bufo marinus* osmotic water transport following treatment with OXY was greater in the winter (cold) months as compared with the summer (warm) months [88]. *Rana catesbeiana* responded to OXY in a similar fashion with a peak at metamorphic climax (Stage XXII, [5]).

Already the premetamorphic larvae of *Salamandra salamandra* responded to OXY ([216], Fig. 2). The response reached its peak upon metamorphosis. It was still noticeable in the juveniles, and to some extent in the adults ([211], Fig. 2). Both the terrestrial phase of the newt (*Triturus vittatus*), and to some extent its aquatic phase, as well as the aquatic phase of *Notophthalmus viridescens*, have shown some response to OXY ([33, 212], Fig. 3).

In the adult *Bufo arenarum*, OXY caused an increase in GFR [209], although apparently not changing the number of glomeruli or their size [208], but by its affect on the reabsorption in the glomeruli of *Rana pipiens* [184]. No effect of OXY was noticed by Stiffler *et al.* [195] in *Ambystoma* larvae. In *Rana esculenta* oxytocin had a clear antidiuretic effect [154].

OXY effect "in vitro" on water movement through isolated bladder and epidermis

The effect of OXY on the isolated urinary bladder of *Rana catesbeiana* took the form of enhancing water permeability [181], and increasing reabsorption in *Rana pipiens* [184]. No such effect was noticeable in the bladder of adult *Rana ridibunda* [211]. However, SCC across the bladder of *Rana esculenta* increased [13]. On the other hand OXY caused water movement through the isolated bladder of *Bufo viridis, Pelobates syriacus, Hyla arborea, Salamandra salamandra* and *Triturus vittatus* [211, 212].

Finally, the water movement across the isolated epidermis showed a marked effect of OXY in adult *Rana ridibunda, Pelobates syriacus, Salamandra salamandra* and *Triturus vittatus* as well as *Xenopus*, but no response in *Bufo viridis* [211, 212].

D. Prolactin (PRL)

Presence of Prolactin

Prolactin-producing-cells were located in the hypophysis of the newt, *Triturus cristatus* [210]. They are confined to the ventral region of the hypophysis in *Cynops* [148]. Purified PRL in the newt *Cynops pyrrhogaster* showed a molecular weight of 23,000, similarly, in *Bufo japonicus* [149, 224, 226]. In *Xenopus* two forms of prolactin were isolated. In bullfrog tadpoles PRL-like hormone was regulated by dopamine [132]. PRL levels increased markedly towards metamorphic climax in *Rana catesbeiana* [161, 128, 227]. In *Bufo japonicus* PRL levels drop when emerging on land [110]. Thus PRL appears to have anti -metamorphic activi-

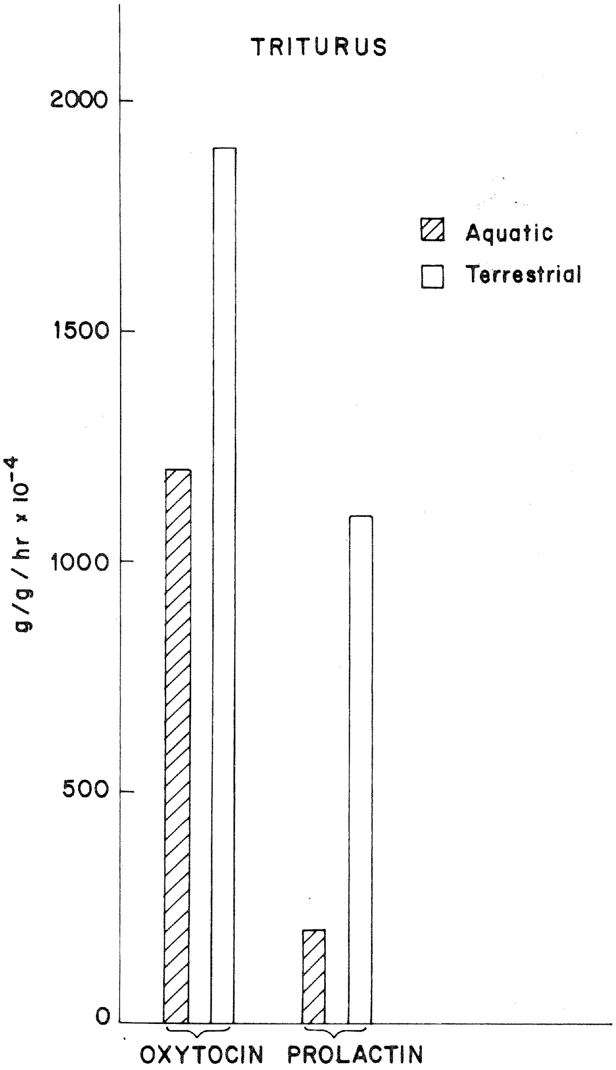

FIG. 3. The response of the aquatic and terrestrial phases of the newt, *Triturus vittatus* to OXY and PRL. The terrestrial phase was more responsive to treatment with these hormones.

ties [134, 163]. The levels increased from 18 ng/ml at stage X to 98–169 ng/ml at stages XXIII-XXV [224]. The neotenic axolotl (*Ambystoma tigrinum*) has more PRL than either larvae or adults [165]. More PRL is released during winter (breeding season) in the newt *Triturus cristatus* [145]. Similarly, in *Bufo japonicus* the high PRL levels were related to breeding in spring [110]. When *Xenopus* was kept outside the water PRL was synthesized, but was not released [85]. PRL binding was highest in kidney except for the aquatic amphibians [218].

Renal binding of PRL sites increased during metamorphic climax [219], but was reduced in dehydrated *Xenopus* [85]. Dehydration caused a drop in PRL binding sites in the kidney and epidermis of *Xenopus* [86, 157].

PRL effect on water balance

The role of PRL in osmoregulation was reviewed by Bern [29] and Brown and Brown [35]. PRL affects water movement into the amphibian. This response was noticeable in *Rana ridibunda* tadpoles just before metamorphosis reaching its peak in the juveniles ([78], Fig. 4). Similarly, in *Bufo viridis*, already the 4-limbed tadpole responded to PRL, but the largest effect was noticeable in the juveniles ([78], Fig. 4). In *Taricha torosa*, PRL caused a lower rate of water uptake [34], partly due to a decreased rate of integumental permeability. In *Xenopus* too, PRL caused increased water uptake [188]. In *Ambystoma tigrinum* larvae PRL caused an increase in body water [175]. In the salamander larva (*Salamandra salamandra*) PRL affected water retention already in the 1-week old larva, and more so in the juvenile salamanders ([216], Fig. 4). In adult *Rana ridibunda* and *Bufo viridis*, PRL has shown a more pronounced effect than in adult *Salamandra* (Fig. 4). Likewise in bullfrog tadpoles PRL caused water retention [41]. PRL also affects permeability of the toad bladder [63], and caused a lowering of the rate of urine production in *Taricha torosa* [34].

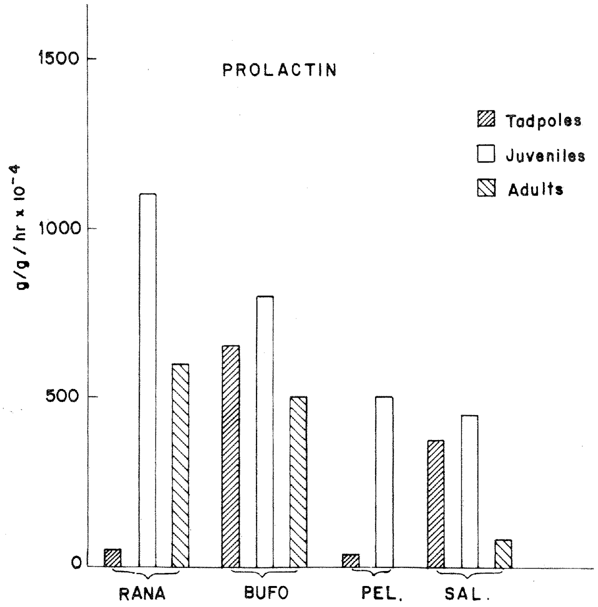

FIG. 4. The response to PRL of *Rana ridibunda, Bufo viridis, Pelobates syriacus* and *Salamandra salamandra* larval and post-metamorphic forms, after 1hr. Note the very low response of *Rana* and *Pelobates* tadpoles and *Salamandra* adults. The highest response can be seen in the juvenile stage.

PRL effect on electrolyte balance

PRL also affects the ion movement. Thus it increased the ion absorbing capacity of *Ambystoma* gills [221], and affected the sodium transport across the epidermis of *Rana temporaria* [105]. It caused an increased sodium content in the axolotl *Ambystoma tigrinum* [175], in *A. gracile* [31], and in *Rana catesbeiana* [66]. In other amphibians: *Rana pipiens, Taricha torosa*, [62], *Desmognathus* [37] *Ambystoma tigrinum* [222]. PRL had no effect on Na^+ levels. PRL restored sodium levels in hypophysectomized *Necturus maculosus* [172]. It depressed sodium transport across isolated skin of *Triturus cristatus* [144,146], and in both *Taricha* and the terrestrial red eft of *Notophthalmus* [40, 42, 44, 45], but did not affect sodium transport in tadpoles of *Rana catesbeiana*. Short circuit current (SCC) increased at metamorphic climax or by treatment with PRL [67]. This was shown also "in vitro" in *Bufo marinus* bladder [189].

In adult *Desmognathus* PRL caused sodium (and Ca^{2+}) retention [220]. Similarly, in the axolotl (*Ambystoma mexicanum*, [221]). However, in bullfrog tadpoles PRL caused a decrease in plasma Na^{+} [41]. In adult, *Triturus cristatus* newts, PRL caused a reduction in sodium transport across the integument [144], and affected SCC [145]. In the aquatic (breeding) phase of the newt, *Cynops pyrrhogaster*, PRL caused a decrease in trans-epithelial transport, TEP [200]. Transport increased greately at stage XXI-XXII in the bullfrog tadpoles [196,197,199]. The effect on SCC was greater in bullfrog tadpoles at stage XXV during spring-summer [198].

PRL effect on water drive

PRL caused the 2nd metamorphosis (water drive) to occur in *Notophthalmus viridescens* [81, 152], and in the salamander *Hynobius retardatus* [155]. PRL caused increase in serum osmolality and thus may provide a cause for the newt's movement into the water [156]. By causing accumulation of mucopolysaccharides in the tissue PRL caused water retention which affected a rise in specific gravity, thus enabling the newt to stay in water.

PRL also stimulated courtship behaviour in hypophysectomized newts [76].

PRL effect on mucus formation

PRL functions to release granules in the gland [103]. Thus it caused increased mucus production in the axolotl *Ambystoma tigrinum* [223], in *A. gracile*, [31], and in *Notophthalmus* [32]. It stimulated mucopolysaccaharide synthesis in *Triturus pyrrhogaster* [131]. The effect of PRL on mucus secretion may be indirect through its effect on testosterone. Testosterone caused the formation of mucus glands in the epidermis and PRL enhanced its action [164]. PRL caused a change from granular to smooth skin in *Taricha torosa* [82, 91]. These changes may be related to the role of the skin in protection from evaporative water loss.

PRL effect on nitrogen balance

PRL stimulated arginase activity in *Bufo bufo* [47, 84,85]. PRL antagonized the urea increase (caused by thyroxine) in *Rana catesbeiana* tadpoles [14], but did not affect the ammonia excretion. PRL caused a decrease in urea excretion in the premetamorphic tadpoles of *Rana catesbeiana*, but did not affect urea excretion in metamorphosing tadpoles [150].

E. The thyroid hormones

Thyroid hormone excretion is largely related to the stages of metamorphic cycles [140], as well as temperature dependant because iodine uptake by the gland is increased with temperature [52, 138]. Thus December frogs showed a low iodine uptake. Kuhn *et al.* found that hormone levels change seasonally peaking in March [201].

Green and Matty [83], reported an increase in sodium transport through the ventral epidermis and bladder of *Bufo bufo* following application of thyroxine. This could not be confirmed by Taylor and Barker [202].

There are reports that thyroxine caused a rise in urea excretion in the axolotl, *Ambystoma mexicanum* [187], or that T_3 caused increased urea excretion in *Rana catesbeiana* [8]. Similar findings were previously reported by Munro [158], and Jaffe and Geschwind [114]. There is also a report that thyroid hormone caused increased ammonia production in *Rana catesbeiana* tadpoles (Stages VIII-XII) [151].

F. Other hormones

The effect of corticosteroids on amphibians has been recently reviewed by Hourdry [164], and Hanke and Kloas [89].

Corticosterone levels in the plasma increase towards metamorphic climax (Stages XXI-XXIV) [113, 228]. Similarly, in *Ambystoma tigrinum* plasma corticosterone levels were low in premetamorphic stages increasing at mid-metamorphosis and peaking towards metamorphic climax [50]. In either *Xenopus* and *Bufo arenarum*, both corticosterone and aldosterone reached their peak at metamorphic climax [51, 121]. Similarly, levels of aldosterone increased in *Rana* towards metamorphic climax [133].

The interrenal cells appear to be more active during summer [119, 120]. In *Hyla arborea* circulating corticosteroids peaked in late spring [141]. Thyroid hormones may be involved in elevating aldosterone levels at metamorphic climax [133, 134]. Other effective groups of peptides stimulating corticosteroid hormones include AVT, ureotensins and angiotensin II [89].

The pituitary gland seems to affect aldosterone secretion [11]. Both AVT and MT enhanced aldosterone levels in hypophysectomized *Xenopus*. In the plasma of *Rana pipiens*, aldosterone levels are only 10% of corticosterone levels [127]. Changes in either osmolality or sodium concentration of plasma (in *Rana*) affected the interrenal secretion [90]. Apparently corticosterone levels declined significantly in dehydrated *Rana pipiens* [126]. Corticosterone caused a drop in the water content of *Xenopus* tadpoles [142]. An increase in water uptake was caused by ACTH in the aquatic phase of *Notophthalmus viridescens, Taricha granulosa* [36]. At the same time ACTH and corticosterone restored the decline in sodium levels [206]. Corticosterone also caused a decline in sodium efflux in *Ambystoma tigrinum* [46]. Thus it caused sodium retention in neotenous *Ambystoma gracile* [31], but no effect on sodium levels in *Rana pipiens*, [62], and in *Desmognathus* [37]. In *Taricha torosa*, ACTH caused sodium retention [38].

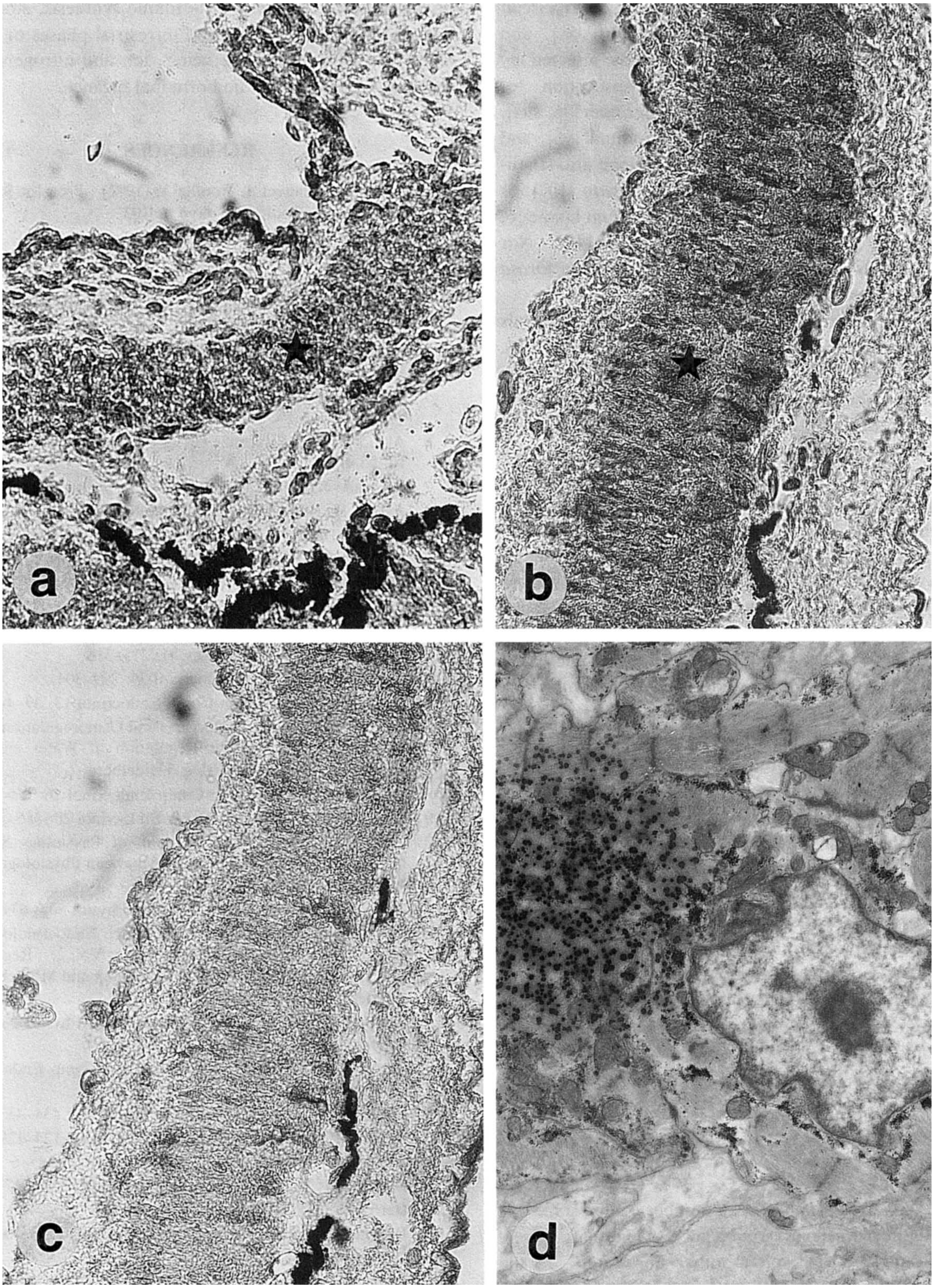

FIG. 5. Atriunatriuretic (ANP) reaction in the heart of a 2-legged *Pelobates syriacus* tadpole (a, ×400), and a tadpole with tail stump just prior to meatmorphic climax (b, ×400). The asterisk (star) depicts the site of immunoreaction. No reaction was observed in controls (c, × 1,000). The ANP cell contains a large number of small secretion granules (d, ×5,000).

Aldosterone stimulated sodium transport through the urinary bladder of *Bufo marinus* [58]. The short circuit current (SCC) through *Necturus* bladder [18, 58], and through *Bufo viridis* skin [159], was similarly affected by aldosterone. Aldosterone stimulated reabsorption of sodium and secretion of K^+ in *Ambystoma tigrinum* [96, 194]. It thus caused elevated levels in plasma sodium [96], and sodium retention in *Triturus* [190]. Aldosterone also stimulated sodium influx through the skin of *Bufo bufo* [107], or through either skin or gills of *Ambystoma tigrinum* larvae [6, 7]. It did not affect water balance in *Xenopus* [142]. Nor did it affect sodium levels in *Rana pipiens, Taricha torosa* [62], or in *Bufo marinus* [153].

Finally, corticesterone caused an increase in urea levels of *Xenopus* tadpoles [142], *Rana catesbeiana* tadpoles [150], or the axolotl [186]. This rise in urea levels in the serum could be due to reduced urea excretion. Urea excretion rose as a result of either aldosterone or cortisol treatment [187]. In *Rana catesbeiana* tadpoles ACTH caused increased urea excretion [150], and in *Rana pipiens* aldosterone enhanced urea production in spring and summer [117].

Angiotensin II (AII), synthesized in several organs (kidney, ovary, pituitary) induces physiological effects that maintain kidney function [162, 176, 191]. In Anura, AII causes tubular antidiuretic and antinatriuretic effects in the kidney [56], and increased water flow through the skin [57]. Treatment with AII caused a water response in, and increased water absorption through the skin of *Bufo punctatus, B. woodhousei* and *Scaphiopus couchi* [101, 102, 203]. Atrial natriuretic peptides (ANP) are peptides localized in the atrial cardiocytes of several vertebrate classes [48, 49, 75]. These peptides have been demonstrated immunohistochemically also in amphibian auricles and vetricles ([160, 178], Fig. 5). It was established that ANP is an osmo-mineral regulating hormone causing diuresis and natriuresis in amphibians [135–137]. In its action it counteracts the effects of AVP, AVT and AII. It causes an increase in GFR, decreased aldosterone and catecholamine production by the adrenal (interrenal), and inhibits secretion of hypophysial hormones [30, 87]. In *Rana*, ANP was shown to inhibit adreno-corticotropic hormone-stimulated adreno-steroid secretion *in vitro* [143]. The distribution of ANP-like material was followed in cardiocytes of larvae, metamorphosing and adult *Bufo* [100, 207].

CONCLUSIONS

In the terrestrial amphibians a number of hormones are present and affect water and ion balance. These are largely AVT, MT and PRL as well as other hormones. In the aquatic stages, aside from PRL, the other hormones are not active as regulators. During that period PRL is the main regulating hormone. In the aquatic adult amphibian, these hormones although present are not actively regulating. The most interesting aspect is in the adult aquatic phase which may last several weeks in urodeles. Here too the hormones although presumably present are not active. There is a need to focus on the dynamic of hormone synthesis, storage and release during the aquatic and terrestrial phases of amphibians. To what extent are water, ion and nitrogen balance affected by changes in the hormonal balance?

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