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INTERACTION OF OSMOTIC AND VOLEMIC COMPONENTS IN INITIATING SALT-GLAND SECRETION IN PEKIN DUCKS

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ABSTRACT.—Pekin Ducks (*Anas platyrhynchos*) were infused with 1,000 mM NaCl. Changes in plasma osmolality (Osm_{pl}); relative plasma volume (RPV); and plasma concentrations of electrolytes, arginine vasotocin, and angiotensin II were determined at initiation of salt-gland secretion and at 5 and 11 h post-infusion. Changes in these parameters and in volume and concentration of secretion produced were not different between the sexes. Although Osm_{pl} and RPV were not related prior to infusion, they were linearly related at the onset of secretion ($r^2 = 0.51$, $P = 0.013$). Osm_{pl} and RPV were equally effective stimuli for secretion. Initial RPV was a strong determinant of secretion volume ($P < 0.01$) and total sodium ($P < 0.001$) and potassium ($P < 0.001$) secreted, but initial Osm_{pl} was not. Plasma arginine vasotocin concentration was increased by NaCl infusion but not by subsequent dehydration. Plasma angiotensin II concentration was not significantly affected by NaCl infusion or by dehydration. These experiments are the first to directly relate the secretory response of the salt glands to the physiological state of ducks prior to salt loading and to describe the interactive simultaneous changes in Osm_{pl} and RPV associated with initiation of secretion. *Received 1 April 1996, Accepted 12 November 1996.*

EXTRARENAL SALT SECRETION by the cephalic glands of marine birds was first observed by Schmidt-Nielsen et al. (1958) when they gave NaCl to Double-crested Cormorants (*Phalacrocorax auritus*). Subsequently, secretion from the "salt" glands also was elicited by many other osmomolytes, and elevation of plasma osmolality (Osm_{pl}) became generally accepted as the primary stimulus for salt-gland secretion (SGS; Peaker and Linzell 1975). Ruch and Hughes (1975) questioned whether elevated Osm_{pl} was the sole effector for secretion, noting that in the absence of a concomitant expansion of the extracellular fluid volume (ECFV), increases in plasma sodium concentration ($[Na^+]_{pl}$) as great as 20% failed to elicit SGS in Pekin Ducks (*Anas platyrhynchos*). This was verified by Hughes (1989a). It was subsequently noted that the Osm_{pl} at the secretory threshold of ducks (primed to secrete by NaCl infusion) was inversely related to ECFV, specifically the interstitial component (Kaul and Hammel 1979, Hammel et al. 1980).

Despite the research noted above, changes in Osm_{pl} and ECFV in response to NaCl challenge, and the relative contributions of these changes to the initiation of SGS, have not been clearly described (Hughes 1989b). We intravenously infused ducks with concentrated NaCl and determined the changes in Osm_{pl} and relative plasma volume (RPV) associated with initiation of SGS. We also assessed the relationship between salt-gland function and a bird's physiological state prior to NaCl loading.

METHODS

In Pekin Ducks, females have smaller salt glands (M. R. Hughes unpubl. data) and larger kidneys (Hughes et al. 1995) than males. When saline is ingested, males produce more concentrated SGS (Hughes et al. 1992) yet are less tolerant of NaCl stress (Hughes et al. 1989, Hughes et al. 1992). Because these differences in the osmoregulatory organs might affect the response of the two sexes to an acute osmotic challenge, we used equal numbers of males and females in our experiments.

Experimental animals.—Twelve Pekin Ducks (mean body mass 3,060 ± SE of 110 g for males, 2,710 ± 120 g for females; $n = 6$ for each sex) were housed in adjacent outdoor enclosures with *ad libitum* 225 mM NaCl drinking water (presented in 85-L plastic wading pools and replenished daily) and duck pellets (Buckerfield's, Abbotsford, British Columbia; sodium, $[Na^+]$, potassium, $[K^+]$, and chloride, $[Cl^-]$, concentrations 83, 153.5, and 99 mM · kg^{-1}, respectively; Hughes et al. 1995). This level of Na^+ intake should not increase Osm_{pl} over its freshwater level (Hughes

et al. 1992) but should enhance the secretory potential of salt glands and the ability of body cells to exclude Na^+ (Ruch and Hughes 1975).

Experimental procedure.—Our experiments followed the guidelines set forth by the Canadian Council on Animal Care and were made alternately on male and female ducks over a period of six weeks. Each bird was fasted overnight with free access to water and weighed with a spring balance. The bill of the bird was cleansed and dried, and spontaneous secretion appearing prior to NaCl infusion was collected into calibrated capillary tubes. Catheters were inserted without anaesthetic into the left and right wing veins for blood sampling and saline infusion, respectively. The blood catheter was kept patent with heparinized isotonic saline between sampling times. The duck sat on a foam-lined restrainer with wings lightly bound to the body with Velcro straps. Its unrestrained head was surrounded by a large funnel that directed SGS into a preweighed plastic cup. The total time from weighing to saline infusion never exceeded 1 h.

After a 5-mL blood sample was taken, 1,000 mM NaCl was infused at 0.3 mL/min for 60 min. Small blood samples (0.5 mL) were taken at 5-min intervals until secretion began. A 5-mL sample was taken at secretion (as well as at 5 and 11 h post-infusion) and immediately divided into two subsamples: 4.5 mL into a chilled Vacutainer tube (containing 0.07 mL 15% K-EDTA and 0.014 mg K-Sorbate) and 0.5 mL into a heparinized 1.5-mL centrifuge tube. Triplicate Strumia microhematocrit tubes were immediately filled from the small subsample and centrifuged with it for 3 min at 15,600 × g. Plasma was transferred into a clean 1.5-mL centrifuge tube and stored at −20°C. The large subsample was kept in ice (maximum time 1 h) until centrifuged at 4°C for 10 min at 3,000 × g to obtain plasma. This was divided into two aliquants, one of which contained 100 μL 0.025 M 0-phenanthroline as an inhibitor of angiotensin-converting enzyme (Dusterdieck and McElwee 1971). The aliquants were stored at −20°C until extracted.

The SGS was collected at 30-min intervals for about 2 h and at longer intervals until secretion stopped. The cups were reweighed, and 1 g of SGS was assumed to be 1 mL. The funnel was rinsed with a known volume of distilled water and the ion content of the wash was determined. The SGS was stored at 4°C until analyzed.

Analytical methods.—All analyses of plasma and SGS were done at least in duplicate. Determinations of $[Na^+]$ and $[K^+]$ were made with an Instrumentation Laboratory Model 943 flame photometer, $[Cl^-]$ with a Buchler digital chloridometer, and Osm_{pl} with a Wescor Model 5500 osmometer. Plasma was extracted using Sep-Pak C18 cartridges prior to radioimmunoassay for concentrations of arginine vasotocin ($[AVT]_{pl}$; Gray and Simon 1983) and angiotensin II $[AII]_{pl}$; Gray and Simon 1985).

Calculations and statistics.—Time to secretion was the interval between the start of NaCl infusion and the first appearance of SGS in the nares. The percentage change of each plasma parameter at secretion was the difference between the pre-infusion value and the value at initiation of SGS divided by the pre-infusion value multiplied by 100. Relative plasma volume was 100 − hematocrit (%).

Statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1990). Sex differences in body mass, time to secretion, volume of secretion, and the total ionic output of the salt glands were analyzed with independent samples *t*-tests (with pooled variances). Blood values from sequential sampling times (pre-infusion, at secretion, and 5 and 11 h post-infusion) were compared using the following statistical model:

$$Y_{ijk} = u + T_i + S_j + B(S)_{jk} + (TS)_{ij} + e_{ijk} \quad (1)$$

for i of 1 through 4, j of 1 and 2, and k of 1 through 12, where Y_{ijk} is RPV, Osm_{pl}, or plasma ion or hormone concentration of the blood sample, T_i is the effect of time of sample, S_j is the effect of sex of bird, $B(S)_{jk}$ is the effect of a particular bird nested within a sex, $(TS)_{ij}$ is the two-way interaction between time and sex, and e_{ijk} is the model error term. Tukey's HSD test was used to evaluate differences among means. Relationships between variables were assessed by linear regression. Data are reported as means ± SE.

Results

Male-female comparisons.—Male and female ducks did not differ significantly in body mass ($P = 0.065$), plasma ionic concentrations (Table 1), Osm_{pl}, RPV, or $[AVT]_{pl}$ and $[AII]_{pl}$ (Table 2) at any sampling time. At secretion, $[Cl]_{pl}$ (but not $[Na]_{pl}$ or Osm_{pl}) increased significantly in both sexes (Table 1). Males and females did not differ in the time required to initiate SGS ($P = 0.84$), secretion volume ($P = 0.68$), or SGS ionic concentrations ($[Na^+]$, $P = 0.84$; $[K^+]$, $P = 0.85$). The $[AVT]_{pl}$ and Osm_{pl} were not correlated in male ducks ($r^2 = 0.06$, $P = 0.23$) and were only weakly correlated in female ducks ($r^2 = 0.31$, $P = 0.06$). $[AII]_{pl}$ was not correlated with RPV in either sex ($r^2 = 0.00$, $P = 0.93$, both sexes).

Salt-gland secretion.—With one exception, all ducks secreted spontaneously during preparation for infusion and ceased secreting before NaCl infusion began. The $[Na^+]$ of this spontaneously formed SGS varied from 94 to 510 mM and was highly predictive of the time (min) required to initiate secretion (time to secretion = $46.8 - 0.05\ [Na^+]$; $r^2 = 0.55$, $P = 0.015$).

All birds secreted, and mean secretion $[Na^+]$ was 576 ± 10 mM in males and 568 ± 15 mM in females ($P = 0.68$). At the start of secretion in

TABLE 1. Plasma ionic concentrations (mM) in saline-acclimated Pekin Ducks (n = 6 for each sex) before and after NaCl infusion[a]. Values are $\bar{x} \pm$ SE.

Parameter	Male	Female
	Pre-infusion	
Na	152.6 ± 3.1A[b]	147.4 ± 3.5A
K	2.7 ± 0.2A	2.6 ± 0.1A
Cl	100.7 ± 4.2A	107.0 ± 3.3A
	Secretion	
Na	159.7 ± 3.4A	153.3 ± 2.1AB
K	3.2 ± 0.1AB	2.9 ± 0.0B
Cl	122.2 ± 4.9B	116.6 ± 2.6AB
	5 hours post-infusion	
Na	164.8 ± 5.8A	160.9 ± 3.1BC
K	4.7 ± 0.8B	3.5 ± 0.3C
Cl	119.6 ± 3.6B	119.5 ± 6.1B
	11 hours post-infusion	
Na	159.7 ± 3.5A	164.1 ± 1.5C
K	3.9 ± 0.2AB	3.5 ± 0.1B
Cl	115.3 ± 4.1B	121.6 ± 2.4B

[a] Ducks infused intravenously with 1,000 mM NaCl at 0.3 mL/min for 1 h.

[b] Within each sex, time periods with different letters differ significantly ($P < 0.05$).

TABLE 2. Plasma osmolality, relative plasma volume (RPV), and plasma concentratons of angiotensin II (AII) and arginine vasotocin (AVT) in saline-acclimated Pekin Ducks (n = 6 for each sex) before and after NaCl infusion[a]. Values are $\bar{x} \pm$ SE.

Parameter	Male	Female
	Pre-infusion	
Osmolality ($mOsm \cdot kg^{-1}$)	295.3 ± 5.8A[b]	291.1 ± 6.6A
RPV (%)	58.5 ± 0.9A	60.5 ± 1.1A
AII ($pg \cdot mL^{-1}$)	21.7 ± 4.4A	39.9 ± 15.3A
AVT ($pg \cdot mL^{-1}$)	14.1 ± 2.6A	16.0 ± 3.1A
	Secretion	
Osmolality ($mOsm \cdot kg^{-1}$)	306.4 ± 7.1A	305.0 ± 5.5AB
RPV (%)	63.2 ± 1.4B	64.5 ± 1.0B
AII ($pg \cdot mL^{-1}$)	26.3 ± 5.9A	23.9 ± 6.3A
AVT ($pg \cdot mL^{-1}$)	26.0 ± 3.9B	24.0 ± 4.7B
	5 hours post-infusion	
Osmolality ($mOsm \cdot kg^{-1}$)	315.9 ± 10.8A	317.1 ± 6.0BC
RPV (%)	63.1 ± 0.5B	64.3 ± 1.3B
AII ($pg \cdot mL^{-1}$)	33.6 ± 8.3A	103.2 ± 42.3A
AVT ($pg \cdot mL^{-1}$)	22.4 ± 2.8B	21.8 ± 2.4AB
	11 hours post-infusion	
Osmolality ($mOsm \cdot kg^{-1}$)	314.1 ± 8.4A	326.2 ± 2.7C
RPV (%)	62.3 ± 0.8B	64.4 ± 1.1B
AII ($pg \cdot mL^{-1}$)	44.7 ± 14.5A	172.9 ± 115.4A
AVT ($pg \cdot mL^{-1}$)	27.6 ± 2.7B	24.2 ± 2.7B

[a] Ducks infused intravenously with 1,000 mM NaCl at 0.3 mL/min for 1 h.

[b] Within each sex, time periods with different letters differ significantly ($P < 0.05$).

response to NaCl infusion, the percentage increases in $[Na^+]_{pl}$, $[K^+]_{pl}$, and $[Cl^-]_{pl}$ were inversely related to their pre-infusion values (Fig. 1). Similarly, percentage increases in Osm_{pl} (r^2 = 0.283, P = 0.075) and RPV (r^2 = 0.176, P = 0.175) tended to be inversely related to their pre-infusion values.

Before NaCl was infused, no clear relationship (P = 0.47) existed between Osm_{pl} and RPV (Fig. 2). At secretion, however, there was a highly significant (r^2 = 0.51,P = 0.013) inverse relationship between Osm_{pl} and RPV (Fig. 2). All birds stopped secreting two or three h after infusion ceased. At this time about 60% of the infused NaCl had been excreted, yet RPV and Osm_{pl}, the two stimuli of secretion, were still at their secretory thresholds, where they remained 11 h post-infusion (Table 2).

Time to secretion (Fig. 3A) was inversely related to the initial RPV (RPV_i), but not to initial Osm_{pl} (r^2 = 0.012, P = 0.73). Total SGS volume (Vol_{SGS}) was strongly and proportionately determined by RPV_i (Fig. 3B), but was not related to initial Osm_{pl} (r^2 = 0.001, P = 0.91). Therefore, RPV_i was also a strong determinant of total ion secretion (Fig. 3C,D).

DISCUSSION

Male and female ducks did not differ in the duration of NaCl infusion required to initiate secretion or in the volume and concentration of SGS that they produced. The ducks drank 225 mM NaCl and should have turned over their body's Na^+ content daily without altering Osm_{pl}. When given water with higher salinity (375 mM NaCl), males have higher Osm_{pl} and produce more concentrated SGS than observed in females, and when birds drank 450 mM NaCl, some males died (Hughes et al. 1992). If sexual disparity in either initiation of SGS or extrarenal NaCl excretion exists, then the differences may be demonstrable only at drinking-water salinities greater than those used in our study.

Ducks sometimes secrete spontaneously when they are handled (Ash 1969, Hughes 1970), which may be due to stress (Peaker and Linzell 1975). With one exception, the birds in our study were secreting at a slow rate before they were handled, but stopped secreting during the placement of the catheters. This suggests that the stress from handling might inhibit secretion. The mechanisms that induce spontane-

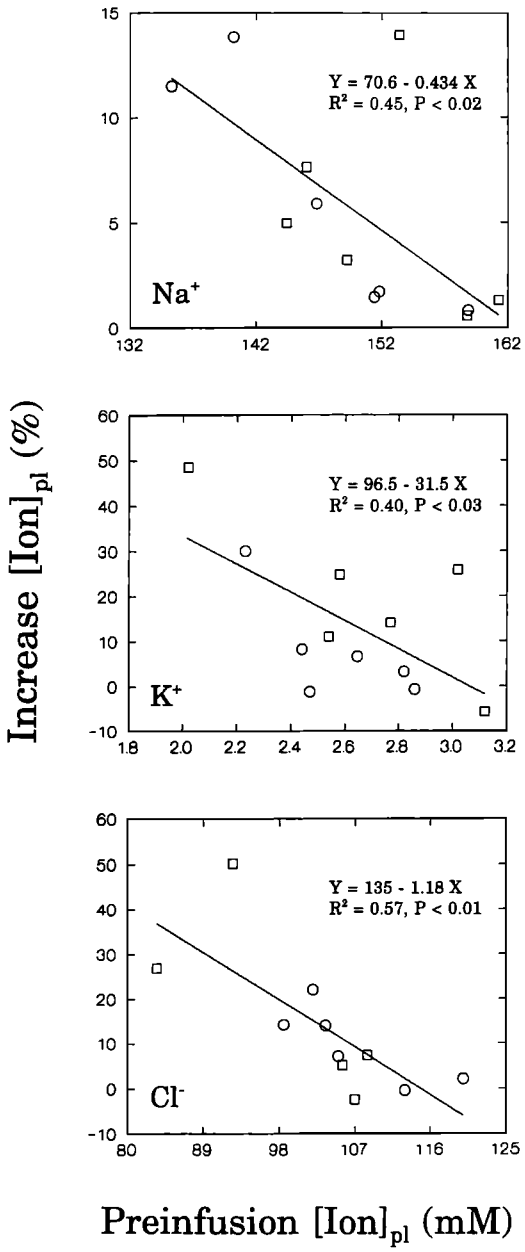

FIG. 1. Percentage increases in plasma ion concentrations of Na^+, K^+, and Cl^- at the start of salt-gland secretion as a function of their pre-infusion values in saline-acclimated male (squares) and female (circles) Pekin Ducks infused intravenously with 1,000 mM NaCl at 0.3 mL/min.

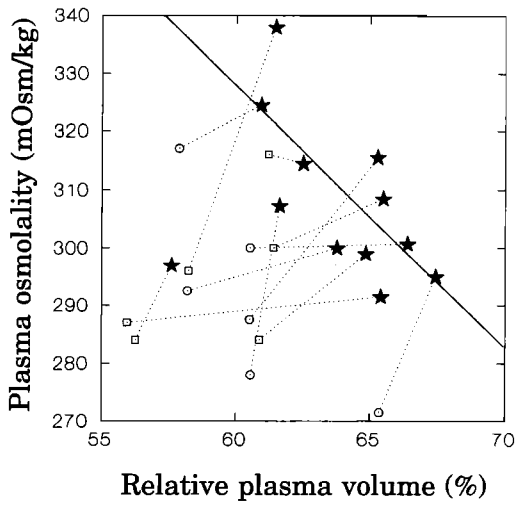

FIG. 2. Plasma osmolality (Osm_{pl}) as a function of relative plasma volume (RPV) in saline-acclimated male (squares) and female (circles) Pekin Ducks infused intravenously with 1,000 mM NaCl at 0.3 mL/min. Equation for line is: $Osm_{pl} = 599 - 4.52 \cdot RPV$ ($r^2 = 0.51$, $P = 0.013$). Dashed lines connect pre-infusion values (squares and circles) with those at secretion (stars).

ous secretion are unclear, because it occurs at lower Osm_{pl} and RPV than predicted as requisite for secretion (Fig. 2).

The role of ECFV expansion in initiating SGS has been debated for a long time (Hughes 1989b). Holmes (1965) suggested that volume or stretch receptors (rather than osmoreceptors) triggered SGS. SGS has been induced by expanding ECFV without increasing Osm_{pl} (Gilmore et al. 1977, Gray et al. 1986, Bokenes and Mercer 1995). However, because some infusates were hyperchloretic, elevated $[Cl^-]_{pl}$ may have triggered secretion. In contrast, ducks denied drinking water for a protracted period eventually secreted despite reduced ECFV, which supports osmotic stimulation (Stewart 1972). Several studies have suggested that total ECFV, the interstitial portion of ECFV (Kaul and Hammel 1979, Hammel et al. 1980), or the change in these volumes (Ruch and Hughes 1975, Hughes 1989a) affect the response of the salt glands to increased Osm_{pl}. Our study is the first to describe the relative stimulatory contributions of Osm_{pl} and RPV in initiating SGS (Fig. 2).

As NaCl was infused, Osm_{pl} and RPV changed simultaneously. Eventually, each bird achieved a unique relationship between Osm_{pl} and RPV that triggered SGS. This combination was positioned on a continuum describing all birds (see Fig. 2). Some ducks began to secrete when RPV was markedly increased, but Osm_{pl} was changed little or not at all, whereas others began to secrete when Osm_{pl} increased with

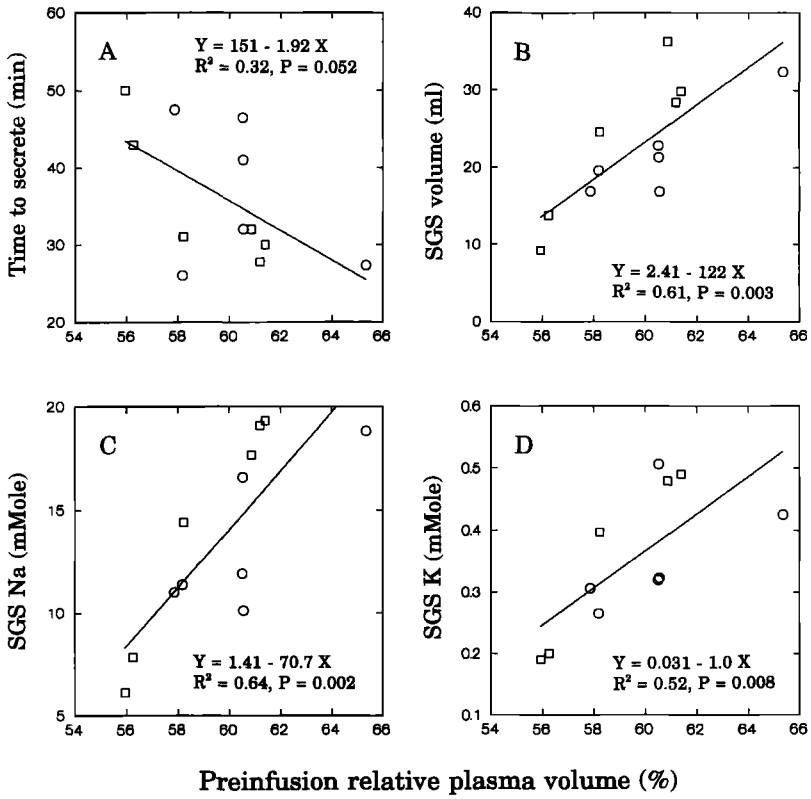

FIG. 3. Relationship between pre-infusion relative plasma volume and (A) time to secretion, (B) volume of secretion, and total amount of (C) Na and (D) K secreted in saline-acclimated male (squares) and female (circles) Pekin Ducks infused intravenously with 1,000 mM NaCl at 0.3 mL/min.

little discernible change in RPV (Fig. 2). These results provide strong evidence that changes in Osm_{pl} and RPV initiate secretion interactively and that increases in Osm_{pl} and RPV may be equally effective stimuli (Fig. 2). This reconciles the disparate observations that both ECFV expansion (Ruch and Hughes 1975, Hughes 1989a) and ECFV reduction (i.e. dehydration; Stewart 1972) induce secretion. It also is consistent with the observation that volume input drives about half the signal-sustaining SGS in ducks previously primed by NaCl infusion (Hammel and Simon 1994, Bokenes and Mercer 1995).

We slowly infused sufficient NaCl (60 min infusion of 1,000 mM NaCl) to increase the body's Na^+ content by about 20%. The infusion induced secretion in all birds within 50 min (Fig. 3A). At secretion RPV and $[AVT]_{pl}$ were elevated, but Osm_{pl} and $[AII]_{pl}$ were not (Table 2). All birds ceased to secrete within two or three h post-infusion, when up to 40% of the infused NaCl remained unexcreted. At that time the birds were dehydrated because body water had been used in forming secretion, and they did not drink during the experiment. Although the increase in $[AII]_{pl}$ was not statistically significant, it may have been great enough to inhibit secretion (Gray et al. 1986), although RPV and Osm_{pl}, the two stimuli of secretion, still were at the secretory threshold.

Möhring et al. (1980) described a positive relationship between $[AVT]_{pl}$ and Osm_{pl} in a study that included only data from ducks before and after acclimation to saline. Gray and Simon (1983) also found a clear positive relationship between $[AVT]_{pl}$ and Osm_{pl} when only data for ducks before and after dehydration were included. Based on these observations (which are essentially two-point regressions), elevation of Osm_{pl} is considered the primary factor regulating increase in $[AVT]_{pl}$ in ducks (Gray and Simon 1983) and other birds with salt glands (Gray and Erasmus 1989a). In our study there was a tendency for Osm_{pl} to increase over time

(significant in females), but $[AVT]_{pl}$ did not change after secretion started (Table 2). Zenteno-Savin (1991) found that ducks increased $[AVT]_{pl}$ in parallel with increases in drinking-water salinity, but did not increase Osm_{pl}. Under a similar protocol, Gray and Erasmus (1989b) found that Kelp Gulls (*Larus dominicanus*) gradually increased Osm_{pl} without altering $[AVT]_{pl}$. In birds with salt glands, the relationship between Osm_{pl} and $[AVT]_{pl}$ remains puzzling.

In summary, male and female Pekin Ducks did not differ in secretory thresholds or secretory competence. Our experiments: (1) demonstrate the influence of the ducks' physiological state, prior to salt loading (especially the RPV), on NaCl secretion by the salt glands; (2) describe secretory threshold as a dynamic interaction of changes in both Osm_{pl} and ECFV (indexed as RPV); and (3) suggest that Osm_{pl} and RPV are equally effective stimulators of secretion.

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