VARIATION IN OSMOREGULATORY PARAMETERS OF CAPTIVE AND WILD HOUSE SPARROWS (*PASSER DOMESTICUS*)

DAVID L. GOLDSTEIN AND AFSHAN ZAHEDI

Department of Biological Sciences, Wright State University, Dayton, Ohio 45435 USA

ABSTRACT.—We examined the regulation of plasma osmolality (P_{osm}), hematocrit (HCT), and urine osmolality and sodium concentration in laboratory-housed and free-living House Sparrows (*Passer domesticus*). Plasma osmolality (mean value = 352 mmol/kg) was quite tightly regulated both within (coefficient of variation [c.v.] = 1.9%) and among (c.v. = 1.7%) individuals maintained on commercial poultry chow in the laboratory. Hematocrit (mean = 0.48) was more variable (c.v. was 7.4% within individuals, 6.9% among individuals). Plasma osmolality, urine osmolality, and hematocrit all increased following 24-h dehydration. Switching from a seed (low sodium) to a cricket (high sodium) diet had no effect on P_{osm}, HCT, or urine sodium, but urine osmolality increased. In wild House Sparrows both P_{osm} (c.v. = 3.6%) and HCT (c.v. = 9.1%) were more variable than in the laboratory, though mean values (341 mmol/kg and 0.50, respectively) did not differ significantly between the laboratory and field. In wild birds, P_{osm} and HCT were negatively correlated, and U_{osm} positively correlated, with ambient temperature. However, osmoregulatory condition of individual birds may vary throughout the year. *Received 27 July 1989, accepted 23 January 1990.*

OSMOREGULATORY homeostasis is an important physiological requirement in free-living animals. In birds, osmoregulation involves the actions of skin, respiratory tract, intestines, and kidneys in defense of several regulated variables, including plasma osmolality and volume. The ability to identify conditions when osmoregulatory homeostasis is not achieved—that is, when the defended physiological variables depart from their normal set points—could be a means to identify periods of environmental stress. To achieve this, one must first define the normally regulated levels for the particular variables, and then measure these in the field. Measurements of the functional state of the controlling organ systems can contribute further to defining physiological condition in the field.

We examined variation in plasma osmolality (P_{osm}) and hematocrit (HCT) in House Sparrows (*Passer domesticus*) maintained in standardized laboratory conditions and in the field. Plasma osmolality is closely regulated in birds. Small increases in P_{osm} will stimulate antidiuretic hormone secretion (Stallone and Braun 1986, Gray and Erasmus 1989) and drinking (Kaufman and Peters 1980). Dehydration-induced changes in P_{osm} are quickly restored when birds regain access to water (Takei et al. 1988). Variations in hematocrit, at least in the short term, are indicative of changes in blood volume (Takei et al. 1988). Given adequate water and electrolytes, one would therefore expect these variables to be maintained at quite constant levels in an individual. Similarly, one might expect that the conditions would vary relatively little among individuals. If so, then these variables could serve as useful indices to the hydrational state of wild individuals.

We were interested in examining three components of variability in P_{osm} and HCT. These were temporal variation within individuals in controlled environments, variation among individuals in those controlled environments, and temporal and interindividual variation in populations of wild birds. In addition, we measured urine osmotic and sodium concentrations in many individuals. These parameters might be expected to vary as the birds defend plasma osmolality in response to changing dietary or environmental osmoregulatory challenges. Our objective was to define the range of variability of these parameters under controlled laboratory conditions, and to provide an interpretive framework to assess changing osmoregulatory demands on wild House Sparrows.

METHODS

Laboratory studies.—We captured House Sparrows (*Passer domesticus*) by mist net in Greene County, Ohio, from populations in rural agricultural areas with scattered residences. Birds were transferred to the laboratory and maintained two or three to a cage at 23°C. Water and commercial chicken mash were provided *ad libitum*. Measurements were made after a minimum

TABLE 1. Variation in plasma osmolality (P_{osm}) and hematocrit (HCT) of House Sparrows maintained for 2 weeks at 23°C and eating commercial bird chow. Data are based on 5 samples collected from each of 15 individuals.

	Within individuals								
	Range			Coefficient of variation[a]			Among individuals[b]		
	Min	Max	$\bar{x}$	Min	Max	$\bar{x}$	$\bar{x}$	Range	c.v.
P_{osm} (mmol/kg)	8	28	14.5	1.0	3.2	1.9	352	32[c]	1.7
HCT	0.04	0.13	0.09	3.5	12.3	7.4	0.48	0.11	6.9

[a] c.v. = 100 × (SD/$\bar{x}$).
[b] Calculated from one value selected at random from each individual; see text.
[c] Minimum and maximum values of P_{osm} were 340 and 372 mmol/kg, respectively.

of 5 days in captivity. Every 3–4 days for 14–17 days, birds were weighed (to the nearest 0.1 g, Mettler top-loading balance) and blood samples were taken by puncture of a brachial vein for analysis of osmolality and hematocrit. All samples were collected between 1300 and 1430. In one group, we withdrew all drinking water for 24 h in the middle of the measurement period. This caused a transient increase in plasma osmolality, and allowed analysis of whether or not P_{osm} returned to the original value after disturbance.

Urine osmolalities were measured on samples (ca. 10 μl) collected both before and after dehydration. Urine was collected by inserting a small cannula with a closed end briefly into the cloaca. Ureteral urine drained from the ureteral orifices into the cannula through a window in its side. The closed cannula end avoided contamination of urine by fluids from the adjacent colon (Goldstein and Braun 1988).

We evaluated the influence of diet on plasma and urine osmolalities and on sodium concentrations in the laboratory in a separate group of sparrows. These birds were first fed seeds (low sodium, 0.02 meq Na^+/g dry food) and then crickets (high sodium, 0.2 meq Na/g dry food). Birds on each diet were given water *ad libitum*. Blood and urine samples were collected after birds had been on each diet for at least four days.

Field studies.—House Sparrows were captured by mist net periodically throughout the year in the same locations as those captured for the laboratory studies. Most sparrows were netted in the morning (0700–1000), but some were captured at other hours throughout the day. Ureteral urine (ca. 15 μl) was collected (as described above) from some birds within 30 s of capture. A blood sample (50–100 μl) was collected from the brachial vein of all birds. We recorded ambient temperature, sex, body mass (measured to the nearest 0.25 g by a calibrated Pesola spring balance), and molt condition at time of capture.

Analyses.—Blood samples were centrifuged for 3 min at 12,000 *g* for separation of cells from plasma, hematocrit was recorded, and plasma was taken for further analysis. Urine was centrifuged, and the supernatant analyzed. We measured osmolality of all fluids by vapor pressure osmometry (Wescor 5500). The storage of samples in heparinized capillary tubes had no measurable influence on sample osmolality. Sodium concentrations were measured in some samples by an ion-specific electrode (Corning). When sample size permitted, analyses were done in duplicate. Osmolality and sodium standards were processed along with each set of samples.

All statistical analyses were performed using a microcomputer-based statistical package (CRISP). Statistical differences were assumed significant if $P \leq 0.05$. Data are reported as $\bar{x} \pm$ SD.

RESULTS

Variation within individuals in the laboratory.—Plasma osmolalities of individual House Sparrows varied somewhat over the 2-week in-laboratory measurement period (Table 1). After a transient increase in P_{osm} caused by 24-h dehydration (see below), plasma osmolality returned to a value not different from that measured before dehydration (mean difference was −1.7 mmol/kg).

Hematocrit (HCT) was more variable than plasma osmolality, with a mean within-individual coefficient of variation of 7.4% (Table 1). We detected no significant difference in HCT before and after dehydration in birds that were dehydrated, and there was no consistent pattern of change in HCT over the course of the measurement period. We conclude that blood sampling did not influence plasma osmolality in a significant way.

Effects of dehydration and diet.—Dehydrated House Sparrows lost weight rapidly ($\bar{x} = 3.9 \pm 0.8$ g, or 14.8% of body mass, lost in 24 h) and experienced significant rises in P_{osm} ($\bar{x} = 41.8 \pm 8.5$ mmol/kg) and HCT ($\bar{x} = 0.028 \pm 0.032$). Urine concentrations changed from hypoosmotic (225 ± 43 mmol/kg) while the birds were fully hydrated to strongly hyperosmotic after they had been dehydrated for 24 h (Table 2). The maximum urine osmolality measured was 920 mmol/kg.

TABLE 2. Effect of 24-h dehydration and diet on blood and urine composition in House Sparrows. Values are mean ± SD (*n*); asterisk indicates significant difference ($P < 0.05$) between seed and cricket diets.

	Diet		
	Commercial, dehydrated	Seed	Cricket
Plasma osmolality (mmol/kg)	396.6 ± 7.3 (7)	343.6 ± 10.2 (7)	347.1 ± 8.0 (7)
Hematocrit	0.51 ± 0.04 (7)	0.52 ± 0.04 (7)	0.51 ± 0.07 (7)
Urine osmolality (mmol/kg)	774.8 ± 136.5 (5)	271.0 ± 88.1 (6) *	401.2 ± 90.6 (6)
Urine sodium (meq/l)	—	99.2 ± 57.4 (6)	113.8 ± 59.1 (6)

Switching diet from seeds to crickets produced no significant changes in hematocrit, plasma osmolality, or urine sodium concentration. The urine osmolality was elevated significantly on the cricket diet (Table 2). The regressions of urinary sodium on osmolality (Fig. 1) were not significantly different on the two diets (ANCOVA).

Variation among laboratory individuals.—We found little variation in the mean value for plasma osmolality among individuals fed the commercial diet in the laboratory (Table 1). The coefficient of variation (c.v.) among individuals, based on mean values of P_{osm} for each individual, was 1.0%. This value was slightly higher (1.7%) when calculated from single randomly selected values from each individual, a situation that more closely resembles the field sampling protocol (in which we took single samples from individuals). For individuals who ate seeds (c.v. = 3.0) and then crickets (c.v. = 2.3%), the coefficients of variation among individuals were slightly higher. The among-individual coefficient of variation calculated from mean values for individuals was 1.2%.

Hematocrit among individuals varied similarly as within individuals. The coefficient of variation was 6.9%, whether calculated from mean values or from randomly selected values.

Blood and urine concentrations in free-living House Sparrows.—The range (306–397 mmol/kg) and the coefficient of variation (3.6%) of P_{osm} measured in wild birds exceeded those measured under laboratory conditions. The overall mean P_{osm} in wild birds (341.0 ± 12.4 mmol/kg) did not differ significantly from that of hydrated sparrows in the laboratory. Plasma osmolality was higher in April than in January, March, and May–October, and was higher in November than in August (Fig. 2). Plasma osmolality correlated inversely with ambient temperature ($n = 180$, $r = -0.22$, $P < 0.005$).

Hematocrit, like plasma osmolality, varied more widely in wild than in laboratory-housed sparrows (overall $\bar{x} = 0.50 \pm 0.045$, c.v. = 9.1%). Significant differences occurred among months (Fig. 2): January > April, July, and August; March > April and July–October; November > July and August. Hematocrit was negatively correlated with temperature ($n = 177$, $r = -0.35$, $P < 0.001$), and positively correlated with plasma osmolality ($n = 177$, $r = 0.14$, $P = 0.05$).

Urine osmolality in wild sparrows ranged from 132 mmol/kg to 658 mmol/kg. Urine osmolality was positively correlated with ambient temperature ($n = 84$, $r = 0.21$, $P < 0.05$) but was not correlated significantly with plasma osmolality. Urinary sodium varied substantially in the field (2.6–179 meq/l). Overall, we found no significant differences among months for either urine osmolality or sodium concentration, and these variables were not significantly correlated with monthly rainfall (data from the National Weather Service). However, urine osmolality was significantly higher in June and July, two particularly dry months during the 1988 drought, than in June 1989, a particularly wet month (Fig. 2). Urinary sodium correlated significantly with urine osmolality in wild birds (Fig. 1). The equation defining this relationship did not differ significantly from those describing the laboratory data for birds on cricket or seed diets.

We found no differences between sexes, and no significant effect of time of day, for any of the variables measured.

DISCUSSION

Plasma osmolality is usually considered a primary regulated variable in birds. We confirm that, under constant environmental conditions, House Sparrows regulate their plasma osmolality within a narrow range, both within and among individuals. Plasma osmolality was not affected by dietary sodium content, at least within a range of sodium contents that would reasonably be encountered in the wild. How-

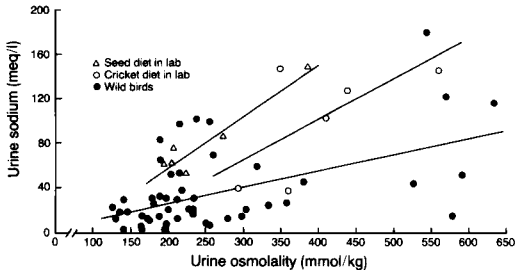

Fig. 1. Urine sodium concentration and osmolality for House Sparrows on two diets in the laboratory and for wild birds. Lines are least squares linear regressions for each group. Equations describing the data are as follows: $U_{Na} = 0.46U_{osm} - 33.6$, $n = 6$, $r = 0.96$ (seed diet); $U_{Na} = 0.36U_{osm} - 42.4$, $n = 6$, $r = 0.80$ (cricket diet); $U_{Na} = 0.14U_{osm} - 1.4$, $n = 47$, $r = 0.54$ (wild birds).

ever, as seen in another population of House Sparrows (Goldstein and Braun 1988), the birds were quite susceptible to dehydration, and plasma osmolality rose rapidly following removal of water.

In Tucson, Arizona, House Sparrow populations are year-round residents in a very hot climate, and it might be expected that their osmoregulatory systems have either adapted or acclimated to this environment. The plasma osmolalities in Ohio birds (355 mmol/l) were actually somewhat higher than in Arizona birds (327–342 mmol/l), and urine osmolalities on a seed diet were lower in the Ohio birds (Goldstein and Braun 1986, 1988). Ohio sparrows appeared less able to maintain balance during dehydration than Arizona birds. Ohio birds lost body mass faster (3.8 g [14.8%] vs. 2.2 g [9.8%] per 24 h) and had a more rapid increase in plasma osmolality (41.8 vs. 33.3 mmol/kg in 24 h) than those from Arizona (Goldstein and Braun 1988). This occurred in the absence of a significant difference in urine concentrating ability between the populations.

Hematocrit (HCT) in the laboratory was much more variable than plasma osmolality. This is consistent with studies that demonstrated that plasma osmolality is more strictly regulated in birds than is blood volume during periods of changing fluid balance (Takei et al. 1988). During short-term variations in hydration, HCT is highly correlated with changes in plasma volume, as extracellular fluid is lost while blood-cell volume remains essentially unchanged (Takei et al. 1988). However, in the longer term, other variables may influence HCT, including age (Gilbert 1969), sex (Sturkie and Newman 1951), and stage of molt (deGraw and Kern 1985). We found no significant difference between the sexes in the birds studied, and no individuals in the laboratory were molting at the time. It is not clear what other factors might contribute to variation in HCT within individuals. For example, variation may simply reflect drinking before we collected blood samples.

As expected, the change in diet from seeds to insects had no significant effect on plasma osmolality. We were surprised that urine osmolality was affected by the change, and that urine sodium concentration was not. In a steady state, sodium intake should equal sodium excretion, and we expected that an increased sodium intake from the cricket diet would increase urinary sodium concentration. The absence of this response may reflect variation in urine flow rate, which together with sodium concentration determines the urinary sodium excretion rate. Independent of variation in urine flow rates, we expected that birds on the higher sodium diet would have a greater proportion of total urine osmolality accounted for by sodium (higher slope in Fig. 1). We did not see this effect. This could reflect different rates of sodium absorption by the intestine in birds on the two diets (Goldstein 1990).

The mean values in laboratory-housed and wild birds for both plasma osmolality (P_{osm}) and hematocrit (HCT) were not significantly different, but both parameters were more variable (higher coefficients of variation) in the field than in the laboratory. Plasma osmolality of wild House Sparrows was negatively correlated with ambient temperature. It is clear that ambient temperature relates only to broad climatic changes, not the microclimate impinging on the birds, and this variable explains only a small percentage of the variation in P_{osm}. Nevertheless, the correlation is highly statistically significant. There are two possible explanations. First, the changing P_{osm} may reflect a changing hydration state. This implies that there is greater hydrational stress for the House Sparrows during the colder months. This certainly is possible as free water may be largely unavailable during cold spells when drinking water and insects are scarce. Nevertheless, the mean osmolalities in both the highest and the lowest temperature ranges were lower than those measured in the laboratory. We cannot say that P_{osm} in winter was elevated above the normally regulated set point. The second possible reason for

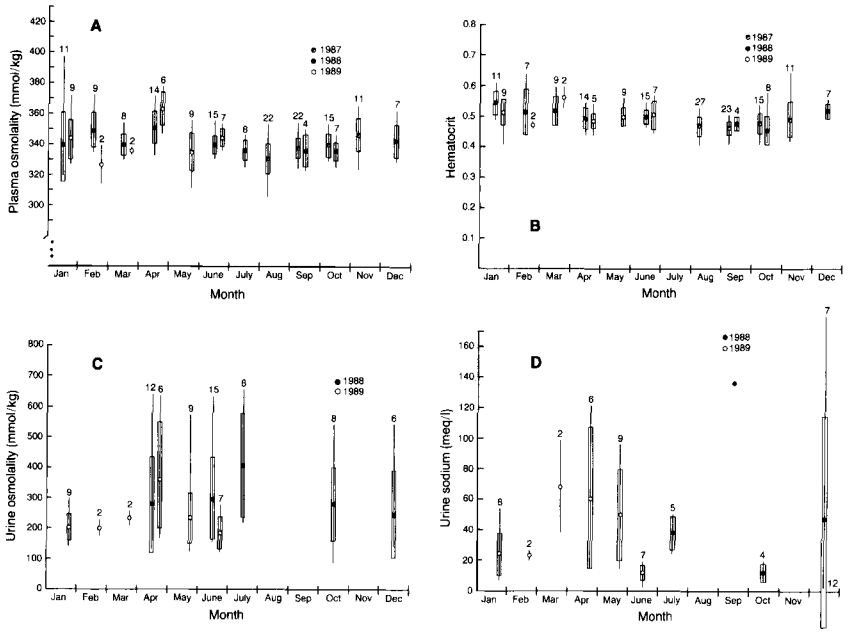

Fig. 2. Annual variation in (A) plasma osmolality, (B) hematocrit, (C) urine osmolality, and (D) urine sodium concentration. Circles indicate mean values, boxes enclose ±1 SD, lines indicate range, and sample sizes are above symbols.

the correlation may be that P_{osm} changed with age. Plasma levels of sodium and chloride (Hughes 1984) and osmolality (Grabowski 1967) change toward adult levels in young post-hatching gulls (*Larus glaucescens*) and chickens (*Gallus domesticus*). Plasma osmolality correlated negatively with temperature in our study. The highest temperatures occurred in summer, a time of year when many of the captured House Sparrows were first-summer juveniles. However, we are not aware of evidence that plasma osmolality actually is age-related in young passerines. We found no significant difference between birds classified as juveniles and adults, though we could not accurately age juveniles. In two other studies of seasonal variation in plasma osmolality, neither found any significant pattern of variation (Vleck 1984, Rooke et al. 1986).

Hematocrit, like plasma osmolality, correlated negatively with ambient temperature. This parallel pattern might suggest a common cause, and the explanations could be similar. Hematocrit changes rapidly with changes in hydration state (Takei et al. 1988), and HCT may change with age (Gilbert 1969). However, other influences may also affect HCT. As in House Sparrows, HCT in Dark-eyed Juncos (*Junco hyemalis*) increased in winter, possibly associated with increased oxygen-carrying capacity during times of high tissue oxygen demands (Swanson 1988). Hematocrit in free-living birds may also vary with the onset of molt (deGraw et al. 1979), with periods of general physiological stress (Rooke et al. 1986), or with changes in total body water (Rooke et al. 1986). We found no difference in HCTs of molting and nonmolting birds. We have no evidence bearing on these other factors. We found no significant differences between HCTs of male and female House Sparrows.

Whereas P_{osm} and HCT are regulated variables, urine osmolality and sodium concentration would be expected to vary as demands on the osmoregulatory system changed. In contrast to the blood variables, urine concentration was positively correlated with ambient temperature. The highest values were recorded during dry days in summer. The measured variability in urine osmolalities (including the absence of a significant correlation with monthly rainfall and the presence of hypoosmotic urines even during the driest times) may relate to variation in drinking before we sampled. Nevertheless, conspicuous water supplies were not available near (ca. 0.5 km) the capture site, and we would expect the physiological condition of at least individuals that did not recently drink to reflect the osmoregulatory demand of the environ-

ment. Consistent with this, birds sampled in October–April, with few (15%) exceptions, produced hypoosmotic urine. This was true also in June 1989, a very wet month when all birds sampled had hypoosmotic urines. In contrast, 40% of birds in June and July 1988, a particularly dry summer, had hyperosmotic urines. Even with unlimited water, urine concentration may change with diet. Still the temperature-related variation in urine osmolality may reflect enhanced demands for water conservation during the hot, dry months. Increased urine (voided cloacal fluid) osmolalities during such times were reported in the Curve-billed Thrasher (*Toxostoma curvirostre*) in the Sonoran Desert of Arizona (Vleck 1984).

Data on urine concentrations reinforce the view that the inverse relationships between P_{osm} and HCT vs. temperature do *not* reflect increased osmoregulatory stress during the colder months. To the contrary, months that are hot and dry appear to impose the greatest demands for water conservation, as might be expected. Seasonal changes in P_{osm} and HCT may reflect the combined influences of temperature, age, and oxygen demand, or perhaps other as yet unidentified factors. It seems that osmoregulatory stress (values for regulated variables outside of their normal range) was rare in the animals we studied. In particular, excessively high (>380 mmol/kg) values of P_{osm} were quite unusual. The highest and lowest values for plasma and urine osmolality occurred scattered through the year, and the highest urine osmolalities measured were close to the values obtained in the laboratory under conditions of acute dehydration. Even in the absence of a generally stressful environment, physiological condition of individual birds may vary depending on their particular interactions with the biotic and abiotic environment.

ACKNOWLEDGMENT

This work was supported by a Research Challenge grant to Goldstein.

LITERATURE CITED

DEGRAW, W. A., & M. D. KERN. 1985. Changes in the blood and plasma volume of Harris' Sparrows during postnuptial molt. Comp. Biochem. Physiol. 81A: 889–893.

———, ———, & J. R. KING. 1979. Seasonal changes in the blood composition of captive and free-living White-crowned Sparrows. J. Comp. Physiol. 129: 151–162.

GILBERT, A. B. 1969. The erythrocyte sedimentation rate and packed cell volume in the domestic fowl with respect to age and sex. Br. Poult. Sci. 10: 109–113.

GOLDSTEIN, D. L. 1990. Effects of different dietary sodium intakes on renal and cloacal sodium excretion in chukars (Aves: Phasianidae). Phys. Zool. 63: 408–419.

———, & E. J. BRAUN. 1986. Lower intestinal modification of ureteral urine in hydrated House Sparrows. Am. J. Physiol. 250: R89–R95.

———, & ———. 1988. Contributions of the kidneys and intestines to water conservation, and plasma levels of antidiuretic hormone, during dehydration in House Sparrows (*Passer domesticus*). J. Comp. Physiol. 158: 353–361.

GRABOWSKI, C. T. 1967. Ontogenetic changes in the osmotic pressure and sodium and potassium concentrations of chick embryo serum. Comp. Biochem. Physiol. 21: 345–350.

GRAY, D. A., & T. ERASMUS. 1989. Control of plasma arginine vasotocin in Kelp Gulls (*Larus dominicanus*): roles of osmolality, volume, and plasma angiotensin II. Gen. Comp. Endocrin. 74: 110–119.

HUGHES, M. R. 1984. Osmoregulation in nestling Glaucous-winged Gulls. Condor 86: 390–395.

KAUFMAN, S., & G. PETERS. 1980. Regulatory drinking in the pigeon *Columba livia*. Am. J. Physiol. 239: R219–R225.

ROOKE, I. J., S. D. BRADSHAW, R. A. LANGWORTHY, & J. A. TOM. 1986. Annual cycle of physiological stress and condition of the Silvereye, *Zosterops lateralis* (Aves). Australian J. Zool. 34: 493–501.

STALLONE, J. N., & E. J. BRAUN. 1986. Osmotic and volemic regulation of plasma arginine vasotocin in conscious domestic fowl. Am. J. Physiol. 250: R644–R657.

STURKIE, P. D., & H. J. NEWMAN. 1951. Plasma proteins of chickens as influenced by time of laying, ovulation, number of blood samples taken and plasma volume. Poult. Sci. 30: 240–248.

SWANSON, D. L. 1988. Seasonal variation of vascular oxygen transport in the Dark-eyed Junco. Am. Zool. 28: 129A.

TAKEI, Y., Y. OKAWARA, & H. KOBAYASHI. 1988. Water intake induced by water deprivation in the quail, *Coturnix coturnix japonica*. J. Comp. Physiol. B 158: 519–525.

VLECK, C. M. 1984. Reproductive season and water stress in a Sonoran Desert bird—the Curve-billed Thrasher. Am. Zool. 24: 5A.