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# Water Balance and Bladder Function in the Namib Desert Sand Dune Lizard, *Aporosaura anchietae* (Lacertidae)

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**We measured field water fluxes and metabolic rates for *Aporosaura anchietae*, a lacertid lizard living in the sand dunes of the Namib Desert, using doubly-labeled water ($H^3H^{18}O$). Mass of males and females was significantly greater in summer 1976–77–autumn 1977 than in summer 1977–78. Water influx, efflux and field metabolic rate was positively correlated with body mass, but body mass loss per day in the field was negatively correlated with mass. Lizards were in negative water balance in summer 1976–77 and autumn 1977 but were in water balance and maintained mass in summer 1977–78. Minimum water requirement for body mass maintenance during the study period was 0.109 and 0.065 $mL\ d^{-1}$ for males and females, respectively. We rarely observed drinking of fog water in these lizards. Water fluxes for *A. anchietae* were similar to juvenile *Uma scoparia* and lower than fluxes for the lizards of the genus *Eremias* from the Kalahari Desert. Bladder fluid mass for field animals was 113 mg and the fluid was hypo-osmotic to plasma (265 vs 410 mOsm/kg). Regulation of plasma sodium concentration occurred if animals were allowed to drink prior to dehydration experiment.**

LIZARDS that inhabit desert sand dunes encounter extremely arid conditions. Typically, summer temperatures are very high, and little vegetation is present as a refuge, whereas precipitation and humidity normally are low. Previous studies on water and electrolyte requirements of the dune lizards *Uma scoparia* (Minnich and Shoemaker, 1972) and *U. notata notata* (Deavers, 1972) indicated that their diets may be very low in water content and that free-ranging *U. scoparia* are unable to maintain weight during dry periods.

The Namib Desert is a coastal desert characterized by precipitation derived principally from periodic advective fogs (Louw and Seely, 1982; Lancaster et al., 1984). The dune system, which extends 100 km inland, is the habitat of many insects which have developed various modes of exploiting the water from fogs (Seely, 1979; Louw and Seely, 1982). It has been inferred that the lizard, *Aporosaura anchietae* (Lacertidae), also takes advantage of condensed water from fogs (Louw and Holm, 1972; Louw, 1972; Louw and Seely, 1982).

*Aporosaura anchietae* are diurnal and feed on a variety of arthropods and seeds (Robinson, 1987; Robinson and Cunningham, 1978). Condensed fog water has been postulated to be an important water source for *A. anchietae*, and in captivity these animals will imbibe 10.8% of their body weight in 3 min (Louw and Holm, 1972). This water is transferred from the stomach to the bladder, a diverticulum of the intestine, within 24 h (Louw and Holm, 1972). Louw and Holm (1972) suggested that the bladder may act as a water storage organ, and recently such a role has been indicated for the bladder of juvenile *Sceloporus jarrovi* (Beuchat et al., 1986).

In this study, we examined aspects of water and salt regulation of *A. anchietae*. Our work was divided into two sections: 1) field measurement of water fluxes and energy metabolism of free-ranging *A. anchietae* with doubly-labeled water ($H^3H^{18}O$) in order to construct field water budgets; and 2) laboratory examination of the possible role the bladder might play in aiding in plasma solute regulation during periods of dehydration.

## Methods and Materials

*Fieldwork.*—Fieldwork was performed on the sand dunes near the Desert Ecological Research Unit (DERU), Gobabeb (23°34′S, 15°03′E), Namibia. Environmental data were recorded by instruments located at DERU. We recorded temperatures using calibrated Lambrecht thermohygrographs, and precipitation using Hellman type rain gauges, modified to also measure fog condensation. Summary of the Namib Desert climate over the 5 yr (1976–81) (Lancaster et al., 1984) was used for comparison with 1976–78 period when this study was performed. The study encompassed three periods in 1976–78; summer 1976–77 (20 Nov.–26 Jan.), autumn 1977 (7–23 May) and summer 1977–78 (3 Dec.–4 Feb.).

We captured lizards (*A. anchietae*) by hand in the sand dunes near the research station. Animals were placed individually in cotton bags and returned to the laboratory at the research station. We recorded the place of collection to insure that lizards were returned to the same location.

In the laboratory, they were weighed, sexed and toe-clipped. Animals for water balance studies were injected with 0.1 mL doubly-labeled water (20 $\mu Ci\ ^3H/mL$, 50 atoms % $^{18}O$). Following an equilibration period of 4 h, we removed and collected blood samples (0.1 mL) by heart puncture in 25 $\mu L$ capillary tubes. The samples were flame-sealed and marked in correspondence with the individual. We then returned the lizards to the field and released them near their point of capture. After 13–17 d, lizards were recaptured and handled as previously described, with a second blood sample removed following weighing. The blood sample was collected and sealed as reported above. We determined final total body water volume by killing the animal and drying it to constant mass in a drying oven (60 C). Initial total body water volume was determined from the allometric relation between body water mass (TBW) and total mass ($TBW = 0.666M + 0.17$, $r^2 = 0.976$, $n = 33$). Sealed fluid samples were refrigerated for storage.

Sealed samples were returned to the Laboratory of Biomedical and Environmental Sciences for analysis of $^3H$ and $^{18}O$ content. Following micro-distillation to obtain pure water, we measured samples for $^3H$ activity using liquid scintillation (Beckman LS 230) and for $^{18}O$ activity by the proton activation method (Wood et al., 1975). Water fluxes and field metabolic rates were calculated using the equations of Nagy (1975). We determined metabolic water production from field metabolic rates assuming 0.65 $\mu l\ H_2O$ formed per mL $CO_2$ produced (Nagy, 1983).

*Laboratory studies.*—We determined total water loss and changes in plasma sodium content on the same animals. We collected 24 lizards and returned them to the DERU laboratory between Feb. and March 1977. Twelve lizards had blood samples removed immediately by heart puncture (25 ga needle, 1 mL syringe) and eight were killed to determine volume and solute concentration of fluid in the bladder. We divided the 12 remaining lizards into two groups, "hydrated" and "dehydrated" animals. The "hydrated" lizards were allowed to drink for 24 h before commencing the experiment, whereas "dehydrated" lizards were not permitted to drink. Lizards in both groups were held individually in sand-filled containers at 25 ± 2 C and room humidity (10–30%).

Following the initial 24 h "hydration" period, we weighed all animals and took blood samples from both "hydrated" and "dehydrated" animals by heart puncture as described previously. Animals were then held for 5–7 d and weighed on alternate days until animals in each group had lost approximately 20% of the body mass measured at the start of dehydration. We then removed a second blood sample and allowed the two groups of animals access to water for 4 h. The change in mass while water was available was assumed to result from drinking.

Blood samples were transferred to 25 $\mu L$ capillary tubes and plasma was separated from whole blood by centrifugation. We sealed capillary tubes with Critiseal or Criticap and refrigerated them. Sodium chloride standards were treated

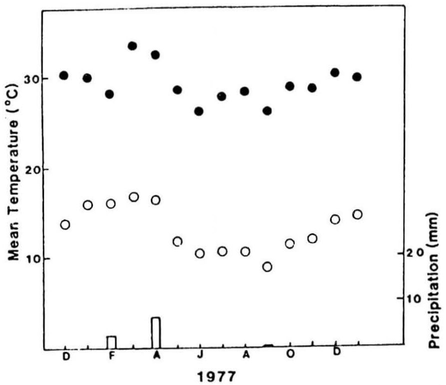

Fig. 1. Daily mean maximum (closed circles) and minimum (open circles) temperature and monthly precipitation (fog and rain) of Gobabeb between Dec. 1976 and Jan. 1978.

in a similar manner to determine changes in concentration with storage.

Quantity of fluid in the bladder for the animals removed from the field was determined gravimetrically (±0.1 mg). We returned animals to the laboratory and quickly dissected them. The bladder was ligated, cut above the ligature, removed and weighed. We removed water by syringe and reweighed the bladder. Bladder fluid was stored in sealed 25 μL capillary tubes and refrigerated.

All plasma and urine samples were air transported to the Laboratory of Biomedical and Environmental Sciences for analyses of osmotic pressure (Wescor 5100) and sodium concentration (flame photometry; Coleman Jr. spectrophotometer).

We regressed daily water fluxes (mL $H_2O$ $d^{-1}$) and field metabolic rate (mL $CO_2$ $h^{-1}$) for the separate sexes against body mass to determine whether allometric relationships were present for these data. Regressions for the individual sexes were then compared using analysis of covariance (Sokal and Rohlf, 1981). If no significant difference between sexes was present, a single regression for the population was calculated.

Two-way ANOVA were used to determine statistical differences among study periods and between sexes for body mass. Paired flux and efflux values were compared statistically with Wilcoxon sign-tests to determine whether lizards were in positive or negative water balance. Least squares linear regression analysis was used for determining the relation between water fluxes and rate of body mass change (data untransformed).

## Results and Discussion

The highest mean maximum temperature was recorded for March and the lowest mean minimum temperature occurred in Sept. (Fig. 1). Measurable quantities of precipitation were collected only in Feb., April and Sept. Mean maximum temperatures for the periods of our field work (summer, 1976–77; late autumn, 1977; summer 1977–78) ranged between 28–31 C with minimum temperatures ranging between 11–16 C.

Body mass differed between sexes ($P < .001$) and also differed among seasons of study ($P < .005$). Both males and females had lower body masses in summer 1977–78 compared to the other periods (Table 1). Body mass change per day was inversely correlated with body mass at first capture (Table 1). Of 10 lizards, which either maintained or gained mass between captures, five occurred in summer 1977–78 (2 ♂, 3 ♀). The proportion of lizards maintaining mass during summer 1977–78 was higher than the other two periods (0.55 vs 0.25 and 0.13).

Body water content did not differ between the sexes when corrected for the difference in body mass. Water efflux was significantly greater than water influx ($P < .001$) in the first summer and autumn but summer 1977–78 lizards were in mass balance ($P > .05$). No difference in the allometric relation for water fluxes or field metabolic rate was observed between sexes ($P > .05$, Table 1).

The regression of water influx against rate of change of body mass (Fig. 2) represents the minimum water requirement for steady-state maintenance of body mass. For our study period, an intake rate of 21.8 μl $H_2O$ $(g.d.)^{-1}$ was necessary in order for *A. anchietae* to maintain mass.

Mass of fluid in the bladder of animals (mean mass 3.958 ± 0.08 g) captured in the field was 113 ± 16.5 mg (n = 7) (no significant correlation with body mass) with a fluid osmotic pressure of 250 ± 38.1 mOsm $kg^{-1}$ and sodium concentration of 52 ± 15.0 mEq $L^{-1}$ (n = 8). Plasma osmotic pressure and sodium concentrations for field animals were 410 ± 4.3 mOsm $kg^{-1}$ and 160 ± 0.9 mEq $L^{-1}$ (n = 12), respectively.

The effect of drinking, then dehydrating, compared with simply dehydrating these lizards is shown in Table 2. Mean mass gain with hydration was 0.384 ± 0.152 g (122.2 ± 3.4% of mass before access to water). We observed no significant change in sodium concentration in hydrated animals after 17.2% of their mass after hydration was lost. However, animals which were dehydrated only (19.8% of initial mass lost) showed an increase of 21 mEq $L^{-1}$ in the plasma sodium concentration, an elevation of 13.2%. At the end of this experiment, the dehydrated-only lizards imbibed twice as much water (159.5 ± 19.1 mg, n = 4) as the initially hydrated group (78.8 ± 2.9 mg, n = 6).

Although our experiments and the previous work of Louw and Holm (1972) show that *A. anchietae* will readily imbibe free water, whether this occurs regularly in the field is questionable.

Table 1. Body Mass and Allometric Regression Equations for Daily Change in Body Mass, Water Influx, Water Efflux and Field Metabolic Rates of *Aporosaura anchietae*. Pooled data for all study periods and both sexes in regressions. Number of measurements in parentheses. $M_i$ = body at time of first capture; M = mean mass during study period.

| | Summer 1976–77 Autumn 1977 | Summer 1977–78 | |
|---|---|---|---|
| Body mass (g) | | | |
| Males | 5.424 ± 0.163 (16) | 4.344 ± 0.235 (4) | $P < .01$ |
| Females | 3.080 ± 0.140 (8) | 2.453 ± 0.042 (5) | $P < .01$ |
| Daily change in body mass (g/day) | BM/d = −0.01$M_i$ + 0.016<br>(F = 7.378, $P < .02$) | (36) | |
| Water influx (mL/d) | Influx = 0.011M + 0.038<br>(F = 4.73, $P < .05$) | (32) | |
| Water efflux (mL/d) | Efflux = 0.014M + 0.042<br>(F = 6.923, $P < .05$) | (32) | |
| Field Metabolic Rate (FMR) (mL $CO_2$/h) | FMR = 0.28M − 0.153<br>(F = 44.134, $P < .001$) | (22) | |

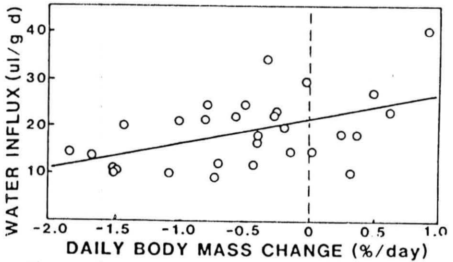

Fig. 2. Least squares linear regression relation between water influx rate (μL $H_2O$/g.d.) and daily body mass change (% body mass change per day). Water influx = 5.341 [% body mass change per day] + 21.78 ($r^2 = 0.261$, $F_{(1,28)} = 9.87$, $P < .005$).

Table 2. Mass Loss and Change in Sodium Concentration of Plasma in Directly-Dehydrated and Initially-Hydrated *Aporosaura anchietae*. Values for sodium are expressed in mEq $L^{-1}$ for initial ($Na_i$) and final ($Na_f$) samples. Expected and observed change between initial and final concentrations are also shown with expected values calculated from the equation of Shoemaker (1964) using the amount of water lost. $\bar{x}$ ± SE (n).

| Group | Mass (g) | Mass loss water loss (mg/100 g) | $Na_i$ (mEq/L) | $Na_f$ (mEq/L) | % Change Observed | % Change Expected |
|---|---|---|---|---|---|---|
| Initially hydrated | | 17.2 ± 1.9 (6) | 159 ± 3.1 (5) | 165 ± 3.7 (5)* | 4.5 | 29.0 |
| (Before hydration) | 3.939 ± 0.147 (6) | | | | | |
| (After hydration) | 4.730 ± 0.265 (6) | | | | | |
| Dehydrated only | 4.463 ± 0.105 (6) | 19.8 ± 1.3 (6) | 156 ± 2.7 (6) | 177 ± 6.4 (6)** | 13.2 | 38.3 |

* n.s.

** $P < .02$.

TABLE 3. WATER FLUXES FOR FIVE SAND DUNE-DWELLING LIZARDS. Only mean values presented.

| Species | Live body mass (g) | Season | Metabolic water (mL $H_2O$/d) | Total influx (mL $H_2O$/d) | Total eflux mL $H_2O$/d |
|---|---|---|---|---|---|
| Lacertidae | | | | | |
| *Aporosaura anchietae* | 5 | Summer–fall | 0.019 | 0.093 | 0.113 |
| | 3 | | 0.009 | 0.072 | 0.088 |
| *Eremias lugubris*[a] | 3.8 | Spring | 0.020 | 0.285 | 0.231 |
| *E. lineoocellata*[a] | 3.3 | | 0.014 | 0.156 | 0.140 |
| Iguanidae | | | | | |
| *Uma scoparia*[b] | | | | | |
| Adults | 20 | Summer | 0.094 | 0.24 | 0.32 |
| Juveniles | 5 | | 0.033 | 0.12 | 0.135 |
| *Uma notata*[c] | 13.3 | | 0.028 | 0.15 | 0.138 |

* Estimated from laboratory only.

[a] Nagy, K. A. et al., 1984.

[b] Minnich, J. E., and V. A. Shoemaker, 1972.

[c] Deavers, 1972.

During our study, *A. anchietae* were generally in negative water balance, and in 83 h of observation by one of us (MDR) during 28 separate fog events, only three lizards were observed to drink fog water condensed on vegetation. Ordinarily, fog water present had evaporated by the time lizards emerged from under the sand. We believe that fog water drinking is uncommon in the inland dunes and does not significantly contribute to this species' overall water relations.

The negative water balance and weight loss which we observed, although not directly connected to the low level of precipitation (compared to 5 yr period) during our study period, probably resulted from low prey availability. These lizards are omnivorous and tenebrionid beetle larvae form a large component of their diet (Robinson, 1987), and reproduction in Namib tenebrionids has been shown to be limited by water availability (Seely, 1973). *Uma scoporia* were reported to lose weight during the North American summer and this observation also was thought to be associated with low prey availability (Minnich and Shoemaker, 1972). If prey were scarce, then fat metabolism may have been necessary to meet energy requirements during 1976. A relative decrease in fat content was reported for the *A. anchietae* populations in 1977 compared to 1976 (Goldberg and Robinson, 1979), and both males and females had lower masses in summer 1977–78 than earlier in 1977 (Table 1). The lower mass may have favored maintenance of water balance, as smaller animals had lower rates of mass change per day (Table 1) and five of the nine animals measured during this period actually gained mass between captures.

The steady-state water requirement for mass balance for *A. anchietae* during our study was estimated to be 0.109 mL $H_2O$ $d^{-1}$ for males (5 g) and 0.065 mL $H_2O$ $d^{-1}$ for females (3 g). The allometric equation for steady-state water requirements of desert (arid/semi-arid) lizards (Nagy and Peterson, 1988) predicts male *A. anchietae* require 0.136 mL $H_2O$ $day^{-1}$ and females 0.091 mL $H_2O$ $day^{-1}$ to maintain mass balance. Our measurements for *A. anchietae* were only 70–80% of these predicted values and as Nagy (1982a) indicated, steady-state flux for *A. anchietae* is below the allometric prediction for maintaining mass balance as is the flux for *Uma notata* (Deavers, 1972).

We also compared water fluxes for male and female *A. anchietae,* two species of *Eremias* (Lacertidae) from the Kalahari Desert (Nagy et al., 1984), and the two North American sand dune-dwelling iguanids, *Uma scoparia* (Minnich and Shoemaker, 1972) and *U. notata notata* (Deavers, 1972) (Table 3). Kalahari lacertids were in positive water balance during the spring (Nagy et al., 1984) and water fluxes are 1.5–2× that of *A. anchietae.* Juvenile *U. scoparia* (5 g) have fluxes very similar in magnitude to male *A. anchietae,* with metabolic water production a greater proportion of total influx. Field metabolic rates of *A. anchietae* were close to rates predicted by Nagy's (1982b) allometric equation as were the field metabolic rates of *E. lugubris* and *E. lineoocellata* (Nagy et al., 1984). The different seasons of measurement and food availability probably are the factors which separate the water budgets of these lacertids.

The bladder studies suggest that *A. anchietae* might use the bladder as a storage site for water similar to juvenile *Sceloporus jarrovi* (Beuchat et al., 1986). The change in plasma sodium between the hydrated and dehydrated treatments is similar to that reported between toads having a full bladder compared with toads having an empty bladder (Shoemaker, 1964). The proportion of fluid in the bladder of *A. anchietae* is lower than that measured for *S. jarrovi* (3 vs 13% of total body mass, respectively) and the osmotic pressure of the urine in the bladder of *A. anchietae* is much higher than that reported for *S. jarrovi* (36 mOsm $kg^{-1}$ for the latter). This may indicate that the animals we collected had been resorbing fluid; Louw and Holm (1972) reported that plasma osmotic pressures of lizards caught in the field were 312 mOsm $kg^{-1}$, while we measured plasma osmotic pressures 100 mOsm $kg^{-1}$ greater for lizards under similar conditions (410 mOsm $kg^{-1}$). The high value we obtained was identical to plasma osmotic pressures recorded after lizards had been dehydrated three weeks in the laboratory (Louw and Holm, 1972). This supports the suggestion from the flux data that free-ranging lizards were partially dehydrated during summer 1976–77 and thus may have resorbed fluid stored in the bladder.

The volumes of fluid imbibed by the lizards at the conclusion of the dehydration study also suggests that the elevated sodium concentration in the plasma resulted from a loss in extracellular fluid. The greater volume imbibed by animals only dehydrated compared with lizards that were allowed to drink before the dehydration began indicates that the former were probably replacing tissue and/or extracellular water to a greater extent than animals which were capable of resorbing bladder fluid. Whether the difference between the quantities which the lizards drank was an actual indication of the difference in level of tissue dehydration is unknown.

Our work does not conclusively show that the bladder is used by *A. anchietae* as a water storage site, but the data are consistent with this hypothesis. In fact, the small volume in the bladder of field animals (113 mg $H_2O$), which would be adequate for only about 1–2 d of mass loss, makes the ecological importance of the bladder questionable during our study period. Full bladders were observed in lizards after drinking (Louw and Holm, 1972) and one of us (MDR) observed bladders containing 200–300 mg $H_2O$ in individuals fed tenebrionid beetle larvae in the laboratory. This suggests that animals maintain water in the bladder during periods of water abundance. Possibly during periods of water stress, lizards may restrict activity and thus reduce evaporative water loss and this allows these lizards to survive for longer periods solely on metabolic water production and the fluid in the bladder.

*Aporosaura anchietae* may also have a nasal salt gland as we observed an encrustation on the nares during laboratory feeding studies. Further studies should examine the relationship between fluid and salt regulation in these lizards, because it is possible that both fluid resorption in a bladder and salt gland secretion occur to maintain water and salt concentrations in tissues and extracellular fluid.

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# A Comparison of the Foraging Behavior of Two Darter (*Etheostoma*) Species

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**Rainbow darters (*Etheostoma caeruleum*) and orangethroat darters (*E. spectabile*) commonly occur in pools and riffles of Ozark streams, occupying similar microhabitats and consuming similar diets. The purpose of this study was to describe and compare the foraging behavior of these two species in pool and riffle habitats in a small Ozark stream. We used 10 min focal animal observations to describe the feeding behavior of these fishes. Both species exhibited a roving search pattern, making frequent short moves and turns across the stream substrate and using head and eye movements to locate prey. Search patterns were not distinguishable between species, although some *E. caeruleum* were much more active than all *E. spectabile* and the other *E. caeruleum*. Each species used two types of quick strikes to capture prey and occasionally spit or coughed sediments or detritus out of their mouth after a capture attempt. Both species foraged more actively in pools, moving a greater distance and making more moves and turns than in riffles. Slower current velocities, finer substrates and lower prey densities in pools may have favored this more active searching pattern in pools. Although a high degree of between-fish variation must be expected in conducting in-stream observations, they can be useful in detecting subtle but potentially significant responses to habitat differences by these species.**

FORAGING has a fundamental role in regulating the dynamics of aquatic communities. Fish alter the structure of prey populations through predation (Carpenter et al., 1987; O'Brien, 1979; Murdoch et al., 1975) and competition with other predators (Werner and Hall, 1979; Magnan and FitzGerald, 1984). Fish also alter their foraging patterns in response to habitat characteristics (Werner et al., 1983a; Mittelbach, 1988). Understanding the factors which affect fish foraging behavior has expanded our understanding of the mechanisms that affect the distribution and abundance of fishes and their prey. Particularly instructive is the way in which some species alter their foraging behavior in response to various environmental stimuli. The behavioral plasticity of fishes may have adaptive significance due to the spatial and temporal variability of aquatic environments (Dill, 1983).

Individual variation in foraging tactics has been documented for several fish species and can be attributed to behavioral, morphological and physiological sources (Ringler, 1983). Environmental features, including both biotic and abiotic factors, also contribute indirectly to variation in feeding behavior. Biotic factors which cause shifts in foraging behavior include changes in prey abundance (Ringler, 1979; Gardner, 1981; Bartell, 1982), prey size (Werner and Hall, 1974), prey type (Brawn, 1969; Ringler, 1979), interspecific competition (Werner and Hall, 1979; Magnan and FitzGerald, 1984), and predation risk (Werner et al., 1983b; Schmitt and Holbrook, 1985).

Several investigators have documented the influence of abiotic factors on fish feeding habits. Turbidity affects reactive distances (Vinyard and O'Brien, 1976; Berg and Northcote, 1985) and feeding rates (Gardner, 1981; Breitburg, 1988). Cover may reduce the efficiency of foraging cutthroat trout (*Salmo clarki*) by hindering their ability to capture food items (Wilzbach and Hall, 1985). Schlosser and Toth (1984) showed that although two darter species have similar diets, their mechanisms of finding prey differ in response to the structure of stream sediments. Aside from these examples, few studies have documented the effects of abiotic factors or human alterations of these factors on fish foraging behavior. In light of increased concern regarding the loss or degradation of fish habitats, this topic deserves more attention.

We initiated this study to describe and compare the foraging behavior of rainbow darters (*Etheostoma caeruleum*) and orangethroat darters (*E. spectabile*), and to determine the effect of habitat characteristics on the foraging behavior