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Seasonal Food Habits of the Coyote in the South Carolina Coastal Plain

Joshua D. Schrecengost[1,*], John C. Kilgo[2], David Mallard[3], H. Scott Ray[4], and Karl V. Miller[5]

Abstract - Spatial and temporal plasticity in *Canis latrans* (coyote) diets require regional studies to understand the ecological role of this omnivorous canid. Because coyotes have recently become established in South Carolina, we investigated their food habits by collecting 415 coyote scats on the Savannah River Site in western South Carolina from May 2005–July 2006. Seasonally available soft mast was the most common food item in 12 of the 15 months we sampled. *Odocoileus virginianus* (white-tailed deer) was the most common food item during December (40%) and March (37%). During May–June, fruits of *Prunus* spp. and *Rubus* spp. were the most commonly occurring food items. Fawns were the most common mammalian food item during May and June of both years despite low deer density.

Introduction

Canis latrans Say (coyote) is historically associated with western North America. However, during the last 50 years, they have expanded their range into the southeastern US, aided by humans and anthropogenic changes in the landscape (Hill et al. 1987). Coyote food habits have been explored in detail throughout much of their historical range (Andelt et al. 1987, Bekoff 1977, Murie 1945). However, because coyotes exhibit temporal and spatial variability in food item use (Bekoff 1977, Cypher et al. 1994), the findings of these studies have limited value in the Southeast. Coyote food habits have been documented in several areas of the Southeast (Blanton and Hill 1989, Gipson 1974, Hall 1979, Hoerath 1990, Lee 1986, Michaelson 1975, Smith and Kennedy 1983, Thornton et al. 2004, Wagner 1993, Wilson 1967, Wooding 1984), but no published record exists for South Carolina or adjacent states. Although there is considerable overlap in the types of food items documented in these studies, the importance of particular food items in the coyote diet differs geographically among study areas and temporally among seasons, probably due to changes in food-item availability. Coyote food habits can also be affected by changes in land-use practices (Gipson and Sealander 1976) and successional changes in vegetation (Andelt et al. 1987).

The effect of coyote predation on game-animal populations has been of interest for decades. In the Southeast, only two studies have focused on specific game animals. Wagner (1993) studied coyote diet during the *Meleagris gal-*

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[1] Georgia Department of Natural Resources, Wildlife Resources Division, 1401 Dean Street, Suite I, Rome, GA 30161. [2] USDA Forest Service Southern Research Station, PO Box 700, New Ellenton, SC 29809. [3] Building 5884, First Division Road, Fort Benning, GA 31905. [4] USDA Forest Service-Savannah River, PO Box 700 New Ellenton, SC 29809. [5] D.B. Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602. [*] Corresponding author - josh_schrecengost@dnr.state.ga.us.

lopavo Linnaeus (Wild Turkey) reproductive season in Arkansas, Mississippi, Alabama, and Florida, and reported Wild Turkey occurred in <2% of scats collected. Blanton and Hill (1989) compared diets of coyotes in areas of high and low *Odocoileus virginianus* Zimmerman (white-tailed deer) densities during the fawning period in Alabama, Kentucky, Mississippi, and Tennessee. Occurrence of deer in coyote scats and stomachs ranged from 9% in low-density areas to 74% in high-density areas during the fawning period. This wide variation in occurrence is consistent with the findings of other southeastern studies. Michaelson (1975) and Wilson (1967) both reported annual deer occurrences <5%, whereas Wooding (1984) reported deer occurrences of 71% during August.

Variability in food habits, even among similar habitats, limits the use of prior studies in determining site-specific ecological impact of coyotes. Detailed data describing coyote use of intensely managed populations such as white-tailed deer are of particular interest. Therefore, our objectives were to determine the breadth of coyote food habits and identify seasonal trends in the coyote diet on the Savannah River Site in South Carolina.

Study Area

Our research was conducted on the 80,000-ha Savannah River Site (SRS) in Aiken, Barnwell, and Allendale counties, SC. The SRS is a US Department of Energy National Environmental Research Park located in the Upper Coastal Plain physiographic province along the Savannah River (Imm and McLeod 2005). General public access to the SRS is heavily restricted. Coyotes were first reported on the SRS in 1986, and since that time, the population has expanded dramatically (Mayer et al. 2005), and coyotes are now observed frequently. Topography of the SRS is gently rolling to flat, and elevation ranges from 20–130 m. Once used for agriculture, SRS is now predominately forested (97%). *Pinus palustris* Miller (longleaf pine) and *Pinus taeda* Linnaeus (loblolly pine) dominate the overstory canopy (68%). Other major vegetative types include swamps and bottomland hardwood (22%) and upland hardwood (7%) forests (Imm and McLeod 2005). Approximately 12% of the total forest stands are <10 years of age (Blake and Bonar 2005). The SRS is intersected by over 2600 km of roads, logging trails, and railroads (Blake et al. 2005).

The white-tailed deer population on the SRS is managed to limit deer-vehicle collisions and deer impact on the environment. Controlled dog hunting is used to maintain a pre-hunt target population of 4000 deer (Johns and Kilgo 2005). Currently, deer population density is estimated at 1 per 26 to 29 ha (H.S. Ray and J.C. Kilgo, unpubl. data). Hunts during the course of this study occurred October through December 2005. In recent years, data collected from the hunts on SRS show a dramatic decline in harvest of fawns and yearlings despite no changes in hunt methodology (H.S. Ray, unpubl. data). This suggests that white-tailed deer recruitment is declining at SRS, coincident with increasing coyote abundance.

The *Sus scrofa* Linnaeus (wild hog) population on SRS was estimated at 900 animals in 2003 (Mayer 2005). Wild hogs are hunted and trapped year round to minimize impact on the environment and vehicle collisions. From May 2005 through June 2006, 172 hogs were killed on SRS. Most wild hog carcasses are disposed of on site, which provides an incidental source of carrion for coyotes.

Methods

We collected coyote scats opportunistically along roads and rights-of-way throughout SRS from May 2005 through July 2006. Especially large or small scats were not collected to avoid inclusion of scats of *Canis familiaris* Linnaeus (domestic dog) and *Urocyon cinereoargenteus* Schreber (gray fox). Scats were subjectively evaluated in the field for relative moisture content and decomposition in an attempt to collect samples <5 days old. Scats were placed in plastic bags labeled with date and location of collection and stored frozen to minimize decomposition. For analysis, scats were oven dried at 65 °C for 72–96 hours, and food items were separated manually. We identified food items macroscopically from hair, tooth, claw, and hoof fragments, as well as plant residues. Dorsal guard hairs were identified microscopically when necessary using the pigment patterns of the medulla (Moore et al. 1974) and compared to reference slides prepared from the University of Georgia Warnell School of Forestry and Natural Resources mammalian collection. White-tailed deer fawn remains were separated from adult deer remains whenever possible by the physical characteristics of the hairs as well as the presence of small hooves. In cases of uncertain age class, the deer remains were included as adult. Plant residues, primarily seeds, were compared to reference manuals and collections of known specimens housed at the Warnell School of Forestry and Natural Resources. We recorded the occurrence as well as a visual estimate of percentage volume for each food item in each scat.

Previous studies have used several terms interchangeably to describe the occurrence of food items in the diet of coyotes (Wagner 1993). We chose to define "percent of scats" as the percent of a sample of scats in which a food item occurs (Table 1), and "percent of occurrence" as the number of times a food item occurs as a percent of total number of occurrences for all food items (Kelly 1991, Wagner 1993). Percent of occurrence data is presented for all food items (Fig. 1), all vegetative food items (Fig. 2), and all mammalian food items (Fig. 3). We grouped some food items due to difficulties in differentiating among species and combined items occurring at low frequencies into an "other" category.

Results

We analyzed 415 scats to evaluate coyote food habits between May 2005 and July 2006 (Table 1). No single food item occurred in all 15 months sampled. White-tailed deer, lagomorphs, and insects, primarily Orthoptera, occurred in 14 months each, and small mammals occurred in 13 months (Table 1). A single food item made up greater than 90% of the scat volume in 227 (54.7%) of the samples we collected.

The coyote diet was dominated by plant matter from May 2005 through November 2005 as well as from June through July 2006 (Fig. 1). The occurrence of individual plant food items consumed varied with expected availability based on known fruiting times of these species (Fig. 2). *Prunus* spp. Linnaeus (wild

Table 1. Percent of scats containing common coyote food items at the Savannah River Site, SC by month from May 2005 through July 2006.

	2005^A								2006^A						
Food item	May (13)	June (53)	July (22)	Aug (51)	Sept (32)	Oct (26)	Nov (26)	Dec (25)	Jan (18)	Feb (27)	Mar (30)	Apr (13)	May (39)	June (31)	July (9)
Plants															
Arachis hypogaea						4			17	4	3	8	3		
Carya spp. (nuts)							8	4		15	13		3		
Crataegus spp.				25	13	15	4	8	6						
Diospyros virginiana				18	78	81	31	8							
Phytolacca americana			5	51	59	77	62	36	17	4	3				
Poaceae (leaves)				4	6		4				3	8	3	10	
Prunus serotina		4	59	10					6	4					22
Prunus spp.	85	43	9	6									54	52	33
Quercus spp. (acorns)							4	8	11		7				
Rubus spp.	23	64	27	2								8	26	58	89
Vaccinium spp.			18	37		4		4	6						
Vitis spp.				30	25	12									
Other^B			5	6		4	8								
Animals															
Aves		2		2		4	4		6	4	10		18	6	11
Castor canadensis				2					6		3				11
Dasypus novemcinctus			5	4				4		4		8	5		
Neotoma floridana		2							11		3	23	5		
Odocoileus virginianus (adult)	15	8	14	6	3		15	40	11	23	37	15	5	10	11
Odocoileus virginianus (fawn)	31	15	18	2									38	23	
Orthoptera	8	21	27	31	31	31	12	8	11		3	31	31	32	44
Procyon lotor				6	3		4			4	7	8	3		
Sciurus spp.	15	3		6	3	4	4	8	6	4	10	8			
Small mammal	8	8	5	10	9	4	8		11	15	10	23	3	10	
Sus scrofa		11	14	10		4		4	6	31	10	8	8	3	
Sylvilagus spp.	8	6	9	6	16	4	4	12	11	31	17	8	5	3	
Other^C					3		8	8	6	4	7		8		

^{A}Numbers in parentheses are sample sizes. ^{B}Includes *Ilex decidua*, *Ostrya virginiana*, *Passiflora incarnata*, and *Pyrus* sp. ^{C}Includes *Canis latrans*, *Didelphis virginiana*, *Lynx rufus*, *Ondatra zibethicus*, *Urocyon cinereoargenteus*, and egg fragments.

plums) occurred in 85% of scats in May 2005 and 54% of scats in May 2006. *Rubus* spp. Linnaeus (blackberries) occurred in 64% of scats in June 2005, 27% of scats in July 2005, 58% of scats in June 2006, and 89% of scats in July 2006. *Prunus serotina* Ehrhart (black cherry) occurred in 59% of scats during July 2005. *Phytolacca americana* Linnaeus (pokeberry) occurred in 51% of scats during August 2005 and 62% of scats during November 2005. *Diospyros virginiana* Linnaeus (persimmon) occurred in 78% of scats during September 2005 and 81% of scats during October 2005.

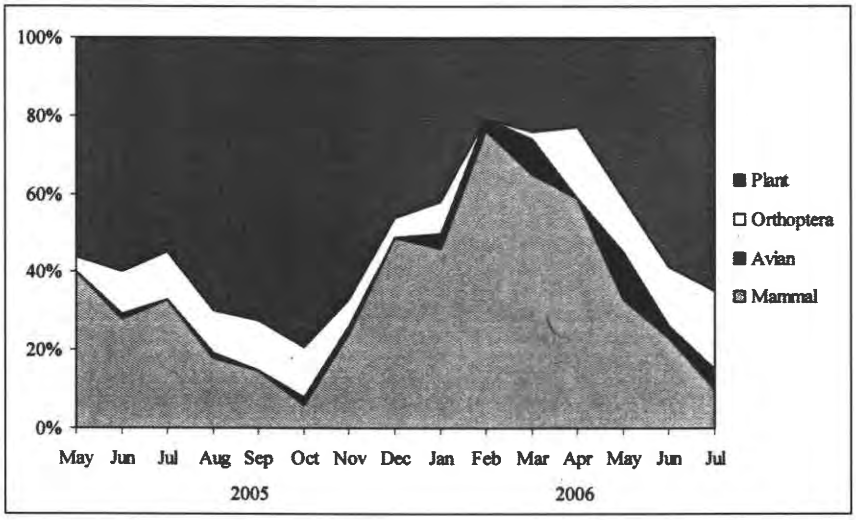

Figure 1. Monthly percent of occurrence for 4 major groups of food items in coyote scats collected on the Savannah River Site, SC, May 2005 through July 2006.

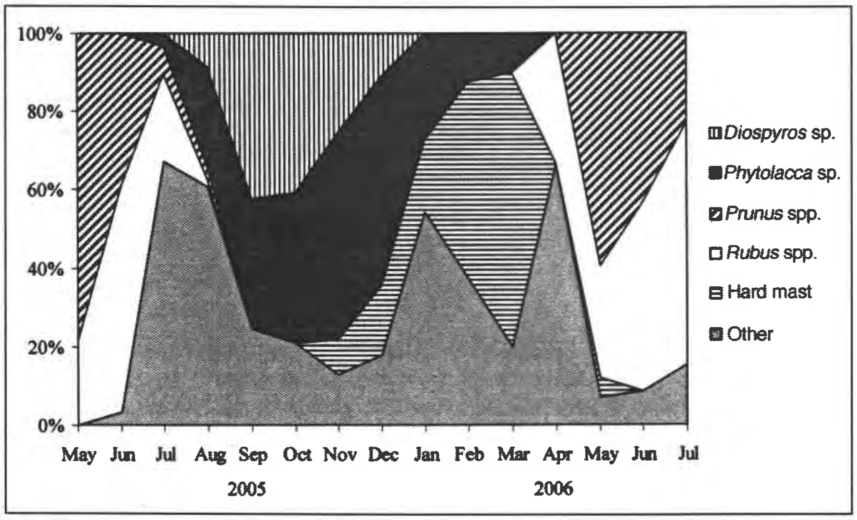

Figure 2. Monthly percent of occurrence for major vegetative food items in coyote scats collected on the Savannah River Site, SC, May 2005 through July 2006.

During December through April, the coyote diet was dominated by animal food items (Fig. 1), although percent occurrence of individual mammalian food items varied throughout the year (Fig. 3). White-tailed deer occurred in 40% of scats during December and 37% of scats during March. Conception dates of white-tailed deer at SRS (Rhodes et al. 1991) plus a 200-day gestation period (Haugen 1959, Verme 1965) place parturition primarily in the months of May and June. During 2005, white-tailed deer fawns were present in scat collected in May (31%), June (15%), July (18%), and August (2%). During 2006, fawns were present in scat collected in May (38%) and June (23%). Wild hogs and *Sylvilagus* spp. (rabbits) each occurred in 31% of scats during February. Orthoptera occurred in 31% of scats during April (Table 1).

Discussion

From spring through late fall, coyotes at SRS fed heavily on soft mast when it was available. However, from December through March, when vegetative food items were less abundant, coyotes relied heavily on mammalian food items. Small- and medium-sized mammals may also be more vulnerable at this time of year due to a decrease in herbaceous cover. Orthopterans, primarily grasshoppers, were common in scats throughout the year, but they rarely comprised a significant portion of the volume of the scats. Similarly, birds were consumed throughout the year, but at a relatively low percent of occurrence. Greatest bird consumption occurred during May 2006 (18%). Although this timing was likely coincidental with avian nesting activity and egg shell fragments were observed in scat, low occurrence during 2005 suggests large annual fluctuations in bird consumption.

Small mammals and lagomorphs appear to be less important in the diets of coyotes at the SRS than elsewhere. Other studies have reported high

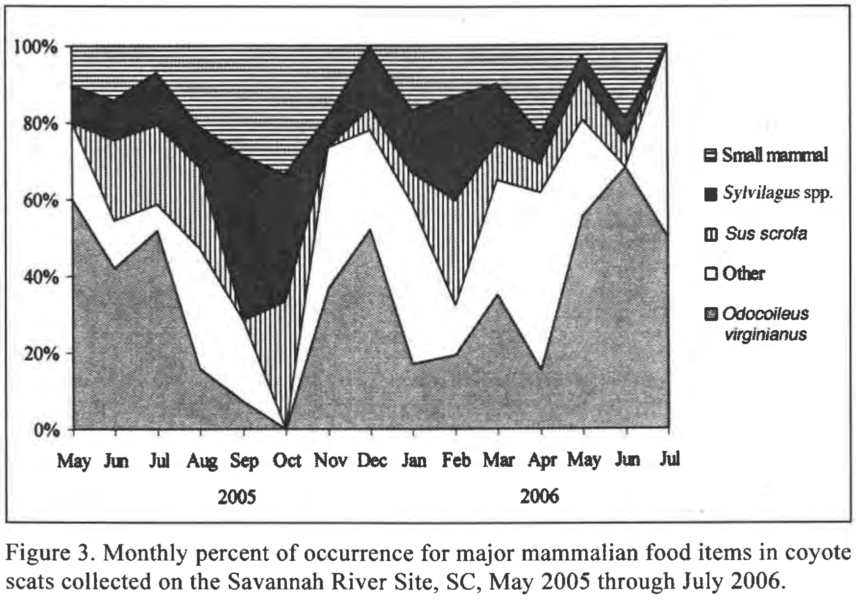

Figure 3. Monthly percent of occurrence for major mammalian food items in coyote scats collected on the Savannah River Site, SC, May 2005 through July 2006.

occurrences of lagomorphs (Bartel and Knowlton 2005, Thornton et al. 2004) and small mammals (Bartel and Knowlton 2005, Hall 1979, Smith and Kennedy 1983) in coyote diets. For example, Blanton and Hill (1989) reported 36.5% frequency of occurrence of *Sylvilagus* spp. in 523 coyote scats and 9 coyote stomachs collected during summer in Mississippi, Alabama, Kentucky, and Tennessee. Bowyer et al. (1983) reported 28.2% annual frequency of occurrence for Rodentia in coyote scats in California. In Louisiana, Wilson (1967) found rodent remains occurring in 75% of coyote stomachs during spring and fall and lagomorph remains occurring in 80% of coyote stomachs during summer. Although both of these groups were present in the diet of coyotes at SRS throughout most of the year, their importance was limited compared to other food items, and occurrence was greatest during winter and early spring (Table 1). Specifically, the highest occurrence of small mammals in coyote scats on SRS occurred during April 2006 (23%), and the highest occurrence of lagomorphs occurred during February 2006 (31%). Although these peak values approach the annual or seasonal occurrences reported in other studies, they were limited to single months. Neither group occurred in >17% of scats collected during any other months (Table 1). Our data does suggest that lagomorphs and small mammals were important relative to other mammalian food items during September and October of 2005 (Fig. 3). However, during this time, the coyote diet was dominated by vegetative food items, and mammalian food items made up <15% of the food items consumed (Fig. 1).

Occurrence of wild hog in scats was greatest during February (31%), corresponding with the peak of hog control (January through March), during which 69 hog carcasses were disposed of on SRS. Similarly, Wagner (1993) found hog remains in 17–25% of scats in Bolivar County, MS and reported peak occurrence coincident with the peak in sport hunting of hogs. Hog remains in scats occasionally contained small hooves, suggesting predation on piglets, but most hog occurrence in scats consisted of the large, coarse hairs of adult hogs. Coyotes undoubtedly scavenge adult hog carrion, but we are aware of no published reports of coyote predation on adult hogs. Nevertheless, we cannot eliminate the possibility of predation on adult hogs, particularly given the somewhat atypical use of other food items by SRS coyotes.

Fruit use by coyotes has been documented by numerous studies (Andelt et al. 1987, Blanton and Hill 1989, Murie 1951, Thornton et al. 2004, Wooding 1984). However, the timing of fruit availability and species use is variable. Wooding (1984) reported persimmons in 67% of scats and stomachs during fall in Mississippi and Alabama, similar to the findings of this study during September through November (31–81%). Blackberry and pokeberry have also been reported at significant levels in several southeastern states (Blanton 1988). However, high occurrence of wild plums in the diet of coyotes has not been previously reported. During the months of May and June, wild plum occurred in 43–85% of the coyote scats collected on the SRS during 2005 and 2006. The differences in occurrence of soft mast within the same region further emphasize the need for locally specific coyote food-habit studies.

White-tailed deer were consumed in every month except October. Road-killed deer carcasses are available to coyotes in limited quantities throughout the year. During 2005, 72 road-killed deer were recovered along the SRS roadways (P.E. Johns, Savannah River Ecology Laboratory, Aiken, SC, unpubl. data) and most were disposed of in wooded areas on site. This explains a portion of the deer remains encountered in coyote scats because we often observed scavenging by coyotes at monitored carcasses. The absence of white-tailed deer in October is coincident with the increase in seasonal soft mast consumption as persimmon and pokeberry fruits became available. Increased use of white-tailed deer during November and December corresponded with the timing of controlled hunts on SRS. Apparently coyotes consumed deer crippled or un-recovered during hunts. We believe it is unlikely that hunting pressure made deer more susceptible to predation. D'Angelo et al. (2003) found that female white-tailed deer on SRS resumed normal movement patterns within 13 hours after hunt-associated disturbances, suggesting that risk of coyote predation likely would not be greatly increased by hunting activity.

White-tailed deer remains also occurred in a large proportion of scats during March 2006 (Table 1). Increased coyote use of deer during late winter has been associated with increased deer vulnerability due to winter severity and deep snows (Patterson et al. 1998). However, winters are mild in South Carolina. Deer-vehicle collision data from the SRS suggests there was no significant increase in availability of deer carrion at this time. Although coyotes may have been killing adult deer, it is more likely that coyotes were returning more often and from greater distances to the available carrion and consuming even portions of the deer hides, and thus hair. This explanation could account for the increased occurrence of deer remains in scats during March.

White-tailed deer fawns were an important component of the diet, occurring in 15–38% of scats during May through July, coincident with the timing of parturition and fawn rearing. During this time, fawns comprised the largest proportion of mammalian food items encountered, although blackberries and wild plums were the most frequently encountered items in scats overall (Table 1). Similarly, Blanton and Hill (1989) reported 31% average occurrence of deer in the summer coyote diet across seven southeastern study areas. Data from Mississippi and Alabama (Wooding 1984) and from Louisiana (Hall 1979) are comparable. Blanton and Hill (1989) observed a decreased use in other food items as fawns became available in areas of high deer density, suggesting that coyotes may select fawns over less profitable food items. Blanton and Hill (1989) used an annual deer-harvest density of 1 per 48 ha or greater to define high-density populations. Deer-harvest density on the SRS was 1 per 372 ha during 2005. On SRS, fawns may be more profitable than alternative food sources despite low deer density (estimated deer density of 1 per 26 to 29 ha). Together with the high occurrence of fawn remains in coyote scats reported herein, several lines of evidence suggest the possibility that coyotes may be impacting deer recruitment at the SRS. These include high coyote-induced mortality among radio-collared fawns during a 2006–2007 study, a 54% decline in the proportion of fawns/doe in the harvest between the periods 1965–1993 and 1997–2006, and a 45% decline in an annual spotlight index from 1991–2007 (J.C. Kilgo and H.S. Ray, unpubl. data). In addition, the increased use of mammalian food items when soft mast availability is limited, suggests that a spring soft-mast failure could result in increased predation of white-tailed deer fawns (Andelt et al. 1987). Our data presents further evidence in support of this theory because increases in mammalian food-item use were correlated with decreases in seasonal soft-mast availability. Additional research is warranted to better understand the potential impacts of the recently established coyote on white-tailed deer and other species in southeastern ecosystems.

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Hydraulic integration and shrub growth form linked across continental aridity gradients

H. Jochen Schenk*[†], Susana Espino*, Christine M. Goedhart*[‡], Marisa Nordenstahl[§¶], Hugo I. Martinez Cabrera[‖], and Cynthia S. Jones[‖]

*Department of Biological Science, California State University, Fullerton, CA 92834-6850; [§]Facultad de Agronomía, Universidad de Buenos Aires, C1417DSE Buenos Aires, Argentina; and [‖]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043

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Both engineered hydraulic systems and plant hydraulic systems are protected against failure by resistance, reparability, and redundancy. A basic rule of reliability engineering is that the level of independent redundancy should increase with increasing risk of fatal system failure. Here we show that hydraulic systems of plants function as predicted by this engineering rule. Hydraulic systems of shrubs sampled along two transcontinental aridity gradients changed with increasing aridity from highly integrated to independently redundant modular designs. Shrubs in humid environments tend to be hydraulically integrated, with single, round basal stems, whereas dryland shrubs typically have modular hydraulic systems and multiple, segmented basal stems. Modularity is achieved anatomically at the vessel-network scale or developmentally at the whole-plant scale through asymmetric secondary growth, which results in a semiclonal or clonal shrub growth form that appears to be ubiquitous in global deserts.

plant hydraulic systems | wood anatomy | hydraulic redundancy | xylem structure and function

In engineering terms, the hydraulic system of a plant is a negative-pressure flow system. This type of hydraulic system, whether natural or man-made, is prone to fail when air bubbles (emboli) are introduced, because under strong negative pressure a single embolism can lead to breakage of the water column unless the air bubble is isolated in a branch or pipe. Both drought and freezing can cause embolisms in plants (1).

Drought-induced embolisms form under negative pressure, when air is pulled into a water-filled conduit from adjacent air-filled spaces or cells, a process known as "air seeding." This common, even daily, event (2–4) can lead to complete failure of the hydraulic system if runaway embolism occurs (5). Two of the three attributes by which plants' negative-pressure flow systems can be protected against failure, resistance and reparability, have been subjects of active research during the last decade (2–4, 6–10). The third attribute, redundancy, has received much less attention as an important drought adaptation but is emerging as a focus of research (11–14). Attributes of redundancy in hydraulic systems of vessel-bearing angiosperms include the numbers of vessels (14), the vessel network topology (12), the number and sizes of pits between adjacent vessels (13, 15, 16), and the division of whole plants into independent hydraulic units (17).

A basic rule of reliability engineering states that the level of independent redundancy should increase with increasing risk of fatal system failure (18); hydraulic engineers routinely increase the safety of man-made pressure-flow systems by designing them to be redundant (19). Redundancy in hydraulic systems (Fig. 1) can vary from a high degree of inter-connectedness (i.e., integrated redundancy) to complete, independent compartmentation (i.e., modular redundancy). In a negative-pressure flow system, integrated redundancy allows alternate water transport pathways around blockages of individual conduits (caused by pathogens or tyloses in plants), while leaving the system vulnerable to runaway embolisms. Only modular redundancy can restrict embolisms to a single conduit or group of conduits; therefore modular redundancy may be expected to be a common trait in plants that face increased risk of hydraulic failure caused by drought (11).

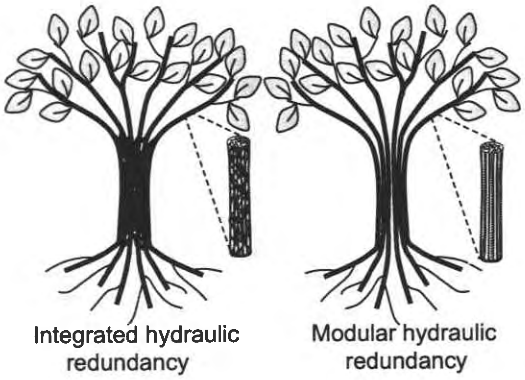

Fig. 1. Integrated and modular hydraulic systems in plants at the level of whole plants and individual stems. Dark lines illustrate pathways of water transport.

Division of plant hydraulic systems into independent hydraulic modules has been reported for a number of shrub species in which asymmetric secondary growth resulting from unequal cambial activity leads to deep segmentation of stems, causing a functional division of the water-conducting sapwood into independent hydraulic modules (17, 20). In some species, stems remain physically connected by nonconducting heartwood (21); others split axially along woody stems and roots into physically separate plants (Fig. 2) (17, 22, 23). Many dominant shrub genera in the world's deserts, *Artemisia*, *Ambrosia*, *Larrea*, and *Salsola*, have this growth form (17). Modular hydraulic redundancy also can be conferred anatomically by reduced vessel contact or lack of intervessel pitting (11, 24) and by isolation of vessels or vessel groups in a fiber matrix (25). Water-filled libriform fibers and fiber tracheids can conduct water (26), but their conductivity is likely to be extremely low and is likely to be zero if they are filled with gas, as has been shown to occur in several tree species (27–29). Anatomical traits that reduce lateral water flow among neighboring vessels or groups of vessels reduce the ratio of tangential and/or radial to axial water flow (11, 24, 30) and result in sectorial patterns of water ascent (31).

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[†]To whom correspondence should be addressed. E-mail: jschenk@fullerton.edu.

[‡]Present address: Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92697-2525.

[¶]Present address: Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia.

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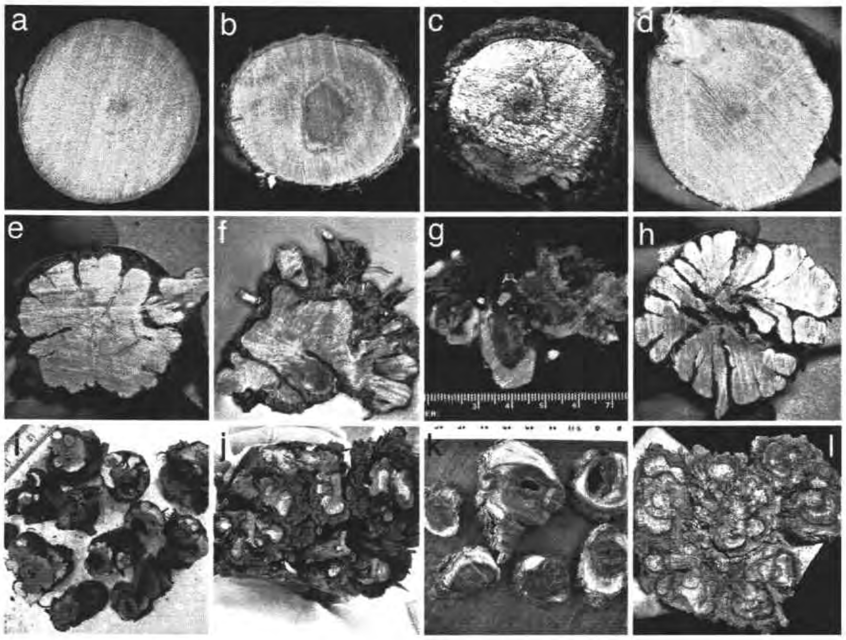

Fig. 2. Representative examples of basal stem shapes for 12 shrub species from North and South America. Stem segmentation indices $S = perimeter\sqrt{\pi}/(\sqrt{area2\pi})$ are listed in parentheses. (*a*) *Rhus glabra* (1.07), Whitehall. (*b*) *Ilex mucronata* (1.10), Coweeta. (*c*) *Baccharis spicata* (1.11), El Palmar. (*d*) *Vaccinium arboretum* (1.14), Whitehall. (*e*) *Salvia mellifera* (2.30), Tucker. (*f*) *Lippia turbinata* (1.42), Cruz de Piedra. (*g*) *Dalea formosa* (2.66), Copper Breaks. (*h*) *Eriogonum fasciculatum* (2.84), Tucker. (*i*) *Junellia aspera* (4.70), La Tranca. (*j*) *Ambrosia dumosa* (4.39), Desert Center. (*k*) *Larrea divaricata* (3.81), Talacasto. (*l*) *Hymenoclea salsola* (4.44), Desert Center.

To quantify the extent of hydraulic integration and its relation to growth form and morphological modularity, we studied 75 dicot shrub species along two transcontinental aridity gradients between 31° and 35° latitude in North America and South America [Table 1 and supporting information (SI) Table S1]. We characterized hydraulic integration by the degree of basal stem segmentation and the lateral spread of dye tracer in basal stems and related both to measures of growth form and wood traits.

Results and Discussion

The degree of basal stem segmentation (S) decreased with increasing mean annual precipitation (MAP) (Fig. 3*a*; Table 2), which in turn was correlated linearly with aridity (the aridity index equals MAP divided by the mean annual potential evapotranspiration; $n = 10$; $r^2 = 0.984$; $P < .0001$). The slope of the relationship between S and MAP was significantly steeper for the North American than for the South American transect (Fig. 3*a*). Stem segmentation was not strongly related to canopy volume ($n = 138$; $r^2 = 0.167$; $P = .051$) but decreased exponentially with increasing canopy height-to-width ratio ($n = 138$; $r^2 = -0.638$; $P < .0001$) and was negatively related to canopy height ($n = 138$; $r^2 = -0.308$; $P < .001$) and the height of the lowest branch above ground ($n = 90$; Wilcoxon Signed Rank Statistic $Z = -2.517$; $P = .012$). The relationship between S and MAP was significant even when MAP, shrub height, and their interaction were included as additional variables in a general linear model to account for the effects of water availability and the biomechanical requirements of taller stems ($r^2 = 0.2809$; effects: MAP, $P = .0019$; shrub height, $P = .0135$; MAP × shrub height, $P = .0399$). Of all shrub species sampled in arid to semiarid environments, 46% had completely split axes (Fig. 2) and therefore consisted of several separate physiological indi-

Table 1. Field sites in North America (United States) and South America (Argentina)

Location	Coordinates	MAP	PET	AI	Seas.	Vegetation
North America						
Desert Center, CA	33°44′ N 115°30′ W	100	1,585	0.06	W	Desert scrub
Tucker WS, CA	33°43′ N 117°37′ W	325	1,143	0.28	W	Sage scrub
Copper Breaks StP, TX	34°06′ N 99°45′ W	660	1,450	0.46	SP	Mesquite savanna
Union, SC	34°39′ N 81°57′ W	1,220	979	1.25	N	Pine forest
Whitehall EF, GA	33°57′ N 83°22′ W	1,250	1,018	1.23	N	Hardwood forest
Coweeta LTER, NC	35°03′ N 83°25′ W	1,850	900	2.06	N	Hardwood forest
South America						
Talacasto, San Juan	31°13′ S 68°39′ W	90	1,082	0.08	S	Desert scrub
La Tranca, San Luis	32°22′ S 67°10′ W	250	1,141	0.22	S	Desert scrub
Cruz de Piedra, San Luis	33°13′ S 66°14′ W	680	1,149	0.59	S	Mesquite savanna
El Palmar NP, Entre Rios	31°53′ S 58°14′ W	1,190	981	1.21	S	Palm forest

AI, aridity index MAP/PET; EF, experimental forest; MAP, mean annual precipitation; N, no pronounced seasonality; NP, national park; PET, mean annual potential evapotranspiration; S, summer maximum; Seas., seasonality of precipitation; SP, spring maximum; StP, state park; LTER, long-term ecological research site; W, winter maximum; WS, wildlife sanctuary.

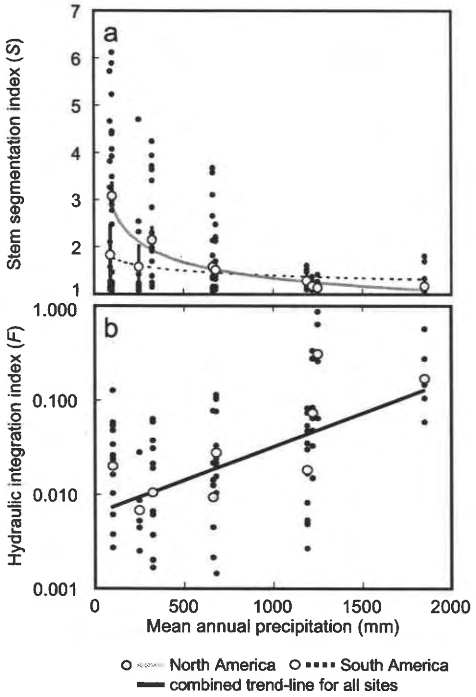

Fig. 3. Degree of hydraulic integration of shrubs as a function of mean annual precipitation (MAP). Black dots are data for individual shrubs, and large circles are geometric means for individual field sites. (*a*) Stem segmentation index *S*. Relationships for North and South America were significantly different: $n = 159$; $F_{\text{continent}} = 10.29$, degrees of freedom (d.f.) = 1, $P = .0016$; $F_{\text{MAP}} = 28.80$, d.f. = 1, $P < .0001$; $F_{\text{continent} \times \text{MAP}} = 4.41$, d.f. = 1, $P = .0373$). (*b*) Hydraulic integration index *F*. Relationships for North and South America did not differ significantly: $n = 86$; $F_{\text{continent}} = 0.68$, d.f. = 1, $P = .4103$; $F_{\text{MAP}} = 8.85$, d.f. = 1, $P = .0038$; $F_{\text{continent} \times \text{MAP}} = 2.55$, d.f. = 1, $P = .1141$).

viduals (17). In contrast, no shrubs from humid environments were completely split; rather, they tended to be single stemmed with more or less circular basal stems. Shrubs growing in the understory of humid warm-temperate forests may well be described as miniature trees, albeit with very short trunks. Shrubs between these extremes in climate tend to be intermediate in their growth forms.

The degree of hydraulic integration calculated from the lateral spread of dye in basal stem cross-sections (index *F*) also increased with MAP (Fig. 3*b*; Table 2), with no significant difference in this relationship between the North and South American transects. The relationship between *F* and MAP remained significant even when the stem area and its interaction with MAP were included in the analysis to account for the possibility that larger stems may tend to have smaller fractions of their wood colored by dye tracer ($r^2 = 0.2572$, MAP, $P < .0001$; stem area, $P = .395$: MAP × stem area, $P = .089$). Functionally, dryland shrubs tend to be much less hydraulically integrated than shrubs in humid environments.

The hydraulic integration index *F* was negatively correlated with fiber wall thickness (Table 2), especially after correction for confounding effects of fiber lumen diameters (Fig. 4), was negatively correlated with the hydraulic diameter of vessels [except for phylogenetically independent contrasts (PICs)], and was positively correlated with vessel density, as previously observed for other species (11). The stem segmentation index *S* was positively correlated with the theoretical implosion resistance of vessels $(t/b)_h^2$ and with sapwood density (Table 2), which decreased with precipitation. The stem segmentation index *S* and integration index *F* were not significantly correlated with each other ($n = 61$; $r = -0.207$; $P = .109$; PICs: $n = 52$; $r = -0.224$; $P = .088$). Stem-splitting shrubs compared with nonsplitting shrubs from dry environments (Table 3) had higher vessel densities, smaller vessel hydraulic diameters, higher wood densities, and higher vessel implosion resistance, indicating strong resistance to drought-induced embolism formation (7, 13, 32).

As predicted by principles of hydraulic engineering, the incidence and degree of hydraulic modularity in shrubs increased with increasing risk of failure resulting from drought. Hydraulic integration thus joins the list of other plant traits that have been observed to correlate with aridity, including the pubescence, sizes, shapes, mass area relationships, and life spans of leaves (33–35) and photosynthetic pathways (36). Because correlation does not prove causation, the question arises as to which factors other than adaptation to drought could explain the relationship observed between hydraulic modularity and aridity. For example, stem segmentation (Fig. 2) might result when drought leads to differential growth or partial dieback of branches, thereby

Table 2. Correlation coefficients for relationships of sapwood traits with the hydraulic integration index, stem segmentation index, and with mean annual precipitation

	Hydraulic integration index $F^{\dagger}$ ($n = 49^{\ddagger}$)		Stem segmentation index $S^{\dagger}$ ($n = 62^{\ddagger}$)		Mean annual precipitation ($n = 62^{\ddagger}$)	
Trait	Uncorr.	PIC	Uncorr.	PIC	Uncorr.	PIC
Vessel density†	0.513**	0.413*	0.114	0.024	0.068	−0.161
Vessel hydraulic diam.	−0.361*	−0.293	−0.210	−0.178	−0.128	−0.021
Fiber wall thickness	−0.495**	−0.434*	0.051	0.303	0.122	0.058
Fiber lumen diam.	−0.092	−0.208	−0.169	−0.083	0.483***	0.378*
$\text{FWTI}_{\%}$	−0.534***	−0.559***	0.205	0.327*	−0.220	−0.247
Fiber wall area, %	−0.088	−0.000	0.269	0.195	−0.366*	−0.299
Fiber lumen area, %	0.094	−0.051	−0.229	−0.141	0.470**	0.364*
$(t/b)_h^2$	−0.163	−0.193	0.371*	0.197	0.380*	−0.219
Wood density	−0.186 ($n = 61$)	−0.215 ($n = 51$)	0.349** ($n = 79^{\S}$)	0.258 ($n = 64$)	−0.565*** ($n = 80^{\S}$)	−0.433** ($n = 64$)

Uncorr., correlations not corrected for phylogenetic effects; PIC, correlations calculated using phylogenetically independent contrasts; diam., diameter; FWTI%, fiber wall thickness index. Coefficients are statistically significant (*, $\alpha = 0.05$; **, $\alpha = 0.01$; ***, $\alpha = 0.001$) after correcting for false discovery rate in multiple comparisons using the Benjamini and Hochberg procedure [Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J R Stat Soc B* 57:289–300].

†Log-transformed.

‡Except for the bottom row, where different sample sizes are noted.

§Each of five species occurred at two sample sites.

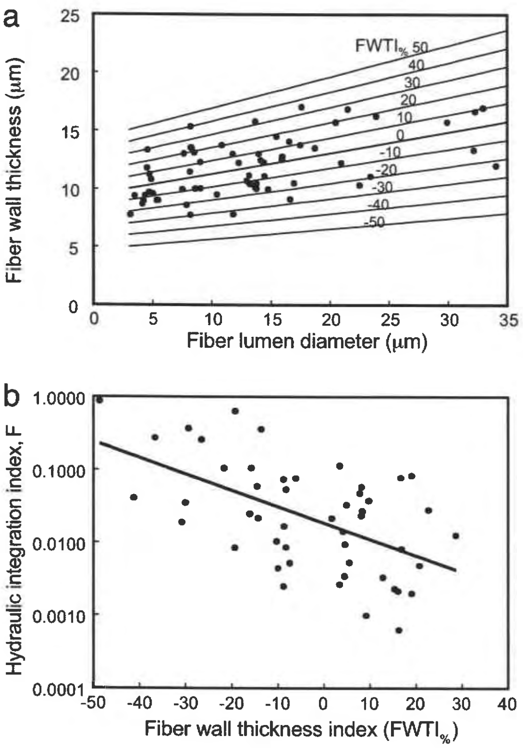

Fig. 4. FWTI%. (*a*) Relationship between fiber lumen diameter (FLD) and fiber wall thickness (FWT): FWTI% = 100 (1 − (0.1798 FLD + 9.4779)/FWT) (n = 62; $r^2 = 0.319$; $P < .0001$). The fiber wall thickness index FWTI% is the coefficient of variation of regression residuals, which is indicated by the thin, labeled lines. (*b*) Relationship between FWTI% and the hydraulic integration index F (n = 49; $r^2 = 0.301$; $P < .0001$).

causing asymmetric growth of the basal stem, as reported by Jones and Lord (23). However, partial dieback and differential branch growth are themselves a consequence of a lack of water sharing among branches and therefore indicate a preexisting modularity. Furthermore, uneven cambial activity preceding eventual stem segmentation begins, at least in some species, when plants are very small, before observed branch die back (23). Could stem segmentation be related to stem mechanics rather than aridity, such that tall shrubs may require round stems for mechanical support, whereas stems of smaller shrubs can split because they do not require much support? The answer is that stem segmentation is significantly related to aridity even when biomechanical constraints associated with increased height are taken into account. Moreover, stem segmentation does not seem to occur in small shrubs from wet environments but does occur in some tall desert shrubs, such as *Larrea tridentata*, which can reach heights of 3.5 m (37).

Could it be that a low degree of hydraulic integration, rather than being a drought adaptation itself, is associated with other structural adaptations that make a hydraulic system resistant to failure? According to the most recent theories about cavitation resistance (12–16), the answer seems to be that hydraulic integration and other structural adaptations are inseparably linked. The connectivity among angiosperm vessels, whether resulting from the number and size of intervessel pits (13) or from the architectural connectedness among vessels (12, 14), is thought to be a crucial adaptation that enables plants to minimize spread of emboli between vessels (12–16). In fact, vulnerability of plant organs to cavitation, as measured by the dehydration, air-injection, or centrifuge methods (38), may be related less to the resistance of individual water-filled xylem conduits to form emboli via wall collapse or air seeding from surrounding intercellular air spaces or gas-filled fibers than to the ability of gas to spread among vessels (12–15). At the organ level, what has been termed "cavitation resistance" in the literature (e.g., 7, 13, 15) probably is better characterized as a combination of resistance and redundancy, namely the resistance of the individual xylem conduits to forming emboli and the degree and type of redundancy of the conduit network (12, 14, 16).

Angiosperm shrubs seem to have evolved two independent ways of building a modular hydraulic system. Through asymmetric secondary growth that leads to fluted sapwood and in some cases to axis splitting (17, 22, 23), plants ensure complete hydraulic isolation of segments. This type of growth is associated with high wood density (Tables 2 and 3), with high implosion resistance of vessels, and therefore probably with high resistance to forming embolisms (6, 7). An alternative strategy to reduce the degree of hydraulic integration seems to be making fewer and larger vessels and surrounding them with a matrix of thick-walled, nonconducting, and possibly gas-filled fibers (25). For plants growing in very dry environments there may be a tradeoff between these two ways of achieving hydraulic modu-

Table 3. Comparison of structural and functional differences in shrub species from dry environments (MAP < 700 mm, AI < 0.6) that have completely split basal stems and species from the same environments that have non-splitting stems

	Species with nonsplitting stems			Species with split basal stems			
Trait	n	mean	SE	n	Mean	SE	P
Stem segmentation, S	27	1.3	0.1	14	3.2	0.3	***
Hydraulic integration, F	21	0.042	0.018	10	0.027	0.008	ns
Hydraulic integration, F, adjusted for split stems†	21	0.042	0.018	10	0.053	0.016	ns
Vessel density, mm^{-2}	27	69.7	6.8	14	95.0	11.2	*
Vessel hydraulic diam., μm	27	55.8	3.0	14	45.8	2.5	*
Fiber wall thickness, μm	27	11.6	0.5	14	11.7	0.6	ns
Fiber lumen diam., μm	27	11.6	1.3	14	9.4	1.5	ns
FWTI%	27	−2.57	3.4	14	2.1	3.3	ns
Fiber wall area, %	27	42.5	2.8	14	49.1	3.1	ns
Fiber lumen area, %	27	12.1	1.9	14	8.5	1.7	ns
$(t/b)^2_n$	27	0.030	0.003	13	0.047	0.007	***
Wood density, g·cm^{-3}	27	0.69	0.02	14	0.78	0.04	*

AI, aridity index; FWTI%, fiber wall thickness index; MAP, mean annual precipitation; ns, not significant. Coefficients are statistically significant (*, $\alpha = 0.05$; ***, $\alpha = 0.001$) after correcting for false discovery rate in multiple comparisons using the Benjamini and Hochberg procedure [Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: A practical and powerful approach to multiple testing. *J R Stat Soc B* 57:289–300]. ns, Not significant.

†Hydraulic integration index F calculated only for the individual stem segment(s) that contained dye tracer.

larity. In vessel-bearing angiosperms, high resistance to embolism formation and vessel implosion is achieved by lowering vessel diameters (13) and increasing the wall-to-lumen ratio of vessels (7). Because hydraulic conductivity of capillaries is proportional to the fourth power of the capillary radius (1), a decrease in vessel diameters must be offset by a concomitant increase in vessel numbers to limit loss in conductivity. Asymmetric secondary growth may be a way to reduce the connectivity among vessels in species with small vessel diameters and high vessel densities (Table 3). High wood density may be a biomechanical requirement for shrubs that have partially or completely segmented stems and therefore lack the mechanical support provided by thicker stems with a core of heartwood. This group includes many of the most cavitation-resistant species from such genera as *Ceanothus*, *Adenostoma*, *Artemisia*, and *Larrea* (7, 39).

The implications of modular hydraulic systems for plant function are numerous. Hydraulic isolation of conduits could allow embolism repair while other parts of the xylem are under tension (10). Under drought conditions, when partial canopy dieback is a frequent occurrence in shrubs (40, 41), hydraulically isolated plant modules with some access to small pockets of water in heterogeneous soil may be able to survive if they are protected from sharing that water with drought-stressed modules (20). In contrast, frost, which also can induce vessel cavitation, is more likely to affect the whole plant equally (42); therefore hydraulic modularity probably does not provide benefits for resistance to or repair of frost-induced embolisms.

Modular hydraulic systems also reduce the spread of runaway embolisms, allow independent stomatal regulation of water use in hydraulic modules, and may help reduce water loss through hydraulic redistribution by restricting flow from one part of the root system to another. In environments not affected by frequent droughts, hydraulic integration seems to be advantageous to shrubs because it allows water and nutrient sharing among modules and rerouting of water flow around pathways blocked by tyloses or pathogens. Most trees in humid forests possess integrated hydraulic systems (31), although both vessel distribution (11) and phylogeny (43) can affect the degree of integration. Hydraulic integration is a trait with important implications for plant structure and function. Highly modular hydraulic systems correlate with the growth form, anatomy, and function of shrubs in dry environments, suggesting that modular hydraulic redundancy is an important, but hitherto largely overlooked, drought adaptation.

Materials and Methods

Field sites were located along transcontinental aridity gradients in North and South America between 31° and 35° latitude (Table 1). Climate data were obtained from nearby weather stations, and mean annual potential evapotranspiration was estimated using a global database (44, 45). At each site, shrubs were sampled during the active growing season using a randomized selection protocol that caused abundant shrub species to have a higher chance of being sampled than less abundant ones. Only healthy shrubs without evidence of partial canopy dieback were sampled. (For a list of species and numbers of individuals sampled at each site see the Table S1) For each shrub, a single, lateral woody root (Ø 2 to 11 mm) was excavated, cut under water, and inserted into a vial containing Acid Fuchsin dye (0.5%). After 1 day, the shrub was cut just below the main branching point, and the basal stem/root crown was taken to the laboratory for analysis of shape and dye-tracer distribution and for measurements of sapwood density and sapwood anatomy. Transverse sections of the basal stem at its most compact point were photographed, and the images were analyzed using SigmaScan Pro software, version 5.0 (SYSTAT Software Inc.).

Shrub growth forms were characterized by measurements of canopy height and widths, height-to-width ratios, canopy volume (calculated as an ellipsoid), and the height of the lowest branch above ground. The degree of physical segmentation of shrubs was characterized by the relationship between cross-sectional area and perimeter of the basal stem's living sapwood and associated undecayed heartwood at the basal stem's most compact point using the formula $S = p\sqrt{\pi}/(\sqrt{A}2\pi)$, with p = stem perimeter, A = basal stem cross-sectional area, and $S = 1$ for a circular area. The degree of hydraulic integration within the basal stem was characterized by measuring the fraction of basal stem cross-sectional area (without bark) colored by Acid Fuchsin dye and calculating a hydraulic integration index as $F = d / A$, with d = area of stem cross-section colored by dye and A = the total area of the basal cross section. Visual distinction between sapwood and heartwood was not possible for many of the species studied, and dye-based methods could not be used without affecting the distribution of Acid Fuchsin dye within the sample. Therefore the total cross-sectional stem area was used to calculate F, and possible effects of total stem area on F were accounted for statistically (as described later). Parameters S and F were log-transformed to meet normality requirements and were analyzed statistically in general linear models as functions of MAP and transect location (North or South America) using SYSTAT software, version 12 . To account for possible effects of biomechanics on the relationship between stem segmentation and aridity, parameter S also was analyzed in a general linear model with MAP, shrub height, and their interaction included as variables. To account for effects of the cross-sectional stem area on parameter F, this parameter also was analyzed in a general linear model with MAP, stem area, and their interaction included as variables.

Sapwood samples from basal stems for analyses of wood anatomy and wood density were softened by boiling and were sectioned and stained. Images of ≈3 mm^2 of transverse sections of sapwood were analyzed in ArcView, version 3.2 (ESRI). Using a drawing tablet, 200 fibers (including libriform fibers and fiber-tracheids) were drawn and measured for wall thickness (FWT) and fiber lumen diameter (FLD), and the entire image was used to determine vessel density, mean vessel hydraulic diameter (46), and the percentages of areas occupied by fiber lumens (FLA) and walls (FWA). A fiber wall thickness index ($FWTI_{\%}$), which included a correction for the relationship between FLD and FWT, was calculated as the coefficient of variation of the residuals of a linear regression of FWT as function of FLD. The theoretical implosion resistance of vessels based on the squared wall thickness-to-span ratio of vessels $(t/b)_h^2$ was measured as described by Hacke *et al.* (7). Sapwood density in basal stems was measured using the Archimedes principle (47). Anatomical traits and wood density were analyzed for their correlation to MAP, the integration index F, and stem segmentation index S. Relationships between non-normally distributed traits were analyzed using Wilcoxon signed rank tests. Linear correlations were calculated for uncorrected trait values and for PICs to account for phylogenetic effects. PICs were calculated using PDAP:PDTREE (48), a module of Mesquite (version 1.1) (49), and Phylomatic (50) was used to generate an initial tree. Most remaining polytomies were resolved using published phylogenies (51–58), leaving only a few unresolved. Any anatomical trait that had a significant association between the absolute value of its standardized independent contrast versus its standard deviation (59–61) was log-transformed (FLD and FWT) or arsine-transformed (FLA and FWA). All branch lengths were set to 1. Statistical significance of correlations was determined in two-tailed tests after correcting for false discovery rate in multiple comparisons using the Benjamini and Hochberg procedure (62, 63).

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BEHAVIORAL ECOLOGY

Form and performance: body shape and prey-capture success in four drift-feeding minnows

Pedro A. Rincón · Markus Bastir · Gary D. Grossman

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Abstract Identifying links between morphology and performance for ecologically relevant tasks will help elucidate the relationships between organismal design and fitness. We conducted a laboratory study to quantify the relationship between variation in body shape and prey-capture success in four drift-feeding minnow species. We offered drifting prey to individual fish in a test flume, counted successful strikes to measure prey-capture success and recorded the position (*X*, *Y* coordinates) of ten landmarks on each fish's outline to delineate the specimen's form. We then quantified shape variation among species and related it to capture performance through thin-plate spline analysis. Body shape varied significantly among species and with specimen size and was the major determinant of capture success, explaining 45–47% of its variability. Prey-capture success at differing velocities differed among species, but once the effects of shape and size were accounted for, those differences were no longer significant. Allometric shape changes appeared responsible for most of the ontogenetic variation in capture performance, although other size-related, non-shape factors also seemed relevant. Fishes with deeper, shorter bodies, more caudally placed median fins and larger, more upward-pointing mouths exhibited greater capture success than more fusiform fish, suggesting that streamlining, which is energetically advantageous for sustained swimming, entails a cost in terms of prey-capture ability. Our findings demonstrate a strong connection between organismal shape and performance and provide empirical evidence of the cost of morphological specialization for fishes in the drift-feeding functional guild.

Keywords Ecomorphology · Ecologically relevant tasks · Morphological costs · Stream fishes · Cyprinidae

Introduction

The relationship between morphology and the use of trophic and spatial resources (i.e., ecological performance) has interested biologists since the time of Darwin (Lack 1947; Wainwright and Reilly 1994). Ultimately, morphology limits an organism's performance at ecologically relevant tasks, although morphology and behavior interact to form a feedback loop with reciprocal influences (Arnold 1983; Wainwright 1994; Ricklefs and Miles 1994). Therefore, establishing the relationship between organismal design and performance at important tasks provides (1) a mechanism for the abundantly reported correlations observed between morphology and ecological traits (Miles et al. 1987; Douglas and Matthews 1992; Norberg 1994) and (2) a basis for subsequent, detailed functional analyses

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P. A. Rincón (✉)
Dpto. Biodiversidad y Biología Evolutiva,
Museo Nacional de Ciencias Naturales,
José Gutiérrez Abascal 2, 28006 Madrid, Spain
e-mail: princon@mncn.csic.es

M. Bastir
Dpto. Paleobiología, Museo Nacional de Ciencias Naturales,
José Gutiérrez Abascal 2, 28006 Madrid, Spain

G. D. Grossman
Daniel B. Warnell School of Forestry and Natural Resources,
University of Georgia, Athens, GA 30602, USA

(Wainwright 1994). There are, however, relatively few explicit, experimental assessments of how morphology affects ecological performance in natural populations.

Organisms for which ecologically relevant tasks can be clearly identified and efficiently measured represent promising systems for elucidating morphology–performance relationships (Norberg 1994; Dewitt et al. 1999; Fulton et al. 2001), and drift-feeding stream fishes comprise just such a system. Drift-feeding fishes also are important components of stream fish faunas worldwide (Matthews 1998); thus, studies of their dynamics have the potential for generality. To briefly describe this system, drift-feeding fishes typically hold relatively stable foraging positions in running water from which they dash to strike at macroinvertebrates carried downstream by the current (i.e., drift) (Hughes and Dill 1990; Hill and Grossman 1993; Grossman et al. 2002). Swimming to hold position against a current may impose substantial energetic costs on drift-feeding fishes (Facey and Grossman 1990), and, at velocities higher than about 5–10 cm/s, current speed can negatively affect the ability of fishes to capture drifting prey (Hill and Grossman 1993; Tyler 1993; Grossman et al. 2002). However, fishes still occupy foraging positions with velocities higher than 10 cm/s because encounter rates with drifting prey generally increase with increasing current velocity (Hughes and Dill 1990; Grossman et al. 2002).

Prey capture is an ecologically relevant task for drift-feeding fishes that should be strongly linked to individual fitness, via its effects on growth. For example, spatial variation in prey-capture success is a major determinant of habitat selection and spatial distribution of individuals within habitat patches (Hughes and Dill 1990; Hill and Grossman 1993; Tyler and Gilliam 1995; Grossman et al. 2002). Spatial and temporal changes in prey-capture success also influence other ecological processes, including: (1) diel activity patterns (Fraser and Metcalfe 1997), (2) growth rates (Wilzbach and Cummins 1986) and (3) foraging mode shifts and niche segregation (Schaefer et al. 1999; Nakano et al. 1999). In addition, capture success of drift-feeding fishes can be measured with reasonable ease, accuracy and realism in the laboratory (Hill and Grossman 1993; Tyler 1993; Grossman et al. 2002).

To our knowledge, the relationship between body morphology and prey-capture success (i.e., ecological performance) has not been quantitatively assessed in drift-feeding fishes. Consequently, we used geometric morphometrics (Rohlf and Marcus 1993) and laboratory experiments on current velocity/prey-capture success to explore the link between morphology and ecological performance in a group of drift-feeding fishes from a southern Appalachian stream. All species examined occupy positions in the water column in Coweeta Creek, N.C., and the influence of current velocity on prey-capture success is the dominant factor determining the focal-point velocities they occupy (Grossman et al. 2002).

Geometric morphometrics can elucidate subtle body shape differences in organisms and relate those to ecological factors (Rohlf and Marcus 1993; Bookstein 1996a; Monteiro et al. 2000). However, their use is not common in ecomorphology (Walker 1997; Adams and Rohlf 2000; Svanbäck and Eklöv 2002) and, to our knowledge, this tool has not previously been used to relate measurements of individual shape and performance. In this study, we utilized it to assess (1) intra- and interspecific variation in morphology and prey-capture performance, and (2) relationships between morphology and foraging success (i.e., ecological performance) of four syntopic drift-feeding minnows (Cyprinidae).

Materials and methods

Study species

Our study species were: rosyside dace (*Clinostomus funduloides*), warpaint shiner (*Luxilus coccogenis*), Tennessee shiner (*Notropis leuciodus*) and yellowfin shiner (*Notropis lutipinnis*). They are members of the "shiner clade", but yellowfin and Tennessee shiners are phylogenetically closest, both placed in the subgenus *Hydrophlox* within *Notropis* (Jenkins and Burkhead 1994; Mettee et al. 1996), and warpaint shiner is closer to them than to rosyside dace (Coburn and Cavender 1993). All four species are common and occur in syntopy in the middle reaches of Coweeta Creek (Little Tennessee River drainage, Macon County, NC, USA), although yellowfin shiner was introduced into the area by man approximately 15 years ago (Menhinick 1991).

The four study species are fairly similar in general external morphology and ecology. They are relatively small with most individuals being less than 80 mm in fork length (FL, length to the fork of the tail), although it is not uncommon for rosyside dace and warpaint shiner to reach lengths greater than 100 mm FL (Menhinick 1991; Jenkins and Burkhead 1994; Mettee et al. 1996). Typically, all four species consume drifting aquatic and terrestrial macroinvertebrates and occupy pools and runs with occasional warpaint and rosyside specimens in the tails or heads of riffles (Outten 1957, 1974; Reisen 1972; Grossman and Freeman 1987; Freeman and Grossman 1992a; Hill and Grossman 1993).

All four species forage both in groups (mono and multispecific) and solitarily (Freeman and Grossman 1992a, b).

Measurement of prey-capture success

The procedures used to assess prey-capture success have been described in detail by Grossman et al. (2002); hence, only the most relevant information is presented here. We captured fishes from Coweeta Creek during the summer of 1998 (water temperature 18–20°C) by seining. Fishes were taken to the laboratory and held in tanks at 18°C with water velocities of about 5 cm/s for 2–3 days before capture success measurements were taken. They were fed rations that approximated maintenance levels (Hill and Grossman 1993) using commercial trout pellets and live *Hyalella azteca* (Amphipoda) 4–7 mm long.

We measured prey-capture success of 107 individuals of the four species (*n*, mean length, range = rosyside dace, 28, 59.4, 40–76 mm; warpaint shiner 29, 64.5, 36–109 mm; Tennessee shiner 26, 51.8, 37–62 mm; and yellowfin shiner 24, 61.5, 42–75 mm) in a 90-cm-long by 35-cm-wide by 35.5-cm-deep test chamber with a Plexiglas viewing port. We recorded the exact positions of specimens during trials using grids marked on both sides and the bottom of the tank. We controlled velocity in the tank using an electric trolling motor with variable speed controls (thrust = 37 lb) placed at the front of the chamber. A honeycomb collimator placed between the propeller and the chamber reduced turbulence in the tank. We conducted foraging trials at 18°C and used live *H. azteca* (4–7 mm long) as test prey. *H. azteca* is easily cultured and was readily consumed by the fishes. *H. azteca* always traveled the length of the chamber without sinking to the bottom and the fishes fed on it using behaviors similar to those exhibited under field conditions (Freeman and Grossman 1992a, b; G. Grossman personal observation). Live *H. azteca* were released into the current 5 cm below the surface via a piece of flexible plastic tubing attached at the upstream screen.

We measured capture success at the fish's focal position at velocities ranging from 5 cm/s to 40 cm/s at 5-cm/s intervals. Fishes always held position in the same area of the test chamber, and we used pilot trials to calibrate motor speeds to produce the desired velocities. A trial began by placing a single test fish in the chamber, allowing it to acclimate at 10 cm/s for 10 min and then delivering prey until it made one capture (a few fishes refused to feed and were not used in trials). We then gradually adjusted the apparatus until the desired velocity was obtained and began releasing prey at approximately 20-s intervals until ten prey had been delivered. An observer recorded prey-capture data and noted both the holding and strike positions of the fish. After completion of the trial, we measured velocities at these locations with an electronic flow meter (Marsh-McBirney 201) accurate to ±0.01 cm/s. Each subject was tested at two or three velocities in a given day in combinations that minimized the effects of fatigue and satiation. Although capture success (proportion of prey captured) was measured at eight different velocities, in this study we only explored the general relationship between morphology and foraging performance at 10, 15, 10 and 25 cm/s and in more detail at 15 cm/s. We chose those velocities because capture success, although still reasonably high, exhibited sufficient variability to make statistical comparisons feasible. We selected 15 cm/s for more in-depth analysis because it is close to the optimal focal velocities used in the field by the four study species (Grossman and Freeman 1987; Hill and Grossman 1993; Grossman et al. 2002).

For a task to be ecologically relevant, individual differences in performance must show some temporal stability and, hence, individual scores in performance tests should be repeatable (Kolok 1999). We only tested fishes once at each velocity and, therefore, could not directly assess repeatability for our performance measurement (capture success at 15 cm/s). However, capture success at 15 cm/s showed a high positive correlation with capture success at both 10 cm/s and 20 cm/s for all experimental subjects both within and among species ($r = 0.81–0.90$, all P values < 0.0001). Test subjects were never tested on the same day at adjacent velocities (e.g., 15 cm/s and 20 cm/s); hence, these data should not be serially correlated. Therefore, prey-capture success appears to meet the prerequisites for an ecologically relevant trait.

Morphological measurements

After the completion of capture success experiments, each fish was measured (fork length, mm) and euthanized with an overdose of MS-222. All experimental procedures were in compliance with the University of Georgia IAUAC policies. We then immediately collected ten landmarks on the profile of the fish (Fig. 1) by recording the position of the following points: (1) anterior-most point of jaw, (2) posterior-most point of neurocranium, (3) anterior insertion of dorsal fin, (4) posterior insertion of dorsal fin, (5) dorsal insertion of caudal fin, (6) ventral insertion of caudal fin, (7) anterior insertion of anal fin, (8) insertion of pelvic fin, (9) insertion of pectoral fin and (10) most posterior point

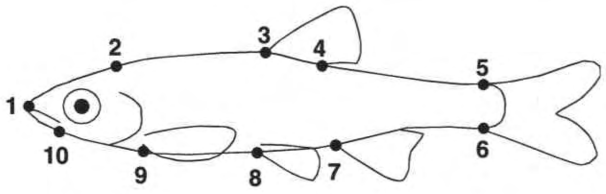

Fig. 1 Location of the ten landmarks used in the morphological analysis. See text for extended landmark definitions

of maxillary (Winans 1984; Wood and Bain 1995). For landmarks not on the outside of body form, we used the projection on the profile (perpendicular to the horizontal axis of the specimen). These, or very similar, landmark configurations can elucidate intra- and interspecific, ecologically relevant shape differences (Winans 1984; Wood and Bain 1995).

We measured landmarks by placing the specimen on its right side on a sheet of water-resistant paper set upon a Styrofoam board with the tip of the snout, the hypural bone and the caudal fin fork aligned along a straight line. We then used a needle to punch holes in the paper at the location of each landmark. A support was employed to ensure that the needle remained perpendicular to the paper (Winans 1984; Wood and Bain 1995). The paper sheets were then scanned and the *X*–*Y* coordinates of each landmark obtained from the digitized images using TpsDig software (Rohlf 2001). To reduce measurement error, all landmark measurements and data analyses were made by one researcher (P.A. Rincón). Reliability of measurements, assessed by repeating the whole process on 20 randomly chosen specimens, was high (correlation between the two sets of inter-landmark distances: $r = 0.986$, $P < 0.0001$).

Statistical analysis

We used geometric morphometrics to quantify inter- and intraspecific variation in size and shape and the relationship between shape and prey-capture success (Bookstein 1991; Rohlf and Marcus 1993; Monteiro et al. 2000). To estimate the size of each fish, we used its centroid size—the square root of the sum of the squares of the distance of each landmark from the centroid (center of gravity) of all the landmarks, which summarizes the dimensions of a specimen in all directions (Bookstein 1991). We removed non-shape variation (location, orientation and scale) and generated a consensus shape for each species using Generalized Procrustes Analysis (Rohlf and Slice 1990) in MORPHEUS software (Slice 1998). We used the thin-plate spline (TPS) function (Bookstein 1991) and the standard formula for the uniform component (Bookstein 1996b) as implemented in the program TpsSpline (Rohlf 2002) to generate shape variables from the aligned specimens. The uniform component of shape variation expresses body shape changes such that sets of parallel lines on the form remain parallel after transformation. That is, shear or stretching occurs uniformly over the entire form. In contrast, non-uniform shape changes affect only localized areas of the landmark configuration (Bookstein 1991).

The TPS function depicts shape changes as deformations of the consensus configuration and yielded scores for a set of 14 partial warps (two times the number of original landmarks minus six), which represented non-uniform shape variation (Rohlf 1991), plus two additional uniform components, reflecting uniform shape changes (Bookstein 1996b). Together, the 16 shape variables accounted for total shape differences and located each specimen in shape space (Bookstein 1996a). This matrix of shape variables was then used in conventional statistical analyses to explore inter- and intraspecific patterns of shape variation and associated differences in prey-capture success (Adams and Rohlf 2000; Svanbäck and Eklöv 2002).

We tested for variation in shape among minnow species and by specimen size by conducting a multivariate analysis of covariance (MANCOVA) on the matrix of partial warp scores, with centroid size as a covariate. The statistical significance of shape differences between pairs of species was assessed with the generalized Mahalanobis distance (corrected for centroid size) between their centroids in multivariate space (Scheiner 1993). Interspecific differences were visualized by comparing the thin-plate spline deformation of each species' mean shape with the reference. Shape changes in relation to size were graphically depicted using multivariate regression of the shape variables matrix onto centroid size using the program TpsRegr (Rohlf 2000).

To elucidate the effects of fish morphology, size and species on prey-capture success, we used General Linear Models with capture success (arcsine square-root transformed) as the dependent variable and different combinations of predictor variables because predictor variables were not completely independent. For example, interspecific differences in performance may be due to variation among species in proximate determinants such as morphology, physiology and behavior. Analogously, changes in performance with size may be attributable to increases in sheer bulk and to size-related shape changes (i.e., allometry). By comparing the change in explanatory power of the whole model and of each factor in particular among models with different subsets of predictors, it is possible to obtain an idea of the relative importance of the potential determinants of performance and the degree of redundancy between them (Myers 1990; Monteiro 1999). The reduction in the residual sum of squares (RSS) produced by a particular model relative to another was tested against the remaining RSS using the *F* statistic (Myers 1990; Dunham and Vinyard 1997; Rincón and Lobón-Cerviá 2002). Then, only for the data at 15 cm/s, the relationship between performance and shape was visualized by regressing partial warp scores against prey-capture success using the TpsRegr program (Rohlf 2000).

Prior to statistical analysis, variables were tested for significant departures from normality and homoscedasticity and none was found (Kolmogorov–Smirnov and Cochran's tests, all $P > 0.05$). Statistical analyses were performed with STATISTICA 6.0 (StatSoft 2001). Capture success was arcsine square-root transformed (Zar 1996), and all statistical results presented below are for the transformed data. However, we have presented untransformed values when they are more informative for the reader.

Phenotypic similarity between species in terms of morphology and performance may be the product of shared evolutionary history (Felsenstein 1985; Harvey and Pagel 1991). Diverse analytical procedures to estimate the effect of phylogenetic relatedness on the observed phenotypic patterns are available (Felsenstein 1985; Martins and Hansen 1997). However, we have assessed the effect of phylogeny on our results non-mathematically because this is relatively straightforward with only four taxa with well-resolved relationships (see "Study species"), and our main interest lies in the functional consequences of morphological variation rather than its causal processes.

Results

Interspecific and allometric variation in morphology

Allometric patterns did not differ significantly among species, as demonstrated by the non-significant species × centroid size interaction in an initial full-factorial MANCOVA (Wilk's $\lambda = 0.6188$, $df = 48$, 250.6, $P > 0.63$). Consequently, the interaction term was removed and we explored morphological variation with a common slope model.

Total body shape (i.e., uniform and non-uniform components) varied significantly with centroid size (i.e., allometry) and among species (common slope MANCOVA, Wilk's $\lambda = 0.0604$, $df = 48$, 259.5 and Wilk's $\lambda = 0.4467$, $df = 16$, 87, respectively, both *P* values < 0.0001). The four species differed morphologically from each other in shape and size, as shown by significant Mahalanobis distances (Table 1). Mahalanobis distances indicated that rosyside dace and Tennessee shiner differed the most morphologically, whereas Tennessee and warpaint shiners were most similar. Yellowfin shiner and rosyside dace were also fairly similar. The remaining differences were intermediate (Table 1). This pattern seemed largely due to morphological similarity rather than similarities in size, because the smallest Mahalanobis distance corresponded to the species pair with the largest size difference (warpaint and Tennessee shiners). Additionally, phylogenetic relatedness and phenotypic similarity (Table 1) were not concordant. For example, yellowfin shiner was most similar morphologically to rosyside dace and least to Tennessee shiner (Table 1). However, rosyside dace and Tennessee shiner are, respectively, the least and most phylogenetically close species to yellowfin shiner of the three species according to current taxonomy.

Most morphological variation, due to both species-specific differences and size-related changes, appeared related to changes in: (1) body depth, (2) length and depth of the caudal peduncle, (3) head size, (4) mouth size and orientation and (5) position and length of the dorsal fin (Fig. 2). Relative to the consensus shape, Tennessee shiner exhibited a marked reduction in body depth over the whole configuration and a notable lengthening of the caudal peduncle. Also, the mouth was smaller and more downturned. Warpaint shiner displayed vertical compression only in the middle trunk area, although not as marked as in Tennessee shiner, and an anterior displacement of the dorsal fin (Fig. 2). In contrast, in yellowfin shiner, the middle trunk showed a marked increase in height. Yellowfin shiner also displayed shortenings of the caudal peduncle and of the dorsal portion of the head and elongation of the dorsal fin. Rosyside dace exhibited enlargement of the head in general (i.e., longer and deeper), and of the mouth in particular. Rosyside dace also showed a deepening of the trunk area immediately

Table 1 Morphological similarity among drift-feeding minnows. Squared Mahalanobis distances for pairwise comparisons between species centroids in multivariate shape space are presented above the diagonal and the associated *F* values below it. The corresponding *P* values are all <0.0001

Species	Rosyside dace	Yellowfin shiner	Warpaint shiner	Tennessee shiner
Rosyside dace	–	9.78	12.39	25.22
Yellowfin shiner	6.328	–	15.67	16.71
Warpaint shiner	9.254	10.468	–	7.21
Tennessee shiner	17.483	10.443	5.169	–

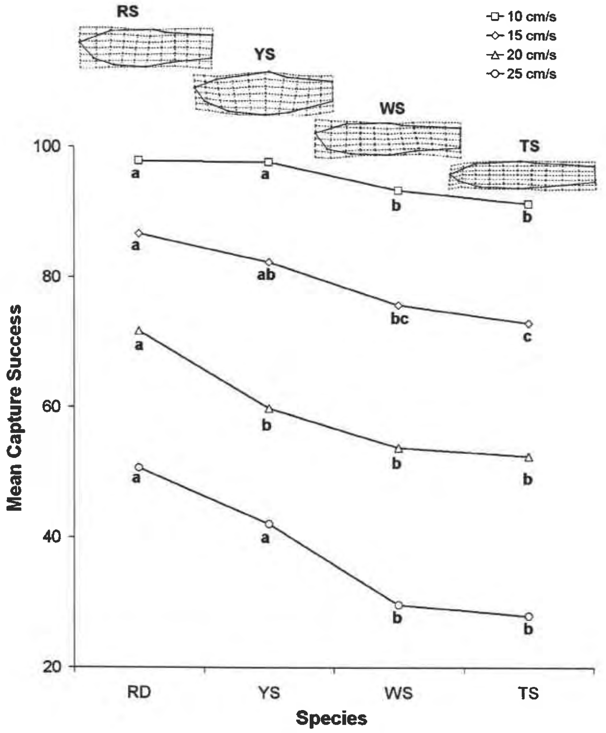

Fig. 2 Mean prey-capture success at 10, 15, 20 and 25 cm/s and average morphological configuration for: rosyside dace (*RD*), yellowfin shiner (*YS*), warpaint shiner (*WS*) and Tennessee shiner (*TS*). Species sharing a *letter* did not differ significantly (least squares comparisons) in mean prey-capture success at a given velocity. Shape changes have been magnified 3× for ease of interpretation. Confidence intervals have been omitted for clarity

anterior to the dorsal fin and, to a lesser extent, of the posterior end of the caudal peduncle, which also was shortened. The dorsal fin of rosyside dace was shorter and more posteriorly located (Fig. 2).

As centroid size increased, the body grew higher, except in the posterior end of the caudal area, for all four species. The mouth became larger and had a more upward orientation, the middle trunk expanded both vertically and horizontally, and the caudal peduncle displayed a marked contraction. The dorsal fin grew longer through a caudal displacement of its posterior insertion and the anal fin became more caudally placed (Fig. 3a). In comparison, smaller specimens showed more slender bodies, smaller, more terminal mouths, elongated caudal peduncles and more anteriorly placed anal fins (Fig. 3a).

Relationships between morphology, size, and prey-capture success

Capture success varied significantly among species and with size at all four velocities (common slope ANCOVA, $F_{3,102} = 4.922–10.051$, $P < 0.003$ and $F_{1,102} = 39.802–53.568$, $P < 0.0001$, in all cases, respectively). These two factors explained 41–47% of the variation in prey-capture success for the four species ($F_{4,102} = 17.995–23.013$, $P < 0.0001$). The use of a common slope model (hereafter Model I) was appropriate because the species × centroid size interaction was non-significant ($F_{3,99} = 1.229–2.118$, $P > 0.1$). A model with centroid size as the only predictor variable explained 30–34% of the variance in prey-capture success ($F_{1,105} = 46.075–53.675$, $P < 0.001$), whereas interspecific differences alone accounted for a lower, but still significant, 14–21% of the variance in foraging performance ($F_{3,103} = 5.827–9.034$, $P < 0.001$).

The pattern of interspecific differences in capture success remained essentially similar at all velocities. Rosyside dace exhibited the highest size-corrected mean capture success and Tennessee shiner the lowest (Fig. 2). Comparisons of least-square (LS) means indicated that rosyside dace mean capture success was always significantly greater than that of Tennessee and warpaint shiners ($t = 3.406–2.557$, $P < 0.02$ and $t = 2.786–3{,}123$, $P < 0.005$, respectively) and than that of yellowfin shiner at 20 cm/s ($t = 2.552$, $P < 0.02$). Yellowfin shiner exhibited significantly higher prey-capture success than Tennessee shiner ($t = 2.202–2{,}993$, $P < 0.03$) and warpaint shiner ($t = 2.215–2.894$, $P < 0.04$) at 10, 15 (Tennessee shiner only) and 25 cm/s. Similar to morphological analyses, patterns in prey-capture success were not concordant with phylogenetic patterns. For example, the two most closely related species (yellowfin and Tennessee shiner) differed significantly with respect to prey-capture success in three of four cases. By contrast, prey-capture success for Tennessee shiner never differed significantly from that of the more distantly related warpaint shiner.

Interspecific differences in capture success appeared largely attributable to differences in morphology. Incorporating the effects of variation in total shape into Model I by adding partial warp scores and uniform components as continuous independent variables increased the variance explained to 58–65% ($F_{16,86} = 1.829–2{,}674$, $P < 0.04$) at 15, 20 and 25 cm/s and to 51% at 10 cm/s (non-significant). In this augmented model (hereafter Model II), centroid size still displayed a significant effect on prey-capture success at all velocities ($F_{1,86} = 10.022–21.141$, $P < 0.0001$), but the species effect was no longer significant ($F_{3,86} = 0.002–1.556$, $P > 0.21$). Removal of the species term yielded Model III, which incorporated the effects of size and shape, and produced almost no reduction in explanatory power (51–57%), except at 25 cm/s (65–56%, although still non-significant). Shape variables

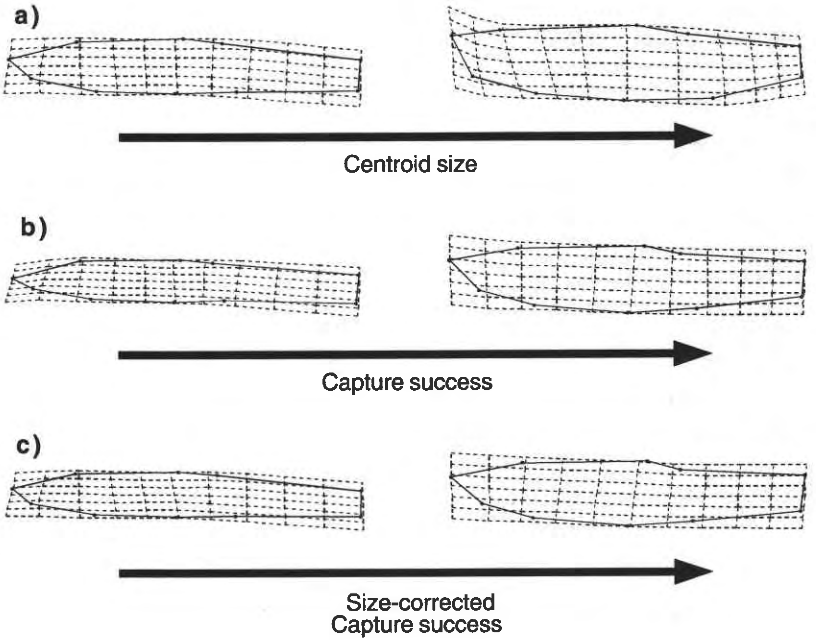

Fig. 3 Changes in morphology associated with variation in centroid size (increases to the *right*) (**a**), capture success (increases to the *right*) (**b**) and capture success after the effect of body size has been mathematically removed (increases to the *right*) (**c**). Shapes at the end of each axis are those corresponding to the lowest and highest values of the axis. Shape changes have been magnified 3× for ease of interpretation

alone (Model IV, no centroid size term) accounted for 45–47% of the variance in prey-capture success ($F_{16,90} = 4.525–6.339$, $P < 0.0001$) which represented a significant decrease in explanatory ability relative to Model III in all four cases ($F_{1,90} = 12.152–24.319$, $P < 0.0001$). Hence, morphological variation was the dominant factor affecting interspecific differences in prey-capture success and also appeared to explain a substantial amount of intraspecific variation (variance explained by size + species + shape = 51–65%, size + shape = 51–57%, size + species = 41–47%; shape alone = 45–47%, species alone = 14–19%, size alone = 30–34%).

Differences in total shape associated with variation in prey-capture success appeared to reflect both allometric and interspecific variation in form (Figs. 2 and 3a). Thus, as capture success increased, the body deepened anterior to the end of the caudal peduncle, and the mouth generally increased in size and was more dorsally oriented. In addition, the caudal peduncle decreased in length, and dorsal and anal fins were positioned more toward the posterior end of the body. Lower capture performance was associated with a slender body, extended caudal peduncle, smaller, more ventrally oriented mouth and more anteriorly placed dorsal and anal fins (Fig. 3b).

Allometric shape changes significantly affected prey-capture success. Centroid size accounted for 12–17% of the 51–57% of total variance explained by Model III (in which the size-free shape variables directly accounted for allometric shape changes). In comparison, when centroid size was the only independent variable (and, hence, acted as a partial surrogate for allometric shape variation), it explained 30–34% of the variance in prey-capture success. Consequently, it appears that allometric variation in shape actually was responsible for a greater proportion of the variation in prey-capture success than changes in sheer bulk. The relevance of allometric morphological variation to prey-capture success is well illustrated by the similarity in shape changes associated with larger size (Fig. 3a) and with increased capture success at 15 cm/s (Fig. 3b)

Discussion

Prey capture is an ecologically significant task with multiple, ecologically relevant consequences for a variety of organisms (Hill and Grossman 1993; Tyler and Gilliam 1995; Nakano et al. 1999; Grossman et al. 2002). To our knowledge, our results provide the first empirical evidence relating prey-capture success (ecological performance) to body shape at both inter- and intraspecific levels in stream fishes. Our data demonstrate that body shape is a major determinant of prey capture for four species of stream minnows. At current velocities between 10 cm/s and 25 cm/s, individuals with deeper bodies, more posteriorly positioned median fins and larger, more dorsally oriented mouths captured greater proportions of drifting prey than did more slender individuals with smaller, more ventrally oriented mouths. The observed morphology–performance link probably reflected the biomechanical consequences of body shape rather than phylogenetic relationships.

Three lines of evidence support this contention. First, species most similar in prey-capture ability were also most similar in shape, but were not most closely related phylogenetically (Harvey and Pagel 1991). Second, the relationship between morphology and performance was consistent whether shape varied between species or due to allometric growth (Ricklefs and Miles 1994). Third, the relationship agreed with biomechanical predictions derived from hydrodynamic theory (Webb 1984a, b; Vogel 1994; Walker 1997). However, although our results appear to represent true morphology–performance relationships, our four species were relatively close relatives, and phylogeny may play a greater role in a different, more varied assemblage (Douglas and Matthews 1992).

Our findings also suggest that prey capture may impose morphological constraints on drift-feeding fishes that differ from those of steady swimming (i.e., cruising or swimming to hold position against the current). We found that increased prey-capture success was associated with (1) deeper, shorter bodies, (2) more posteriorly placed median fins and (3) larger, more dorsally oriented mouths. Hydrodynamic theory and empirical evidence show that (1) and (2) improve maneuverability, but result in poorer steady swimming performance. Conversely, streamlining enhances steady swimming performance (Webb 1983, 1984a, b; Taylor and McPhail 1985a, b, 1986; Taylor and Foote 1991; Vogel 1994; Walker 1997). Maneuverability is defined as the ability to modify steady, forward locomotion rapidly and precisely and, thus, includes not just turning, but also accelerating, braking, etc. (Breder 1926; Walker 1997).

The spatial distribution and videographic analysis of the capture strikes of drift-feeding fishes clearly support our results because both show that swimming when striking at prey involves substantial turning and accelerating and is unsteady (Grant et al. 1989; Hughes and Kelly 1996; Rincón and Grossman 2001). Therefore, shapes favoring maneuverability should perform those attacks more efficiently. In contrast, using different experimental procedures, Schaefer et al. (1999) found that more fusiform longear sunfish *Lepomis megalotis* captured more prey than deeper bodied bluegill *L. macrochirus* as water velocity increased.

By showing that a more fusiform body shape reduces capture success, our results suggest that streamlining can have a cost for drift-feeding fishes. However, drift-feeding fishes often spend long periods of time holding position (i.e., presumably swimming steadily) against the current (Bachman 1984; Hughes and Dill 1990; Webb 1991; Hughes and Kelly 1996). Although holding position in a stream actually seems to require much unsteady swimming (McLaughlin and Noakes 1998), more fusiform shapes should still result in lower energetic costs (Vogel 1994). Therefore, our results support Bisson's et al. (1988) suggestion that the morphology of drift-feeding fishes represents a compromise between the conflicting demands of prey capture (maneuverability) and holding position (sustained swimming).

The ecological consequences of this compromise (i.e., more streamlined individuals in areas of faster currents and deeper-bodied specimens in slower habitats) have been documented at both inter- and intraspecific levels and at multiple spatial scales (Thomas and Donahoo 1977; Taylor and McPhail 1985b; Taylor 1988; Bisson et al. 1988; Taylor and Foote 1991; McLaughlin 1994; Nicieza 1995). Some have argued that the costs of sustained swimming would exclude deep-bodied fishes from high-velocity areas, whereas more fusiform specimens would suffer a competitive disadvantage in slow-flowing water due to lower prey-capture efficiency (Bisson et al. 1988). Although, several studies have documented that more streamlined fishes have superior sustained swimming performance (Thomas and Donahoo 1977; Taylor and McPhail 1985b; Taylor and Foote 1991; Hawkins and Quinn 1996; Petterson and Brönmark 1999), our results provide the first evidence that more fusiform species also displayed reduced capture success.

Lower prey-capture success is not the only potential drawback of streamlining. For example, predator avoidance may also contribute to the trade off between streamlining and robustness. More fusiform shapes show lower burst swimming performance and, hence, probably reduced escape ability (Taylor and McPhail 1985a, b). Therefore, higher predation pressure may have constrained the emergence of more streamlined shapes in certain circumstances (Taylor and McPhail 1985a; Walker 1997).

We found that body shape varied significantly among species and with size, and that both types of variation affected foraging performance. Interspecific differences in morphology were the main factor influencing interspecific variation in capture success once the effect of size was removed mathematically. This result was surprising, because the four species appear superficially to be quite similar in morphology. In addition, our analysis did not take into account a number of non-shape traits (e.g., thermal physiology, muscle composition, etc.) that also may affect performance (Sidell and Moerland 1989; McLaughlin and Kramer 1991). The "species" term in Model I acted as a surrogate for differences in both morphology and these hypothetical factors and was statistically significant. However, once the effects of morphology were explicitly incorporated (Model II), the species term was no longer significant and retained little explanatory power. Consequently, unmeasured, non-shape factors seemed to contribute little to the observed interspecific differences in capture performance.

Similarly, our results indicate that allometric shape variation was substantially more important for capture success than other potential, size-related factors. As size increases, both shape and non-shape traits (e.g., muscle properties and motor patterns) vary with it, and variation in both types of traits may produce size-linked changes in performance (Richard and Wainwright 1995; James et al. 1998; Hernandez 2000). Once the partial warp scores explicitly accounted for the effect of shape variation, centroid size represented the influence of those other, non-shape factors. The effect of centroid size remained statistically significant in Models II and III. However, its explanatory power decreased from 30–34% to 12–17%, and inclusion of this term into a model with only morphological variables produces a more modest increase in explanatory power than the addition of shape variables to a size-only model (7–11% vs. 21–24%). Therefore, larger size seems to result in increased prey-capture success mostly, though not exclusively, through size-related changes in shape.

Because of the ability of geometric morphometrics to separate shape and non-shape variation in morphology, our results provide clear support for the hypothesis that allometric shape changes through ontogeny may play an important role in size-related variation in ecological performance (Emerson 1978; Galis 1993; Svanbäck and Eklöv 2002). The ecological effects of size variation have been abundantly documented (Peters 1983; Schmidt-Nielsen 1984; Werner and Gilliam 1984; Rincón and Lobón-Cerviá 2002) and allometric growth is the norm among animals (McMahon 1973). Therefore, the effects of allometric shape changes on performance are likely to be widespread and should receive attention in future studies of ontogenetic effects on resource use and ecological performance.

In summary, we have identified a strong relationship between body shape and prey-capture success (ecological performance) and have shown that morphological specialization in the form of streamlining incurs costs for drift-feeding fishes (i.e., reduced prey-capture success). Such costs, most likely the consequence of decreased maneuverability, were predicted by hydrodynamic theory and have been invoked to explain phenomena such as resource polymorphisms and spatial segregation in both lake and stream fishes (Webb 1983; Bisson et al. 1988; Walker 1997; Robinson et al. 2000; Svanbäck and Eklöv 2002). Our findings provide support for those claims and also suggest that the diverse demands placed on morphology by different ecological tasks and their evolutionary and ecological consequences deserve further attention; we showed drift-feeding fishes to be a promising system to further explore these questions.

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