- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183–190.
- GREENE, H. W. 1993. What's good about natural history. Herpetol. Nat. Hist. 1:3.
- INGER, R. F. 1992. Variation of apomorphic characters in stream-dwelling tadpoles of the bufonid genus Ansonia (Amphibia: Anura). Zool. J. Linn. Soc. 105: 225–237.
- KORKY, J., AND R. G. WEBB. 1973. The larva of the Mexican toad Bufo cavifrons Wiegmann. J. Herpetol. 7: 47–49.
- LEE, J. C. 1996. The Amphibians and Reptiles of the Yucatán Peninsula. Cornell Univ. Press, Ithaca, New York.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.
- LIMBAUGH, B. A., AND E. P. VOLPE. 1957. Early development of the Gulf Coast Toad, *Bufo valliceps Wieg*mann. Amer. Mus. Novit. 1842:1–32.
- LIPS, K. R., AND J. SAVAGE. 1996. Key to the known tadpoles (Amphibia: Anura) of Costa Rica. Stud. Neotrop. Fauna Env. 31:17–26.
- LÖTTERS, S. 1996. The neotropical toad genus *Atelopus*: checklist—biology—distribution. M. Vences and F. Glaw Verlags BbR., Köln, Germany.
- MCDIARMID, R. W., AND M. S. FOSTER. 1981. Breeding habits of the toad *Bufo coccifer* in Costa Rica, with a description of the tadpole. Southwest. Natur. 26: 353–363.
- MENDELSON, J. R., III. 1994. A new species of toad (Anura: Bufonidae) from the lowlands of eastern Guatemala. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 166:1–21.
- ——. 1997a. The systematics of the Bufo valliceps group (Anura: Bufonidae) of Middle America. Unpubl. Ph.D. Diss., Univ. Kansas, Lawrence.
- . 1997b. A new species of toad (Anura: Bufonidae) from Oaxaca, Mexico, with comments on the status of *Bufo cavifrons* and *Bufo cristatus*. Herpetologica 53:268–286.
  - —. 1997c. A new species of toad (Anura: Bufonidae) from the Pacific Highlands of Guatemala and southern Mexico, with comments on the status of *Bufo valliceps macrocristatus*. Herpetologica 53:14– 30.

—. 1998. Geographic variation in *Bufo valliceps* (Anura: Bufonidae), a Widespread Toad of the United States and Middle America. Sci. Pap. Nat. Hist. Mus. Univ. Kansas 9:1–12.

- PORTER, K. R. 1962. Evolutionary relationships of the *Bufo valliceps* group in Mexico. Unpubl. Ph.D. Diss., Univ. Texas, Austin.
- SAVAGE, J. M. 1960. Geographic variation of the toad, Bufo marinus. Copeia 1960:233–236.
- SHANNON, F. A., AND J. E. WERLER. 1955. Notes on amphibians of the Los Tuxtlas Range of Veracruz, Mexico. Trans. Kansas Acad. Sci. 58:360–386.
- STEBBINS, R. C., AND N. W. COHEN. 1995. A Natural History of Amphibians. Princeton Univ. Press, Princeton, New Jersey.

Accepted: 18 January 1999.

#### Appendix I

### SPECIMENS EXAMINED

Bufo macrocristatus.—GUATEMALA: HUEHUE-TENANGO: Santa Cruz Barillas, 1650 m (KU 104115). MEXICO: CHIAPAS: 6.8 km E Rayón Mescalapa (UTA A-27857–59).

Bufo marinus.—BELIZE: CAYO: Río On, 8.7 mi N San Luis (KU 157685). COSTA RICA: PUNTARENAS: Rincon de Osa, 5 m (KU 104288). HONDURAS: SAN-TA BARBARA; 4 km SW Quimistan, 175 m (KU 68328); FRANCISCO MORAZAN: El Zamorano, 850 m (KU 104116). PANAMA: SAN BLAS: Camp Sasardi, 12 m (KU 116723). PERU: MADRE DE DIOS: Cuzco Amazonico, 15 km E Puerto Maldonado, 200 m (KU 205826).

Bufo valliceps.—GUATEMALA: HUEHUETENAN-GO: Carretera Camoja Grande–Nenton, Km 361, 795 m (UTA A-48106). MEXICO: HIDALGO: 38.5 km SW Huejutla (UTA A-19233–36). USA: TEXAS: Tarrant County, drainage off Davis Rd., across street from campus [UTA] police station (UTA A-45074).

*Bufo tutelarius.*—MEXICO: OAXACA: stream on slope opposite W slope Cerro Baúl, 8.8 km rd km N Colonia Rodulfo Figueroa, 1100–1200 m (UTA A-51647–52; MZFC 10138).

*Journal of Herpetology*, Vol. 33, No. 2, pp. 328–330, 1999 Copyright 1999 Society for the Study of Amphibians and Reptiles

# Dispersal of Namaqua Fig (Ficus cordata cordata) Seeds by the Augrabies Flat Lizard (Platysaurus broadleyi)

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Several recent studies have identified lizards as seed dispersal agents (Iverson, 1985; Whitaker, 1987; Traveset 1990; Valido and Nogales, 1994). Hence, it is reasonable to hypothesize that fig eating lizards such as Ctenosaura similis (Roberts and Heithaus, 1986) and Platysaurus broadleyi (Whiting and Greeff, 1997) may disperse fig seeds. Figs typically produce either small red figs that are dispersed by birds (Coates Estrada and Estrada, 1986; Bronstein and Hoffmann, 1987; Lambert and Marshall, 1991; Compton et al., 1996), or green odoriferous figs that are dispersed by bats (Kalko et al., 1996). Ants often play an important secondary role in moving seeds from feces to good quality germination sites (Roberts and Heithaus, 1986; Kaufmann et al., 1991). An array of mammal species as diverse as monkeys and agoutis also disperse seeds, but they are often seed predators (Roberts and Hei-

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thaus, 1986). Aquatic animals such as turtles (Moll and Jansen, 1995) and fish (Conceição de Souza-Stevaux et al., 1994; Horn, 1997) disperse the seeds of riparian figs.

Ficus cordata cordata produces small red figs, typical of a tree whose seeds are dispersed by birds. The microhabitats of this tree and the Augrabies flat lizard (Platysaurus broadleyi) closely coincide with each other. This small cordylid lizard (adult snout-vent length range: 64-84 mm) is restricted to rocky outcrops in the Northern Cape Province and southern Namibia, and is particularly abundant along the Orange river (Branch and Whiting, 1997), where it seeks refuge in deep crevices. In previous studies we showed that adult P. broadleyi feeding underneath Namaqua fig trees consume an average of one fig every three minutes (Whiting and Greeff, 1997) and that large groups of more than a hundred lizards (maximum recorded = 134) aggregate underneath fruiting fig trees (Whiting and Greeff, 1999).

We evaluated the possibility that *P. broadleyi* disperses Namaqua fig seeds by comparing germination success and germination speed of un-ingested (control) seeds to seeds ingested by lizards and sympatric vertebrates (hyraxes and birds) that also feed on figs. We quantified the distance over which this lizard can act as a disperser and measured the energy content of figs to determine the energetic gain to the lizard.

During April 1996 we studied a population of *P. broadleyi* at Augrabies Falls National Park (28°35'S, 20°20'E), Northern Cape Province, South Africa where the Namaqua fig is a dominant component of the vegetation. See Branch and Whiting (1997) and Whiting and Greeff (1997) for a detailed description of the study area.

We performed a systematic search for all fig trees on the southern bank of the Orange river, within the confines of the park, and noted whether a tree was growing in a sandy or rocky substrate. Of the 92 trees we surveyed, only three (3.3%) grew in sand and these probably germinated in rock crevices later covered by sand.

We collected feces containing fig seeds from P. broadleyi, birds (mostly Onychognathus nabouroup and Pycnonotus nigricans), and rock hyraxes (Procavia capensis). These were the only diurnal animals observed to feed on figs, although primates (Papio ursinus and Cercopithecus aethiops) may sometimes eat figs. Uneaten fruit was also collected underneath trees. These samples were transported to Pretoria for germination trials. Seeds that were not parasitized by fig wasps were removed from feces and figs. Groups of five seeds were isolated from 10 figs and 10 fecal pellets of each of the three possible dispersers. The seeds were planted in two seed trays (each seed in its own compartment) with coarse sand and placed in a temperature regulated room at 25 C with a 14:10 L:D regime. Seeds were watered daily with distilled water and germination was scored with the first appearance of the leaves above the soil surface. The experiment ran for 35 d.

There was no significant difference between the germination success of the four treatments (Kruskal-Wallis, P = 0.092; Table 1), but there was a significant difference in the germination time between the four treatments (Kruskal-Wallis, P = 0.0169; Table 1). A

TABLE 1. Germination success expressed as the number of the 5 seeds in each block that germinated, and the time to germination for the averages of each block of 5 seeds, only considering seeds that germinated.

Treat-	Germination success $(N = 20)$			Days to germination			
		SE	Range	Mean	SE	Range	Ν
Control	2.40	0.30	0–5	24.35	0.97	16.7-33	19
Lizard	2.35	0.33	0–4	20.56	0.85	14–25	16
Bird	1.70	0.34	0–5	23.44	1.10	18–35	15
Hyrax	1.45	0.28	0–4	25.31	1.04	19–34	16

post hoc comparison of mean ranks revealed that seeds eaten by lizards germinated significantly (P < 0.05) faster than those eaten by hyraxes.

Even though we could not show that digestion by lizards enhanced germination success or reduced time to germination, our results suggest that seeds are not adversely affected. The decrease, albeit non-significant, in germination time of lizard ingested over control seeds might be important in harsh and dry environments where seeds have little time to establish themselves after brief and erratic rains.

The rock hyraxes that commonly feed on figs (Smithers, 1971; Compton et al., 1996), also inhabit microhabitats suitable for germination. However, hyrax-ingested seeds germinated significantly slower than lizard-ingested seeds, and many of the seeds eaten by hyraxes were so damaged that they could not be used in the germination trials. Through thorough mastication, mammals commonly reduce the viability of seeds (Compton et al., 1996). Other studies have found that digestion of seeds can increase (birds; Compton et al., 1996) or reduce (fish; Horn, 1997) germination speed or increase the variance in germination time (bats; Izhaki et al., 1995).

To obtain a quantitative impression of the distances over which P. broadleyi may be able to disperse seeds we scanned the surrounding rocks for fecal pellets and measured the distance to the nearest fruiting tree (N = 2 trees). Fresh fecals immediately stick to the rocky substrate and therefore provide an accurate measure of the dispersal effort of the lizard. Platysaurus broadleyi feces containing fig seeds were recorded at an average of 120.0 m (N = 18 fecals, SD = 40.7), ranging from 57 to 187 m from the nearest fig tree. These lizards can thus serve as relatively long distance dispersers. The high numbers of lizards consuming large number of figs beneath fruiting trees (Whiting and Greeff, 1997) have the potential to disperse large numbers of seeds. This evidence suggests that P. broadleyi could be an important seed disperser of F. c. cordata at Augrabies.

Uneaten ripe figs were collected from a tree and brought to the laboratory for calorific analysis with a CP400 mini bomb calorimeter. Figs were oven dried at 60 C. Due to their small size, five groups of five or six figs were ground up together, weighed, and pressed into a pellet, which was loaded into the bomb calorimeter. The figs had an average dry weight of 0.0928 g (N = 29) and contained an average of 22.280

kJ/g (SE = 0.263, N = 4 groups of six fruit and one of five).

The energy content of the figs is similar to the 22.6 kJ/g recorded for insects (Golley, 1961). In terms of energy, one single fig must therefore be the equivalent of many black flies (*Simulium* spp.), which is the most common prey of *P. broadleyi*. Since the lizards do not digest seeds, our estimate of the digestible energy content is liberal, but the fig may represent a substantial reward to the lizard. Another benefit to eating figs in this arid environment is their high water content (87.2% of the pulp of *F. burtt-dawyi*; Compton et al., 1996). It therefore appears as if both the lizards and the fig trees gain from this feeding-dispersal relationship awaits further study.

Acknowledgments.—Nico van der Walt and the National Parks Board are thanked for permission to work at Augrabies and excellent support during our stay. We are grateful to Steve Compton and an anonymous referee for their helpful comments. We thank Jaco Delport for performing the energy analysis.

#### LITERATURE CITED

- BRANCH, W. R., AND M. J. WHITING. 1997. A new Platysaurus (Squamata: Cordylidae) from the Northern Cape Province, South Africa. African J. Herpetol. 46:124–136.
- BRONSTEIN, J. L., AND K. HOFFMANN. 1987. Spatial and temporal variation in frugivory at a neotropical fig, *Ficus pertusa*. Oikos 49:261–268.
- COATES ESTRADA, R., AND A. ESTRADA. 1986. Fruiting and frugivores at a strangler fig in the tropical rain forest of Los Tuxtlas Mexico. J. Trop. Ecol. 2:349– 358.
- COMPTON, S. G., A. J. F. K. CRAIG, AND I. W. R. WA-TERS. 1996. Seed dispersal in an African fig tree: birds as high quantity, low quality dispersers? J. Biogeography 23:553–563.
- CONCEIÇÃO DE SOUZA-STEVAUX, M., R. R. B. NEGREL-LE, AND V. CITADINI-ZANETTE. 1994. Seed dispersal by the fish *Pterodorus granulosus* in the Paraná river basin, Brazil. J. Trop. Ecol. 10:621–626.
- GOLLEY, F. B. 1961. Energy values of ecological materials. Ecology 42:581–583.
- HORN, M. H. 1997. Evidence for dispersal of fig seeds by the fruit-eating characid fish *Brycon guatemalen*sis Regan in a Costa Rican tropical rain forest. Oecologia 109:259–264.
- IVERSON, J. B. 1985. Lizards as seed dispersers? J. Herpetol. 19:293–294.
- IZHAKI, I., C. KORINE, AND Z. ARAD. 1995. The effect of bat (*Rousettus aegyptiacus*) dispersal on seed germination in eastern mediterranean habitats. Oecologia 101:335–342.
- KALKO, E. K. V., E. A. HERRE, AND C. O. HANDLEY. 1996. Relation of fig fruit characteristics to fruiteating bats in the new and old world tropics. J. Biogeography 23:565–576.
- KAUFMANN, S., D. B. MCKEY, M. HOSSAERT-MCKEY, AND C. C. HOROVITZ. 1991. Adaptations for a twophase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). Amer. J. Bot. 78:971–977.
- LAMBERT, F. R., AND A. G. MARSHALL. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. J. Ecol. 79:793–809.

- MOLL, D., AND K. P. JANSEN. 1995. Evidence for a role in seed dispersal by two tropical herbivorous turtles. Biotropica 27:121–127.
- ROBERTS, J. T., AND E. R. HEITHAUS. 1986. Ants rearrange the vertebrate-generated seed shadow of a neotropical fig tree. Ecology 67:1046–1051.
- SMITHERS, R. H. N. 1971. The mammals of Botswana. Mus. Mem. Natl. Mus. Manum. Rhodesia 4:1–340.
- TRAVESET, A. 1990. Ctenosaura similis Gray (Iguanidae) as a seed diperser in a central American deciduous forest. Amer. Midl. Natur. 123:402–404.
- VALIDO, A., AND M. NOGALES. 1994. Frugivory and seed dispersal by the lizard *Gollotia galloti* (Lacertidae) in a xeric habitat of the Canary islands. Oikos 70:403–411.
- WHITAKER, A. H. 1987. The roles of lizards in New Zealand plant reproductive strategies. New Zealand J. Bot. 25:315–328.
- WHITING, M. J., AND J. M. GREEFF. 1997. Facultative frugivory in the Cape flat lizard, *Platysaurus capensis* (Sauria: Cordylidae) Copeia 1997:811–818.

AND ———. 1999. Use of heterospecific cues by the lizard *Platysaurus broadleyi* for food location. Behav. Ecol. Sociobiol. In press.

Accepted: 19 January 1999.

Journal of Herpetology, Vol. 33, No. 2, pp. 330–334, 1999 Copyright 1999 Society for the Study of Amphibians and Reptiles

## The Timing and Pattern of Myogenesis in Hymenochirus boettgeri

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Differences in the relative timing of homologous developmental events among closely related species, known as heterochronies, may provide valuable clues in understanding evolutionary relationships (McKinney, 1988; McNamara, 1995). Examining the timing of myogenic events is a relatively easy and effective method for finding heterochronic events. For example, whether muscle proteins and myofibrils appear before or after multinucleation can be determined through histological techniques (Kielbowna, 1981). Simple observations of live specimens can pinpoint functional landmarks such as first twitch (spontaneous or due to external stimuli) and first heartbeat.

Heterochronies are known to exist in amphibian myogenesis, particularly in the formation of axial muscles. A common pattern of muscle development, as seen in the common Eurasian spadefoot toad (*Pelobates fuscus*), begins in the myotome with the appearance of mononucleated myotomal myoblasts, which then fuse to form elongated, multinucleated muscle cells (Kielbowna, 1981). The muscle fiber then synthesizes myofibrils, which is followed by first twitch (see Radice et al., 1989 for review). *Xenopus lae*-