
MICROHABITAT CHARACTERISTICS OF EGG DEPOSITION SITES USED BY RETICULATED FLATWOODS SALAMANDERS

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Abstract.—The Reticulated Flatwoods Salamander (*Ambystoma bishopi*) is one of three southeastern U.S. ambystomatid salamanders that deposit eggs in ephemeral wetlands without standing water. Eggs typically hatch from inundation by rising water levels during the late fall or early winter. We described microhabitat characteristics of *A. bishopi* egg deposition sites from three ephemeral wetlands on Eglin Air Force Base, Florida during the 2011–2012 winter breeding season. Specifically, we estimated vegetation characteristics and microtopography for 57 egg deposition sites and for paired random sites without eggs. Egg deposition sites were best described by a model that included higher amounts of herbaceous vegetation and increased microtopography (i.e., concave depressions). Herbaceous vegetation is also an important component of larval occupancy and is used by metamorphs and adults. Management of breeding wetlands should include methods that increase cover of herbaceous vegetation, which will likely benefit all life-stages for this federally endangered salamander.

Key Words.—*Ambystoma bishopi*; endangered species; habitat selection; oviposition; wetland restoration

INTRODUCTION

Ambystomatid salamanders have a diverse suite of reproductive strategies, but most members of the genus in the eastern U.S. migrate to breeding wetlands on rainy nights, then court and lay eggs in water-filled wetlands (Petranka 1998; Lannoo 2005). In contrast, three species, Reticulated Flatwoods Salamander (*Ambystoma bishopi*), Frosted Flatwoods Salamander (*A. cingulatum*), and Marbled Salamander (*A. opacum*) migrate to wetlands on rainy, fall/winter nights, court, and lay eggs in dry wetland basins (Anderson and Williamson 1976; Petranka and Petranka 1981a; Hill 2013). Eggs of these species are capable of persisting in the dry basin for over two months (Hassinger et al. 1970; Anderson and Williamson 1976) prior to the wetland filling with water. The breeding sites of flatwoods salamanders (i.e., *A. bishopi* and *A. cingulatum*) fill with water in the fall and winter months of sufficiently wet years. This period of time, when wetlands are not inundated, creates a considerably more complex suite of variables for females to navigate when selecting microhabitat for oviposition within the wetland relative to most other species in the genus. This unique strategy has implications for successful hatching and subsequent larval survival. Female *A. opacum* frequently select sites at intermediate elevations along elevational gradients within the basin (Petranka and Petranka 1981a), but also appear to select nest sites under grass clumps when available (Figiel and Semlitsch 1995). Specific vegetation characteristics may be important for oviposition site selection for flatwoods salamanders as

well. There are noteworthy differences in the reproductive biology of flatwoods salamanders and the Marbled Salamander. An individual Marbled Salamander lays its entire clutch of eggs in a single depression formed by the female and attends its clutch for part or all of the period from laying to inundation-induced hatching (Petranka 1990). In contrast, flatwoods salamanders lay small groups of eggs in multiple locations within a wetland, and do not attend their dispersed clutches (Anderson and Williamson 1976).

The Reticulated Flatwoods Salamander is a federally endangered species and much of its natural history is not well understood (USDI FWS 2009). Some descriptive work has been conducted on the egg deposition habitat of the closely related Frosted Flatwoods Salamander, but eggs are challenging to locate, making them difficult to study. Further, until 2007 *A. bishopi* and *A. cingulatum* were considered a single species (Pauley et al. 2007), so no investigations of egg deposition have been directed towards Reticulated Flatwoods Salamanders. The work by Anderson and Williamson (1976) is an important starting point, because their work suggested *A. cingulatum* uses a variety of egg deposition sites, including the base of bushes, small trees, and clumps of grass. However, no formal analyses have been conducted to compare use versus availability. We examined the egg deposition microhabitat of Reticulated Flatwoods Salamanders. Understanding the microhabitat characteristics and timing of Reticulated Flatwoods Salamander eggs occurring on the landscape as well as persistence of eggs can inform application and

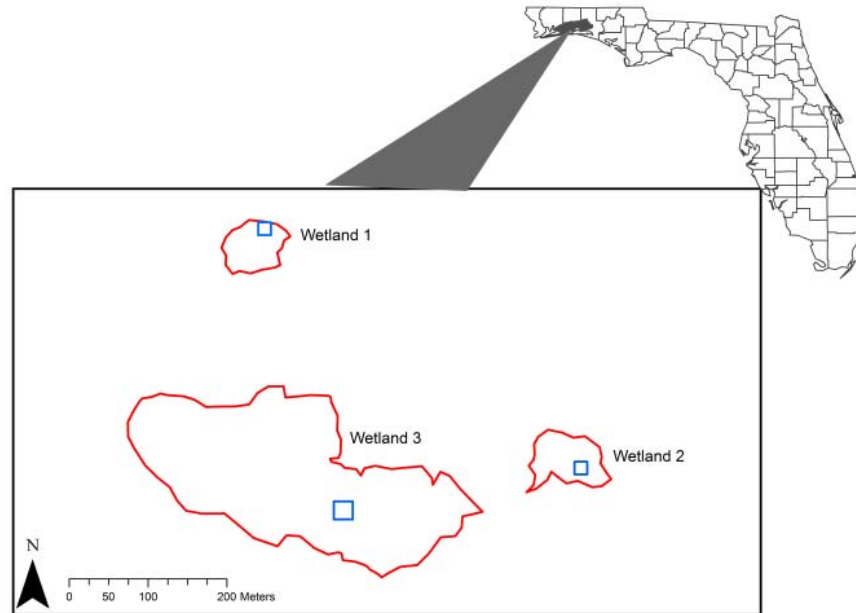


FIGURE 1. Perimeters of Wetlands 1, 2, and 3 (red outlines) with areas searched (blue boxes). Wetland sizes were 0.4, 0.5, and 5.0 ha, respectively. Egg deposition sites of *Ambystoma bishopi* were studied from December 2011 through January 2012 on Eglin Air Force Base, Florida.

timing of management activities, such as prescribed fire and other restoration actions.

MATERIALS AND METHODS

Study area.—We evaluated egg microhabitat in three ephemeral wetlands on Eglin Air Force Base, Okaloosa County, Florida from December 2011 through January 2012. The wetlands used in this study had open overstories (range of % canopy cover: 15.2–46.5%; Gorman et al. 2013) dominated by Slash and Longleaf Pine (*Pinus elliottii* and *P. palustris*), Swamp Tupelo (*Nyssa sylvatica* var. *biflora*), Pond Cypress (*Taxodium ascendens*), and Myrtle Dahoon (*Ilex cassine* var. *myrtifolia*), open to dense midstories dominated by young Myrtle Dahoon, Chapman’s St. John’s-wort (*Hypericum chapmanii*), and Swamp Titi (*Cyrtilla racemiflora*), and understories dominated by Wiregrass (*Aristida* sp.), Longleaf Threeawn (*Aristida palustris*), Rosette Grass (*Dichantheium* sp.), and Flattened Pipewort (*Eriocaulon compressum*), along with a richly diverse mix of subdominant forbs and graminoids (range of herbaceous cover: 31.2–53.8%; Gorman et al. 2013). During the fall/winter breeding season (i.e., including adult migration through typical timing of metamorphosis in a sufficiently wet year) of *A. bishopi*, monthly rainfall from October 2011 through April 2012 averaged 8.77 cm (low = 0.18 cm; high = 16.10 cm) in northwest Florida and was well below average, which was 13.46

cm for this time period (National Weather Service. 2013. Available from www.ncdc.noaa.gov [Accessed 26 June 2013]).

Sampling.—We began searching for Reticulated Flatwoods Salamander eggs on 8 December 2011 and continued this initial effort through 22 December 2011. The initial approach followed a systematic sampling design. We established multiple survey plots that were oriented along a transect that started in the ecotone surrounding the wetland and followed the long axis of the wetland. Plots were spaced every 20–40 m along the transect (we used the longer spacing in the largest wetland to allow complete coverage across the basin). At both ends of the transect (i.e., within the ecotone), we also established two additional egg searching plots perpendicular to the transect, as the ecotone is thought to be important for salamander use (Palis 1996). Each plot consisted of five, 1 × 1 m quadrats in a line that was centered on the transect. Because the three wetlands varied in size (0.4, 0.5, and 5.0 ha, respectively) they contained different numbers of plots. The three wetlands had eight, 11, and 14 plots, respectively, resulting in 165 quadrats; however, five quadrats (at separate plots) were not included because a large tree or other obstruction obscured the majority of the quadrat. This approach was extremely unsuccessful at locating eggs (n = 1 egg deposition site located), so we opted to try an alternative approach.



FIGURE 2. *Ambystoma bishopi* breeding wetland (wetland 2) on Eglin Air Force Base, Florida. (Photographed by Thomas A. Gorman).

The more successful approach that yielded the data presented herein was conducted over an eight-day period from 29 December 2011 to 5 January 2012. We searched for Reticulated Flatwoods Salamander eggs when wetlands were dry. We focused search efforts on portions of the wetlands where in previous years we captured larval Reticulated Flatwoods Salamanders (Gorman et al. 2009). These areas were dominated by dense herbaceous vegetation and a moderate canopy cover (Gorman et al. 2009) and were consistent with breeding site descriptions for *A. cingulatum* (Sekerak et al. 1996). These areas varied in size, but ranged from approximately 250 m² to 400 m² (Fig. 1). We searched these areas of habitat (Fig. 2) completely during the daylight hours by crawling, carefully parting vegetation and lifting debris. Flashlights were used in some cases to make eggs more visible after parting vegetation.

When we located a group of eggs we flagged the site and then selected a paired site using a random compass bearing and a random distance between 1–3 m from the center of the egg deposition site. We defined an egg deposition site as a location containing one or more eggs adjoining each other or separated by < 2 cm. Because females can carry over 100 eggs (Goin 1950), but deposit them in small batches (as in *A. cingulatum*, Anderson and Williamson 1976), we do not refer to a clutch of eggs but use the term egg deposition site.

We estimated vegetation characteristics in 10 × 10 cm plots for 57 egg deposition sites and paired random sites. These plots were aligned with the cardinal directions, and placed so that the egg or group of eggs was in the center of the plot. Within each 10 × 10 cm plot, we visually estimated percent cover of herbaceous vegetation and percent cover of litter using the midpoints of six categorical cover classes (0–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100%) established by Daubenmire (1959). Further, we counted the number of

individual *Dichanthelium* spp. plants, number of individual *Eriocaulon* sp. plants, and number of individual *Xyris* sp. plants. Based on our initial observations in 2010–2011 we expected that these plants would be important for egg deposition, because both *Eriocaulon* sp. and *Xyris* sp. have basal rosettes that we predicted would maintain moisture around eggs prior to inundation. Lastly, we visually estimated microrelief in a 2 × 2 cm plot that was nested in the 10 × 10 cm plots and centered on the group of eggs or on the random point. We assigned microrelief categorically (i.e., concave, convex, or planar) based on small elevation changes along perpendicular axes (on the compass directions) through the 2 × 2 cm plot (modified from Zedaker and Nicholas 1990).

We monitored these egg deposition sites approximately once per week after the sites were found until no live eggs remained. We calculated persistence time from the date of first observation to the last date we saw at least one viable egg. Eggs considered viable included: (1) those with clear and intact egg envelopes containing visible embryos; (2) those with slightly clouded but intact egg envelopes that still contained healthy-looking embryos; and (3) eggs with clear but ruptured egg envelopes containing moving embryos. Because gravid females arrived at these wetlands from 10 November 2011 through 24 January 2012 (Thomas Gorman and Carola Haas, unpubl. data), it is possible that eggs were present for more than a month before we began searching or were laid shortly before we found them; therefore, we could not calculate survival estimates. Unfortunately, we were not able to consistently record development stages of embryos. Eggs were often located under basal rosettes of leaves, or in crevices, and we were concerned about disturbing the eggs or the microhabitats, especially because of their tendency to adhere to nearby materials.

Analyses.—We used a conditional logistic regression for matched pairs data to estimate habitat selection (Compton et al. 2002; Gorman and Haas 2011) of egg deposition sites. Similar to a paired t-test, this approach focuses on the differences between used sites and paired random sites. This analysis is recommended for animals with limited mobility. Moreover, by limiting our random plots to areas within 1–3 m of used plots, the analysis provides for a more realistic comparison of use and availability and allowed for us to collect the random and used habitat variables at the same time so that availability did not change. Ultimately, this framework allowed for a more accurate assessment of the choices female salamanders are making at the time of egg deposition. We developed a model set that consisted of 14 models and combined six variables that were hypothesized to be important to egg deposition sites (Table 1). We hypothesized that structure or species

Gorman et al.—Microhabitat and egg sites of *Ambystoma bishopi*.

TABLE 1. Three overarching hypotheses to explain oviposition site selection of *Ambystoma bishopi* were tested using a suite of models. Variables included are used as the model name. Data were collected at three wetlands on Eglin Air Force Base, Florida.

Hypotheses	Models and associated variables
<i>Hypothesis 1: Females select egg deposition microhabitat based on the structure or composition of vegetation.</i>	
	1. Herbaceous vegetation
	2. <i>Dichantheium</i> spp.
	3. <i>Eriocaulon</i> spp.
	4. <i>Xyris</i> spp.
	5. Herbaceous vegetation + <i>Dichantheium</i> spp.
	6. Herbaceous vegetation + <i>Eriocaulon</i> spp.
	7. Herbaceous vegetation + <i>Xyris</i> spp.
	8. <i>Dichantheium</i> spp. + <i>Eriocaulon</i> spp. + <i>Xyris</i> spp.
	9. Herbaceous vegetation + <i>Dichantheium</i> spp. + <i>Eriocaulon</i> spp. + <i>Xyris</i> spp.
<i>Hypothesis 2: Females select egg deposition microhabitat based on micro-topography and ground-surface structure.</i>	
	10. Litter
	11. Microrelief
	12. Microrelief + Litter
<i>Hypothesis 3: Females select egg deposition microhabitat by seeking micro-depressions in areas with dense herbaceous vegetation cover.</i>	
	13. Herbaceous vegetation + Microrelief
<i>Global Model:</i>	
	14. Herbaceous vegetation + <i>Dichantheium</i> spp. + <i>Eriocaulon</i> spp. + <i>Xyris</i> spp. + Microrelief + Litter

TABLE 2. Descriptive statistics of 57 used sites (eggs of *Ambystoma bishopi* present) and 57 random sites from three breeding wetlands on Eglin Air Force Base, Florida.

	%Litter	%Herbaceous	Microrelief			# of <i>Eriocaulon</i> spp.	# of <i>Dichantheium</i> spp.	# of <i>Xyris</i> spp.
			%concave	%planar	%convex			
Used mean	37.1	62.0	61.4	36.8	1.8	2.79	0.25	0.68
Used SE	4.1	4.0	-	-	-	0.26	0.09	0.19
Random mean	43.9	41.2	21.1	78.9	0.0	2.04	0.51	0.35
Random SE	4.3	4.2	-	-	-	0.27	0.13	0.11

omposition of the vegetation could be important (Hypothesis 1) because plants that form basal rosettes (such as species of *Dichantheium* and *Eriocaulon*) might protect eggs from desiccation and/or predators or because a mucus-like substance produced by some species of *Xyris*, which occur at our sites (e.g., *Xyris ambigua*; Tobe et al. 1998), might help to reduce desiccation of eggs. We hypothesized that microrelief and litter might be important (Hypothesis 2) as eggs laid in crevices or small depressions or among dense leaf litter might be less vulnerable to desiccation or hard freezes. We also considered the possibility that both vegetation and microrelief would be important (Hypothesis 3) in oviposition site selection. To evaluate the models we used an information-theoretic approach and Akaike’s Information Criterion (AIC_c) that was corrected for small sample size (Burnham and Anderson 2002). After model construction we evaluated multicollinearity of variables to avoid over-fitting of models using Pearson correlation coefficient and no variables were highly correlated (all correlations were ≤ 0.34). Within the information-theoretic framework the model with the lowest AIC_c is considered to have the best balance of statistical parsimony and goodness of fit

and models with $\Delta > 2$ are considered to be less supported by the data (Burnham and Anderson 2002). Our analyses were conducted in SAS 9.2 (SAS Institute Inc., Cary, North Carolina, USA) using PROC Logistic and a Strata statement to identify matched pairs between the used and random sites.

RESULTS

We located 57 *A. bishopi* egg deposition sites at three breeding wetlands on Eglin Air Force Base, Florida (Table 2). We located two egg deposition sites at wetland 1, 16 at wetland 2, and 39 at wetland 3. We observed from one to 12 eggs ($\bar{x} = 5.5$) at each egg deposition site (Fig. 3). In the previous year, we located one egg deposition site that contained at least 17 eggs. All eggs were deposited terrestrially and we did not observe any females attending eggs. Although we did not observe females laying eggs, we do monitor water levels in these wetlands, and the wetland basins were dry from before females arrived in November through January.

TABLE 3. Modeling results from a logistic regression of egg microhabitat selection of *Ambystoma bishopi* (n = 57) at three breeding wetlands on Eglin Air Force Base, Florida (k = # of parameters, AIC_c = second-order Akaike's Information Criteria [i.e., for small sample sizes], ΔAIC_c = the change in AIC_c , and w_i = the relative amount of support for the model). The remaining models were omitted from the table, because ΔAIC_c was >12.

Model	k	AIC_c	ΔAIC_c	Log-Likelihood	w_i
Herbaceous veg. + Microrelief	2	58.43	0.00	1.00	0.78
Global	6	61.27	2.84	0.24	0.19
Microrelief	1	66.61	8.17	0.02	0.01
Microrelief + Litter	2	67.04	8.61	0.01	0.01
Herbaceous vegetation	1	70.08	11.65	0.00	0.00

We located many more eggs using the targeted approach, but egg-searching remained a time-consuming process. For instance, on 5 January 2012, two observers searching wetland 3 for a combined total of 8.5 h located 13 egg deposition sites. Of the egg deposition sites that we first found in late December and early January, we observed at least one viable egg persisted for a minimum of eight weeks at one egg deposition site, seven weeks at five sites, and six weeks at four sites. Because of drought, the wetlands did not fill and only one egg deposition site became inundated while the eggs were still viable, and this small puddle in the wetland soon dried again.

Microhabitat selection.—Our modeling suggested that female *A. bishopi* select egg deposition habitat by seeking micro-depressions in areas with dense herbaceous vegetation cover (Table 2). The most highly supported model out of the 14 *a priori* models was a model that included herbaceous vegetation and microrelief ($AIC_c = 58.43$, $w_i = 0.78$; Table 3). *Ambystoma bishopi* used sites that had 1.5 times higher amounts of herbaceous vegetation and were 2.9 times more likely to have concave microrelief than random sites (Table 2). Odds ratios of coefficients predicted a 2.2% increase in the chance of a site being used with every 1% increase in herbaceous cover and the odds of a concave site having eggs was 5 times greater than the odds of a convex or planar site (Table 4). The second most supported model was > 2.0 ΔAIC_c from the most highly supported model ($AIC_c = 61.27$, $\Delta AIC_c = 2.84$, w_i

= 0.24; Table 3) and represented the fully additive global model, which included all the variables (Table 1). While this model received some support, the inclusion of microrelief and herbaceous vegetation drove the strength of this model, because all the other variables were not significant. The remaining 12 models all received very limited support from the data and were > 8 ΔAIC_c from the top model (Table 3).

DISCUSSION

Our findings that female Reticulated Flatwoods Salamanders select egg deposition habitat by seeking micro-depressions in areas with dense herbaceous vegetation cover (Fig. 4) might be related to egg and/or larval survival. Placing eggs in a depression or crevice and sheltering them under the base of a plant may help conserve moisture and reduce the risk of freezing, predation, and/or fire damage (see Powell et al. 2013). Anderson and Williamson (1976) noted that eggs of Frosted Flatwoods Salamanders shrank considerably when exposed to dry conditions. We also observed eggs shrinking and swelling as substrate moisture changed. Also, as in *A. cingulatum* (Anderson and Williamson 1976; Hill 2013), eggs of *A. bishopi* usually adhered to each other and within an egg deposition site were arranged in a clumped or in a somewhat linear pattern.

Once hatched, larvae may not initially be able to travel far in the shallow basins, so hatching within suitable larval habitat may be important for larval survival. Wetland habitat occupied by larvae of Reticulated Flatwoods Salamanders was best described by higher amounts of herbaceous vegetation and lower levels of canopy cover (Gorman et al. 2009) and similarly, larval Frosted Flatwoods Salamanders have been shown to be associated with diverse herbaceous cover (Sekerak et al. 1996). Selection of adequate sites by females may have implications for hatchling survival until they attain sufficient mobility to choose their own cover and foraging areas. Both recent metamorphs and adult salamanders have also been observed using Wiregrass and other graminoids (Jones et al. 2012), so it is apparent that all life-stages are tied to the presence of

TABLE 4. Parameter coefficients, odds ratios, and 95% confidence intervals for the most highly supported model of egg microhabitat selection of *Ambystoma bishopi* at three breeding wetlands on Eglin Air Force Base, Florida.

Parameter	Coefficient	Estimate	Odds Ratio	
			Low	High
Microrelief	-1.5933	0.203	0.078	0.533
Herbaceous vegetation	0.0213	1.022	1.007	1.037



FIGURE 3. Two *Ambystoma bishopi* eggs in a small depression on Eglin Air Force Base, Florida. (Photographed by Kelly C. Jones).



FIGURE 4. View of microhabitat used by Reticulated Flatwoods Salamanders (*Ambystoma bishopi*) for egg deposition on Eglin Air Force Base, Florida. (Photographed by Kelly C. Jones).

herbaceous plants. Management practices (such as fire) that increase herbaceous vegetation in breeding wetlands will likely benefit all life-stages of this species.

Managing wetlands directly for microrelief is likely to be more challenging. This has been accomplished when creating or completely restoring wetlands (e.g., Barry et al. 1996); however, this level of restoration may not be necessary in functionally intact or nearly intact wetlands. Rather, indirectly managing for herbaceous species of plants may have different effects on substrate. In some wetland systems, microtopography varies as a result of species-specific production and decomposition rates (Rocheffort et al. 1990), so managing for plant diversity will likely facilitate heterogeneity of microrelief. Herbaceous vegetation is limiting in many flatwoods salamander breeding wetlands (Bishop and Haas 2005; Gorman et al. 2013) because of competition with woody vegetation or reduced seed production in the absence of growing-season fire. Plant diversity can be influenced by the presence of microtopography, with different species using different portions of the microtopographical continuum. Similarly, consumption of fine fuels may have an impact on the topography, such that fire will burn the duff accumulation in the wetlands heterogeneously and therefore may be another mechanism for creating suitable microrelief for flatwoods salamanders. Peat fires, in particular, can result in creation of depressions within flatwoods wetlands (pers. obs.). Benscoter et al. (2005) found that fire increases the abundance of hollows relative to hummocks.

The maintenance and creation of microrelief in these wetlands may be an important topic for future research on flatwoods salamanders. Microrelief has implications for plant diversity and both should be integrated into wetland restoration goals (see Vivian-Smith 1997; Bruland and Richardson 2005). Our observations did not reveal any evidence of excavation of egg deposition

sites by females (i.e., soil did not appear to be freshly disturbed). The one observation of a Frosted Flatwoods Salamander in the process of laying did not include excavation (Hill 2013), but this has been observed in Marbled Salamanders (Petranka and Petranka 1981b).

This behavior may be more likely to occur in species such as Marbled Salamanders, which deposit all eggs in one location as opposed to flatwoods salamanders which lay eggs in multiple locations. Previous authors have mentioned the prevalence of burrows (Means et al. 1996) and burrowing crayfish (Goin 1950; Ashton 1992; Sekerak et al. 1996; Palis 1997) in wetlands that support flatwoods salamanders and even described eggs being deposited at the mouth of crayfish burrows (Anderson and Williamson 1976). Our observations did not include any eggs associated with crayfish burrows, but the relationship between burrows and flatwoods salamanders in general could be an area worthy of further study (e.g., Ashton 1992).

Further investigations into oviposition site selection based on elevation gradients within a wetland basin would be interesting, as these gradients have been shown to influence oviposition site selection in Marbled Salamanders (Jackson et al. 1989; Petranka 1990). However, elevation gradients within ephemeral wetland basins are often associated with significant shifts in vegetation structure, and it may be difficult to isolate those factors (but see Croshaw and Scott 2006). Woody encroachment in the higher and/or lower elevation portions of wetlands may narrow the range of suitable sites available to females for oviposition, and sites with high densities of diverse herbaceous vegetation across a wide range of elevations within the wetland would be ideal for these types of investigations. Selection of elevation gradients by Marbled Salamanders has been linked to soil moisture and/or microhabitat characteristics (Petranka and Petranka 1981a; Petranka 1990; Figiel and Semlitsch 1995).

We confirmed that *A. bishopi* does deposit eggs terrestrially, singly or in small clusters, and with no prolonged attendance by the female, similar to the breeding behavior of *A. cingulatum* (Anderson and Williamson 1976; Hill 2013). Egg deposition sites differed distinctly from random sites. Restoration of known flatwoods salamander breeding sites and other potential Reticulated Flatwoods Salamander breeding wetlands is in progress at Eglin Air Force Base. Canopy cover is responding well to treatments, but herbaceous vegetation has been slow to recover at some wetlands (Gorman et al. 2013). Taking into consideration all life stages will be critical to successful management and recovery of this species.

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