

Declines in Ravine-inhabiting Dusky Salamanders of the Southeastern US Coastal Plain

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Abstract - Gully-eroded and steephead valleys on Eglin Air Force Base in the Florida panhandle were sampled for the abundance of four species of ravine-inhabiting, plethodontid salamanders in two separate periods, 25 years apart. In this interval, *Desmognathus auriculatus* (Southern Dusky Salamander) appears to have gone extinct and the abundance of *D. cf. conanti* (Spotted Dusky Salamanders) has decreased by about 68%. There was no change in the average abundance of *Eurycea cirrigera* (Two-lined Salamander). *Pseudotriton ruber* (Red Salamanders) declined in ravines from which larger populations of *D. auriculatus* disappeared, but increased in ravines from which smaller populations of *D. auriculatus* had disappeared. There was a slight increase in the average abundance of *P. ruber* in ravines that were inhabited by *D. cf. conanti*, but those changes in *P. ruber* abundance were unrelated to the changes in the abundance of *D. cf. conanti*. Declines in populations of *D. auriculatus* were also noted in Louisiana and Georgia; evidence suggests that all of these declines began in the mid-1970s. There are several potential causes of the regional declines, but no single explanation appears sufficient to explain declines in all populations. Feral pig rooting eliminates the larval seepage habitat of desmognathine salamanders and may be partly responsible for the declines on Eglin Air Force Base.

Introduction

Extinction and precipitous population declines in amphibians have been reported for many species the world over, even from relatively pristine habitats (Houlahan et al. 2000, Stuart et al. 2004). These examples primarily involve the anurans, frogs and toads. Disappearances of individual species are the most well-known examples (e.g., *Rheobatrachus silus* Liem [Gastric-brooding Frog; Ingram and McDonald 1993], and *Bufo periglenes* Savage [Golden Toad; Crump et al. 1992]), but in some locations, entire faunas of unrelated frog species have declined catastrophically (Laurance et al. 1996, Lips 1998). Reports of declining salamanders have been fewer (Blaustein et al. 1994b, Dodd 1997), less convincing (Pechmann et al. 1991), or restricted to a small portion of the species' range (Dodd 1997, Means et al. 1996).

The largest salamander family, Plethodontidae, has not been implicated in precipitous declines (Hairston and Wiley 1993). Declines in plethodontid populations would be especially important to an ecosystem because these salamanders are often extremely abundant and, in many locations, are an important source of high-quality energy for a variety of predators (Burton and Likens 1975, Petranksa and Murray 2001).

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Like many streamside-inhabiting plethodontids, *Desmognathus auriculatus* Holbrook (Southern Dusky Salamander) has been reported as an abundant inhabitant of streams in the southeastern US Coastal Plain (Means 1974, 1975, 2000). While some population declines were noticed in the mid-1970s (Means cited in Dodd 1997, 1998), these were considered to be within the range of normal population fluctuations. A recent report by Dodd (1998) that the species had disappeared from one locality in peninsular Florida, however, suggested that other populations of the species might have declined. If so, this would be the first example of a general decline in any plethodontid and, if part of a general species-wide or area-wide pattern, could have important consequences for the ecosystem processes in their stream and ravine habitats.

In this paper, we use data from surveys of salamander abundance in streams in the western Florida panhandle in two periods, twenty-five years apart, to assess whether there is a general decline in the abundance of *D. auriculatus* and the abundances of three other plethodontid salamanders that occur in the same (*Eurycea cirrigera* Green [Two-lined Salamander], *Pseudotriton ruber* Latreille [Red Salamander]) or similar (*D. cf. conanti* Rossman [Spotted Dusky Salamander]) habitats. We report what appear to be precipitous declines and perhaps extinctions of many populations of *D. auriculatus*, declines in the populations of *D. cf. conanti*, and the effects of those declines on the abundance of the syntopic species *P. ruber* and *E. cirrigera*.

Methods and Materials

Natural history

Dusky salamanders (subfamily Desmognathinae of the lungless family Plethodontidae) are found widely distributed in the US east of the Mississippi River, with outliers in eastern Texas, Oklahoma, and Arkansas (Conant and Collins 1998, Petranka 1998). Many occur in or adjacent to mountain stream habitats of the Appalachian Mountains or other interior highlands, with the exception of one high-elevation terrestrial species and one burrower (Petranka 1998). A number of species live in the low-elevation Coastal Plain, a band of land skirting the southeastern corner of the US from New Jersey to Texas. There, many populations of dusky salamanders, along with other streamside-dwelling plethodontids, live in ravine habitats that approximate the mountain stream habitat of the interior highlands (Means 2000).

Cool, humid ravines are critical habitats for Coastal Plain plethodontid salamanders because ravines offer refuge from the intense mid-summer heat and desiccation (Means 2000). The Florida panhandle is better endowed with ravines that provide optimum plethodontid habitat close to the seacoast than any other part of the extensive Coastal Plain from Virginia to eastern Texas, because the area uniquely possesses a special type of ravine called "steephead" (Means 1975, 1991, 2000). Steepheads are formed by spring sapping of surficial groundwater aquifers in deep, porous deposits of sand.

Whereas classic gully-eroded ravines are usually dry in their first-order reaches (Strahler 1964) unless it has recently rained, water flows permanently all along steepheads where spring water emerges from the toe of steep slopes. This water is characterized by relatively constant temperatures year-round (19–22 °C) and constant chemical composition. The perennial seeps associated with steepheads, therefore, are ideal habitats for mountain stream-loving salamanders (Means 2000).

Steepheads and ravines across the Florida panhandle are populated by Red Salamanders, Two-lined Salamanders, and one of three species of *Desmognathus* (Means 1975, 2000). The endemic species *D. apalachicola* Means and Karlin occupies ravines in the Apalachicola, Ochlockonee, and lower Chattahoochee drainage basins (Means and Karlin 1989). Habitats further west are occupied by a *Desmognathus* that appears to be an undescribed species (D.B. Means, unpubl. data) that we refer to here as the *D. cf. conanti*. Additionally, Means (1975) discovered that in the western part of the Florida panhandle, several small drainages emptying independently into the Gulf of Mexico are occupied by *D. auriculatus*, instead of *D. cf. conanti*. Although *D. auriculatus* is more generally found in swampy habitats in other areas of Florida, the other desmognathines are not. Population genetic data is consistent with extremely low to negligible rates of movement of *D. apalachicola* and *D. cf. conanti* among ravines (Blouin 1986). In this paper, we present data taken in the streams that, up through the mid-1970s, were occupied either by the *D. auriculatus* or *D. cf. conanti*.

Study area and data

The principal study area is a group of 129 deep, shaded, cool steepheads and ravines on Eglin AFB in Santa Rosa, Okaloosa, and Walton counties, FL (Fig. 1). We also examined data from other localities on Eglin AFB and elsewhere in the Florida panhandle. Salamanders were collected by D.B. Means on all visits to sites between 1969 and 1998 (some sites were sampled more than once), with one or more other people assisting 22% of the time. Salamanders were collected in a standard fashion: suitable-appearing microhabitats were investigated by crawling on hands and knees and scraping decomposing litter from the substrate using either the hands or a potato rake. Sometimes we used the side of the boot to scrape back the top few centimeters of decomposing litter off the top of small mucky depressions.

The data in this paper were apportioned over two time periods about 25 years apart, 1969–1975 and 1 October 1997–30 September 1998. In the 1970s, all specimens were collected and preserved. In the 1990s, all salamanders were counted, but only a few larvae and one or two metamorphosed specimens were collected and preserved.

Field surveys on Eglin AFB were grouped in the following manner: 1) all localities in which *D. auriculatus* had been collected in the 1970s; 2) all localities in which *D. cf. conanti* had been collected in the 1970s; 3) a new set of 37 localities in which *D. auriculatus* was endemic; and 4) a new set of 40 localities in which *D. cf. conanti* was endemic. Sites of the latter two groups

had not been visited previously by the authors. We collected for a minimum of one hour at all the localities, except in those few that had been altered by impoundment, sedimentation, or some other gross mechanical disturbance that left the site with very little suitable habitat for plethodontids. Most of the

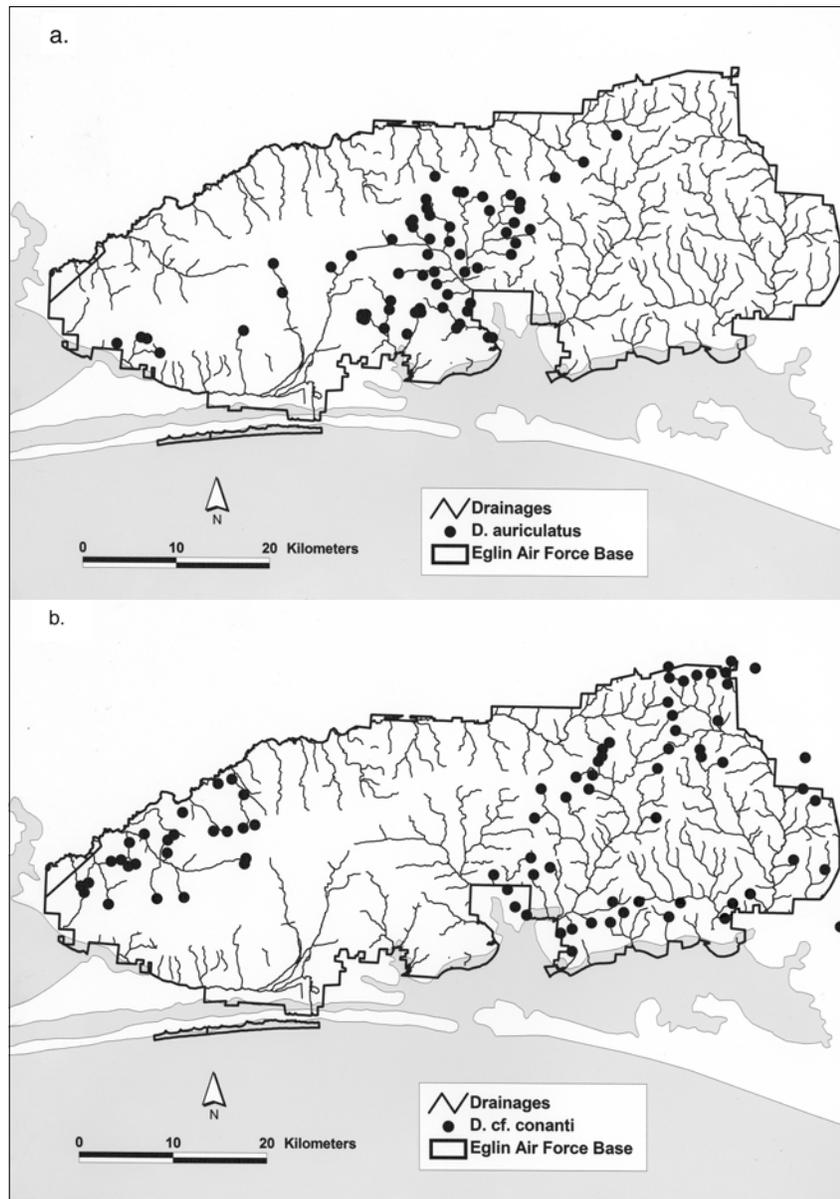


Figure 1. Distribution of steepheads and ravines in which (a) *Desmognathus auriculatus* and (b) *D. cf. conanti* are endemic on Eglin Air Force Base and vicinity, Santa Rosa, Okaloosa, and Walton counties, FL.

Eglin AFB ravines have remained in the same, relatively pristine ecological condition over the 25 years of this study. No logging of the slope hardwood forests ever took place in the steephead habitats, and the surrounding sandhill uplands have remained undeveloped. The hydrology of steephead streams is driven by the seepage of large, surficial aquifers so that water flow is relatively continuous and nonfluctuating, even during the most severe droughts (Means 1991, 2000; Wolfe et al. 1988).

Statistical analyses

Statistical analyses were performed on catch per unit effort (CPUE): in this case, the number of animals captured per hour of searching (hereafter denoted as rate of capture). Analyses of CPUE perform best when there is little variation among samples in the search time. For these data, the coefficients of variation in number caught (0.76 to 1.48) exceeded those in search time (0.32 to 0.71). The difference is more marked in the matched comparisons of catch and effort for each individual ravine. We assume that detection probabilities did not change over time.

Results

The two species of *Desmognathus* have declined dramatically since the 1970s, and *D. auriculatus* is effectively extinct in these ravines (Table 1). In the 1970s, the average rate of capture of *D. auriculatus* in 26 ravines was 8.65 salamanders per hour. No salamanders of this species were seen in the 1990s, neither in the same ravines sampled in the 1970s nor in 37 novel ravines. The change in capture rate in the 26 ravines sampled twice is significant (matched pairs $t = 7.18$, $P < 0.001$).

In the 1970s, *D. cf. conanti* was more abundant than *D. auriculatus*, with an average rate of capture in 26 ravines of 13.56 salamanders per hour (Table 1). This rate was lower in 22 of the same ravines in the 1990s, an average decline of about 68%. The difference in rate of capture between visits to the same ravines is significant (matched pairs $t = 4.16$, $P < 0.001$). Prior sampling cannot explain this change; there is no significant difference in rate of capture between resampled ravines and ravines surveyed for the first time in the 1990s (average rate of 4.40 salamanders per hour, $t = 0.14$, NS).

Table 1. Average rate of capture plus one standard error of four salamander species in ravines designated by the desmognathine species that was present in the 1970s.

Species	Ravine type					
	<i>D. auriculatus</i>			<i>D. cf. conanti</i>		
	1970s	1990s old	1990s novel	1970s	1990s old	1990s novel
<i>D. auriculatus</i>	8.65 (1.29)	0	0	-	-	-
<i>D. cf. conanti</i>	-	-	-	13.56 (2.12)	4.66 (1.12)	4.40 (1.05)
<i>P. ruber</i>	4.95 (1.17)	5.80 (1.12)	5.83 (0.82)	2.83 (0.57)	3.61 (0.77)	3.06 (0.55)
<i>E. cirrigera</i>	2.59 (0.59)	2.99 (0.72)	4.60 (0.67)	3.63 (1.57)	3.67 (0.74)	2.85 (0.44)

Data for *P. ruber* exhibit three interesting patterns. First, in both sampling periods and for novel or resampled ravines, *P. ruber* was more abundant in *D. auriculatus* ravines than in *D. cf. conanti* ravines (Table 1). Across sampling periods, the rates of capture of *P. ruber* in *D. auriculatus* ravines averaged about 5.3 salamanders per hour, but only about 3.2 salamanders per hour in *D. cf. conanti* ravines. The difference between ravine types was significant ($F = 7.74, df = 1, 168, P = 0.006$).

Second, the overall abundance of *P. ruber* has not changed across time. The rates of capture of *P. ruber* increased by 17–27% across the decades, but the large variation among ravines precludes this difference from being statistically significant.

Third, although on average there was no change in *P. ruber* abundance, the changes in a subset of ravines showed a strong pattern (Fig. 2). In ravines that had been inhabited by *D. auriculatus*, the change in *P. ruber* abundance was positively correlated with the change in *D. auriculatus* abundance ($r = 0.46, P < 0.05$). Ravines that suffered greater declines in *D. auriculatus* abundance also had declines in *P. ruber*, whereas ravines that lost small populations of *D. auriculatus* actually exhibited increases in *P. ruber* abundance. In ravines that were inhabited by *D. cf. conanti*, there was no relationship between the change in *P. ruber* abundance and the change in the abundance of *D. cf. conanti*.

The rates of capture of *E. cirrigera* were comparable between *D. auriculatus* and *D. cf. conanti* ravines (3.4 and 3.5 respectively), but they

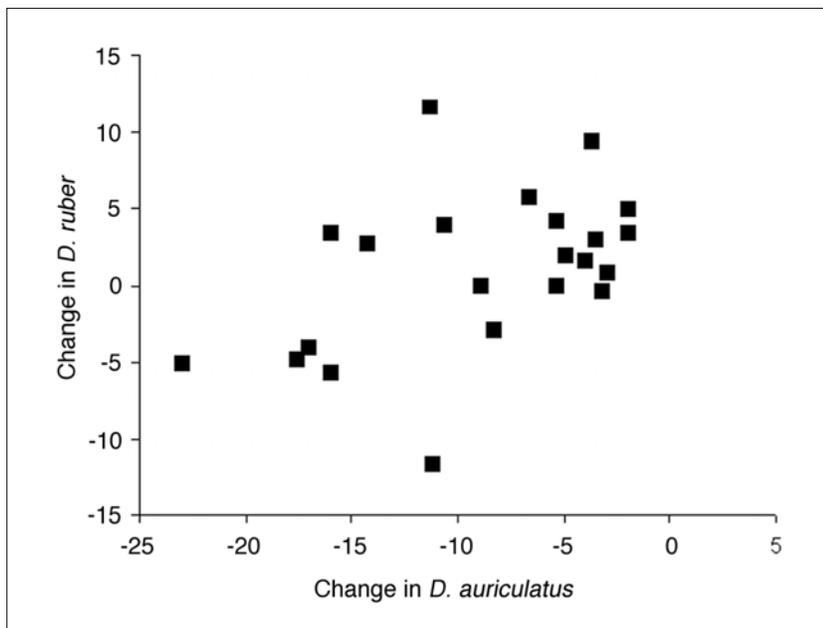


Figure 2. The relationship of the change in rate of capture of *P. ruber* between the 1970s and 1990s to the change in the rate of capture of *D. auriculatus* in the same ravines across the same interval.

exhibited no consistent change across sampling periods or ravine types (Table 1). Neither the magnitude nor the direction of change in the rate of capture of *E. cirrigera* in a ravine was related to either the type of ravine (*D. auriculatus* or *D. cf. conanti*) or the magnitude of change in the desmognathine population in the ravine.

It is unlikely that these results are artifacts of sampling. The percentage decrease in average rates of capture of the two *Desmognathus* species between decades far exceeds the percentage decrease in average sampling durations between the 1970s (1.60 hours, s.e. = 0.20) and 1990s (1.31 hours, s.e. = 0.19). Moreover, rates of capture of the other species were either higher (*P. ruber*) or comparable (*E. cirrigera*) in the 1990s to the rates in the 1970s, which should not be the case if our results were driven entirely by the slightly shorter sampling durations in the 1990s. While our method did not control for a variety of factors that can affect detection probabilities (e.g., recent rainfall history, air temperature; see MacKenzie et al. 2002), variation in these factors should have increased the variance among ravines within each period, which makes the difference in rates of capture between periods more notable and the statistical tests of these effects conservative.

Discussion

The decline of *D. auriculatus*

Once the most abundant salamander in the steepheads and floodplain swamps it occupied, *D. auriculatus* now appears to be entirely absent from the 185,600-ha Eglin Air Force Base. It is possible, at least in theory, that by sampling only twice, we have inadvertently sampled high and low points of normal population fluctuations. However, for this to be the case, all 129 populations of the two desmognathine species would have to be fluctuating synchronously, which seems unlikely. Even if this were the case and all desmognathines were in the same numerical trough, we would have expected to find at least a few individual *D. auriculatus* in the nearly 80 hours spent searching 63 ravines.

Desmognathus auriculatus is also missing from several other localities in Florida where it had been abundant in the early 1970s (based upon collection records in the Florida State and Louisiana State museums and the Coastal Plains Institute). *D. auriculatus* was abundant in the Ochlockonee River floodplain (below Old Bainbridge Road in Leon County), but have not been seen since 1971. In the Telogia Creek floodplain (Liberty County), no *D. auriculatus* have been seen since 1974. The last Southern Dusky Salamander in Deep Springs Canyon, a large steephead of Econfinia Creek (Bay County), was observed in 1976, in spite of many efforts to find it there in the 1990s (D.B. Means, pers. observ.).

Perhaps the most striking decline, for historical reasons, has occurred at Silver Glen Springs, FL (Marion County). Neill (1951) brought formal attention to this population by naming it *D. f. carri*, which was subsequently placed in the synonymy of *D. auriculatus* (Means 1974, Rossman 1959). Neill's

(1951) type series contained a collection of 22 juveniles and adults taken on 12 November 1950 and another of 18 juveniles and adults collected on 29 January 1951. On 25 November 1958, Rossman (1959) found *D. auriculatus* abundant at this site, collecting 36 specimens, and Christman's (1970) report was based on 91 specimens he collected from three sites including Silver Glen Springs. D. Rossman (LSU Museum of Natural History, Baton Rouge, LA, pers. comm., 1999) said that Silver Glen Springs was the most robust population of *D. auriculatus* he had seen at that time. On 16 February 1972, S.P. Christman and D.B. Means found 9 specimens in one person-hour of searching in the vicinity of the spring boils, and the species was common in the surrounding hardwood bottomland swamps ($n = 10$; 1.5 person-hours). On three collecting trips between June 1994 and March 1995 to collect *D. auriculatus* at Silver Glen Springs, R. Franz and K. Dodd were unsuccessful (Dodd 1998), but Christman found two or three individuals in November 1995 (Dodd 1998).

The four habitats discussed above were high quality, extensive habitats that previously supported large populations of *D. auriculatus*, but which produced few or no specimens after about 1975. In fact, there are only two localities in the Florida panhandle where *D. auriculatus* has been found recently: Monkey Creek in the Bradwell Bay Wilderness Area on the Apalachicola National Forest in Wakulla County and a large cypress swamp on the Apalachicola National Forest in southern Liberty County, about 18 km west of the Monkey Creek site. Both sites are acidic, blackwater swamps and are very different habitats in comparison with the rheophilic ravines.

Desmognathus auriculatus has also declined or been extirpated in other states. At a site on Anderson Branch of Hunters Creek, GA (Irwin County), one larva and 26 juveniles and adults were collected on 15 December 1971 and 25 January 1972 in 6 person-hours of effort. The site was revisited 14 years later in 1986, and no *D. auriculatus* were found in 3 hours of intensive collecting, while on 18 March 1995, with 4 hours of vigorous searching, one small juvenile was found. Of 2789 *D. auriculatus* specimens in southern Louisiana museum collections from the Florida parishes, only 14 (0.5%) were collected after 1975. On the basis of localities, *D. auriculatus* was collected from only 2 of 75 historic localities since 1980. On the other hand, 21% of the *D. cf. conanti* in collections were taken after 1975, and the species has been collected in 11 of 71 localities since 1980 (Boundy 2005; J. Boundy, Louisiana Department of Wildlife and Fisheries, Baton Rouge, LA, pers. comm.).

Based on the accumulated evidence, a widespread decline or extirpation of *D. auriculatus* has taken place in many Coastal Plain localities. In the ravines on Eglin AFB, *D. cf. conanti* has also declined. It is important to note that all of these declines may have begun at approximately the same time, in the mid-1970s. A similar conclusion was reached for the timing of the extinction of *D. auriculatus* in Devil's Millhopper in central Florida (Dodd 1999). We do not have comparable data on abundance of *D. apalachicola* or the rarer *D. monticola* Dunn, and there is no evidence from our field work, or that of other herpetologists in the area, that these species have undergone any comparable decline.

Changes in *P. ruber*

The abundance of *P. ruber* in ravines inhabited by *D. cf. conanti* showed no significant change between the 1970s and 1990s, but their abundance in *D. auriculatus* ravines changed in proportion to the magnitude of the *D. auriculatus* decline. Ravines that had held larger populations of *D. auriculatus* showed declines in their *P. ruber* populations and ravines that had held smaller desmognathine populations showed increases. One hypothesis for this pattern is that the loss of Southern Dusky Salamanders represented a significant loss of prey for *P. ruber*, which is a well-known predator of other salamanders (Gustafson 1993, Petranka 1998). The failure to see a similar pattern in the *D. cf. conanti* ravines could be ascribed to the possibility that *D. auriculatus* was a more important resource for *P. ruber* than is *D. cf. conanti*, a possibility bolstered by the observation that, in the 1970s, average *P. ruber* abundance in *D. auriculatus* ravines was 75% higher than their average abundance in *D. cf. conanti* ravines. Of course, a second, equally viable hypothesis is that the changes in *P. ruber* abundance were driven by factors other than changes in the desmognathine abundance; those factors could be the same as those that affected the desmognathines or they could be entirely different.

Potential causes of the declines of desmognathine populations

Any explanation for the widespread declines and extinctions in *D. auriculatus* and *D. cf. conanti* must account for the absence of any negative effect on the syntopic *P. ruber* and *E. cirrigera* or the abundance of the other members of the genus *Desmognathus* in north Florida. The major hypotheses include one or more of the effects posited to cause amphibian declines in other regions (overcollecting, acid rain, ultraviolet-B radiation, toxic substances, disease), and the indirect effects of *Sus scrofa* Linnaeus (feral pigs) on habitat structure.

It is possible that different factors have combined to affect different populations and that there is no single cause for these declines. The simplest explanation is that D.B. Means over-collected every population that he sampled in the 1970s. This hypothesis is unlikely for three reasons. First, quantitative studies in other streamside communities indicate that a far greater collecting effort would be necessary to create a long-term loss of animals (Hairston 1986, Petranka and Murray 2001). Second, only the desmognathines declined, not the hemidactylines, which were collected in the same samples. Third, the hypothesis is inconsistent with the fact that the densities of the desmognathines were just as low in ravines that had not been sampled in the 1970s as in those that had. In addition, the population in Monkey Creek within the Bradwell Bay Wilderness Area seems to be thriving despite periodic collections by D.B. Means from this population.

Three causes of other amphibian declines—acid rain, ultraviolet-B (UV-B) radiation, and toxic substances—are unlikely to be important in these cases. For one reason, the effects would have to be confined to two species of *Desmognathus* and not to other, syntopic plethodontids. In addition, the

habitats used by these species seem unlikely to be affected by these factors. Florida receives fairly high levels of acid rain (Brezonik et al. 1980), but *D. auriculatus* inhabits some of the most naturally acid wetland habitats in the Coastal Plain (Means 1999). In fact, as already mentioned, it is in acid swamps that known populations still exist. One might expect acid rain to affect *D. cf. conanti*, which exclusively occupies ravines in which aquifer water or rainfall is circumneutral to slightly acid, yet this species remains extant, albeit in lower abundances. While ambient ultraviolet-B (UV-B) radiation causes significant embryonic mortality in some amphibian species (Anzalone et al. 1998; Blaustein et al. 1994a, 1995), the more susceptible populations studied to date occur at high elevations (1190–2000 m) and breed in shallow lakes and other wetlands that are open to full sunlight. The habitats of the plethodontid salamanders reported here are much lower in elevation (0–200 m) and densely forested. In addition, the plethodontids live in microhabitats that are naturally protected from UV-B such as in decomposing leaf litter and water, or under logs, rocks, and the soil surface beneath moss or fern ground cover. While toxic substances such as heavy metals, herbicides, and pesticides cannot be discounted (Diana and Beasley 1998), their effects must be very selective among species in order to account for the patterns documented here.

Disease caused by a microbial pathogen is a plausible cause of the declines noted here (Faeh et al. 1998). Differential susceptibility to a pathogen could be correlated with phylogenetic affinity, which would account for the selective nature of the declines and the differential severity between *D. auriculatus* and *D. cf. conanti*. The persistence of populations in and around the Monkey Creek area might be explained by a simple failure of the pathogen to invade those populations, even though it would have invaded all of the surrounding populations.

The effect of feral pigs on habitat structure is a prime candidate for some of the declines. Feral pigs eat and uproot plants (Hardin 1994, Lipscomb 1989), eat animals (Douglass and Winegarner 1977, Wood and Roark 1980), modify the soil by mixing organic and mineral layers (Ebenhard 1988), and mechanically disrupt microtopographic relief of seepage wetlands, thereby altering microhydrology (Layne 1997; D.B. Means, pers. observ.; Randall et al. 1997). The first evidence of feral pig rooting in an Eglin AFB steephead was not noticed until 26 February 1975. However, during 1997–1998, severe feral pig damage was observed in 77 of 160 (48%) steepheads and ravines, moderate damage in 19 of 160 (12%), light damage in 3 of 160 (2%), and little or no evidence of recent pig rooting was recorded for 61 (38%) steepheads and ravines.

There are limited data that feral pigs eat salamanders (Singer et al. 1982, Springer 1977), but the more likely effect of feral pig rooting is to alter the larval habitat of the desmognathines, and perhaps thereby have a greater effect on these species than the hemidactylines. The larvae of both *D. auriculatus* and *D. cf. conanti* in steepheads are found on small, sandy, seepage sites with only a thin sheet-flow (2–5 mm) of water and covered with a veneer of decomposing,

multicolored leaf litter. *Psuedotriton ruber* hatchlings are found in such habitats for a short while until they are about the size of the largest desmognathine larvae, at which time they move into deeper, mucky pools. The larvae of *E. cirrigera* are most commonly found in flowing water where seepage collects in small rivulets, and larger *E. cirrigera* larvae are also found in mucky or wet peaty sites with *P. ruber*. Suitable habitat for desmognathine larvae is confined to the upper reaches of the steephead, whereas patches of mucky habitat for hemidactyline larva occur throughout the stream course. Repeated pig rooting transforms the gentle seepage slopes that are habitat for desmognathine larvae into flat, submerged beds of deep organic matter—exactly the habitats preferred by the larger *P. ruber* and *E. cirrigera* larvae. Besides adult salamanders hiding under leaf and twig litter on seepage slopes, *Diplocardia mississippiensis* Smith (earthworms) in the soil are probably what pigs are seeking in the seepage slopes. Once a seepage slope has been converted to a mucky pool, further pig rooting does not change the habitat preferred by the hemidactyline larvae.

While it is likely that feral pigs have affected the desmognathines in Eglin AFB ravines, the wider disappearance of *D. auriculatus* from diverse localities across the species range in which there is no evidence of feral hog depredations suggests either that a more pervasive agent, such as a pathogen, is acting or that there is no single cause for the species decline. Those few localities (Monkey Creek, Apalachicola National Forest) in which *D. auriculatus* still can be found are highly acidic, flatwoods swamps. Possibly, the acidity of blackwater environments precludes pathogens such as viruses, bacteria, and chytrid fungi, all known pathogens that negatively affect amphibians (Lannoo 2005). A range-wide survey of all known populations of *D. auriculatus*, plus a search for new localities, should be mounted immediately. There should also be a search for any candidate pathogens in this species. Discovering declines such as those reported here, and determining their cause, highlights the importance of establishing a nationwide biomonitoring program (Bishop and Pettit 1992, Kim and Knutson 1986, National Research Council 1993).

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