Detecting Enigmatic Declines of A Once Common Salamander in the Coastal Plain of Georgia

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Abstract - For amphibian species suspected of undergoing enigmatic declines, it is important to determine the effort required to confidently establish species absence. *Desmognathus auriculatus* (Southern Dusky Salamander) has purportedly gone from being quite common throughout the southeastern US Coastal Plain to now being enigmatically rare. We used repeated standardized surveys of 5 historically occupied streams and their adjacent riparian zones between 2007 and 2010 to estimate detection rate of Southern Dusky Salamanders. We detected Southern Dusky Salamanders at 3 of 5 historic sites. Mean detection rate across streams known to be occupied at least once during the study was moderately low (mean ± 1 SE = 0.20 ± 0.12 for a double-sampled 50-m survey), improved at 2 sites with increasing time since drought, and varied among streams. For comparison, we evaluated detection rates of several other stream salamanders and found those rates to range from 0.37 (± 0.07) for *Eurycea quadridigitata* (Dwarf Salamander) to 0.08 (± 0.01) for *Siren intermedia* (Lesser Siren). Based on mark–recapture along a 200-m section of stream and the associated riparian habitat at the site where Southern Dusky Salamanders were most often detected, we estimated 43 (± 15) and 97 (± 161) individuals to be present February–May 2009 and October 2009–May 2010, respectively. Despite abundant adults, Southern Dusky Salamanders were the only species that we failed to detect as larvae; however, we observed many newly metamorphosed Southern Dusky Salamanders—usually under logs with saturated soil and often near entrances to crayfish burrows. Our results generally support the characterizations of Southern Dusky Salamanders as having become enigmatically uncommon. Because landcover change in the study area has been minimal, we suspect habitat damage from *Sus scrofa* (Feral Pig) may be responsible for the variation in Southern Dusky Salamander presence and abundance among sites. Because of the low detectability of Southern Dusky Salamanders, future work to identify factors driving Southern Dusky Salamander distribution and abundance will require intensive sampling at sites to provide robust estimates of occupancy or population size.

Introduction

Amphibian population declines are recognized as a large component of an accelerating and complex biodiversity conservation crisis (Berger et al. 1998, Collins 2010, Pounds et al. 1999, Wilcove and Master 2005). Multiple and different factors can contribute to population declines and local extirpation including interactions

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with invasive species, habitat loss and degradation, climate change, over-exploitation, ultraviolet radiation, contaminants, and emerging infectious pathogens (reviewed by Blaustein and Kiesecker 2002, Collins 2010, Collins and Storfer 2003, Lannoo 2005, Semlitsch 2003). Ultimately, any specific decline is likely the result of multiple interacting factors (Blaustein and Kiesecker 2002), and identifying the etiological agents of a decline is often a challenge.

The apparent decline of *Desmognathus auriculatus* (Holbrook) (Southern Dusky Salamander) populations across large portions of the species' range is an example of an "enigmatic" amphibian decline (Graham et al. 2010). Southern Dusky Salamanders are found exclusively within the coastal plain of the southeastern United States. The southeastern US is a global hotspot for salamander diversity, but declines of some species such as *Ambystoma cingulatum* Cope (Frosted Flatwoods Salamander) and *Notophthalmus perstriatus* Bishop (Striped Newt) have been documented. These declines are largely attributed to habitat loss and alteration (Means 2005, Palis and Means 2005). Southern Dusky Salamanders inhabit swamps and blackwater creeks, and were routinely described as the most common and abundant salamander in blackwater habitats (Means and Travis 2007). However, the species has conspicuously declined across its range including at sites within large protected areas (Beamer 2005, Dodd 1998, Means and Travis 2007). Causes of decline may include impacts of *Sus scrofa* L. (Feral Pig), disease (Graham 2006), and habitat loss and alteration; however, no cause has been conclusively linked to the decreases in Southern Dusky Salamander detection throughout its range (Means 2005).

For species that are difficult to detect due to rarity or cryptic behavior, monitoring and conservation planning can be challenging. Even demonstrating that management is necessary for a species such as Southern Dusky Salamanders is complex. Predecline reports of species counts do not reliably quantify search effort (Dodd 1998), and in some cases salamanders of other species may have been counted as sightings of Southern Dusky Salamanders (Beamer and Lamb 2008, Graham et al. 2010). Because few historical data exist to quantify the magnitude of declines, future management of the species must rely on the most reasonable assessments of historical population estimates, combined with robust monitoring approaches that maximize efficiency of survey efforts. Short, simple surveys are often insufficient to reliably determine a species' absence at a site (Dodd and Dorazio 2004). To address this issue quantitatively, managers and conservation biologists need tools that will provide reasonable assurance that failure to find the species is not a false negative.

Our goal was to estimate detection and abundance patterns among historic Southern Dusky Salamander sites at Ft. Stewart, GA, and to use this information to further evaluate the steps required to adequately monitor this species throughout its range. To meet this goal, we determined the level of sampling necessary to determine confidently that Southern Dusky Salamanders (and other stream salamanders for comparison) are no longer present at a site, and we provide an estimate of population size for Southern Dusky Salamanders at one occupied site. Based on our experience and results, we propose a tiered process for evaluating causative agents of suspected range-wide population declines in rare and secretive species.

Field–Site Description

We focused the field-based portion of this study within the boundaries of Ft. Stewart, GA. Fort Stewart is located approximately 30 miles west of Savannah and has been in operation since 1940. All of our sampling locations were in the northwest area of the installation within the Canoochee River system (Fig. 1). The area is characterized by frequently burned flatwoods and sand hills, and networks of slow-moving blackwater creeks. Genetic evidence has shown that the only Desmognathine salamander found in this area is the Southern Dusky Salamander (Beamer and Lamb 2008).

Site selection on Ft. Stewart began in August 2007 when the creeks that were dry the previous year from a prolonged drought filled with some late summer rains. Using information from recent surveys (Graham 2006), and consultations with the military base's biologist (Dirk Stevenson), we identified 4 initial sites with historic records of Southern Dusky Salamanders for this study. We later added a fifth site where it was suspected and we later confirmed that Southern Dusky Salamanders might occur. The proximity of these sites allowed us to sample all of them repeatedly over a 1- to 4-day period, which provided an opportunity to assess detection probabilities for Southern Dusky Salamanders and other species at those sites. The majority of sites were characterized by a shallow, braided stream network with stands of *Taxodium distichum* L. (Bald Cypress) and *Nyssa aquatica* L. (Water

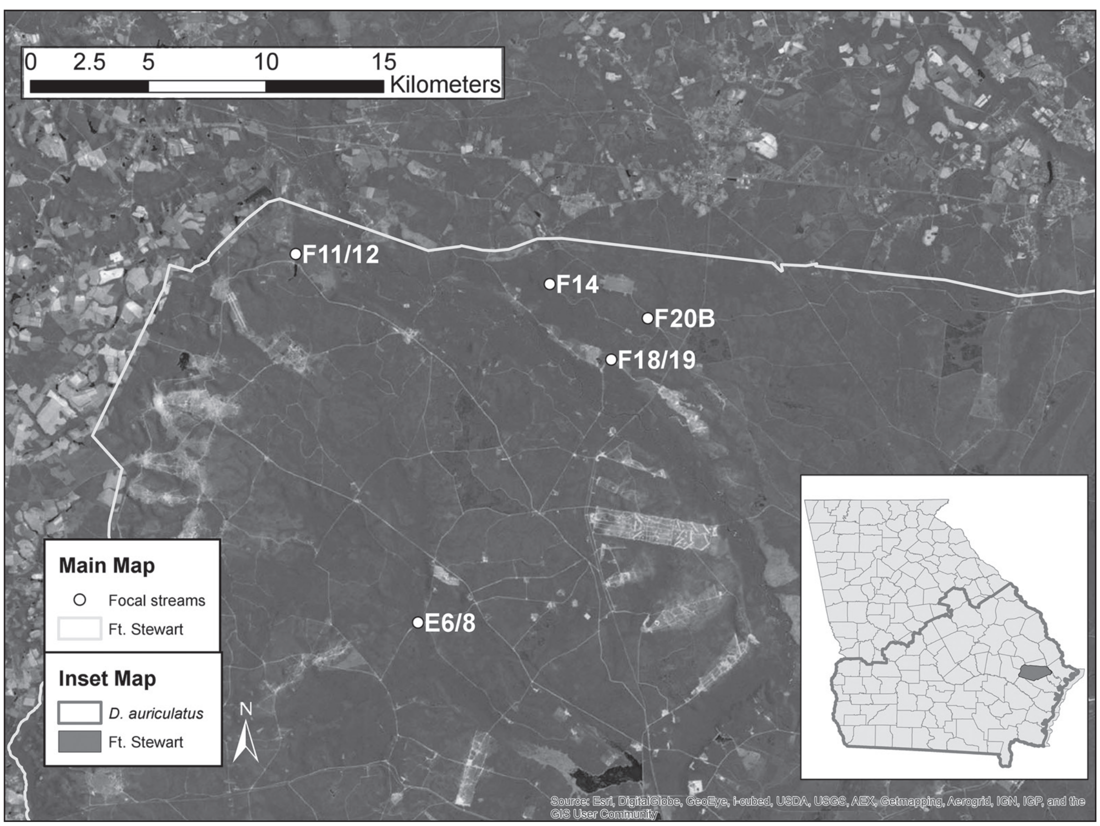

Figure 1. Location of the study sites found within Ft Stewart, GA. The imagery shows the relatively undeveloped watersheds within which the focal streams are located.

Tupelo). One site (F11/12) was a deeply channeled, quick moving creek that was atypical of the region. Though F11/12 did not fit the classic description of Southern Dusky Salamander habitat, it was a listed historical site.

Methods

Sampling methodology

From November 2007 to January 2008, we conducted preliminary sampling at all sites except F14 to evaluate methods for Southern Dusky Salamander surveys. In February 2008, we established four 50-m transects along the water line during each site visit, and we sampled these transects twice (up and back) on 2 consecutive days. This procedure was followed in February, March, April, and May of 2008, and twice more in February 2009. In March, April, May, October (1 and 29), and December 2009 and April and May 2010, we only made a single-day sampling visit to all sites (Fig. 2). During each sample pass, we dip-netted an area ~1-m wide out from the water line as well as raked the leaf litter and turned all cover objects >5 cm in diameter in a 1-m swath directly adjacent to the water line. Activities on the military base made it routinely difficult to travel to site F11/12, so we eliminated

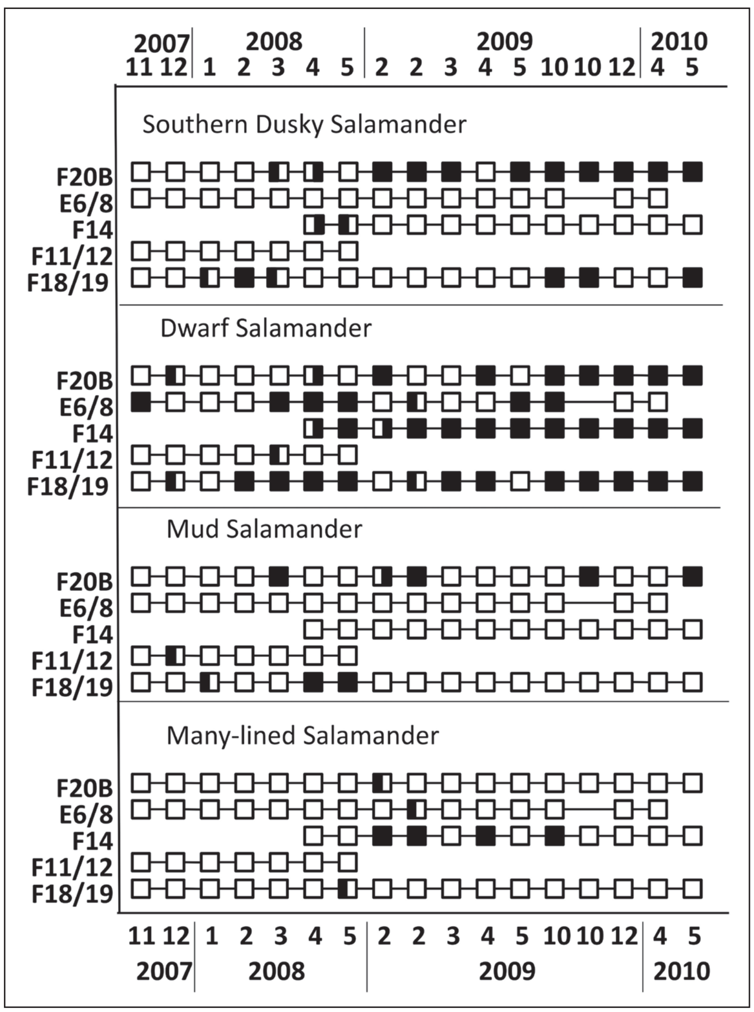

Figure 2. Irregular detection of Southern Dusky Salamanders, Dwarf Salamanders, Mud Salamanders, and Many-lined Salamanders at 5 focal study sites on Ft. Stewart, GA. Dates range from November 2007 to May 2010. Months listed twice were sampled at the beginning and the end of that month. Hollow symbols represent no detection, and shaded symbols indicate a positive detection. The amount of shading (1/2 vs. full) indicates whether the species was detected on one or both consecutive days of sampling (respectively). Left-side shading indicates the species was detected on Day 1 and right-side shading indicates detection on Day 2. Samples from March 2009–May 2010 were single-day samples only.

this site from our regular sampling protocol after May 2008. In April 2008, we identified a new site (F14) for Southern Dusky Salamanders. From May 2008 to May 2010, we focused only on 4 sites: F18/19, E6/8, F20B, and F14. At each site on each sample day, we surveyed 4 consecutive 50-m transects twice each (once up and once back). Data on water temperature, water depth, soil temperature, pH, dissolved oxygen, and conductivity were collected at E6/8, F11/12, F18/19, and F20B on five occasions from November 2007 to January 2008, but do to few detections of Southern Dusky Salamanders during that period we were not able to model the influence of those factors on detection rate. In November 2008, we collected site-level variables at E6/8, F14, F18/19, and F20B, including percentage of area covered in leaf litter, depth of leaf litter, and percentage of riparian zone with signs of pig activity (assessed visually in 10% increments).

For all Southern Dusky Salamanders (and occasionally, for other species) captured, we recorded species, life stage (adult or larva based on the absence or presence of gills, respectively), sex, snout–vent length, total length, and wet mass. Data on capture location (water, leaf litter, or cover object) and capture technique were recorded for most, but not all encounters. All Southern Dusky Salamanders were uniquely marked using visible implant elastomer (VIE) and then released at their original capture location (University of Georgia IACUC #A2007-10190).

Analyses

Data from all sampling occasions were used to describe general patterns of species richness and capture numbers across sites. We used data from sampling months during the period February 2008–May 2010 to calculate the detection probability for each species at each site, and then we calculated a mean detection probability and standard error among all streams or only those streams where a species was detected during our study. We report this as the mean probability and standard error of detecting the species at a site, assuming it is present, during a double–sampled 50-m survey (up and back) of the water line. We extrapolate this value to derive the mean cumulative probability of missing a species during consecutive surveys of a stream, which provides a guideline for the number of surveys required to ensure sufficient sampling effort. We calculated these probabilities for Southern Dusky Salamanders and for 4 other sympatric species (*Eurycea quadridigitata* [Dwarf Salamander], *Pseudotriton montanus* [Mud Salamander], *Siren intermedia* [Lesser Siren], and *Stereochilus marginatus* [Many–lined Salamander]). We included these other members of the stream salamander assemblage in our analysis to demonstrate the efficacy of these survey methods for species occupying similar habitats as Southern Dusky Salamanders.

Detection probability was calculated in the manner detailed above, rather than the more formalized calculations offered by programs such as Presence (MacKenzie et al. 2006), which would require sampling of a larger number of sites. A Bayesian approach may have provided a viable alternative (Kéry 2009); however, we did not explore that option. For all species except Southern

Dusky Salamanders, we only used streams where at least one individual was detected during the sampling period to estimate detection probability. To assess general patterns of detection probability for Southern Dusky Salamanders*,* we used 2 different approaches. First, we used all study sites (E6/8, F11/12, F14, F18/19, and F20B) where Southern Dusky Salamanders were historically present. The second, more conservative approach, involved only using the 3 sites where Southern Dusky Salamanders were detected during our sampling efforts beginning in February 2008. We felt the first, more liberal approach, was worth exploring for 2 reasons. First, while we never detected Southern Dusky Salamanders at E6/8 or F11/12, the species had been found at both streams within the past 14 years (D. Stevenson, The Orianne Society, Athens, GA, pers. comm.). Second, we failed to detect the species consecutively from one month to the next at several of the sites, and on consecutive days in 6 cases at 3 different streams (Fig. 2). Thus, these 2 analyses bracket detection rates for Southern Dusky Salamanders at these historic sites.

Site F20B provided a sufficient number of Southern Dusky Salamander recaptures to estimate population size using a robust design framework in Program MARK (Williams et al. 2001). Because this species undergoes metamorphosis in late spring in Georgia (Means 2008), and we only captured individuals post-metamorphosis, we consider primary sampling periods to be delimited by May sampling periods—the period after which one might begin to capture individuals from a new cohort. Specifically, we divided samples into 3 primary sampling periods (February 2008–May 2008, February 2009–May 2009, and October 2009–May 2010), with 7, 7, and 5 secondary sampling periods in each, respectively. In all models, immigration and emigration were fixed at zero, and survivorship was assumed to be equal across primary sampling occasions. We evaluated 3 models; in each, hypothesized abundance parameters across sample occasions were unique, but models varied based on assumptions about capture/recapture probabilities (*p*) across occasions (Table 1). The number of parameters that could be estimated for models was limited because the population size of this species was low even at the site where it was the most abundant. Despite the limited ability to explore a large number of model structures, we feel that our targeted approach strikes an appropriate balance between ignoring issues of detection probability altogether and over-stepping the analytical constraints inherent to small datasets.

Table 1. Hypothesized models of capture/recapture probabilities and associated support for Southern Dusky Salamanders at stream F20B, Ft. Stewart, GA. The "primary only" model indicates detection probability was set to vary only across primary sampling occasions (see Methods for details), while the "all occasions" model represents a scenario in which detection probability varies across each visit to the site. The p = c(.) model represents a constant capture and recapture probability.

Model	AICc	ΔAICc	AICc weight	Model likelihood
$p = c(.)$, N(t)	74.26	0.00	0.52	1.00
$p = c$(time specific, primary only), N(t)	74.43	0.17	0.48	0.92
$p = c$(time specific, all occasions), N(t)	143.41	69.15	0.00	0.00

Results

Physical conditions

Water levels and other conditions showed dramatic variation temporally. Water-quality variables at E6/8, F11/12, F18/19, and F20B varied temporally. Dissolved oxygen varied remarkably over the sampling period from a mean across all sites of 40% and 44% (range = 23–63%) in November and December 2007, respectively, to a mean of 80% (range = 73–86%) in January 2008. Mean water pH across sites was low (4.92; range = 4.49–5.79) and relatively stable temporally. Average litter depth showed little variation across sites, with a low mean value of 2.0 cm at E6/8 and a high mean value of 2.4 cm at F18/19. Similarly, the percentage of plots covered by leaf litter (as measured in November 2008) varied little, ranging from 86% at F20B to 94% at F11/12. The percentage of area turned recently by Feral Pigs was 78% and 67% at E6/8 and F14, respectively. In contrast, we observed no pig activity at sites F18/19 and F20B.

Species- and assemblage-level summary data

Between November 2007 and May 2010, we spent ~800 person hours sampling amphibians on Ft. Stewart, including at least 160 person hours each at the 4 localities believed to be the most likely to yield Southern Dusky Salamanders. We captured 443 salamanders of 8 different species (Table 2). The Dwarf Salamander was the most frequently detected salamander species followed by the Many-lined Salamander, Southern Dusky Salamander, and *Plethodon ocmulgee* (Ocmulgee Slimy Salamander). Larvae were the most frequently detected life stage for Southern Two–Lined Salamanders, Lesser Sirens, and Many-lined Salamanders, while adults were more commonly found for Mud Salamanders and Dwarf Salamanders. No larval Southern Dusky Salamanders were captured.

We captured a total of 41 Southern Dusky Salamanders at 3 sites (F18/19, F20B, and F14) with 1 recapture of the only individual caught at site F14, and 8

Table 2. Captures of salamanders from Ft. Stewart, GA, study sites. Numbers indicate the count of individuals located at each site.

	Sites				
Species	E6/8	F11/12	F14	F18/19	F20B
Desmognathus auriculatus Holbrook (Southern Dusky Salamander)	–	–	1	7	33
Eurycea cirrigera Green (Southern Two-lined Salamander)	–	28	–	1	–
Eurycea quadridigitata Holbrook (Dwarf Salamander)	41	1	119	55	16
Pseudotriton montanus Baird (Mud Salamander)	–	1	–	5	11
Siren intermedia Barnes (Lesser Siren)	–	–	8	19	–
Siren lacertina L.(Greater Siren)	–	1	–	–	–
Stereochilus marginatus Hallowell (Many-lined Salamander)	–	–	55	1	1
Plethodon ocmulgee Highton (Ocmulgee Slimy Salamander)	–	–	8	2	30

individuals recaptured at least once from F20B (yielding 0.06 captures/person-hr). Ninety-four percent of Southern Dusky Salamander captures were of individuals found by turning cover along the stream bank or just at the water line. One individual was located while raking leaf litter, and 1 was dip-netted from the stream. No Southern Dusky Salamanders were found at site E6/8 or F11/12. Southern Dusky Salamanders ranged in size from 22 to 68 mm SVL and 42 to 122 mm TL, with an average mass of 2.5 g (range = 0.3–5.0 g). Of the 34 individuals on which we attempted to make a sex determination, 11 were female, 7 were male, and 16 were recently metamorphosed juveniles. Two of the 11 females were gravid upon capture (found in March 2008 and February 2009). Fourteen of the 16 recently metamorphosed juveniles were found during or after the fall of 2009.

Detection probability

Assuming all study sites were occupied, we estimate that the mean detection probability (± 1 SE) for Southern Dusky Salamanders when double-sampling a 50-m transect was 0.15 (± 0.10). The mean detection probability for Southern Dusky Salamanders among the 3 sites where we found the species during our study was 0.20 (± 0.12). These detection rates were intermediate to other salamander species observed among the same streams during our study (Table 3). The mean detection probability for Dwarf Salamanders (0.37 ± 0.07) was the highest among all salamander species we encountered.

In terms of sampling effort, to be ≥90% confident that a species that was not detected at a site was indeed not present, the average minimum number of double samples of a 50-m transect would be 5, 11, 19, 24, and 27 for Dwarf Salamanders, Southern Dusky Salamanders, Mud Salamanders, Many-lined Salamanders, and Lesser Sirens, respectively (Table 3). These estimates do not address variation in detection among sites. For example, detection is often a function of density, and at F20B, where we captured the majority of Southern Dusky Salamanders, we detected individuals on 45% of samples. In contrast, we detected Southern Dusky Salamanders at F14 and F18/19 during only 6% and 11% of samples, respectively. Our estimates of mean detection probability assume that detection remained constant through time for the sample period used; however, detection of some salamander species appears to have increased at some sites after March 2008 (e.g., Southern Dusky Salamanders at F20B), which was approximately 6 months after the drought broke (Fig. 2).

Population status at F20B

We recorded 40 captures of Southern Dusky Salamanders (of 33 individuals) within a 200-m length of stream and riparian area at Site F20B, with 7 recaptures of marked animals. We were able to execute 3 models, which allowed us to assess the effects of variation in capture/recapture probability on estimates of population size. The model assuming constant p and the model assuming p varied among primary sampling occasions had nearly identical support based on comparisons using Akaike's Information Criterion (AIC; Table 1). Model averaging (± unconditional SE) of these 2 models for second and third primary periods yielded abundance estimates of 43 (± 15) and 97 (± 161) individuals per 200-m length of riparian forest, respectively. The model assuming *p* varied among primary sampling occasions was responsible for the larger estimate of mean abundance and its associated high unconditional standard error in the model averaging results for Period 3. The constant *p* model for that period provides an estimate of abundance that is more similar to that in Period 2 (40 ± 16 individuals). Estimates for the first primary period were non-identifiable in the period-dependent model, and were estimated to be suspiciously low in the constant-*p* model (4.5 ± 3.2 individuals). The estimate for individual capture probability generated by the constant-*p* model for site F20B was low (0.07). For the model where capture/recapture probability was allowed to vary across primary periods, *p* was only identifiable for Periods 2 and 3, but each value was similar to that from the constant-*p* model (0.09 ± 0.03 and 0.02 ± 0.02, respectively).

Table 3. Mean detection probability and associated probability of missing a species if present across a range of sampling numbers for select salamander species at Ft. Stewart, GA, between November 2007 and May 2010. A "sample" refers to a double-search (up and back) of a 50-m transect along the water line including dip-netting all areas within 1 m of water line, and raking all debris and searching all cover 1 m above the water line. For each species, the minimim number of samplesat which one would have a ≤0.10 (*) and ≤0.05(**) chance of not detecting the species after a specified number of visits. Note that only a subset of sample numbers are shown.

	Species					
	Southern Dusky Salamander[A]	Southern Dusky Salamander[B]	Dwarf Salamander[B]	Mud Salamander[B]	Many-lined Salamander[B]	Lesser Siren[B]
Mean detection probability (SE)	0.15 (0.10)	0.20 (0.12)	0.37 (0.07)	0.11 (0.03)	0.09 (0.07)	0.08 (0.01)
No. sites where species was detected	-	3	5	3	3	2
# of samples	Probability species was present, but not detected					
1	0.85	0.80	0.63	0.89	0.91	0.92
2	0.73	0.64	0.39	0.79	0.83	0.85
3	0.62	0.51	0.24	0.70	0.75	0.78
4	0.53	0.41	0.15	0.62	0.68	0.72
5	0.45	0.33	0.10*	0.55	0.62	0.66
7	0.33	0.21	0.04**	0.44	0.51	0.56
11	0.17	0.09*	0.01	0.27	0.35	0.40
15	0.09*	0.04**	0.00	0.17	0.24	0.28
19	0.05**	0.01	0.00	0.10*	0.16	0.20
24	0.02	0.00	0.00	0.06	0.10*	0.13
25	0.02	0.00	0.00	0.05**	0.09	0.12
27	0.01	0.00	0.00	0.04	0.08	0.10*
31	0.01	0.00	0.00	0.03	0.05**	0.07
35	0.00	0.00	0.00	0.02	0.04	0.05**

[A]Estimates based on detection rate among 5 streams where the species was historically reported present.
[B]Estimates based on detection rate among streams where streams where the species was detected during this study.

Discussion

Our results generally support other recent characterizations of Southern Dusky Salamanders as having gone from historically "common" to enigmatically uncommon in various parts of the species' range (Graham et al. 2010, Means and Travis 2007). On Ft. Stewart, Southern Dusky Salamanders were difficult to detect at most sites, except after February 2009 at a single site (F20B). Means and Travis (2007) report catching 8.65 Southern Dusky Salamanders per person-hour during the 1970s in the Florida Panhandle, and Graham et al. (2010) found 6 Southern Dusky Salamanders at F18/19 in 1 hour of searching in 2006. The number of Southern Dusky Salamanders captured by Graham et al. (2010) in 1 hour in 2006 is comparable to the total number we captured over 31 months at the same site. There were historic reports of Southern Dusky Salamanders at E6/8 and F11/12 within the past 14 years (D. Stevenson, pers. comm.); however, we estimate the probability that *S*outhern Dusky Salamanders were present but went undetected at E6/8 or F11/12 during our study period is <0.005. Thus it would be reasonable to conclude that Southern Dusky Salamanders have declined at Ft. Stewart. However, by focusing on extensive sampling of 5 focal streams over a 31-month period rather than single, concurrent samples over broad geographic areas (e.g, Graham et al. 2010), our results suggest that drought effects on local populations could limit detection for several years, and make it difficult to distinguish sites where the species is temporarily undetectable from sites where the species is genuinely rare or absent.

All of our study streams were dry from August 2006 through October 2007, and this was the second prolonged drought within a decade. Though occupancy of some stream-breeding salamanders can remain high during drought years (Price et al. 2012), extreme droughts are linked to amphibian population declines at other sites within the region (Daszak et al. 2005). We found that 2 years post drought, dusky salamanders became relatively common and easy to detect at one historic site (F20B), while remaining rare or absent at other nearby historic sites. The best evidence that drought was the major factor initially driving low salamander detection was the low detection rates of Dwarf Salamanders at all sites from November 2007 through February 2008 (Fig. 2). Dwarf Salamanders are widespread and abundant in forested blackwater habitats in the region. From November 2007 through April 2009, detection of Dwarf Salamanders increased among all sites, and by October 2009 we found Dwarf Salamanders in large numbers at every site sampled (Fig 2). We continued to detect Dwarf Salamanders in high numbers on every visit at 3 sites from October 2009 through May 2010.

Detection of Southern Dusky Salamanders followed a similar pattern at sites F20B and F18/19, with no detections in November and December 2007, periodic detections from January through May 2008, and then consistent detections at F20B from February 2009 through May 2010 (Fig. 2). However, unlike Dwarf Salamanders, we only saw a consistent increase in Southern Dusky Salamander detection at F20B, and F20B was the only site where we ever detected multiple individuals during a visit. Estimates from mark–recapture at F20B indicated that individual capture probability was low. Low capture probability may explain why Southern Dusky Salamanders are difficult to detect at sites where abundance is also low.

The absence or low abundance of Southern Dusky Salamanders at historic sites proximate to one site where they remain relatively common suggests that local factors are important determinants of Southern Dusky Salamander abundance. Large amounts of habitat have been altered across the range of Southern Dusky Salamanders; however, it is unlikely that habitat loss is linked to the apparent rarity of Southern Dusky Salamanders in Georgia and within Ft. Stewart. First, watersheds across Georgia with historical Southern Dusky Salamander populations have lost little forested wetland habitat between 1974 and 2005, and forested wetland remains the second largest land-cover class within historical Southern Dusky Salamander watersheds in Georgia (Maerz 2010). Second, Southern Dusky Salamanders appear increasingly rare even in watersheds contained within large protected areas such as Ft. Stewart, where the watersheds that include our focal sites have not experienced any significant land-cover change over the past 30 years (Maerz 2010). We hypothesize that the most likely factor contributing to the rarity of Southern Dusky Salamanders and potentially other salamanders is the activity of Feral Pigs. We observed extensive pig damage at sites E6/8 and F14, where Southern Dusky salamanders were rare or extirpated. In contrast, we did not observe any comparable hog damage at F20B, where Southern Dusky Salamanders were regularly detected, or at F18/19, which was our second best site for detecting the species. Our observations are consistent with those of Means and Travis (2007) for Southern Dusky Salamanders in Florida where the species appears to have declined and is now characterized as rare concurrent with extensive damage by Feral Pigs.

We feel it is important to note that despite our finding numerous breeding adult Southern Dusky Salamanders at F20B, that species was the only one we failed to detect as larvae at Ft. Stewart. Sampling for larval salamanders is a common approach for rapid inventory and monitoring because it is often a relatively highly detectable life stage for many species (Graeter et al. 2013). We successfully detected larvae of several uncommon salamander species with few if any adult detections, so the failure to detect larval Southern Dusky Salamanders despite captures of breeding adults is notable. Moreover, we observed many newly metamorphosed Southern Dusky Salamanders in 2009 and 2010. One metamorphic Southern Dusky Salamander was captured in a dip net at the wetted edge of F18/19, but the remainder of metamorphic Southern Dusky Salamanders were found under logs away from the main stream channel. In many cases, the soil was saturated with the water table near the soil surface, and the metamorphic Southern Dusky Salamanders were often positioned within pooled water and near entrances to crayfish burrows. Little is known about the larval natural history of Southern Dusky Salamanders, which hampers our ability to fully understand the factors that regulate the species' distribution and abundance and identify causes of local declines. We speculate that larval Southern Dusky Salamanders may occur in subsurface waters around blackwater streams, which would limit the effectiveness of stream sampling to detect larvae, and could also contribute to the species' sensitivity to the impacts of Feral Pig damage to soils along the margins of blackwater streams.

As with any species, evaluating factors potentially affecting Southern Dusky Salamander distribution and abundance depends on establishing accurate patterns of occupancy among sites. Because detection rates for the species can be low and sensitive to recent weather events such as drought, it will be necessary to be strategic when selecting sites for comparison and to maximize survey effort at those sites in order to detect a relationship between environmental factors and species occurrence. Our study lays the groundwork for a more rigorous future assessment connecting environmental factors such as land-cover change or Feral Pig damage to the current status of Southern Dusky Salamanders in Georgia. Our study can be used to inform the amount of sampling that may be required to confidently determine Southern Dusky Salamander presence or absence. Detection is not an intrinsic property of a species (Mazzerolle et al. 2007); however, it is reasonable to use estimates from prior studies and other sites to guide future research.

Collectively, the work we have done suggests a series of steps that will optimize resources applied to assessment, monitoring, and management of rare or cryptic wildlife. First, it is important to estimate sampling effort required to detect species with a desired level of confidence. Once a desired, robust sampling effort is determined, then a subset of sites selected across an identified gradient (e.g., land-cover change or habitat alteration by invasive species) should be sampled. Further, more-intense monitoring efforts such as mark–recapture studies can be conducted within a subset of occupied habitats (Conroy et al. 2008). More-robust data on occupancy and abundance among sites along an environmental gradient will allow for rigorous tests of whether specific factors are contributing to the current status of species within a region. This approach contrasts with the more traditional approach of sampling all (or most) historical sites to assign presence or abundance and then correlating variables post hoc to that pattern. In most cases, sampling effort may be insufficient due to low detection, researchers will have little confidence in assigning presence or absence, and causal inferences may be weak. We recognize the value of searching for post hoc correlations when there is no clear mechanism explaining declines; however, when reasonable hypotheses can be formulated, we believe that resources diluted in sampling many sites would be better allocated to more focused sampling of mechanistic gradients established a priori. The effort required to document the enigmatic decline of a rare species is considerable. A combination of environmental gradients identified a priori and occupancy-based surveys provides a framework that will likely yield the most efficient use of limited resources.

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