California Tiger Salamander Biology and Conservation

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Workshop Topics

1) How is the CTS different from other tiger salamanders?
2) Where does it occur and what limits its distribution?
3) Why has it declined and what are the greatest threats?
4) How to identify the different stages in the CTS life cycle.
5) Life history, demography, and population dynamics.
6) Ecology: habitat attributes, prey, and predators.
7) Movements, metapopulations, and landscapes.
8) Strategies for avoidance, minimization, conservation, and recovery
9) Survey methods, requirements, and strategies

Key Facts for Understanding CTS

- Breed in ponds – develop as aquatic larvae
  - ponds must hold water until at least May
- Larger ponds are better (but not permanent ponds)
- The CTS is primarily a terrestrial beast
  - live in small mammal burrows
  - observed to move >1.5 km overland
- Large areas of <u>contiguous or interconnected habitat</u> is what's needed for its conservation
  - CTS coexist with certain human land uses
  - Habitat loss (and hybridization) are the main threats

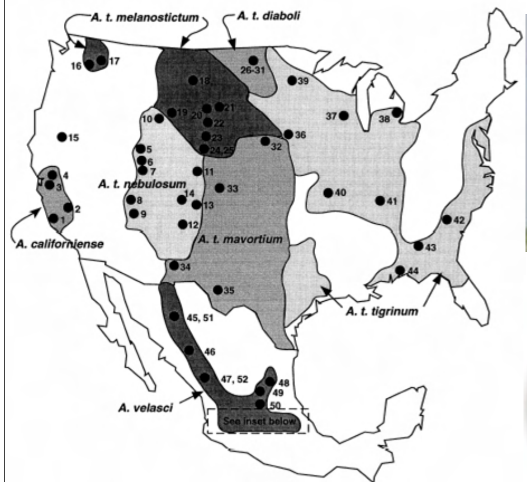
Getting your own permit

- Start early! It will likely take a year (or more)
  - talk to agency representatives throughout process
- FWS requirements
  - B.S. in biology (or equivalent experience)
  - Course work in herpetology (or eq. exp.)
  - Study/survey design experience (5 surveys/40 hrs)
  - Handling experience (>25, including >5 larvae)
  - Familiarity with habitats
  - Familiarity with co-occurring amphibians
  - Ability to identify vegetative components of habitat

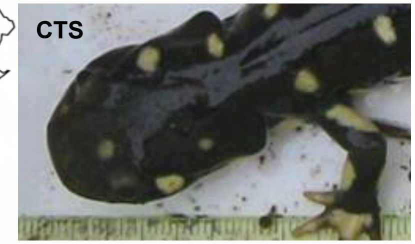
What is a CTS

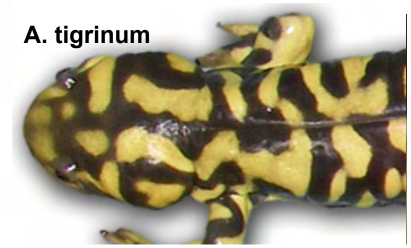
- **Amphibian**
  - aquatic eggs, thin scale- less skin
- **Salamander**
  - four legs and a tail
- **Mole salamander**
  - Family Ambystomatidae
- **Tiger salamander**
  - large terrestrial salamanders and the only group to <u>occupy grasslands</u>
- ***Ambystoma californiense***

Pattern and Head Shape Differ From *Ambystoma tigrinum*



Shaffer and McKnight 1996

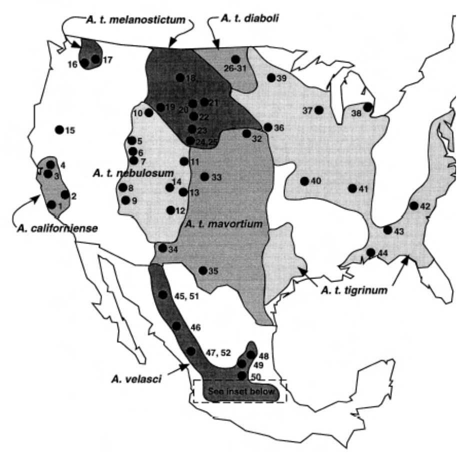




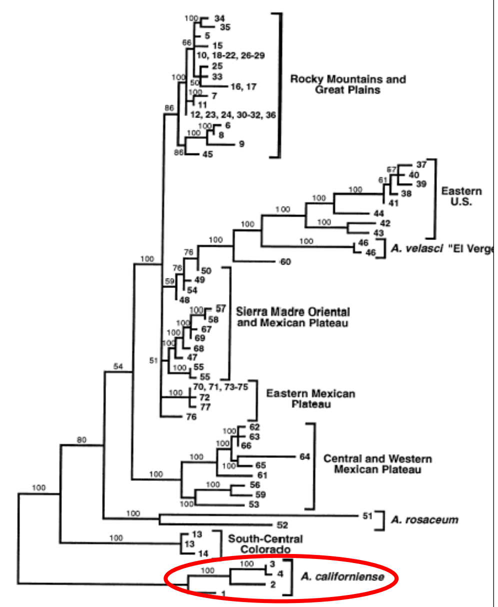
CTS larvae are smaller and are not known to become sexually mature larvae (paedomorphs)

CTS is Genetically Different

(est. 3-5 million years independent evolution)



Shaffer and McKnight 1996



CTS Genetics

<u>Six Genetic Groups</u>

Sonoma

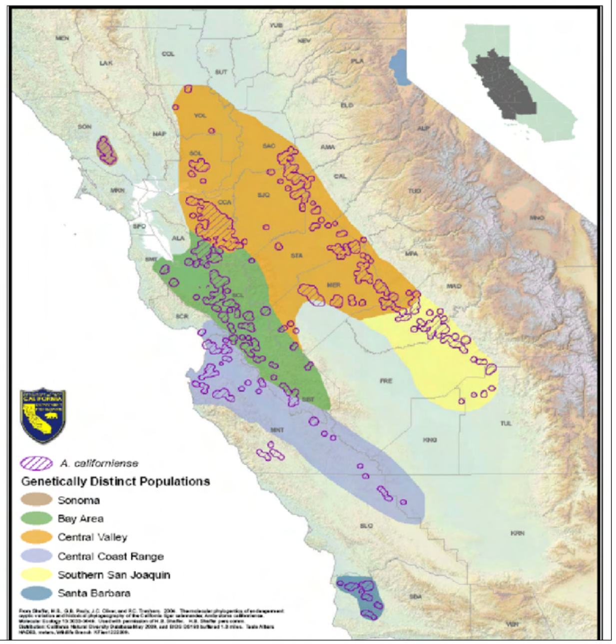
Central Valley

Bay Area

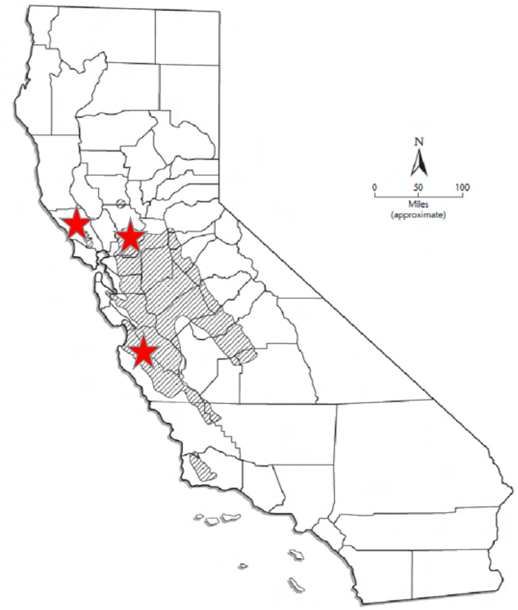
Southern San Joaquin

Central Coast Range

Santa Barbara



CTS Distribution

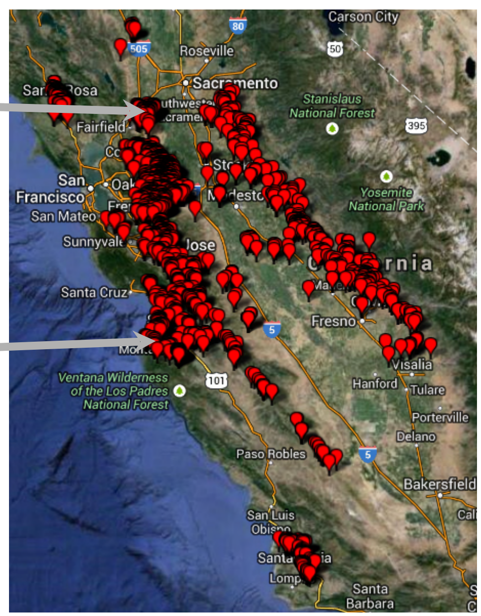


- extremely broad range
  - to 3900 ft in Coast Range
  - to 1200 ft in Sierra foothills
- habitat/climate differs
  9 to 38 in rainfall
- often generalizing based on studies from a few sites

Focal populations

Jepson Prairie Preserve:
9 years of data (2005-2013)

Hastings Natural History Reservation:
6 years of data (1992-1997)

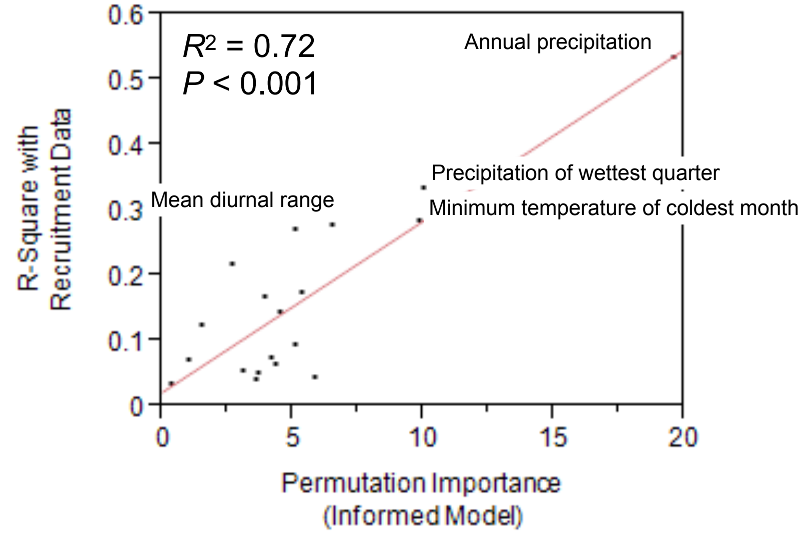


Climatic factors significantly correlated with recruitment

Bioclim variable	Sign	R^2
Annual precipitation	+	0.53
Precipitation wettest quarter	+	0.33
Minimum temperature of coldest month	+	0.28
Mean diurnal range	-	0.28
Precipitation wettest month	+	0.27
Precipitation coldest quarter	+	0.22

Searcy, C. A. & H. B. Shaffer 2016. *The American Naturalist*.

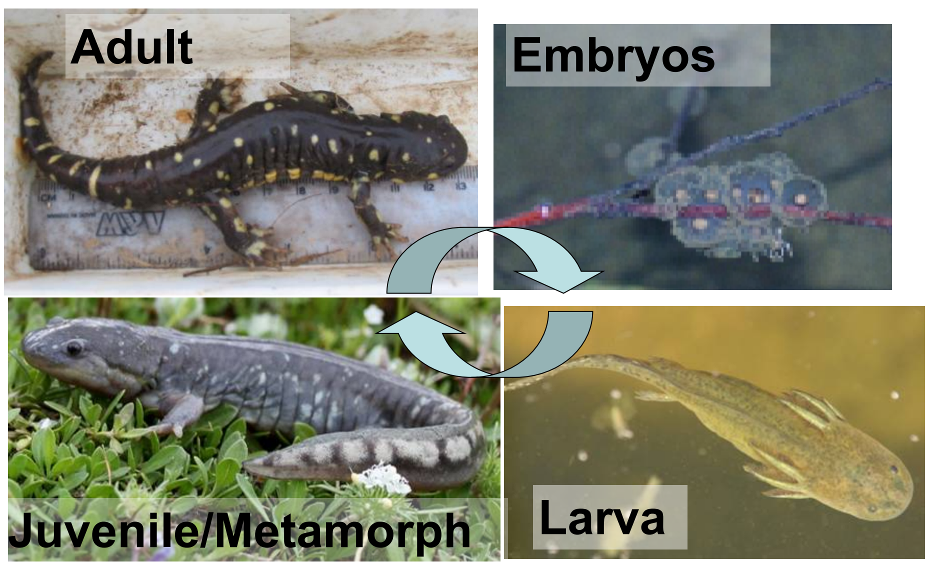
Agreement between factors associated with recruitment and spatial distribution



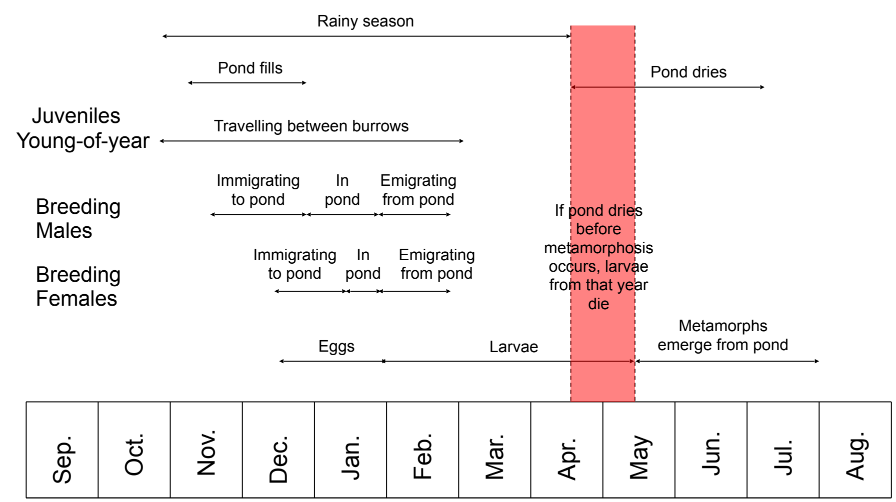
Habitat Basics

- Aquatic Habitat
  - Vernal Pools*
  - Ponds*
  - Ditches
- Upland Habitat
  - Grassland*
  - Oak savanna*
  - Oak woodlands
  - Sometimes chaparral and shrublands

Basic Life Cycle and Morphology



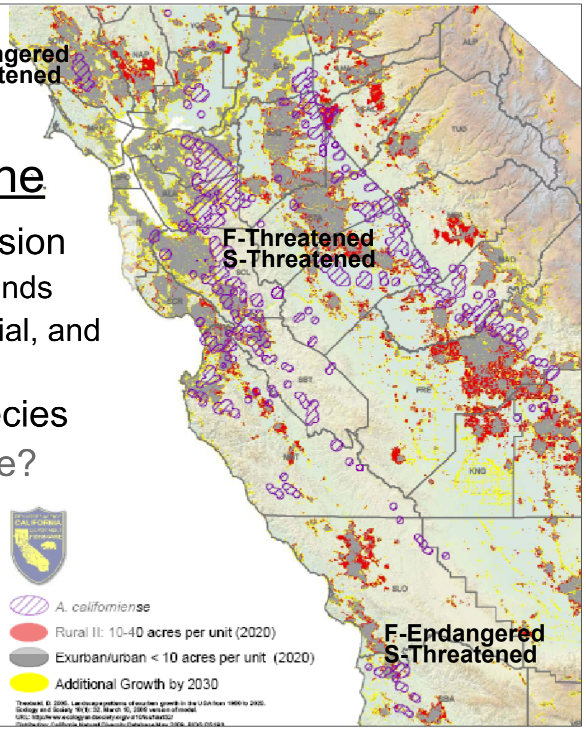
CTS Life Cycle



Causes of Decline

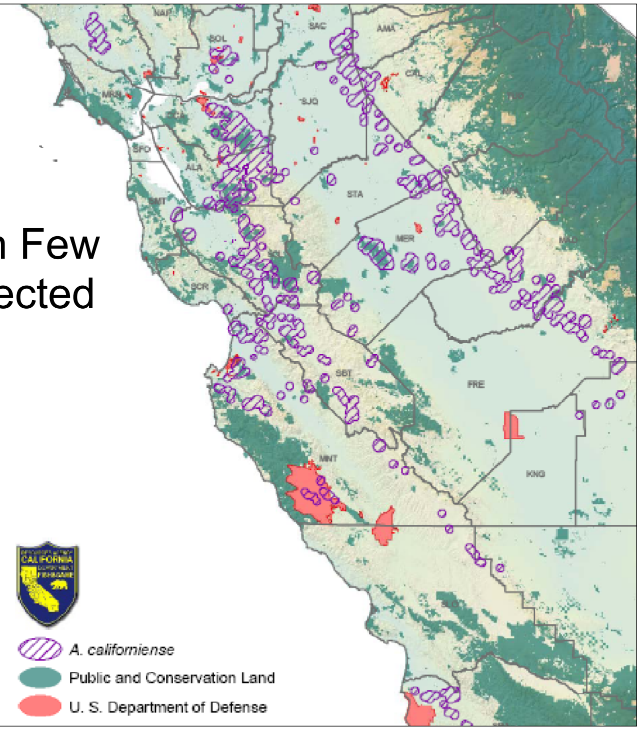
- #1 – Habitat Conversion
  - of wetlands and uplands
  - to cropland, residential, and urban uses
- #2 – Introduced Species
- #3 – Climate Change?

*From: CDFG 2009 Status Evaluation



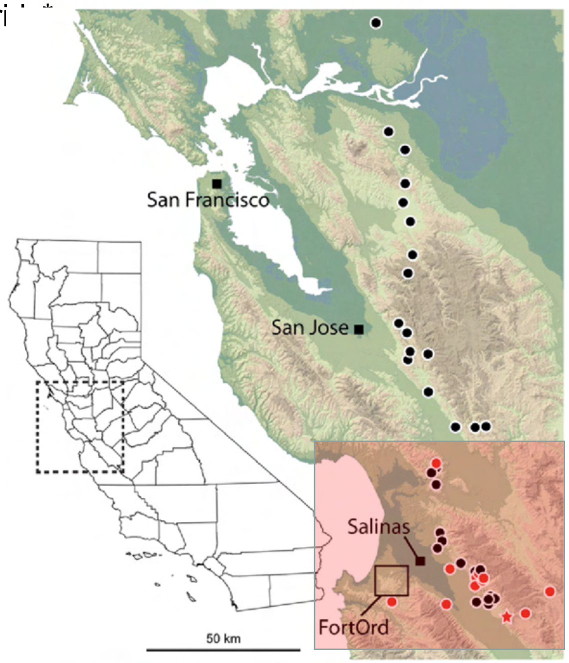
- CTS Occur On Few Currently Protected Lands

*From: CDFG 2009 Status Evaluation



Cause of Decline *#2 - Hybri

- initial introduction
  - South of Salinas
  - 1940s
- discovered late 1990s
- situation evolving



Introductory Main Points

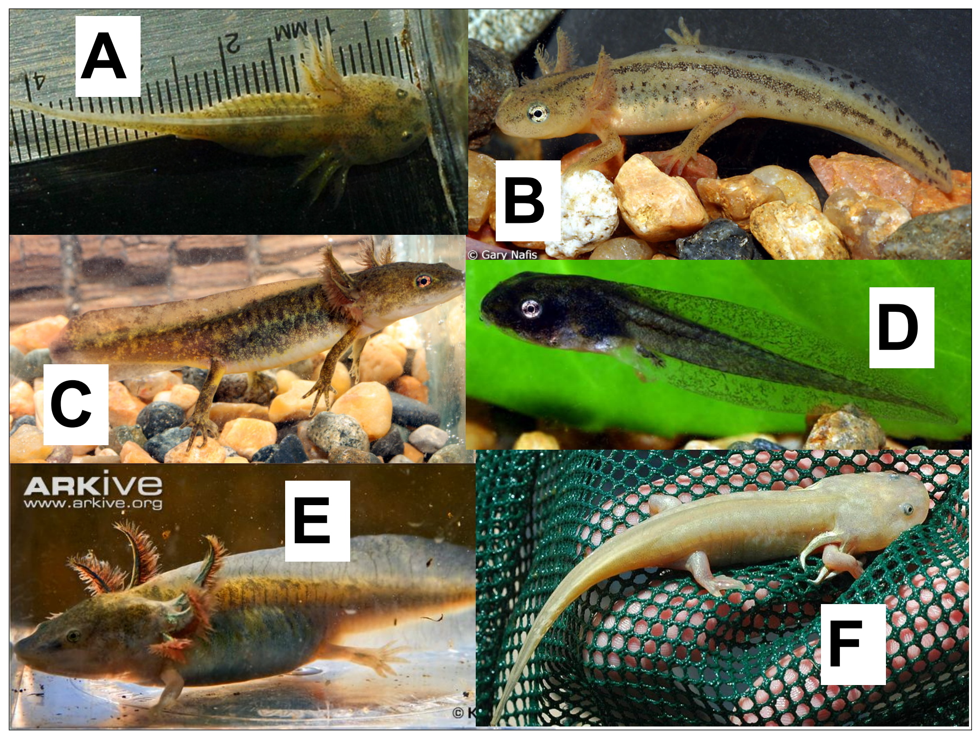
- CTS habitat and range
  - Breed in ponds
  - Upland habitat with grasslands
  - From Yolo Co. to Santa Barbara Co. in areas with appropriate climate
- Annual cycle driven by rainfall and pond drying
- Key threats/reasons for listing
  - Habitat loss
  - Hybridization

Embryo Identification/Morphology

- 2-3 mm diameter
- whitish to grey to yellow
- w/jelly 4.5-10 mm
- attached to vegetation or other materials
- singly or small clusters
- grape-like (each in its own separate membrane)
- Detectable mainly Dec-Feb

Larvae - Identification/Morphology

- Fish-like
- Feathery external gills
- Four legs
- 30 to 150 mm
  - 1 to 6 inches
- Color variable
- No stripes or real pattern
- Potentially detectable year-round (mainly March-June)

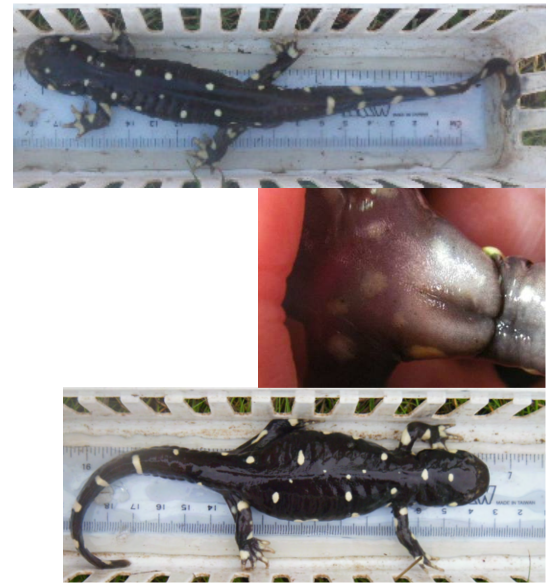


Adult Identification/Morphology

- 6-10 inches long
- NO nasolabial groove
- black to light brown background
- white to light yellow rounded spots
  - size/amount of spots varies
- toes pointed
  - NOT squared

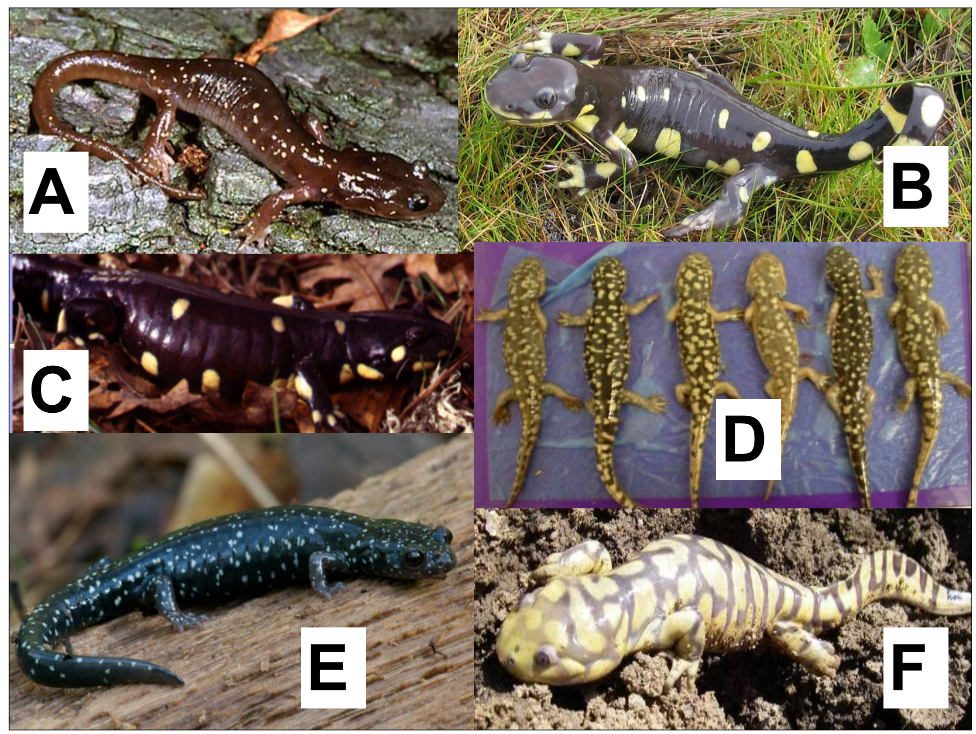
Sexing Adults

- Males have longer tail and a swollen vent
- Females appear fat when they are gravid with eggs
- Both sexes have a laterally compressed tail



Immature Age Classes

- Metamorphs
  - At metamorphosis
  - Muddy color patterns
  - Remnant gill stubs
  - 100-150 mm long
    - 4 – 6 inches
  - Fat
- Juveniles (after 1st summer)
  - Resemble adults, but smaller



Hybrids

- Genetic test needed for conclusive ID
  - Adults with barring are suspicious
  - Giant larvae are suspect also (CTS larvae usually <6” total length)

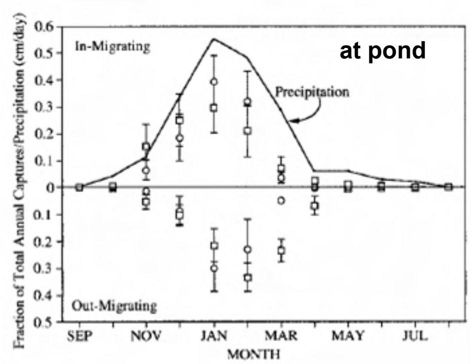
Identification – Main Points

- Embryos are distinctive and detectable
  - Single embryos alone or in clumps
- Larvae are easily differentiated from newt larvae by larger size and no eye stripe
- Metamorphs have muddy/blotchy color
  - Often with remnants of gills/fins
- Juveniles and adults
  - Black/brown background with cream/yellow spots
  - Lack nasolabial groove, pointed toe tips
- Hybrid/Natives?
  - Genetic test required for conclusive ID
  - Large size and odd color patterns *suggest* hybrid

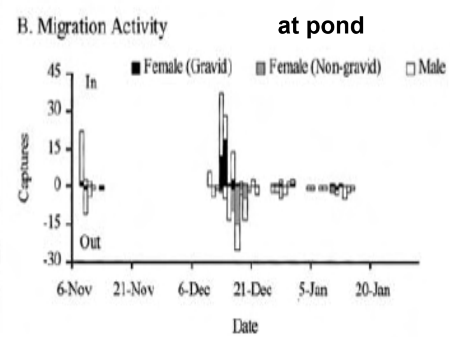
Group Exercise 1 - Identification

- In a group of 3-4 discuss the different stages of *A. californiense* and how you would identify them.
- What other amphibians might you encounter in the same ponds?
  - What species could cause problems?
  - In what regions do these species occur?

Timing of Captures: Adults At Ponds



Trenham et al. 2000 (Monterey Co.)



Cook et al. 2006 (Sonoma Co.)

Activity differs by region!
Largely driven by rainfall.

Adult/juvenile movement period

Positively correlated with date at which annual precipitation reaches 0.56 in. (Jepson Data)

Year	Start	End
05-06	29-Nov	27-Feb
06-07	14-Nov	22-Feb
07-08	11-Nov	20-Feb
08-09	2-Nov	2-Mar
09-10	14-Oct	24-Feb
10-11	24-Oct	2-Mar
11-12	11-Oct	15-Mar
12-13	17-Nov	20-Mar
Overall	30-Oct	28-Feb

Adult/juvenile movement period

Positively correlated with Nov. rainfall, negatively correlated with Feb. rainfall (Jepson Data)

Year	Start	End
05-06	29-Nov	27-Feb
06-07	14-Nov	22-Feb
07-08	11-Nov	20-Feb
08-09	2-Nov	2-Mar
09-10	14-Oct	24-Feb
10-11	24-Oct	2-Mar
11-12	11-Oct	15-Mar
12-13	17-Nov	20-Mar
Overall	30-Oct	28-Feb

Weather Patterns

1) Even during migratory periods, CTS are active on the surface for a small fraction of the days.

1) Surface activity is driven by weather.

Adult/Juvenile Activity

Out of a ~140 day activity season, 95% of the movement occurs on 15 days (11% of days)

Year	Movement Days
05-06	21
06-07	16
07-08	18
08-09	6
09-10	11
10-11	23
11-12	14
12-13	13
Average	15.25

Correlations

- Movement days are correlated with:
  - Precipitation (+)
  - High minimum temperature (+)
  - Humidity (+)
- However, amongst nights when rain is predicted (~32 per year), there is no clear rule for when CTS will be active

Metamorph emergence period

Positively correlated with Mar. rainfall (Jepson Data)

Year	Start	End
04-05	19-May	20-Jun
05-06	30-May	10-Jul
07-08	14-May	20-May
08-09	23-May	10-Jun
09-10	21-May	26-Jun
10-11	2-Jun	30-Jun
11-12	1-Jun	19-Jun
12-13	7-May	18-May
Overall	17-May	3-Jul

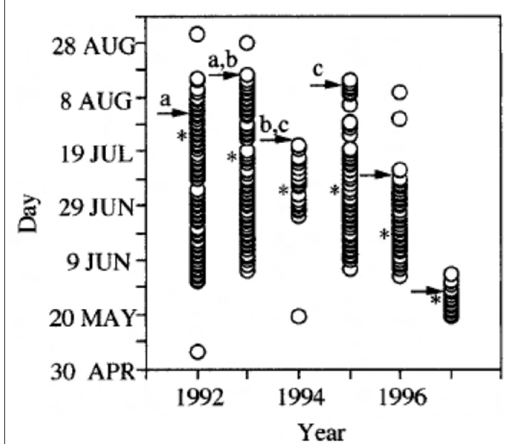
Metamorph emergence period

Year	Start	End
04-05	19-May	20-Jun
05-06	30-May	10-Jul
07-08	14-May	20-May
08-09	23-May	10-Jun
09-10	21-May	26-Jun
10-11	2-Jun	30-Jun
11-12	1-Jun	19-Jun
12-13	7-May	18-May
Overall	17-May	3-Jul

Positively correlated with drying date of breeding pond (Jepson Data)

Dates of Metamorph Capture

Monterey Co. (1992-1997)



Trenham et al. 2000

Contra Costa Co. (1992-1993)

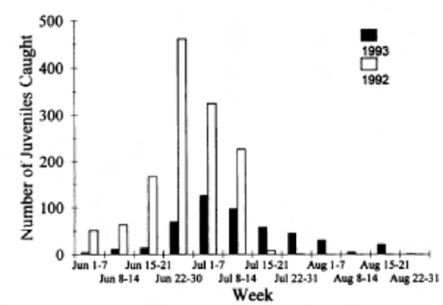


Fig. 3. Number of juvenile *Ambystoma californiense* caught by week in summer 1992 and summer 1993, Contra Costa County, California. Numbers of individuals include original captures and recaptures.

Loredo and Van Vuren 1996

Conclusions – To Avoid Migrating Salamanders

Avoid activities that will impede salamander movement in the terrestrial environment:

a) after the first ~0.5 inches of rain in the fall until mid-March

b) from mid-May until the breeding ponds are dry

Breeding pond occupancy

Positively correlated with first 0.82 in. after the end of October (Jepson Data)

Year	Start	End
05-06	2-Dec	5-Jul
06-07	14-Nov	25-Feb
07-08	11-Nov	17-May
08-09	2-Nov	9-Jun
09-10	12-Dec	25-Jun
10-11	21-Nov	29-Jun
11-12	15-Dec	18-Jun
12-13	17-Nov	17-May
Overall	11-Nov	29-Jun

Breeding pond occupancy

Year	Start	End
05-06	2-Dec	5-Jul
06-07	14-Nov	25-Feb
07-08	11-Nov	17-May
08-09	2-Nov	9-Jun
09-10	12-Dec	25-Jun
10-11	21-Nov	29-Jun
11-12	15-Dec	18-Jun
12-13	17-Nov	17-May
Overall	11-Nov	29-Jun

Positively correlated with drying date of breeding pond (Jepson Data)

Conclusions – Avoiding in Ponds

Avoid activities in the aquatic habitat:

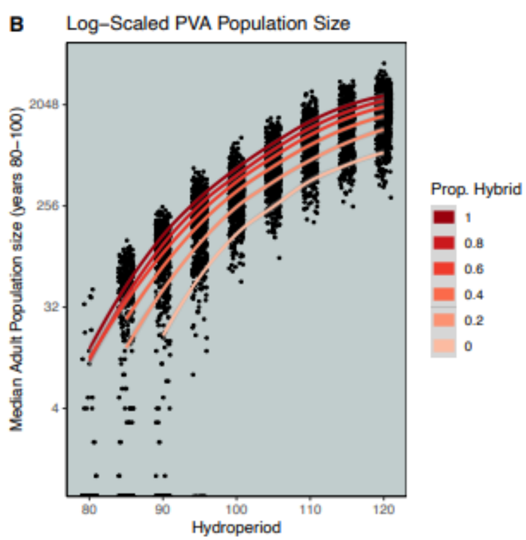
-Once ~0.8 in. have accumulated after the end of October

-Until the pond has dried for natural vernal pools or until late dry season for artificial ponds

Relationship to Hydroperiod

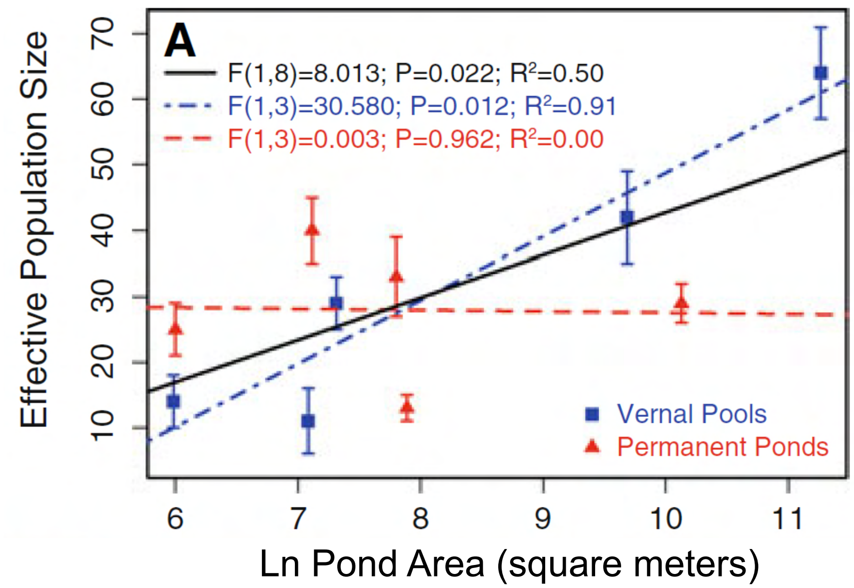
Year	Average Breeding Date	Average Date of Metamorph Emergence	Average Number of Days in Pond
05-06	22-Dec	19-Jun	178
07-08	5-Jan	16-May	131
08-09	14-Feb	31-May	106
09-10	21-Jan	6-Jun	136
10-11	10-Jan	16-Jun	157
11-12	15-Mar	11-Jun	88
12-13	14-Dec	12-May	148

Hydroperiod Modeling



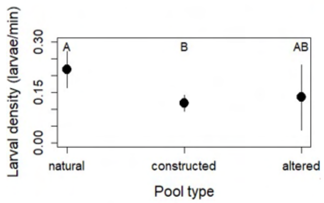
R. Cooper PhD Dissertation

Pond Size Influences Population Size

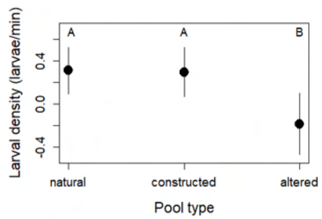


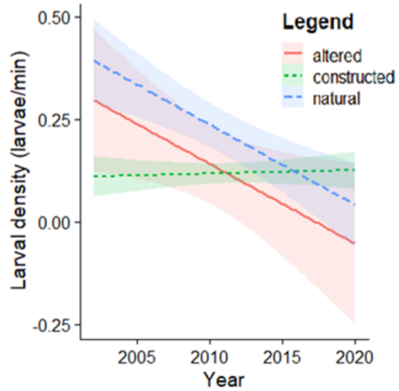
Constructed Pools Can Provide High Quality Habitat

Raw densities: natural pools are best



Marginal densities corrected for pond size: constructed and natural pools are equal





Cook et al. 2023

Aquatic Habitat – Important Issues

- Vernal pools and playa pools (CTS natural habitat)
  - Constructed ponds (more common today)
- Hydroperiod
  - Must persist into May (July or August, even better)
  - Permanent ponds often unsuitable due to predators
- Pool area and depth
  - Bigger pools = more metamorphs
  - Deeper pools = >hydroperiod
- Vegetation? Water quality?
  - With or without vegetation
  - Often with livestock waste

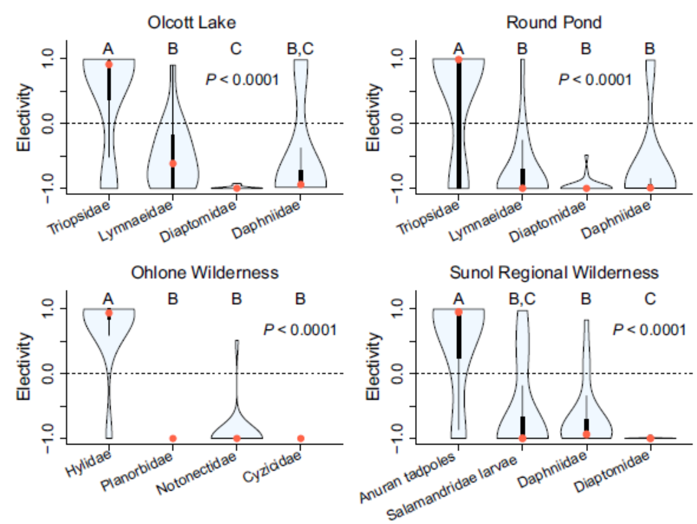
Aquatic Prey and Predators

- Prey
  - Zooplankton (cladocera, copepods)
  - Macrocrustaceans (California clam shrimp, vernal pool tadpole shrimp*)
  - Insect larvae (corixids, notonectids)
  - Newt larvae
  - Pacific chorus frog tadpoles
  - Snails

  *endangered prey
- Predators
  - Avocets
  - Herons
  - Terns
  - Garter snakes
  - Adult newts
  - Bullfrogs*
  - Crayfish*
  - Fish*
  - Insect larvae (dytiscid beetles, giant water bugs)*

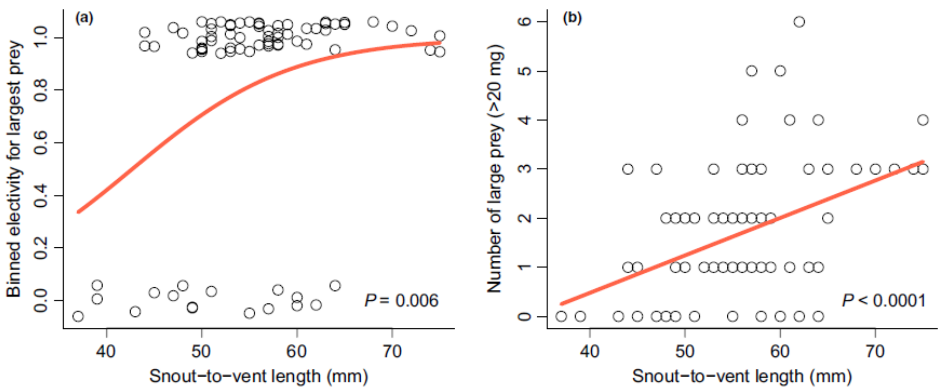
  *a big problem with permanent ponds!

CTS Larvae Prefer Large Prey…



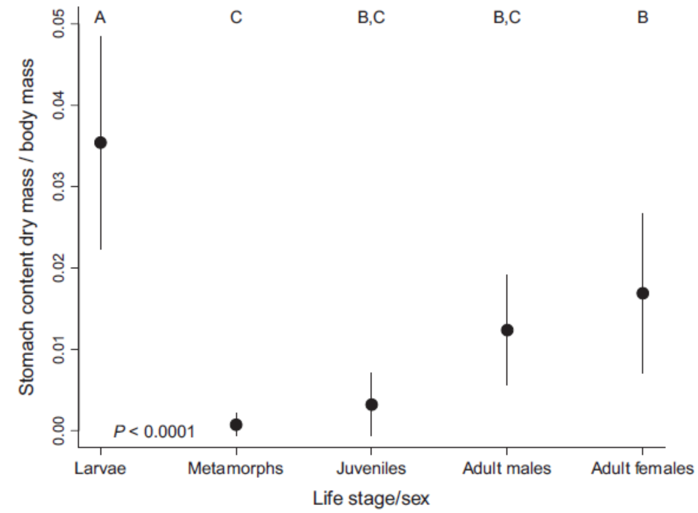
Messerman et al. 2021

…Once It Fits In Their Mouth

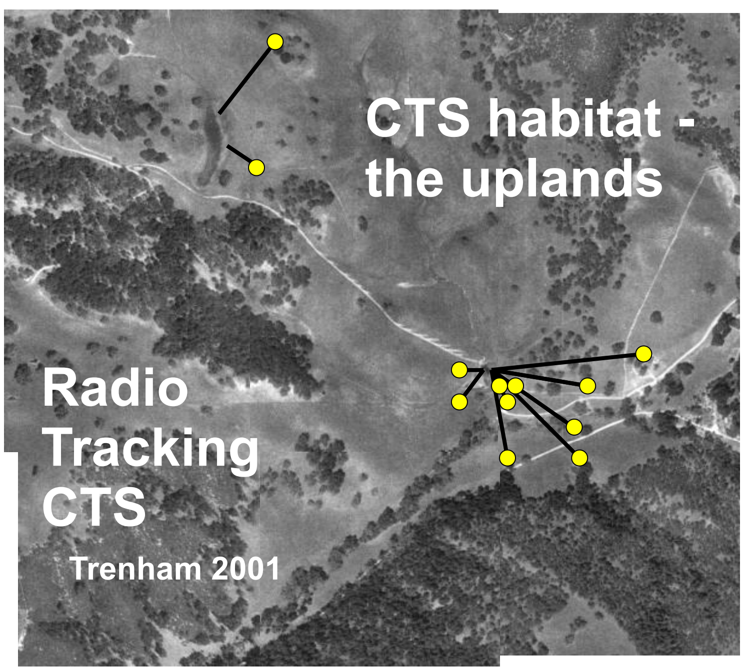


Messerman et al. 2021

Vernal Pools Have Abundant Prey



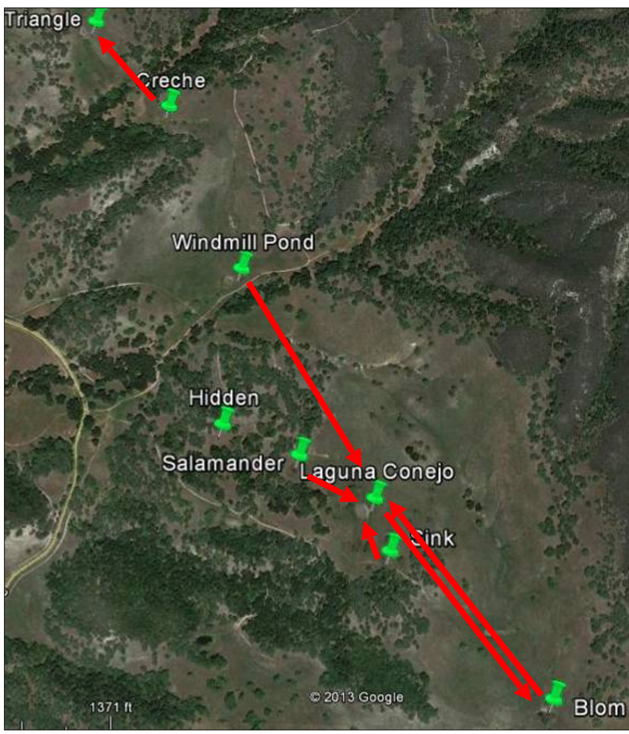
Messerman et al. 2021



CTS Live In Small Mammal Burrows




FIBER-OPTIC VIDEO
courtesy of Michael Van Hattem

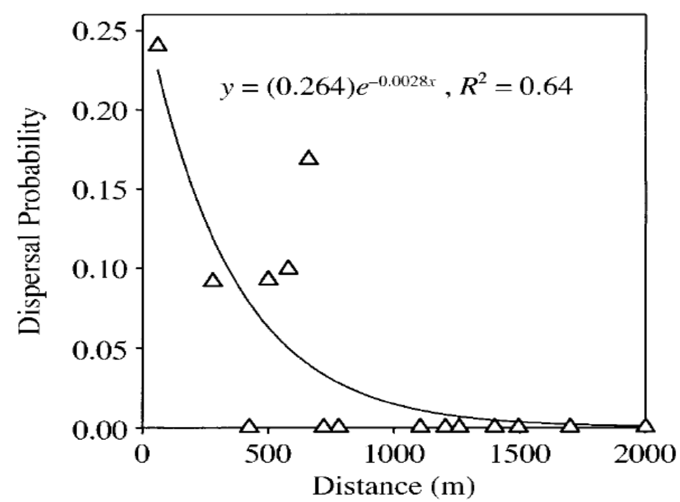


Landscape Ecology

- ~20% moved between ponds
- Most moved <600 m
- Estimated some disperse up to 1 to 2 km

• **Trenham et al. 2001 Ecology**

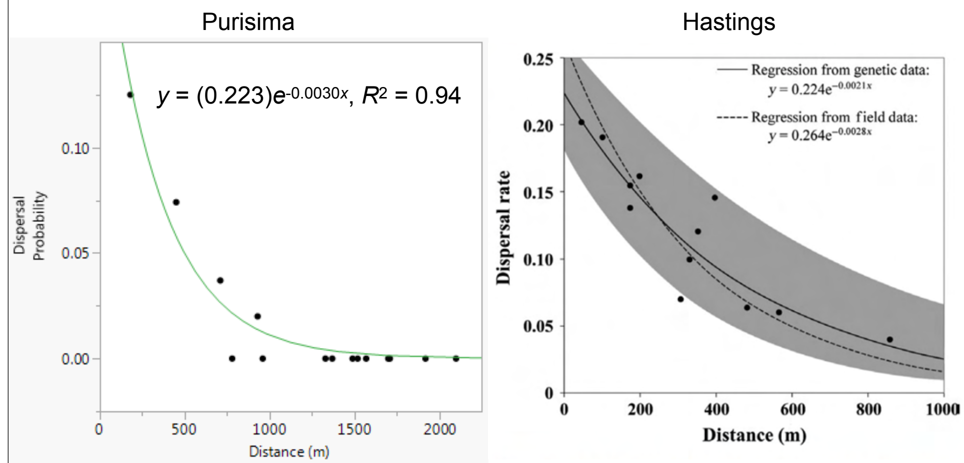
Probability of Dispersal vs. Distance



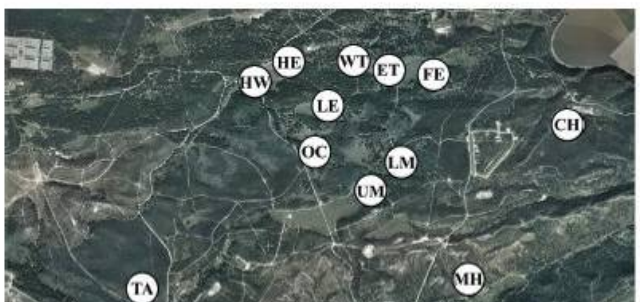
Source: Trenham, P. C., W. D. Koenig, and H. B. Shaffer. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology 82: 3519-3530.

Santa Barbara CTS

All dispersal studies provide similar estimates



Fort Ord Genetic Evaluation of Recent Migration History



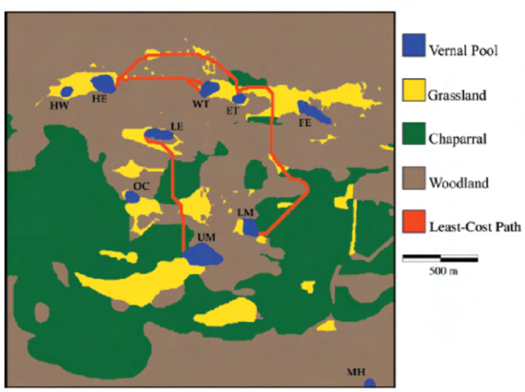


Fig. 4 Habitat map showing least-cost paths between breeding ponds for four interpopulation dispersal corridors. The least-cost paths shown are those that most closely fit the relative mean dispersal rates. The paths were calculated as having one cell width, but are drawn as wider for visualization. Population acronyms correspond to those used in Table 1.

Data suggest grassland and chaparral favored over woodland for migration

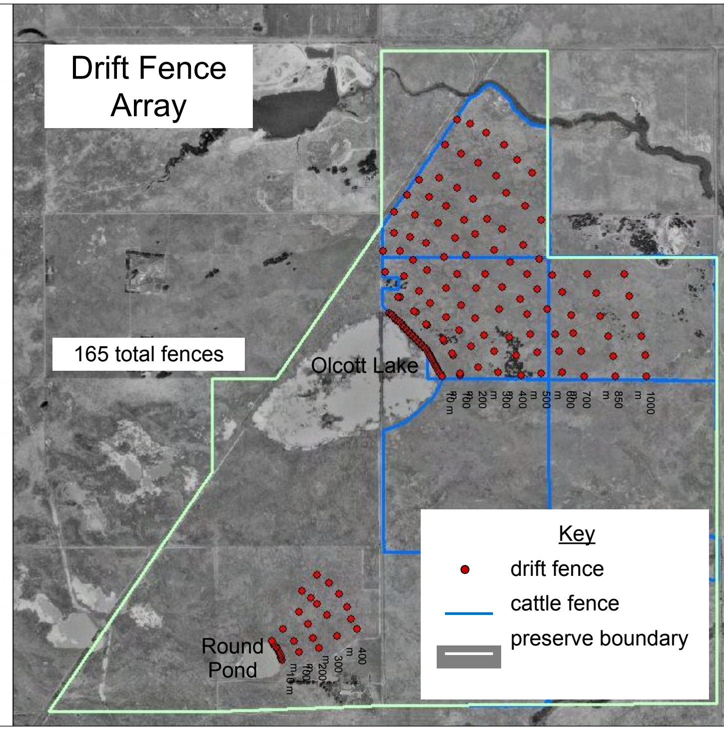
Wang et al. 2009

Landscape Habitat Points

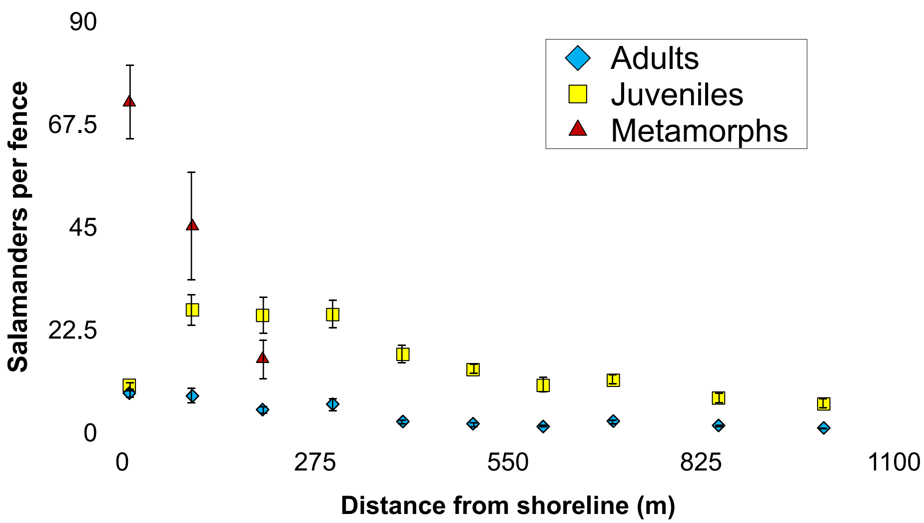
- Major upland habitats – for burrows/migration
  - grassland
  - oak woodland
  - chaparral/sage scrub
- Most do not remain near edge of pond
  - 680 m observed
  - ~800 m genetically estimated
- Movement between ponds 1 - 2 km expected

Upland Habitat Main Points

- After metamorphosis, CTS are almost always underground
- Occupy mainly ground squirrel and gopher burrows
  - Emerge to move to pond or another burrow
  - Emerge only at night, usually when raining
- Aestivation has not been observed
- Most do not remain near edge of pond



Age Classes Are Distributed Differently



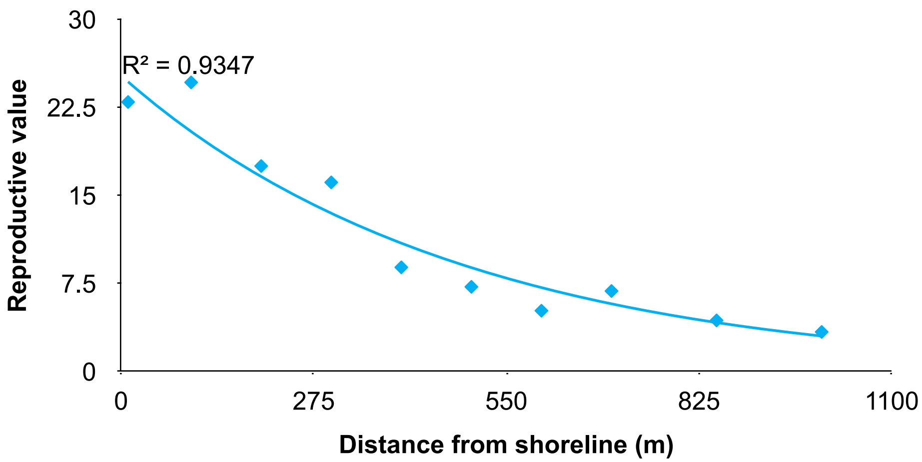
What is the relative importance of the different age classes?

Adult

Juvenile

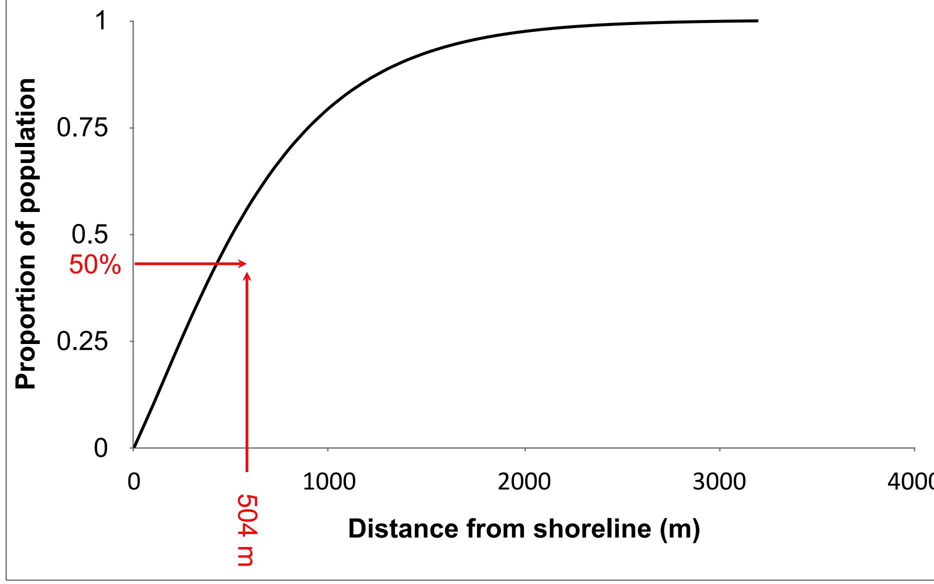
Metamorph

Reproductive value declines with distance from pond

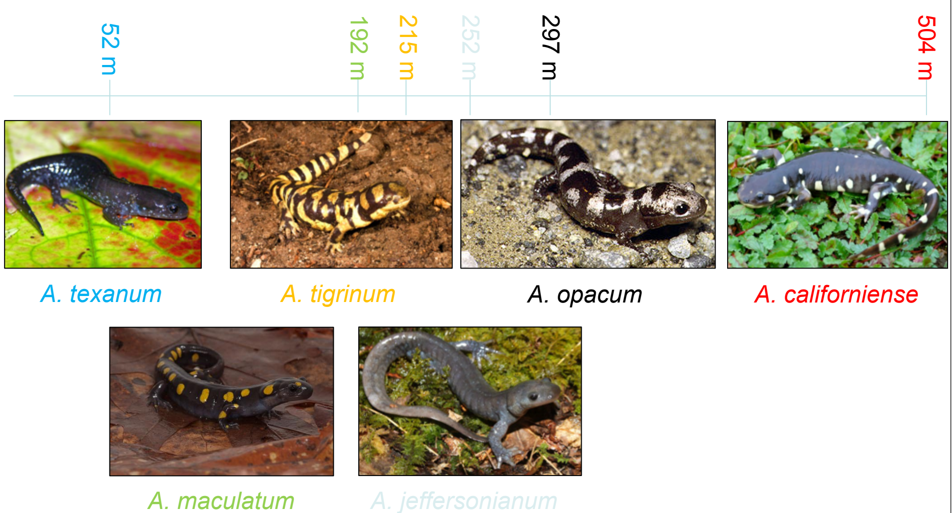


Searcy, C. A. & H. B. Shaffer. 2008. *Conservation Biology*.

Protecting 50% of the Population

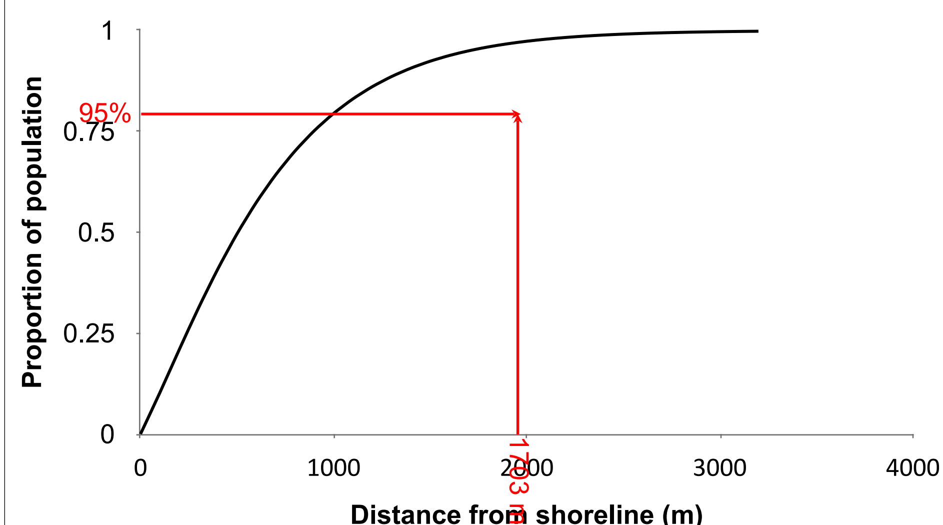


Average *Ambystoma* Migration Distances



Searcy, C. A. et al. 2013. *Biological Conservation*.

Protecting 95% of the Population



Pattern recognition

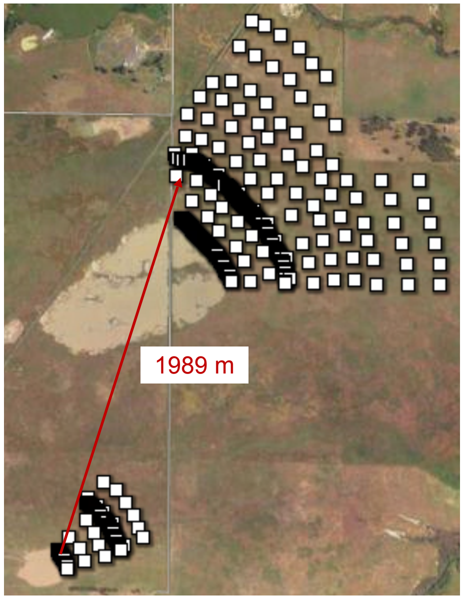
How far does the average salamander move in a season?

- Average rate = 150 m/night
- Most adults are active for 2 to 5 nights during both immigration and emigration
- (150 m/night)(3.5 nights) = 525 m
- This is pretty similar to the 504 m estimate from the integration method

How far can a salamander move in a season?

- We know that a rate of 188 m/night is sustainable for at least 6 nights in a row
- There are 10 to 19 nights with appropriate weather conditions during both immigration and emigration
- (188 m/night)(10 nights) = 1880 m
- Even in a dry year, a salamander should be capable of migrating 1703 m

Longest observed migration



Jepson Study - Conclusions

- The two methods agree very well.
- The average adult probably travels ~500 meters from the pond – almost twice the distance of any of its congeners.
- There is no reason to doubt that the top 5% of migrants travel 1703 m or more from the pond edge.
- The 2092 m buffer currently used by USFWS is within the ecophysiological capacity of the salamander in most years and is within the 95% confidence interval of the integration method.

How many acres/hectares to protect 95% of CTS?

- About how many hectares/acres are encompassed by a pond buffered by 1.7 km?

$$AREA = \Pi r^2$$

- r = 1,703 m
- hectare = 10,000 m^2
- hectare = 2.5 acres

~9,000,000 m^2

= ~900 ha

= ~2,250 acres

Group Exercise

- You are responsible for designing habitat restoration for a failing vineyard in Sonoma County.
- The property is 500 acres and currently has no ponds, but CTS breed in ponds on a neighboring property.
- List at least 5 priority actions for restoring CTS to this site.

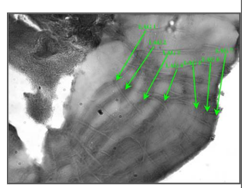
Multi-species conservation

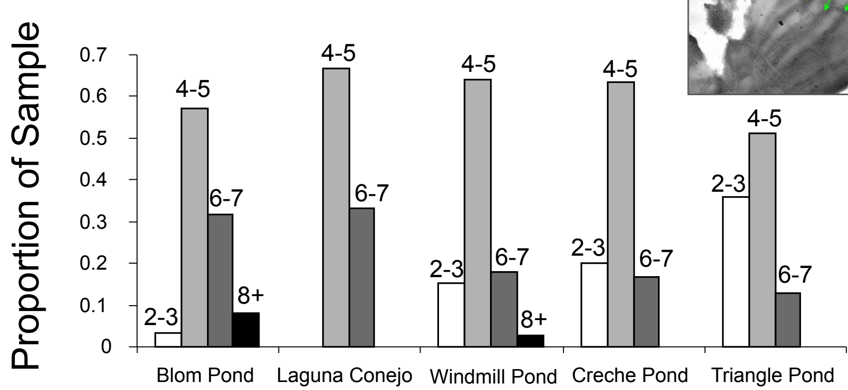
- Due to their large habitat requirements, California tiger salamanders can serve as an umbrella species for conservation of vernal pool grasslands in central California.
- Vernal pools are a bastion for rare California endemics; 89 other listed species also live within the 2092 m buffer around California tiger salamander breeding ponds.

Modeling Population Extinction Risk

- Key demographic parameters:
  - Age at maturity: 1-5+ years
  - Fecundity: ~ 800 eggs per female
  - Larval/embryonic survival: 0-10%
  - Metamorph/Juvenile survival = ~50%
  - Adult survival = ~70%

Demography: Age of Adults Differed Among Five Ponds in Carmel Valley





Trenham (unpub. data)

- Modeled probability of extinction most sensitive to
  - 1) *subadult survival
  - 2) adult survival
- This emphasizes importance of minimally disturbed upland habitat
- Trenham and Shaffer, 2005, Ecological Applications

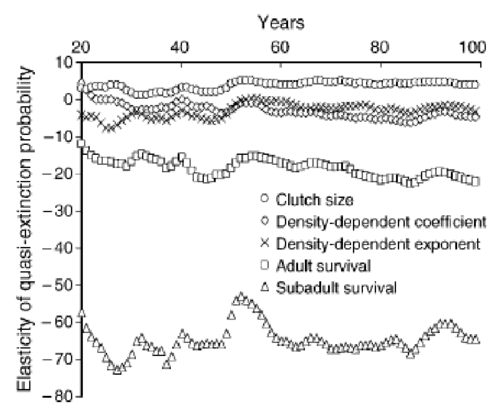
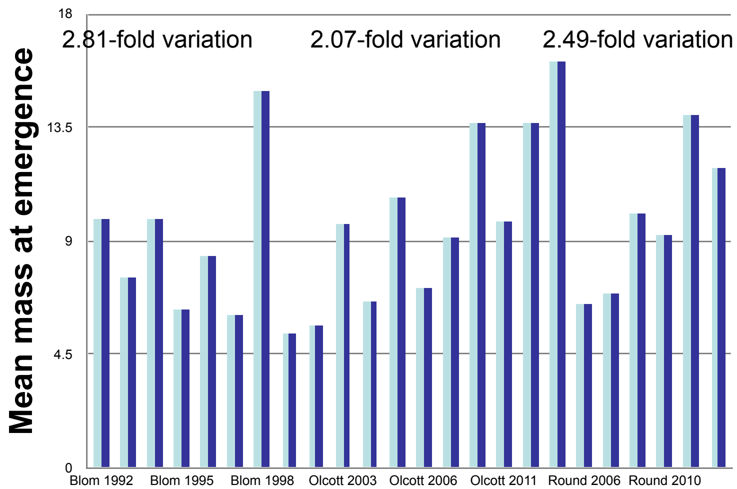


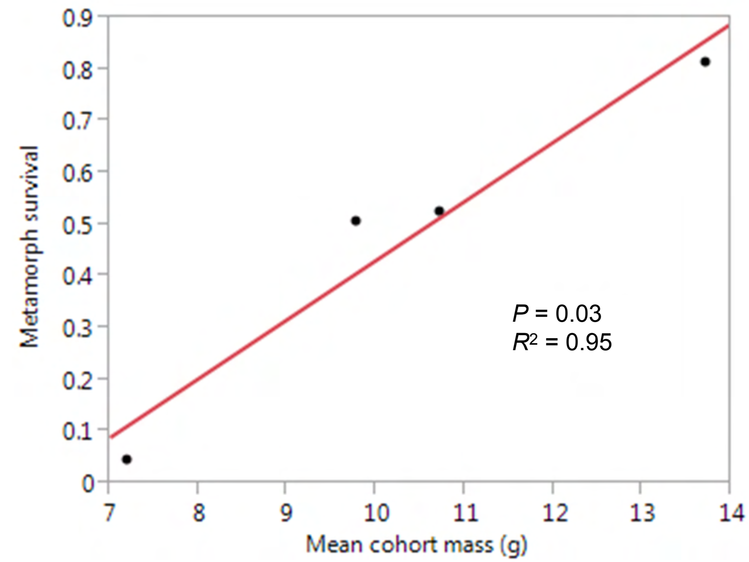
FIG. 5. Estimated elasticity values for cumulative quasi-extinction probabilities in response to perturbations of mean vital rates. Symbols represent elasticity in response to perturbation of various model parameters: subadult survival, adult survival, coefficient and exponent in larval density-dependent survival function, and number of eggs deposited per breeding female. Five adult females was the quasi-extinction threshold. The baseline model parameter values for this analysis were those indicated in Table 1. Elasticities for <20 years are not plotted because few extinctions occurred before this time, and as a result estimates of extinction probabilities and elasticities during this interval are highly variable and unreliable. Methods for elasticity analysis of density-dependent stochastic models are adapted from Morris and Doak (2002).

Variation in Metamorph Quality

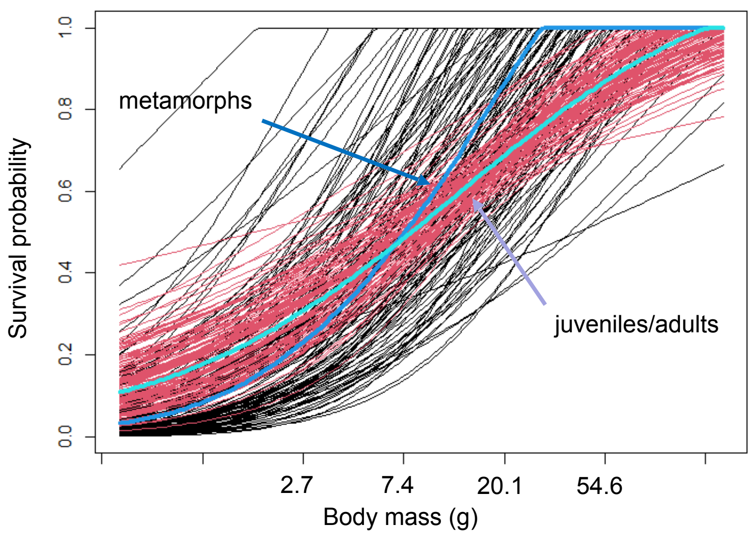


Searcy, C. A. et al. 2014. *Ecology*.

Cohorts with higher average mass had higher average survival

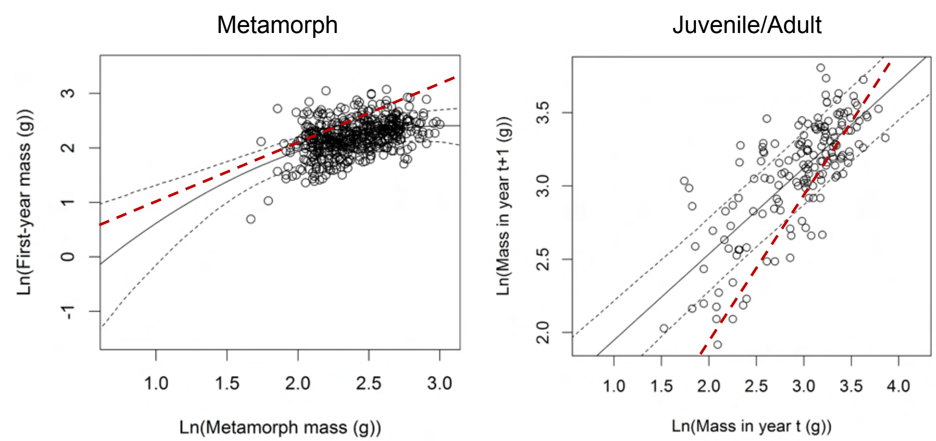


Individuals with higher mass have higher probability of survival

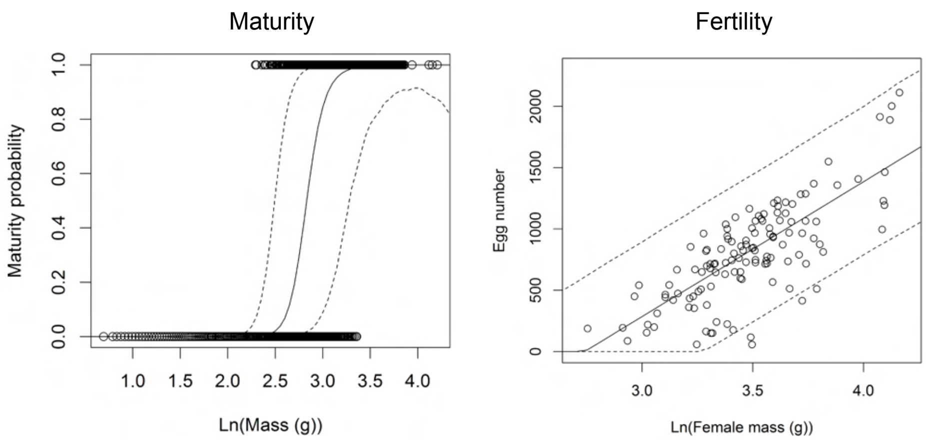


Messerman et al. 2023

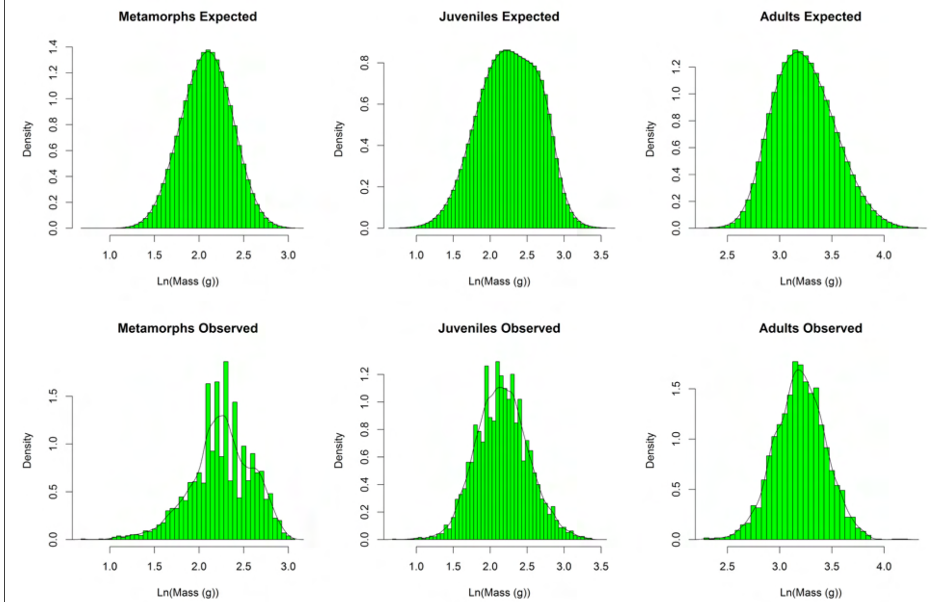
Growth



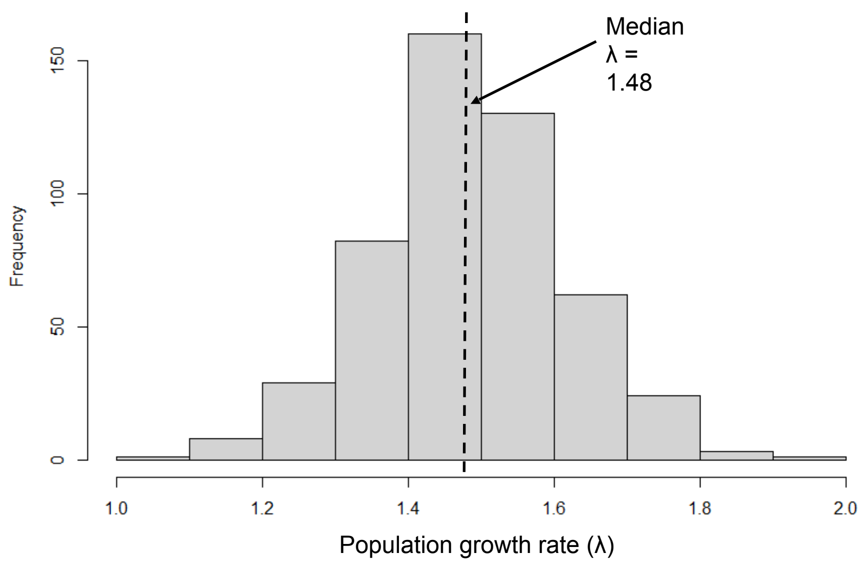
Reproduction



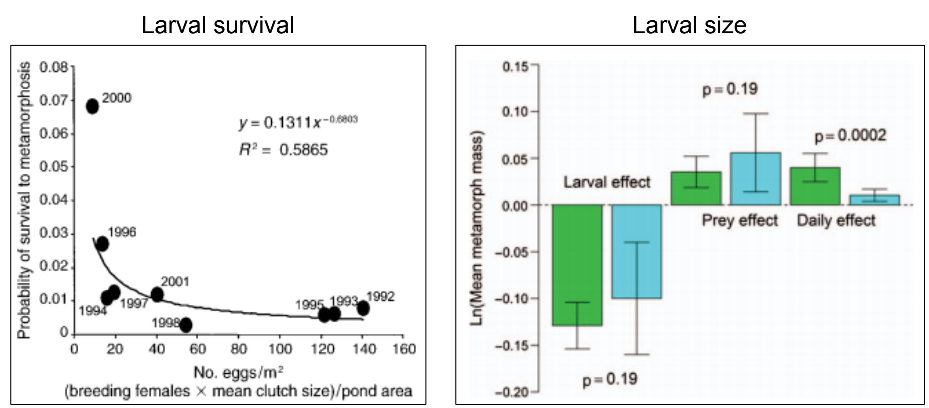
Stable Size Distribution



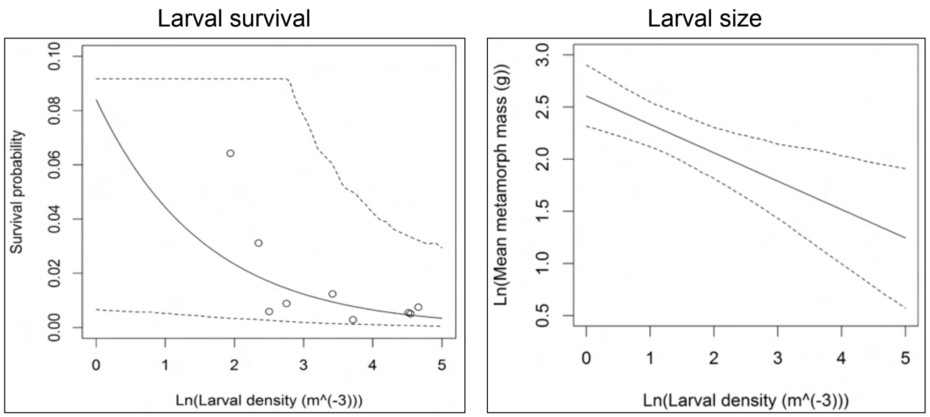
Population Growth Rate



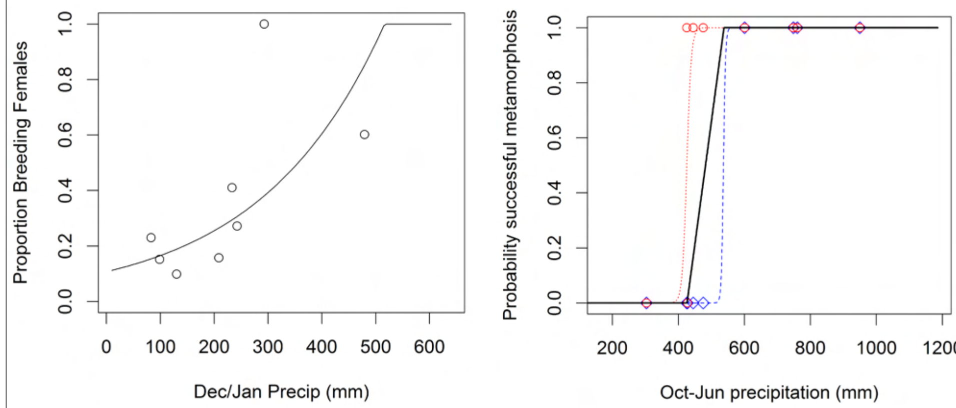
Density-dependence



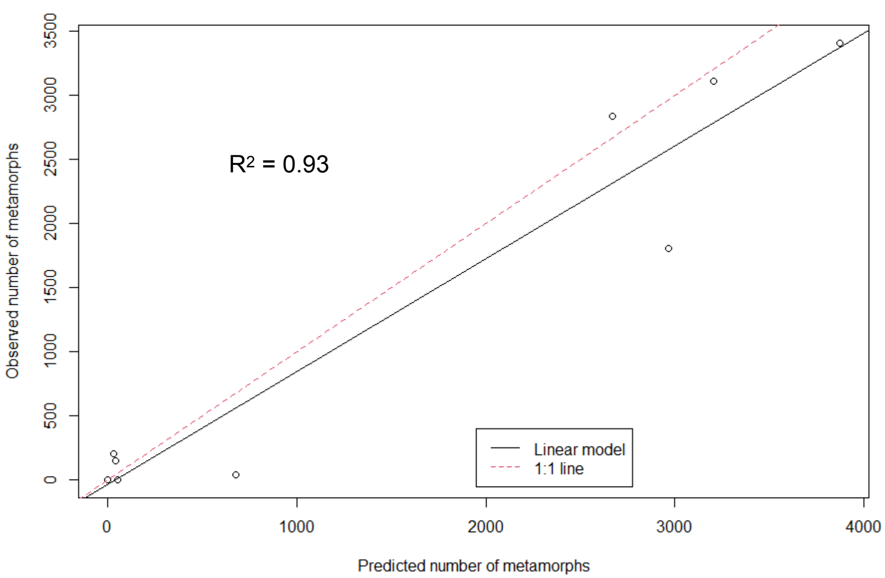
Density-dependence



Climatic Stochasticity



Population Dynamics



Demographic Rates

Embryonic/larval survivorship = 2%

Terrestrial survival pre-maturity = 50%

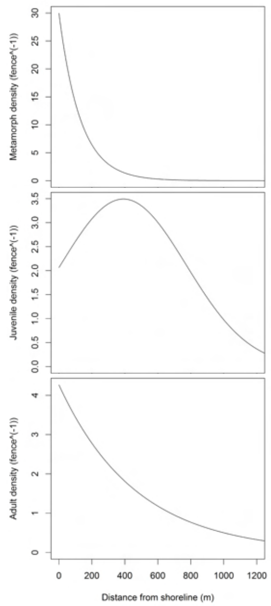
Average age at maturity = 3 years

Terrestrial survival post-maturity = 78%

Frequency of complete reproductive failure = 22%

Mean breeding frequency = 38%

Minimum Dynamic Area

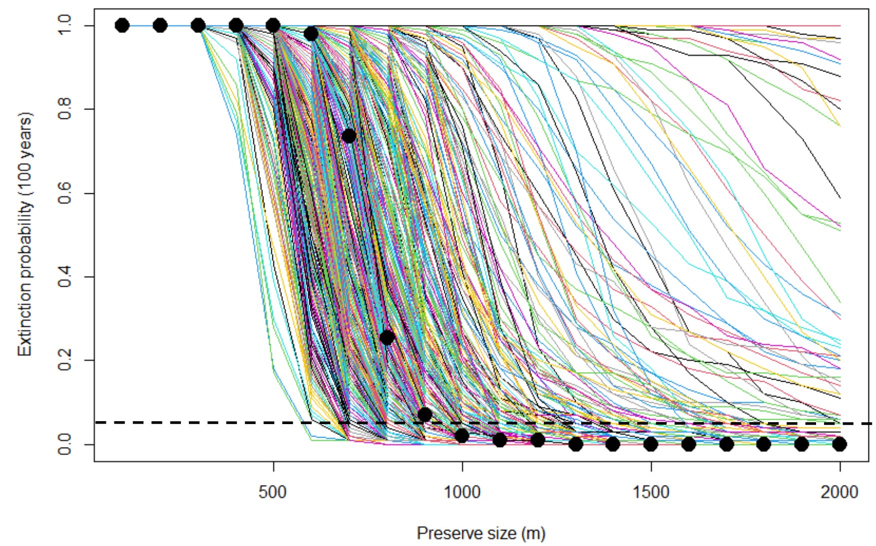


Metamorphs

Juveniles

Adults

Population Viability Analysis

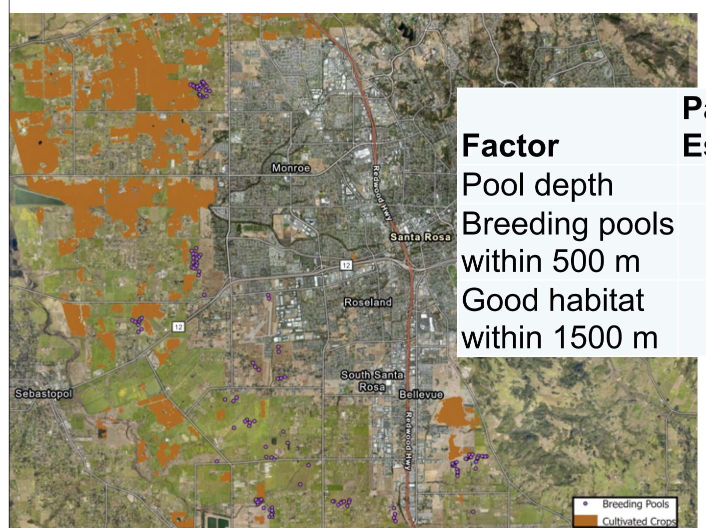


Actual Landscapes

Jepson Prairie

Hall Preserve

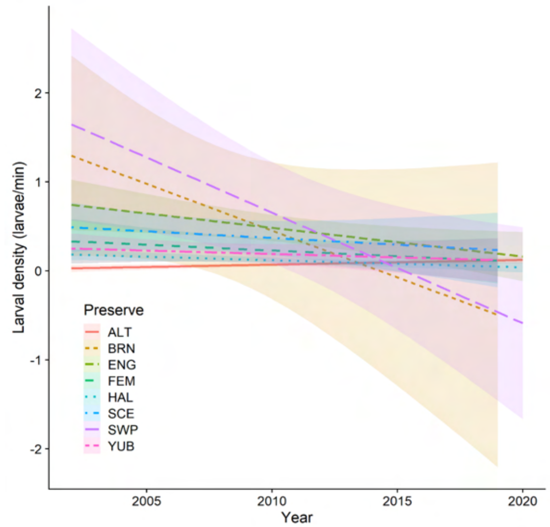
Terrestrial Density Dependence



Factor	Parameter Estimate	P-value
Pool depth	0.382	<0.0001
Breeding pools within 500 m	0.362	<0.0001
Good habitat within 1500 m	0.253	<0.0001

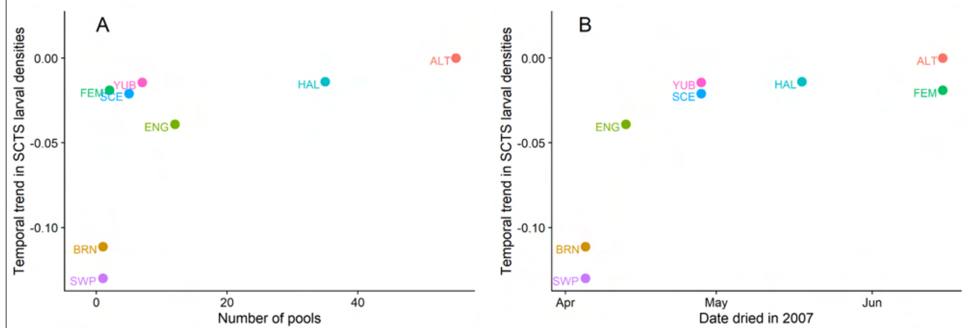
Sonoma DPS is in trouble!

Larval densities across 118 pools (most of the DPS) decreased by 48% between 2002-2020.



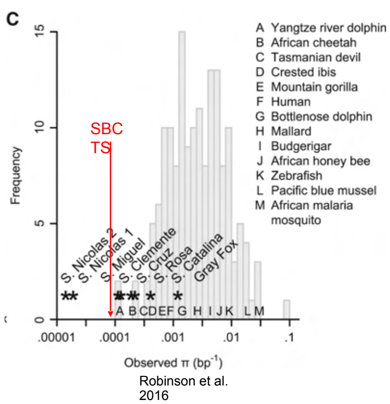
Stokes et al. 2021

Importance of metapopulation dynamics for demography

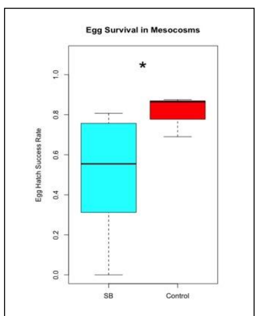


Stokes et al. 2021

Santa Barbara DPS is in trouble!

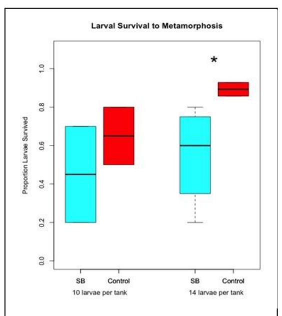


Robinson et al. 2016



Egg survival to hatching was **lower** in SBCTS animals.

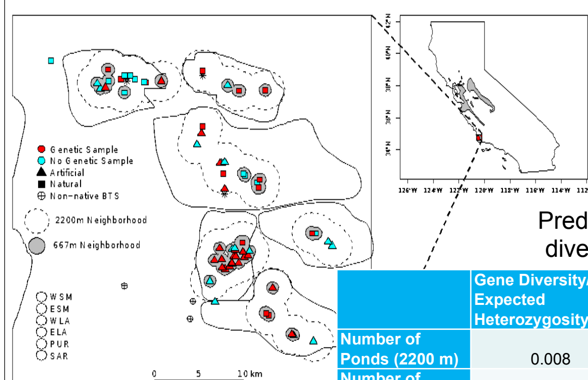
SBCTS: 49.8%
Control: 77.9%



Larval survival to metamorphosis was **lower** in SBCTS animals.

SBCTS: 31.5%
Control: 56.5%

Importance of metapopulation dynamics for genetic diversity



Predictors of genetic diversity (*P*-values)

	Gene Diversity/ Expected Heterozygosity	Observed Heterozygosity	Allelic Richness	Nucleotide Diversity
Number of Ponds (2200 m)	0.008	1×10^{-08}	1.1×10^{-06}	0.00002
Number of Ponds (667 m)	0.00029	9.85×10^{-06}	2.3×10^{-06}	0.0001
Proportion of Natural Ponds (2200 m)	1.71×10^{-05}	1.35×10^{-05}	1.93×10^{-05}	0.00005

E. Toffelmier PhD Dissertation

Demography – Main Points

- Female CTS can produce large numbers of eggs
  - but most breeders are at least 2 yrs old
  - and they don't breed every year
- Survival probability is size dependent
- Some individuals can live 10+ years
  - Most don't ever make it to metamorphosis
- Population size is much more sensitive to upland survival than to larval survival

Conservation Strategies

- Protect occupied landscapes
  - Ideally >2250 acre blocks; minimally 780 acres
  - With multiple breeding ponds
    - 7+ if possible
    - Some ponds should be larger
- Maintain/promote habitat connectivity
  - Minimize effects of new or improved roads
  - Maximize natural habitat between ponds
  - Construct additional ponds

Aquatic Habitat - Managing for CTS

- Modify/manage ponds to maintain appropriate hydroperiod
- Eliminate predators by periodic drying
- Maintain existing berms/remove excessive siltation
- Create additional ponds
- Allow livestock grazing (esp. vernal pools)

Upland Habitat-Managing for CTS

- Maintain habitat connectivity between ponds and uplands AND between ponds
- Maintain natural habitat, especially near breeding ponds
- Maintain burrowing mammal populations
- Effects of grazing unknown, but anecdotally positive

Aquatic Sampling

- Dip nets
- Minnow seine
- 1/8" mesh or smaller
- Move through the water quickly
- Neither works well in deep ponds

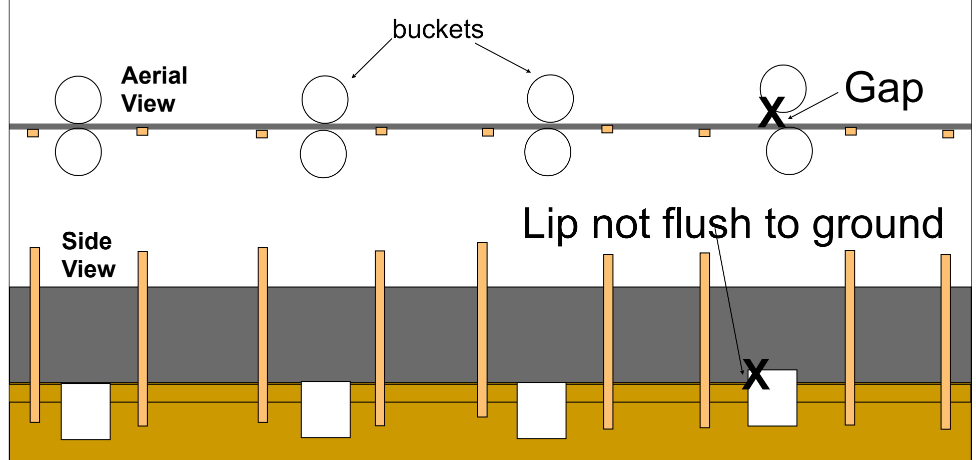
Alternate Aquatic Detection Methods

- Minnow traps (left)
- Visual embryo surveys
  - "egg grid" shown below

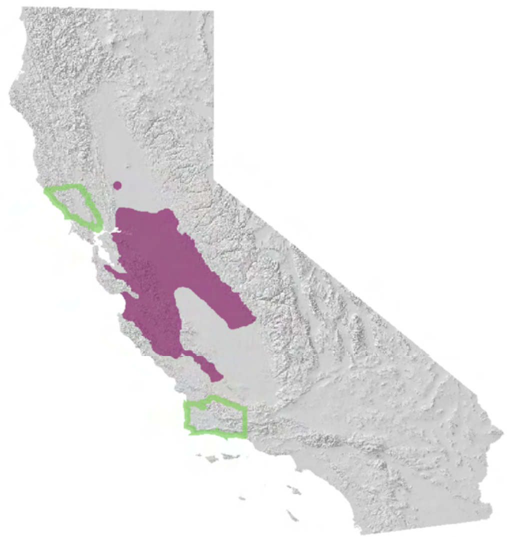
Figure 9. Southern trap line facing west.

Sue Orloff, Ibis Associates (2007)

Upland Sampling - Drift Fences with Pitfall Traps



First Consideration – Are You In The Range?
(check with agencies for latest range info)



CA Dept. of Fish and Game

Sampling for CTS – CDFW/USFWS Guidance
requirements for a negative determination

- 1) Site assessment – assess upland and aquatic habitat onsite and within 2 km
- 2) If pond within 2 km and upland habitat only…
  - Two seasons of drift fence sampling
  - ≥1 ft tall drift fence with pitfalls ≥ 90% site perimeter
  - Pitfall buckets <33 ft apart, ≥ 2 gallon buckets
  - Traps opened for rain events <u>Oct. 15 – Mar. 15</u>
- 3) If potential breeding habitat on-site
  - 2 seasons aquatic sampling for CTS larvae
    - Sample >10 days apart in March, April, and May
    - Sample using dipnets and seines (if none detected in dipnets)
  - One season drift fence sampling as above
    - With drift fences also around potential breeding habitat

USFWS/CDFG Reports

- Provide Complete Information
  - Dates and times sampled
  - Rainfall/temperature data for area during study period
  - Records of all animals captured
  - Photographs of representative specimens
  - Photographs of sampling apparatus
  - Records of all communications with USFWS
  - For aquatic sampling, calculations of the total effort expended/area covered each time

CTS Basics – Final Review

- Aquatic Habitat – just for breeding
  - Good ponds are temporary but dry only after May
  - Bigger, longer lasting ponds are better
- Upland Habitat – the rest of their lives
  - On land CTS occupy small mammal burrows
  - Many move hundreds of meters from ponds
  - Only return to ponds to breed (not even every year)
- Landscape Considerations
  - More ponds = more security against local catastrophes
  - For connectivity, ponds should be 1-2 km or less apart
- Weather/Rainfall
  - drives migrations and population dynamics