

Title: Abundance and phenology patterns of two pond-breeding salamanders determine species interactions in natural populations

Authors: Thomas L. Anderson¹, Daniel J. Hocking², Christopher A. Conner¹, Julia E. Earl³, Elizabeth B. Harper⁴, Michael S. Osbourn¹, William E. Peterman⁵, Tracy A. G. Rittenhouse⁷, and Raymond D. Semlitsch¹

Erratum:

The original manuscript by Anderson et al. (2015) contained a data manipulation error that affected several sections of the numerical results, and a few of the overall conclusions. Below, we outline the nature of the analytical error, report a brief summary of how the results change, what the correct results should be, and list the important biological interpretations those changes.

Data Analysis:

The data used in Anderson et al. (2015) were initially aggregated by calendar year and pond to obtain the total number of adult and metamorphosed individuals for ringed and spotted salamanders. This resulted in a data frame that looked similar to the hypothetical example below:

Year	Pond	Metamorphs	Adults	...
2004	1	100	200	...
2005	1	75	300	...
...				

However, the ringed salamander life cycle encompasses two calendar years, due to their fall breeding phenology (roughly equivalent to saying is the start of a biological “year” is August), resulting in a misalignment of adult and metamorph abundances that represented a single breeding cohort. In the example above, metamorphs in 2004 actually came from breeding adults in 2003, 2005 metamorphs come from 2004 breeding, etc. In other words, the 200 adults in the above example are what produce the 75 metamorphs in 2005, not the 300 adults in 2005. Thus, the data used in the original analysis was incorrectly aligned, as we had not adjusted for the ringed salamander life cycle.

While the misalignment of adult and metamorph abundances were not a problem for spotted salamanders in the same way, as their life cycle is contained with a single calendar year, this error affects the analysis of their responses because the correct ringed salamander abundance to use as a predictor of spotted salamander response variables would be from the previous year, not the same year.

In total, correcting these changes to the data eliminates five of twenty data points for analyzing abundance and survival of each species, because these response for metamorphic ringed salamanders in 2004 would have no predictors based on adult ringed salamanders (*Intraspecific* and *Interspecific models*, respectively). Additionally, there are no ringed salamander metamorph values or spotted salamander values corresponding to ringed salamander adults from 2007, as the fences were not monitored in 2008. Our use of a random effect of Year now represents the year during which ringed salamanders bred. Analysis of SVL and date of emigration also now have a reduced sample size because of what predictors go into the models, though not to the same degree as abundance or survival, as individual-level measurements were used and the pond/year random effects account for interdependence of values.

Results:

Summary of changes to the Results: The ranking of models was different for two out of four response variables for *A. annulatum*, and four out of four responses for *A. maculatum* (Tables E1-E2). The significance of parameter estimates for individual covariates mostly remains the same between versions of the Results, as does the direction (positive or negative) of the effects. We note the exceptions that did change in Tables E3-E4. The results pertaining to the relationship of size and date of metamorphosis remain unchanged (1st paragraph of original Results section).

Results, based on correct analysis:

For *A. annulatum*, the best supported model for all response variables was the joint effects model, which contained both intra- and interspecific effects (abundances and timing of breeding of both species (Table E1). Conspecific and heterospecific female abundances showed positive and negative relationships with metamorph abundance, respectively, with the positive effect being slightly stronger (Table E3). The date of breeding in *A. maculatum* also had a significant but weaker positive effect (Table E3). Metamorph SVL showed a negative relationship with *A. maculatum* female abundance, and positive relationships with the date of *A. maculatum* breeding, conspecific breeding date, and *A. annulatum* metamorph abundance, all of which were relatively equal in strength (Table E3). Metamorph emigration date showed negative relationships with conspecific date of breeding and metamorph abundance, the former of which was three times stronger than the latter. Emigration date also showed a positive relationship with female abundance and date of breeding of *A. maculatum*, with the effect of abundance being nearly twice as strong. Survival of *A. annulatum* showed a positive relationship with *A. maculatum* breeding date and *A. annulatum* female abundance, and a negative relationship with *A. maculatum* female abundance.

For *A. maculatum*, the density model was the top model for metamorph abundance and date of emigration (Table E2). The interspecific model had the highest support for SVL and the phenology model had the highest support for survival (Table E2). Metamorph abundance showed a positive relationship with *A. annulatum* metamorph abundance and female conspecific abundance, and a negative relationship with *A. annulatum* female abundance (Table E4). Metamorph SVL of *A. maculatum* had positive relationships with both *A. annulatum* metamorph SVL and emigration date, with the latter effect being almost twice as strong (Table E4). Metamorph emigration date showed a positive relationship with increasing conspecific female abundance, and negative relationship with increasing *A. annulatum* female abundance that were of approximately equal strength in their respective directions (Table E4). Survival of *A. maculatum* was positively related to date of conspecific breeding, and negatively related to metamorph emigration date and date of breeding of *A. annulatum*, the last of which exerted the strongest influence (Table E4).

Discussion

Changes to primary conclusions:

The original Discussion in Anderson et al. (2015; 1st paragraph of Discussion) stated three primary summary points. The first point states that:

“We found that combinations of intra- and interspecific effects best explained metamorph abundance and survival in natural populations of each species.”

This point is still valid, as the top model for each response variable contained several significant covariates of each species.

The second conclusion from Anderson et al. (2015) stated that:

*“The relationships between each effect and the response variables also supports the hypothesis that early-breeding *A. annulatum* negatively affects recruitment of the spring-breeding *A. maculatum*, matching experimental studies (Anderson and Semlitsch 2014).”*

This general point is still accurate. However, the hypothesized mechanism behind these effects changes for some responses. Previously, we identified that negative effects on *A. maculatum* manifested from metamorphs of *A. annulatum*. In the new results, female abundance of *A. annulatum* was negatively related to abundance and survival of *A. maculatum*. Both adults and metamorphs of *A. annulatum* represent different aspects of predation risk to *A. maculatum*, with the former being a better representation of larval density and the latter a representation of final recruitment of *A. annulatum*. Our new results indicate that larval *A. annulatum* were more important, in a negative way, on *A. maculatum* abundance and survival.

The third point from the original conclusion states that:

*“Our results also indicate metamorph size and date of emigration within each species were affected by different processes (largely intraspecific effects for *A. annulatum* and combinations of intra- and interspecific interactions for *A. maculatum*), which contribute to different size-date relationships that have implications on terrestrial survival and adult fitness.”*

This underlined section above is largely incorrect now, and it would be more accurate to say that size and date were affected by combinations of intra and interspecific process for both species.

A new result, which partly contradicts statements in the original text, is that female abundance of *A. maculatum* was negatively related to metamorph abundance and survival of *A. annulatum*, which could indicate larval competition between the two species has a negative effect on their recruitment. This contradicts our original statement that high reproductive effort of *A. maculatum* potentially facilitated *A. annulatum* recruitment (1st paragraph on p 769). The amalgamation of these results with the previous negative relationships (e.g., *A. maculatum* female abundance on *A. annulatum* metamorph emigration date) all align to suggest that *A. maculatum* has a larger negative effect on *A. annulatum* than we previously suspected.

The remaining Discussion sections (beginning p 770, paragraph 2) are largely unchanged by the new results.

Table E1: Model selection results for metamorphs of ringed salamanders (*Ambystoma annulatum*). All models included Pond and Year as random intercept terms. Abbreviations in the table are defined as follows: “1” = intercept only, Con = conspecifics, Het = heterospecific, Meta = metamorph, ♀ = adult females, Abun = abundance, Date = Julian date of female breeding migration (Con or Het), or Julian date of metamorph emigration (with Meta), and SVL = snout-vent length. ω is the AIC weight. r^2 shows the marginal and conditional values. Bold models are the most highly supported models. Sample size is listed below each response.

Response	Model	Covariates	Δ AICc	K	ω	Marginal
Abundance N = 15	Joint	Con ♀ Abun + Con ♀ Date + Het ♀ Abun + Het ♀ Date	0	7	1	0.49/0.49
	Density	Con ♀ Abun + Het ♀ Abun	20.3	5	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	91.9	5	<0.001	
	Phenology	Con ♀ Date + Het ♀ Date	525.1	5	<0.001	
	Inter	Het ♀ Abun + Het ♀ Date	989.9	5	<0.001	
	Null	~1	1244.6	3	<0.001	
SVL N = 2243	Joint	Con ♀ Abun + Con ♀ Date + Het ♀ Abun + Het ♀ Date	0	9	0.8533	0.37/0.87
	Phenology	Con ♀ Date + Het ♀ Date + Con Meta Date	3.6	7	0.1431	
	Intra	Con ♀ Abun + Con ♀ Date + Con Meta Abun	11	7	0.0035	
	Density	Con ♀ Abun + Het ♀ Abun + Con Meta Abun	38.4	7	<0.001	
	Inter	Het ♀ Abun + Het ♀ Date	2665.2	6	<0.001	
	Null	~1	2728.6	4	<0.001	
Date N = 2243	Joint	Con ♀ Abun + Con ♀ Date + Het ♀ Abun + Het ♀ Date	0	9	1	0.31/0.71
	Intra	Con ♀ Abun + Con ♀ Date + Con Meta Abun	22.8	7	<0.001	
	Phenology	Con ♀ Date + Het ♀ Date	27.4	6	<0.001	
	Density	Con ♀ Abun + Het ♀ Abun + Con Meta Abun	39.9	7	<0.001	
	Inter	Het ♀ Abun + Het ♀ Date	4057.8	6	<0.001	
	Null	~1	4076.6	4	<0.001	
Survival N = 15	Joint	Con ♀ Abun + Con ♀ Date + Het ♀ Abun + Het ♀ Date	0	7	0.82	0.10/0.10
	Density	Con ♀ Abun + Het ♀ Abun	3	5	0.18	
	Intra	Con ♀ Abun + Con ♀ Date	80.8	5	<0.001	
	Inter	Het ♀ Abun + Het ♀ Date	420.6	5	<0.001	
	Phenology	Con ♀ Date + Het ♀ Date	429.3	5	<0.001	
	Null	~1	516.3	3	<0.001	

Table E2: Model selection results for metamorphs of spotted salamanders (*Ambystoma maculatum*). All models included Pond and Year as random intercept terms. Abbreviations in the table are defined as follows: “1” = intercept only, Con = conspecifics, Het = heterospecific, Meta = metamorph, ♀ = adult females, Abun = abundance, Date = Julian date of female breeding migration (Con or Het), or Julian date of metamorph emigration (with Meta), and SVL = snout-vent length. ω is the AIC weight. r^2 shows the marginal and conditional values. Bold models are the most highly supported models. Sample size is listed below each response.

Response	Model	Covariates	ΔAIC_c	K	ω	R2
Abundance	Density	Het Meta Abun + Con ♀ Abun	0	6	1	0.45/0.99
N = 15	Joint	Het Meta Abun + Het Meta SVL + Het Meta Date + Con ♀ Abun + Con ♀ Date	40.1	8	<0.001	
	Phenology	Het Meta Date + Con ♀ Date + Het ♀ Date	114	6	<0.001	
	Inter	Het Meta Abun + Het Meta SVL + Het Meta Date	186.2	6	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	218.3	5	<0.001	
	Null	~1	274.1	3	<0.001	
SVL	Inter	Het Meta Abun + Het Meta SVL + Het Meta Date	0	7	0.88	0.52/0.69
N = 1225	Joint	Het Meta Abun + Het Meta SVL + Het Meta Date + Con ♀ Abun + Con ♀ Date	3.9	9	0.12	
	Phenology	Het Meta Date + Con ♀ Date + Het ♀ Date	108.4	7	<0.001	
	Density	Het Meta Abun + Con ♀ Abun	187.6	8	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	208.2	7	<0.001	
	Null	~1	226.9	4	<0.001	
Date	Density	Het Meta Abun + Con ♀ Abun	0	8	0.9985	0.15/0.32
N = 1225	Joint	Het Meta Abun + Het Meta SVL + Het Meta Date + Con ♀ Abun + Con ♀ Date	13	9	0.0015	
	Intra	Con ♀ Abun + Con ♀ Date	23.3	7	<0.001	
	Inter	Het Meta Abun + Het Meta SVL + Het Meta Date	24.7	7	<0.001	
	Null	~1	33.9	4	<0.001	
	Phenology	Het Meta Date + Con ♀ Date + Het ♀ Date	35.3	7	<0.001	
Survival	Phenology	Het Meta Date + Con ♀ Date + Het ♀ Date	0	6	0.9945	0.28/0.75
N = 15	Density	Het Meta Abun + Con ♀ Abun	10.4	6	0.0055	
	Joint	Het Meta Abun + Het Meta SVL + Het Meta Date + Con ♀ Abun + Con ♀ Date	19.6	8	<0.001	
	Inter	Het Meta Abun + Het Meta SVL + Het Meta Date	107.4	6	<0.001	
	Intra	Con ♀ Abun + Con ♀ Date	123.8	5	<0.001	
	Null	~1	160.2	3	<0.001	

Table E3: Parameter estimates of top models for each response of metamorphic ringed salamanders (*Ambystoma annulatum*). Upper and Lower C.I. are 95% confidence intervals. AMMA = *Ambystoma maculatum*, AMAN = *A. annulatum*, Meta = metamorph, ♀ = adult females, Date = breeding immigration date of adult females or emigration date of metamorphs, Abun = abundance, and SVL = snout-vent-length. For covariates that were in the top model in the original results, a change in the significance or direction of the relationship is indicated as follows: *switch from non-significant to significant; ^switch from significant to non-significant; + switch from negative to positive relationships and significant; - switch from positive to negative relationship and significant.

Response	Covariate	Estimate	Std. Error	z/t-value	lower	upper
Abundance (N = 15)	(Intercept)	4.083	0.670	6.092	2.519	5.619
	Het ♀ Date	0.489	0.084	5.821	0.324	0.655
	Het ♀ Abun*	-1.429	0.151	-9.459	-1.730	-1.136
	Con ♀ Abun	2.226	0.107	20.890	2.020	2.438
	Con ♀ Date^	-0.022	0.128	-0.175	-0.273	0.229
SVL (N =2243)	(Intercept)	41.599	3.158	13.171	34.978	48.264
	Con Meta Abun	1.205	0.335	3.596	0.557	1.869
	Het ♀ Abun	-2.357	0.744	-3.167	-3.793	-0.810
	Het ♀ Date	1.829	0.454	4.033	0.875	2.713
	Con ♀ Date ⁺	1.687	0.320	5.277	1.049	2.306
	Con ♀ Abun	-1.279	0.709	-1.805	-2.682	0.095
Date (N =2243)	(Intercept)	150.942	7.900	19.106	134.699	167.506
	Con Meta Abun*	-3.821	1.344	-2.842	-6.460	-1.051
	Het ♀ Abun ⁺	3.882	1.805	2.151	0.137	7.706
	Het ♀ Date	6.064	2.941	2.062	-0.450	12.054
	Con ♀ Date	-9.212	1.281	-7.192	-11.696	-6.351
	Con ♀ Abun^	2.451	2.840	0.863	-3.388	8.018
Survival (N = 15)	(Intercept)	-7.075	0.794	-8.909	-8.920	-5.255
	Het ♀ Date	0.337	0.083	4.047	0.174	0.501
	Het ♀ Abun	-1.396	0.152	-9.183	-1.698	-1.101
	Con ♀ Abun	2.034	0.107	18.997	1.826	2.247
	Con ♀ Date^	0.078	0.129	0.602	-0.175	0.331

Table E4: Parameter estimates of top models for each response of metamorphic spotted salamanders (*Ambystoma maculatum*). Upper and Lower C.I. are 95% confidence intervals. AMMA = *Ambystoma maculatum*, AMAN = *A. annulatum*, Meta = metamorph, ♀ = adult females, Date = breeding immigration date of adult females or emigration date of metamorphs, Abun = abundance, and SVL = snout-vent-length. For covariates that were in the top model in the original results, a change in the significance or direction of the relationship is indicated as follows: *switch from non-significant to significant; ^switch from significant to non-significant; + switch from negative to positive relationships and significant; - switch from positive to negative relationship and significant.

Response	Covariate	Estimate	Std. Error	z/t-value	lower	upper
Abundance (N = 15)	(Intercept)	4.292	0.958	4.480	1.957	6.630
	Het Meta Abun ⁺	0.543	0.112	4.845	0.325	0.766
	Con ♀ Abun*	3.155	0.283	11.164	2.623	3.735
	Het ♀ Abun	-2.900	0.244	-11.878	-3.394	-2.434
SVL (N = 1225)	(Intercept)	32.067	1.446	22.181	28.877	35.261
	Het Meta Date	5.005	0.316	15.843	4.361	5.618
	Het Meta SVL	3.022	0.247	12.220	2.510	3.503
	Het Meta Abun [^]	0.128	0.176	0.727	-0.212	0.494
Date (N = 1225)	(Intercept)	226.536	11.862	19.098	203.287	249.784
	Con Meta Abun	1.699	2.483	0.684	-3.167	6.565
	Het Meta Abun [^]	2.522	2.567	0.982	-2.509	7.553
	Con ♀ Abun	34.317	11.349	3.024	12.073	56.561
	Het ♀ Abun	-38.996	10.198	-3.824	-58.984	-19.008
Survival (N = 15)	(Intercept)	-7.163	1.409	-5.083	-9.925	-4.401
	Het ♀ Date	1.285	0.127	10.155	1.037	1.533
	Con ♀ Date ⁻	-2.075	0.181	-11.453	-2.430	-1.720
	Het Meta Date	-0.222	0.075	-2.963	-0.369	-0.075