INFLUENCE OF CANOPY COVER AND CLIMATE ON EARLY LIFE-STAGE VITAL RATES FOR NORTHERN RED-LEGGED FROGS (*RANA AURORA*), AND THE IMPLICATIONS FOR POPULATION GROWTH RATES

By

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A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

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December 2017

ABSTRACT

INFLUENCE OF CANOPY COVER AND CLIMATE ON EARLY LIFE-STAGE VITAL RATES FOR NORTHERN RED-LEGGED FROGS (*RANA AURORA*), AND THE IMPLICATIONS FOR POPULATION GROWTH RATES

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Many amphibian species are in decline due to habitat loss and changing climates. Understanding how habitat characteristics and climate influence vital rates, and if they act in concert or in opposition can inform management decisions. This study investigated the potential interaction of canopy cover and climate on early stage vital rates of northern red-legged frogs. Demographic data were collected from sample populations in experimental canopy cover treatments across a latitudinal distribution. Rearing cages were used to estimate hatch success, and mark-recapture surveys to estimate tadpole survival. Ambient air temperature was used as an index of climate because it is easily relatable to the effects of climate change and collected at fine scales without specialized equipment. Estimates from field data, along with published accounts were used in a matrix modeling analysis to evaluate if tadpole survival impacted population growth rates.

Egg hatch success did not differ between canopy treatments or among sites. Canopy cover did affect tadpole survival rates, but not tadpole development time. The effect of canopy over on tadpole survival varied depending on which population was

being evaluated. There was no evidence that the effect of canopy cover on tadpole survival was dependent on air temperature. Tadpole survival rates did impact population growth rates.

This research shows that the effect of canopy cover on early stage vital rates for this species is variable between populations, but not due to differences in average air temperatures. For some populations the effect of canopy cover on tadpole survival was large enough to change projected population growth rates from stable to decreases of 30%. These results demonstrate that manipulating canopy cover can influence tadpole survival sufficiently enough to alter population trajectories. However, the variable effects of canopy cover on vital rates suggest a universal management strategy through canopy cover manipulation will not have equal impacts across populations.

ACKNOWLEDGEMENTS

I would like to thank Dr. Brian Hudgens for supporting this research intellectually, his mentorship, and securing the funding opportunity. Thanks to committee members Dr. Daniel Barton and Dr. Matthew Johnson for their feedback and guidance, and to Dr. Barton for serving as committee chair. Thanks to the research and administrative staff at The Institute for Wildlife Studies (Arcata, California, USA). I would also like to extend gratitude to the cooperating land owners and management agencies who provided access to field sites and logistical support; The Mendocino Redwood Company LLC, Green Diamond Resource Company, Humboldt Bay National Wildlife Refuge (USFWS), and the United States Army Corps of Engineers - Willamette Valley Projects. This material is based upon work supported by the US Army Corps of Engineers, Humphreys Engineer Center and Support Activity Contracting Office under Contract No. W912HQ-15-C-0051. Any opinions, findings and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the US Army Corps of Engineers, Humphreys Engineer Center and Support Activity Contracting Office.

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INTRODUCTION

Amphibians are experiencing declines and extinctions at unprecedented rates (McCallum 2007). Nearly half of all described amphibian species are experiencing some decline, while one third of described amphibian species are listed as globally threatened by the International Union for Conservation of Nature (IUCN, Stuart et al. 2004). A variety of sources contribute to amphibian declines, but availability of suitable habitat appears to have a significant role in driving population dynamics and species diversification (Ficetola and De Bernardi 2004, Porej et al. 2004, Cushman 2006). In at least one study, existing habitat characteristics at the site level appear to be a stronger determinant of species occurrence than either historic conditions or habitat characteristics at larger spatial scales (Piha et al. 2007).

One important local habitat characteristic influencing amphibian vital rates is vegetation in and around the breeding sites (Williams et al. 2008). For example, canopy cover is negatively associated with somatic growth rates and survival of tadpoles for several anuran species (Werner and Glennemeier 1999, Thurgate and Pechmann 2007). Werner and Glennemeier (1999) found American toad (*Bufo americanus*), wood frog (*Rana sylvatica*) and leopard frog (*Rana pipiens*) tadpoles experienced poorer survivorship in closed canopy systems compared to open canopy systems.

Thurgate and Pechmann (2007) investigated survivorship differences for tadpoles of the endangered dusky gopher frog (*Rana sevosa*) and the relatively common southern leopard frog (*Rana sphenocephala*) in closed and open canopy systems. Survivorship to

metamorphosis was greater for dusky gopher frogs in open-canopy artificial ponds than in shaded artificial ponds. The effect of shading was less influential for southern leopard frogs. The authors suggest the differences in the species' trajectories between the endangered dusky gopher frog and the more common southern leopard frog are, at least in part, due to the different responses to closed canopy breeding sites.

Climate has also been implicated as an influential force on amphibian vital rates and life history characteristics (Daszak et al. 2005, Pounds et al. 2006, and Todd et al. 2010). Because climate can be influenced by latitude and elevation, amphibian species that exist across wide latitude and elevation ranges, like northern red-legged frogs (*Rana aurora*), also exist across a range of climates. For such species, survival may depend on a combination of local climates and habitat characteristics. Understanding how a species' vital rates are related to habitat characteristics in different climates provides managers and ecologists a tool to evaluate the effects of changes habitat management and climate change on amphibian population trajectories.

For this thesis work, I evaluated the effect of canopy cover on northern red-legged frog early stage vital rates, determined whether the effect varied across different climates, and projected growth rates associated with different tadpole survivorship rates for populations that demonstrated a clear signal of canopy effects. Specifically I asked four basic questions: 1) does canopy cover influence egg hatch success and/or tadpole survival, 2) if canopy cover influences hatch success or tadpole survival, does the effect change depending on location within species range, 3) if the effect depends on location with species range, can the differences among canopy treatments be attributed to the

different climates at those locations, and 4) does the observed variation in survival between treatments have a meaningful influence on population growth rates?

Study System

Northern Red-legged frogs are a Ranid species (family *Ranidae*). The Ranid frog family is globally distributed, represented on every continent except Antarctica. Species descriptions and modern genetic based cladistics place nearly 700 species in the family, representing nearly a quarter of all extant frog species (Scott 2005). Northern red-legged frog latitudinal distribution extends from the Northern California coast (USA) northward to coastal British Columbia (Canada). Longitudinal species distribution extends from low elevations in the Cascade and Sierra Nevada mountain ranges westward to the Pacific coastline (Stebbins 1951, and Storm 1960). This distribution of populations covers latitude and elevation gradients, with the potential for different climate and vegetative conditions. In the United States of America, Northern red-legged frogs are listed as vulnerable in California (California Department of Fish and Wildlife 2017), sensitive in Oregon (Oregon Conservation Strategy 2016), and not listed with elevated conservation status in Washington State. For Northern red-legged frogs, breeding generally begins as early as October in the southern end of its range in California (personal observation), and in January to February in Oregon (Storm 1960). The species generally breeds in permanent and ephemeral pools, and slow moving reaches of streams and rivers.

MATERIALS AND METHODS

To determine whether canopy cover has an impact on northern red-legged frog early life stage vital rates, egg hatch success and tadpole survival data were collected in open and closed canopy areas at seven breeding sites. Two experimental enclosures (see below) were created in each field site to create contrasting canopy cover treatments. Subsamples of eggs were reared and hatched in-situ to estimate hatch success, and mark-recapture methods were used to estimate tadpole survival. Mark-recapture models estimating tadpole survival for different site and canopy treatment groupings were compared to determine if the effect of canopy varied for different populations. Climate was integrated into mark-recapture models to determine if the differences in tadpole survival estimates were due to differences in climate. Estimates of vital rates from field data, along with published accounts, were then used to parameterize population projection matrices to determine if variation in canopy effects on early stage vital rates between treatments produced consequential differences in population trajectories.

Field Sites

Field sites were distributed across the southern half of the species latitudinal range, spanning approximately 560 km from Fort Bragg, California, USA to Sweethome, Oregon, USA which included sites with a range of different climate conditions (Table 1, Figure 1). Field sites were selected for accessibility, a mosaic of canopy cover amounts, and a recent history of breeding activity.

Sites included a variety of water body types including seasonal or ephemeral pools, permanent ponds, and artificial water bodies such as abandoned quarries and reaches of reservoirs. Land management between the sites included federal agencies and private industry ownership (Table 1). Sites varied in vegetation abundance and species composition, as well as hydroperiod and growing season phenology.

Figure 1. Image showing approximate locations of field sites. Outline showing approximate range of Northern red-legged frogs in Oregon and California, in lighter color. Three letter acronyms are site names, see Table 1. Image source: Google earth V 7.1.7.2606. (12/13/2015). Image Landsat/Copernicus, Data LDEO-Columbia.

Table 1. Locations of field sites, listed from North to South. UTMs (Universal Transverse Mercator) are projected in WGS 84, zone 10. Site abbreviations and description are, FOS = Abandoned quarry adjacent to Foster reservoir; APG = Slough in the Applegate management unit of Fern Ridge reservoir; FCR = Pond within the Tufti management unit at Fall Creek reservoir, HCR = Pond located below toe of dam at Hills Creek reservoir, BLG = Ephemeral pond located within Big Lagoon timber management tract near Orick, CA., REF = Ephemeral pool/wetland located on Humboldt National Wildlife Refuge, Humboldt County, CA., DYL = Semi-permanent pond located near Doyle Creek in Fort Bragg, CA. USACE = United States Army Corps of Engineers; GDRC = Green Diamond Resource Company; USFWS = United States Fish and Wildlife Service, MRC = Mendocino Redwood Company. Elevation is approximate.

Site	General Location	UTM	Elevation (m)	Water body type	Land manager/owner
FOS	Linn County, Oregon	526000 E 4918614 N	215	Abandoned quarry	USACE
APG	Lane County, Oregon	472547 E 4878592 N	121	Reservoir	USACE
FCR	Lane County, Oregon	519330 E 4866634 N	243	Ephemeral pool	USACE
HCR	Lane County, Oregon	546082 E 4840188 N	384	Pond	USACE
BLG	Humboldt County, California	413039 E 4551472 N	250	Ephemeral pool	GDRC
REF	Humboldt County, California	398054 E 4503620 N	3	Seasonally inundated wetland	USFWS
DYL	Mendocino County, California	431741 E 435551 N	102	Ephemeral pool	MRC

Experimental Enclosures

Within each site, two experimental enclosures (hereafter mesocosms) were created by erecting drift fence material to enclose a section of aquatic area. Mesocosms were placed to maximize contrast in canopy cover between the treatments. Drift fences consisted of 122 cm tall woven ground cover material and supported with 122 cm tall non-painted, non-treated wooden ground stakes. The woven ground cover was a UV stabilized, permeable polypropylene material, which allowed the transfer of water and nutrients but restricted tadpoles and hatchlings from passing through.

The bottoms of the drift fences were buried in a shallow trench or secured by cloth tubes filled with pea gravel (< 2 cm river rock aggregate; hereafter gravel tubes). The pea gravel was treated with a bleach solution and thoroughly rinsed prior to filling the gravel tubes to avoid transfer of invasive species or pathogens. Gravel tubes were approximately 10 cm in diameter and 1.5 m long. Each gravel tube was carefully placed on top of an approximately 20 cm wide strip of material at the bottom edge of the drift fence, and overlapped each other by approximately 10 cm.

Mesocosms were constructed to be roughly circular and traverse the aquatic and terrestrial environments. Within each site, habitat conditions were kept as consistent as possible between mesocosms. Mesocosms were designed to be similar in size, and to include shallower (near bank) and deeper parts of the water column. With the exception of the open canopy mesocosm at FOS, each mesocosm incorporated edges of the water bodies to allow for recently transformed metamorphs to emigrate from the aquatic

environment. At FOS, there were no practical areas to place the open canopy mesocosm which included pond edges. The open canopy mesocosm at this site was placed in an area in the middle of the water body that contained a small island of dry land and vegetation onto which metamorphs could migrate. Similarity between mesocosms was determined by visual comparisons during initial site visit and time of setup.

Canopy Cover

In order to ensure that mesocosms within each site differed in canopy cover, canopy cover over each mesocosm was quantified using a Solar Pathfinder™ (The SolarPathfinder Company, Linden, Tennessee, United States of America). The Solar Pathfinder™ device estimates the percent of solar light reaching the point of measurement. This is accomplished by tracing the reflection on a semi-transparent polycarbonate dome of obstructions overhead and on the horizon onto a template sheet underneath the dome (Appendix A). Canopy cover is then estimated as the difference between the amount of light reaching the site and total possible under unobstructed conditions (100%). Using the Solar Pathfinder™ device, measurements of canopy cover were taken only once during any time of the year and estimates of monthly canopy cover were calculated from the template sheet (Appendix A). Paired t-tests were performed for each site (a total of six different t-tests) to determine if monthly canopy cover was different between treatments during the survey period (January through July).

Temperature Data

Mean weekly air temperature was used as an index of climate differences between sites. Air temperature was chosen to represent climate in this study because it can be easily retrieved from historical records or collected on site with little effort for managers. Air temperature can also be measured on fine spatial scales without specialized equipment, and is directly relatable to potential effects of climate change at the breeding site level.

Temperature data were recorded using HOBO® UA-001-08 eight kilobyte data loggers (Onset Computer Corporation®; Bourne, Massachusetts, United States of America). A single data logger was placed in a location within each site, approximately halfway between the mesocosms, and suspended from emergent or bankside vegetation to record ambient air temperature. Each data logger was set to take temperature measurements once per hour. Temperature data from HOBO data loggers were collected at least once during the field season for each site, and when the study period was completed. After temperature data were verified and corrected, hourly temperature readings were averaged over a 24 hour period beginning 12 am (00:00 hours) and ending at 11 pm (23:00 hours) the same calendar day. Daily averages were then used to calculate mean weekly temperatures over seven day periods, corresponding to each date of site visit plus the 6 days prior to each site visit.

Differences in mean weekly air temperatures between sites were evaluated with a Tukey-Honestly Significant Difference (TukeyHSD) test for multiple comparisons on a fitted analysis of variance (ANOVA) general linear model. All statistical analyses for

temperature, and for each following section, were done using the R statistical software program (R core team 2017).

Temperature Data Corrections

Some temperatures from the data loggers recording air temperature were unavailable or corrupted. Data sets with suspect or missing air temperatures from dataloggers were plotted against PRISM climate datasets (PRISM Climate Group, Oregon State University), to check for consistencies between the two data sets for periods just prior to and after the missing data points from the dataloggers. PRISM datasets and datalogger data sets were also compared to check for divergence between the two datasets for the suspect data from the dataloggers. The PRISM climate datasets used for comparisons corresponded to the beginning and ending times of the datalogger sets and had a 4 km scale resolution. Missing air temperature data and data determined to be inaccurate were replaced with data from the PRISM climate datasets specific to each site.

Egg Hatch Success

To estimate egg hatching success, eggs from 2-5 sample egg masses per site were caged within individual mesh-fabric enclosures (hereafter rearing cages). A subsample of 25 eggs from each egg mass was placed in a rearing cage in each of the two experimental mesocosms. Rearing cages were built from untreated, unpainted wooden frames covered with tulle fabric. Rearing cages measured approximately 45 cm width x 45 cm length x 90 cm height. The tops of the rearing cages were left open to facilitate observations of egg development. Rearing cages were placed next to each other in a row within each

mesocosm, and secured with wooden ground stakes. Rows of rearing cages within a site were oriented in the same direction. The position within rows of egg samples from the same egg mass was randomized to account for possible effects of being in an exterior versus interior rearing cage.

Rearing cages were checked once every seven to ten days to determine numbers of hatched and unhatched eggs, development stages of unhatched eggs, and numbers of non-viable embryos. During each check, rearing cages were removed from their anchors and slowly lifted to water surface until eggs, tadpoles or egg cases were visible. If there were unhatched eggs during a check, the rearing cage was placed back into its original position and unhatched eggs were allowed to develop further. During intermediate and final cage checks, some cages had holes in the mesh fabric and repairs were made as necessary.

The total number of eggs present immediately prior to hatching was often less than the 25 originally placed in the rearing cages. Because the fate of these eggs was unknown, hatch success was calculated as the proportion of hatched eggs to the total available to hatch, rather than the original number of 25 eggs. The number of hatched eggs used in the calculation was the highest total count either of tadpoles present, or of empty egg cases (assumed to be the remaining vitelline membrane). Total available to hatch was calculated as the sum of the number of hatched eggs plus the number of unhatched non-viable eggs. Mesocosm and site specific mean hatch success was determined as a weighted average (i.e. mesocosm or site specific sum of hatched eggs divided by sum of total available to hatch).

Nonparametric analyses were used because variances could not be estimated for some mesocosms or sites, and because some mesocosms and sites had very small samples sizes. Variances were not able to be estimated for some treatment and sites because some mesocosms had only one rearing cage that produced hatch success data, some mesocosms had the exact same hatch success for all the rearing cages, and some sites had fewer than 4 total rearing cages. Mesocosm and site effects on ranks of egg hatch success were fit with an ordered logistic regression model using the R package MASS (Venables and Ripley 2002). Significance of overall treatment and site effects were determined from type 2 ANOVA sum of squares reductions using the R package car (Fox and Weisberg 2011).

Tadpole Mark-Recapture

Mark-recapture data were collected throughout the tadpole development period at five of the previously identified seven field sites. Excessive growth of reed canary grass (*Phalaris arundinacea*) at APG resulted in no tadpole captures, and dense submerged woody debris at BLG limited tadpole captures to only two animals, and thus these two sites were excluded from the tadpole survival analysis.

Sample populations of tadpoles for mark-recapture came from tadpoles hatched from naturally-occurring and seeded egg masses in each mesocosm. Seeding egg masses into mesocosms was accomplished by cutting the vegetation that egg masses were attached to and transferring them using a five gallon bucket filled with water. After transferring, the vegetation attached to the egg mass was secured to a bamboo stake.

After hatching, tadpole size and development were monitored by dipnet sampling during each site visit to determine if tadpoles were large enough to mark (between 20mm and 40mm depending on site). Site visits were conducted no less frequently than once every 10 days.

Once large enough to mark, tadpoles from each mesocosm were captured, marked, and released. Tadpoles were captured by dipnetting and using partially submerged funnel traps. Traps were set at randomly selected places around each mesocosm. No trap was in place for longer than 8 hours during any visit, and all traps were closed and pulled from the field sites at the end of the sampling day. On multiple visits for each site, trapping and dip-netting were done outside the mesocosms to determine if any marked animals escaped.

Prior to marking, animals were anesthetized with a solution of Tricaine Methanesulfonate (MS-222) in an immersion bath. MS-222 was chosen as method for anesthesia due to the high recovery rates. Anesthesia was conducted using procedures outlined in Anholdt et al. (1998) and Grant (2008), but at the lower concentration of 0.02 used by Anholdt et al. (1998). Anesthesia solution was buffered with sodium bicarbonate, and neutral ph was verified using disposable ph test strips. Water for immersion and recovery baths was sourced from the natal ponds where tadpoles were captured. Up to three animals at a time were placed in immersion baths and monitored for response to external stimuli to determine if full anesthesia was reached. Typically, full anesthesia was reached in 2-5 minutes.

Once under anesthesia, tadpoles were marked with Visible Implant Elastomer (VIE) tags, (Northwest Marine Technologies Inc., Shaw Island, Washington, USA). Each animal was marked with a four-tag color coded sequence, with two tags on either side of the tail. Tags were injected between the epidermis and muscle tissues using a 0.3 cc insulin syringe with a 29 gauge needle. One pair of tags was placed on the dorsal side and the other pair on the ventral side of the tail. Each pair of tags was adjacent to each other and located near where tail muscle telomeres meet the fins.

After marking, tadpoles were placed in the recovery bath and monitored for recovery. Full recovery was then determined by monitoring tadpoles in holding containers, watching for active swimming and burst swimming when gently prodded. Tadpoles that had fully recovered were released into the same mesocosms from which they were captured. Water for recovery baths, pre and post-marking holding containers were refreshed between batches of tadpoles.

Methods for animal manipulation including anesthesia and recovery, capture, marking and confinement to mesocosms followed those approved in my Institutional Animal Care and Use Committee (IACUC) protocol (number 15/16.W.59-A).

Tadpole Data Collection

For field sites FOS, FCR, HCR, REF, and DYL there were at least four sampling occasions for both mesocosm treatments. Resampling in the closed mesocosm at HCR ended when water levels in the pond dropped suddenly between the third and fourth site visits, and all tadpoles disappeared. These disappearances could have been caused by tadpoles escaping through an undetected hole in the mesocosm or a mass predation event

precipitated by the receding water. Raccoons (*Procyon lotor*) patrol the banks regularly, and large wading birds like Great blue heron (*Ardea herodias*) are commonly observed in the field site. The FCR closed treatment ended after the fourth sampling occasion when water levels dropped rapidly in this mesocosm between the fourth and fifth sampling occasion and all the animals vanished abruptly. The apparent extirpation of this sample population could have been caused by a rapid metamorphosis following the dropping water levels. A more plausible explanation is that low water levels facilitated high predation rates by juvenile and adult bullfrogs (*Lithobates catesbeianus*), which were commonly observed within the mesocosm. There was no detectable hole in the drift fence.

Tadpole Data Analysis

Two important sources of variation in tadpole vital rates which influence recruitment into the metamorph life-stage are: 1) daily survival rates, and 2) the overall length of time of the tadpole stage. Survival and stage length were estimated separately.

Mark-Recapture Analysis

Daily survival rates were estimated using the RMark package (Laake 2013) in R. Multistate models were used to evaluate these data because each mesocosm represents a unique grouping of animals analogous to the different states of animals in the multistate model framework (Arnason 1973, Schwarz et al. 1993). Recapture probabilities were constrained to zero for survey days on which sites were not visited.

Although a few (14 of 583 total recaptures) animals were recaptured outside of the original mesocosms they were released in, no animals were recaptured inside a different mesocosm than the one of original release. Because the proportion of animals recaptured outside their original mesocosm was extremely low, and those tadpoles were captured near their original mesocosm, dispersal among mesocosms could be effectively represented as 0.

During model fitting, two candidate model sets were created. The first model set was created to determine the most appropriate representation of recapture probability (p). Assuming that survival varied independently among all mesocosms, recapture probability was evaluated as 1) a single estimate across all mesocosms and sites, 2) different estimates for each site with a single estimate for both mesocosm treatments within a site, 3) no site differences but different estimates for mesocosm treatments (open or closed canopy) within sites, 4) additive site and treatment effects, and 5) different estimates for each site with different effects of treatment type for each site. For each of these parameterizations, p was assumed to be either 1) the same across all sampling occasions, or 2) a function of total animals captured in a survey day for each mesocosm, reflecting the effort spent capturing during each visit.

Once the best fitting parameterization for p was determined, only that model structure for p was used when fitting different models of daily survival rates (S). To determine if tadpole survivorship was influenced by the canopy cover treatment, a second candidate model set was built and evaluated. This model set contained parameterizations of S as 1) a single estimate across all mesocosms and sites, 2) different estimates for each

site but with a single estimate for both mesocosm treatments within a site, 3) no site differences but different estimates for mesocosm treatments (open or closed canopy) within sites, 4) additive site and treatment effects, and 5) different estimates for each site with different effects of treatment type for each site. Climate was also fit to models with different parameterizations of S, as a linear function of mean weekly air temperature to determine if there was a treatment by temperature interaction. Nonsense estimates (e.g. S = 1 or 0), and inflated standard errors tend to occur when attempting to estimate parameters with relatively sparse data, in particular for models with large numbers of parameters (k). Because of this, a time dependent model where S varied between sampling occasions is not included in the reported final candidate model set for S.

At some point, tadpoles transformed into metamorphs and emigrated from the pond. Because tadpoles were marked on the tail, which is lost to reabsorption during the transformation process, the tags were unrecoverable even if the animal is recaptured. To account for the apparent loss of animals due to transformation, instead of actual loss due to mortality, the mark-recapture dataset for each mesocosm was truncated when at least half of the animals caught in a survey day were considered metamorphs (> Gosner stage 42-43, Gosner 1960). While this method does not account for all the uncertainty between apparent and actual mortality, the timing when at least half the animals caught in a day were metamorphs was interpreted as the first indication that the population has transitioned from mostly tadpoles to mostly metamorphs. For each of the sites this transition happened relatively shortly after the first metamorph was detected, usually within one to two weeks.

Models within each candidate model set were assessed for relative support using Akiake information criterion corrected for small sample size (AICc) (Akiake 1973, Burnham and Anderson 2002), and by model weight. Comparison among candidate models using AICc assumes that data are not overdispersed, where overdispersion is represented as ĉ values (Burnham and Anderson 2002). Overdispersion was checked for using a bootstrap simulation. The bootstrap simulation was completed by recreating multiple alternate datasets in R, with the mark-recapture parameters (e.g. timing of entry into the marked populations, recapture probability, and survival probability) informed by estimates from the general model evaluated with the field data. The bootstrap resampling and evaluation process was completed 100 times. If results from the bootstrap simulation suggest overdispersion is prevalent (i.e. average ĉ values from the bootstrap simulation are greater than the observed ĉ value form the original data set), final AICc values can be adjusted to Quasi AICc (QAICc) to account for the overdispersion (Burnham and Anderson 2002). If the average ĉ value from the bootstrap simulation is smaller than the observed ĉ from the original data, AICc values are not adjusted.

Once the top-performing model was selected and if it contained a site effect, treatment effect, or combination of both, 95% lower and upper confidence limits (LCLs and UCLs) were used as a measure of significance. Comparison of the LCLs and UCLs on the transformed parameters (survival estimates) for pairs of sites, or pairs of treatments within a site, and whether the LCLs and UCLs for the estimated canopy effects (log odds ratios) encompassed zero were used to determine if there was a clear signal of a treatment effect. If the range of confidence limits between the estimates did

not show any overlap, and if the confidence limits on the estimated canopy effects did not encompass zero, this was interpreted as compelling evidence for a treatment effect. Estimated canopy effects for each site were calculated by combining the estimates for the average treatment effect and the site specific treatment effect of the untransformed betas. Standard errors for the site-specific estimated canopy treatment effects were calculated using the delta method in Rmark package (Laake 2013).

Tadpole Tag Loss

Although infrequent, some tag loss was observed during recapture occasions. For tadpoles with complete sequences but partially lost individual tags (i.e. some of the elastomer tag was still visible), the individual tags were reinjected. If an individual tag was completely lost, the remaining tag colors and their position within the original sequence were recorded.

Partial color sequences in the field were cross-checked against the known color sequences used for each mesocosm, and animals with missing tags were matched with a short list of possible animals. In some cases, it was possible to reduce the list to a single individual animal based on when combinations were used, recaptures of other tadpoles with similar combinations, tadpole development, and which mesocosm animals were released in because there was effectively no dispersal between mesocosms. Multiple recaptures of tadpoles with the same partial combination, although rare (19 of 583 total recaptures) were assumed to be the same animal. In most cases partial combinations could be assigned to multiple possible marked individuals. If all possible matches were originally marked on the same date, the unidentified animal was assigned to one of the

possible matches at random. If at least one of the possible matches was originally marked on a different date, the unidentified animal was assigned an identification corresponding with the earliest possible, or the latest possible entry date into the marked population (early and late datasets). It was assumed no animals completely lost all four tags.

The general model for the mark-recapture tadpole survival analysis was evaluated using both the early and late entry datasets to look for differences in survival estimates. In the event that both data sets returned estimates without substantial differences for every survival parameter (i.e. differences between analogous tadpole survival estimates, less than one standard error apart, measured using the smaller of the two comparable standard errors), then either dataset could be used and the choice to use one over the other would be arbitrary. If however, at least one set of analogous survival parameters were greater than one standard error apart, the choice of the data set to use was based on which produced estimates with the smaller of the standard errors on the untransformed betas (β). The remainder of the survival analysis was done using the chosen data set. Results from the global model used in dataset selection evaluated with the early and late entry datasets are reported in Appendix B.

Tadpole Stage Length

Tadpole stage length for each mesocosm was estimated as the length of time from when the tadpole sampling started to the first sampling occasion when more than half of the animals caught (marked or unmarked) were metamorphs. A set of generalized linear models were compared to determine if tadpole stage length varied between treatments or sites. For each model the response variable was the estimate of the tadpole stage length.

A total of four models were built, one with no effect (null model), one each for site only and treatment only effects, and one for both site and treatment effects. AICc scores from each model were compared to determine the best representation of differences in tadpole stage lengths between canopy treatments and/or sites. Lower AICc scores taken as supporting evidence for better representation of differences. Because the HCR and FCR closed treatments ended abruptly as a result of rapid drying which likely facilitated predation rates greater than ambient levels, estimates of the tadpole period for these treatments were excluded from the models. Because of unbalanced data (HCR and FCR missing estimates for the closed treatments), in addition to the small sample sizes, an interaction model could not be evaluated to determine if tadpole stage length differed between mesocosms for each site.

Population Growth Rates

Pre-breeding stage-based (Lefkovitch) matrices (Lefkovitch 1965), were created to determine if canopy differences may have an effect on stable stage population growth rates (λ) through their influence on tadpole survival rates. For each site where significant differences in tadpole survival between mesocosm were observed, population growth rate matrices were created corresponding to the different estimates of tadpole survival and stage length. Matrices were built for the point estimate for tadpole daily survival, LCL and the UCL for each mesocosm at each site evaluated. For each matrix, only tadpole survivorship or tadpole stage length varied while all other vital rates were kept consistent. The matrix transition elements were calculated from 10 total parameters (Table 2), and

were either estimated directly from data from this study, or appropriated from published accounts.

Table 2. Basic matrix showing parameterization for transition rates. E = combined early life stages, J = Juvenile, A = Adult

	J1	**J2**	**A**
J1	0	0	$(F_b * E_m)* [(H * S_h) * (S_d^n) * M_s]$
J2	$J1_s$	0	0
A	0	$J2_s$	A_s

Published accounts of breeding success (F_b) for northern red-legged frog adult females are scarce, but Licht (1974), suggests that adult females are breeding every year, or at least had eggs available for collection during laboratory experiments (i.e. $F_b = 1$). Eggs per mass (E_m), was estimated as the average eggs per mass across all sites divided by two assuming a 1:1 sex ratio. Average eggs per mass was estimated from counts of eggs in digital photos taken of egg masses at each site. Hatch success (H), was estimated from the rearing cage experiment. Hatch success was averaged across treatments or across sites, dependent on the results from the statistical tests for significant differences between sites or treatments. Published accounts estimate total survivorship rate from egg to metamorphosis at 0.0064 Licht (1974). Under the assumption that post-hatchling tadpoles in my research had comparable survival rates as Licht (1974), S_h was estimated as [0.0064/ average survivorship of tadpoles from my research]. To obtain a stage specific survival rate for tadpoles (S_d^n), the daily survival estimates (S_d) from each mesocosm was raised to the estimates of number of days (n) in the tadpole stage

estimated for each breeding site. Metamorph survival (M_s) values were taken from Licht (1974).

In his research, Licht (1974) estimated a combined adult and juvenile survival rate, as well as an adult only survival rate. However, there is not enough information in that study to determine juvenile only survival with high confidence. Assuming that juvenile survival is likely more similar to that of adults than metamorphs due to their shared behavioral traits (e.g. emigration from natal ponds and overwintering dormant cycles), a single value was used for both J_s and A_s. Because juveniles are not reproductively active in their first year (Licht 1974), the matrix includes a transition rate from first year juvenile ($J1_s$) to second year juvenile ($J2_s$). The matrices evaluated here also assume second year juveniles are not reproductively active. All survivorship rates were assumed to be similar between sexes.

To determine the relative contribution of the early stages to population growth, an elasticity analysis was done (Caswell 2000). Elasticities were calculated analytically using eigenvalues and eigenvectors (de Kroon et al. 1986), in the R software program. Elasticities were evaluated using a matrix with the mean value of for the early stage survival rates for the mesocosms included in individual matrices used in the analysis above.

RESULTS

Canopy Cover

Canopy cover was different between treatments for most sites during the survey period from January through July (Table 3). The greatest observed difference in mean canopy cover between treatments for the study period was for HCR at 54.07 %, while the smallest difference was for BLG at 9.93 % (Table 3).

Table 3. Average canopy cover (from Jan. to July), across seven field sites in Oregon and California. Difference is open minus closed averages. Pr (>|t|) = p-value from paired t-tests evaluating differences in monthly canopy cover between treatments. Each paired t-test compared seven data points for monthly canopy cover in each mesocosm for each site.

Site	Avg. open (se)	Avg. closed (se)	Difference	Pr (>|t|)
FOS	28.78 (5.11)	56.71 (7.75)	27.93	0.0127
APG	31.89 (12.97)	62.71 (11.28)	30.82	0.0987
FCR	10.50 (4.34)	59.07 (11.70)	48.57	0.0051
HCR	7.50 (2.69)	61.57 (2.81)	54.07	< 0.0001
BLG	89.78 (4.61)	99.71 (0.18)	9.93	0.0748
REF	7.00 (1.63)	36.35 (3.17)	29.35	< 0.0001
DYL	12.50 (1.17)	60.21 (11.59)	47.71	0.0061

Temperature

Because sites DYL, REF, HCR, FCR, and FOS were they only ones to yield both egg hatch success and tadpole survival data, they were the only sites included in the temperature analysis. The average of the daily mean air temperatures during tadpole study periods was highest for FCR at 17.313 C°, and lowest for REF at 12.106 C°, with DYL, HCR and FOS at 12.313 C°, 13.868 C°, and 16.612 C° respectively. Results from the TukeyHSD multiple comparisons test on differences in range of temperatures between sites suggested significant differences in mean weekly air temperature between DYL with FCR and FOS (adjusted P = <0.0001 and 0.001), but not REF or HCR (adjusted P = 0.999 and 0.645); significant differences between REF with FCR and FOS (adjusted P = 0.001 and 0.003) but not HCR (adjusted P = 0.641), marginal differences between HCR with FCR (adjusted P = 0.06) but none with FOS (adjusted P = 0.159), and no difference between FCR with FOS (adjusted P= 0.923), (Figure 2).

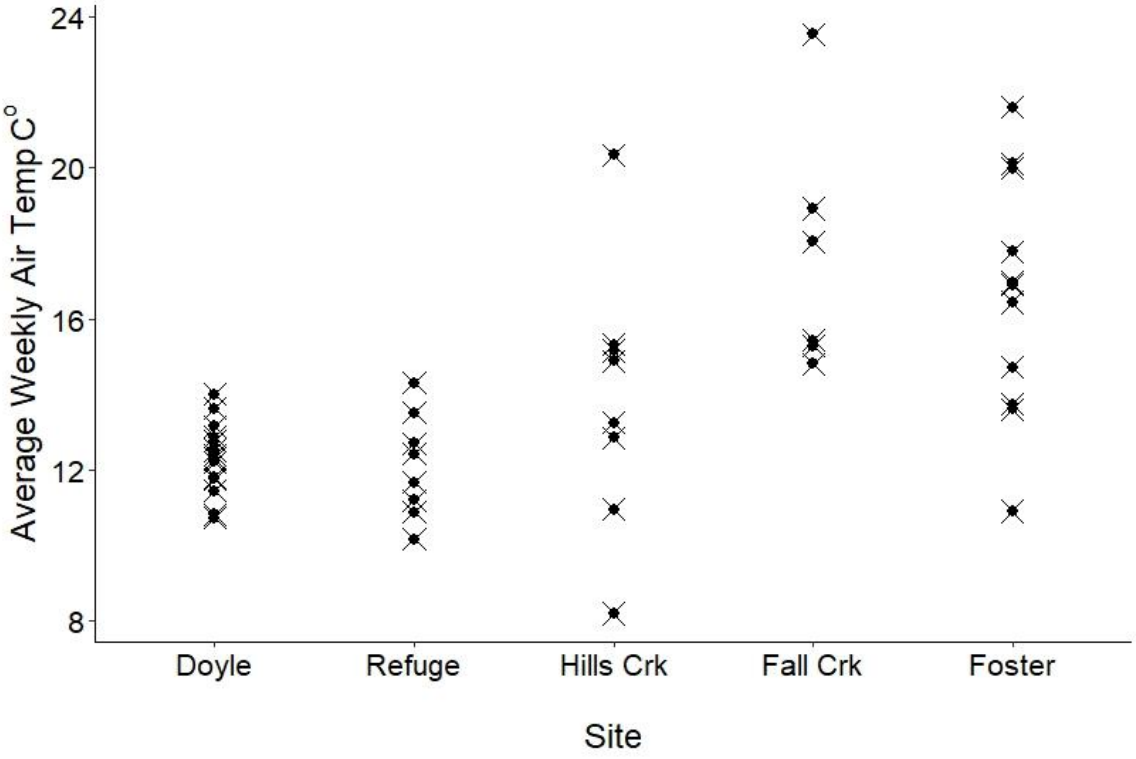


Figure 2. Figure showing average weekly air temperature comparisons between field sites in Oregon and California. Field sites are ordered from South to North. Weekly air temperatures are for the tadpole study period in each site, beginning at the earliest data either mesocosm was surveyed and ending on the latest date either mesocosm was surveyed.

Egg Hatch Success

The total number of rearing cages within a mesocosm used to calculate hatch rates varied from 1 to 5 (Table 4). Two of the four cages installed in the open mesocosm at REF were recovered with no egg cases or tadpoles. One of the cages in the closed mesocosm at REF was recovered with only one tadpole and one egg case, and another was recovered with only 3 tadpoles and no egg cases. All other individual rearing cages, were recovered with a total of at least 10 tadpoles and cases.

Average hatch success was greater than 80% in all mesocosms except for the closed treatment at REF. There was not a significant difference in hatch success between canopy treatments across sites ($\chi^2 = 0.247$, df = 1, P = 0.619). No differences in hatch success were observed between sites ($\chi^2 = 9.188$, df = 6, P = 0.163).

Table 4. Table showing calcualted hatch success by site and canopy treatment. μ Hatch = average hatch rates in treatment type. Range = lowest and highest individual rearing cage hatch success.

Site	(N) cages Open	(N) cages Closed	μ Hatch Open	μ Hatch Closed	Range Open	Range Closed
FOS	4	4	0.95	0.94	0.87 – 1.0	0.87 – 1.0
APG	5	5	0.96	0.96	0.88 - 1.0	0.92 – 1.0
FCR	2	2	0.95	1	0.93 – 0.96	1.0
HCR	5	5	0.82	0.95	0.54 – 1.0	0.88 – 1.0
BLG	1	2	1	1	1.0	1.0
REF	2	5	1	0.35	1.0	0 – 1.0
DYL	2	1	1	1	1.0	1.0

Tadpole Mark-Recapture

A total of 1931 tadpoles were captured, marked and released across five field sites. Total length of time for surveys varied from 20 days in the HCR open treatment to 106 days in the DYL closed treatment. Average number of days from previous sampling occasion to next varied from 6.67 days in HCR closed treatment to 8.38 days in the DYL closed treatment (Table 5).

The late entry dataset was selected to complete the survival analysis because daily survival could not be estimated for all the mesocosms under the general model using the early entry dataset. In addition to the inability to estimate survival for all mesocosms, for the mesocosms in which survival was estimated, the uncertainty associated with the untransformed parameters was greater for the early entry dataset compared to the late entry dataset. Although the late entry dataset was chosen to complete the tadpole survival analysis, the top model from the late entry dataset model selection table was evaluated with early entry dataset. Those results did not qualitatively differ from the conclusions of the tadpole survival analysis using the late entry dataset. The results reported below are based on the late entry dataset.

The overdispersion ($\hat{c}$) value from the model run with the original data was 3.637. The bootstrap simulation was run 100 times and returned a mean $\hat{c} = 7.203$, which gives a derived $\hat{c} = 0.504$. The derived $\hat{c}$ and the scaling factor was rounded up to one, and the model selection table did not change.

The top performing recapture probability model estimated p for each mesocosm treatment, and as a function of daily number of animals caught in each treatment. This model carried 100 percent model weight and had an AICc score > 100 points lower than the next best fitting model. Among the suite of models evaluated for tadpole survival, the model that included a treatment by site interaction had the lowest AICc score and carried 98.1% model weight (Table 6). The next best fitting model included both site and treatment as factors, but without an interaction between the two variables. There was no evidence for a linear or quadratic relationship between air temperature and tadpole survival.

The highest estimated daily survival from the top model was for the FOS open treatment at 0.9857 (SE = 0.0087, CI = 0.9533, 0.9957). The lowest estimated daily survival was for the HCR open treatment at 0.8717 (SE = 0.0337, CI = 0.7898, 0.9247) (Figure 3). The lower and upper confidence limits between treatments overlapped for FOS, FCR and REF, whereas for DYL and HCR the limits show a clearer separation between treatments.

Table 5. Mark-recapture and survey effort data during the study period in 2016. N (marked) = total number marked and released in each treatment. Recaptures = total number of recapture events, Individuals recaptured = uniquely identifiable individuals recaptured across survey period. Begin date = date of first survey day when tadpoles were marked, and End date = date of survey day when 50% or more of animals caught were metamorphs and tadpole period was estimated to be over. Visits = number of visits to each treatment which resampling efforts took place, Avg. interval = average number of days from previous sampling occasion to next.

Site	N (marked)	Recaptures	Individuals recaptured	Begin date	End date	visits	Avg. interval
FOS OP	250	69	61	Apr. 19	Jun. 14	9	7
FOS CL	248	160	103	Apr. 19	Jun. 28	11	7.22
FCR OP	48	6	6	May 6	Jun. 15	6	8
FCR CL	28	10	8	May 6	May 30	4	8
HCR OP	234	17	14	Apr. 20	Jun. 7	8	6.85
HCR CL	164	87	72	Apr. 21	May 11	4	6.67
REF OP	225	66	54	Mar. 9	May 4	9	7
REF CL	266	82	68	Mar. 9	May 4	9	7
DYL OP	250	56	45	Feb. 16	May 19	13	7.58
DYL CL	218	30	29	Feb. 16	Jun. 1	14	8.38

Table 6. Model selection table showing different parameterizations for tadpole survival (S). Models are ordered by relative evidence for model fit as AICc. N(k) = number of parameters included in the model, AICc = corrected Akiake information criterion, ΔAICc = difference in AICc from the top model, weight = model weight, Deviance = model deviance. Parameterization; (site) = parameter estimated for each site, (treatment) = parameter estimated for treatment type, (*) interaction between adjoining terms, (temp) = average weekly ambient air temperature, (^{2}) = quadratic term, (.) = single parameter estimated for all sites and treatments collectively.

Model	**N(k)**	**AICc**	**ΔAICc**	**weight**	**Deviance**
S(site * treatment)	30	3869.73	0.000	9.81E-01	694.715
S(site + treatment)	26	3877.84	9.105	1.03E-02	712.005
S(site + treatment * temp)	28	3878.96	10.226	5.90E-03	709.037
S(site)	25	3882.22	13.485	1.15E-03	718.427
S(temp)	22	3883.97	15.239	4.81E-04	726.297
S(site + temp)	26	3884.14	15.407	4.42E-04	718.307
S(treatment + temp)	23	3885.09	16.358	2.75E-04	725.379
S(treatment + temp + temp^2)	24	3886.27	17.535	1.52E-04	724.517
S(treatment * temp)	24	3887.11	18.379	1.00E-04	725.361
S(.)	21	3888.33	19.601	5.43E-05	732.695
S(treatment)	22	3889.69	20.961	2.75E-05	732.019

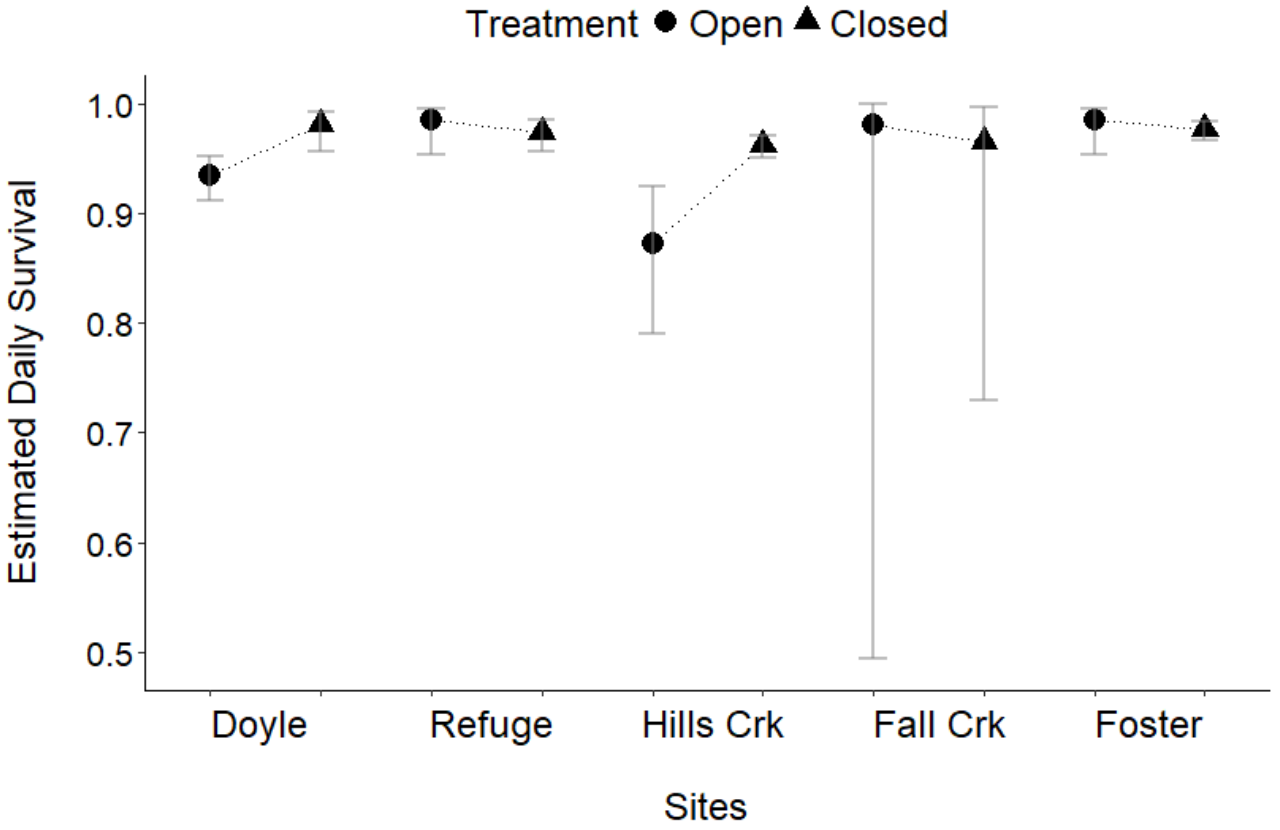


Figure 3. Tadpole Daily survival estimates from the top performing tadpole survival model in the candidate model set, S(site * treatment), p(meso * catch), ψ(fixed0). Grey error bars are lower and upper confidence limits.

Table 7. Tadpole survival analysis model results from top model in candidate model set S(site * treatment), p(meso * catch), ψ(fixed0). β's are estimates of the canopy effect (log odds ratio between treatments) on tadpole daily survival specific to each site. SE are standard errors, LCL and UCL are 95% lower and upper confidence limits. Estimate (S), SE, LCL, and UCL are the real transformed (derived) survival parameter estimates from the model output.

Canopy effect					**Real (transformed) parameter estimates**				
Site	**β**	**SE**	**LCL**	**UCL**	**Site * Treatment**	**Estimate (S)**	**SE**	**LCL**	**UCL**
DYL	-1.294	0.477	-2.228	-0.360	DYL CL	0.981	0.008	0.956	0.992
					DYL OP	0.934	0.010	0.912	0.952
REF	0.575	0.665	-0.728	1.878	REF CL	0.974	0.007	0.956	0.985
					REF OP	0.985	0.009	0.953	0.995
HCR	-1.324	0.335	-1.980	-0.667	HCR CL	0.962	0.005	0.951	0.971
					HCR OP	0.872	0.034	0.790	0.925
FCR	0.582	2.339	-4.002	5.166	FCR CL	0.966	0.040	0.729	0.997
					FCR OP	0.980	0.039	0.493	1.000
FOS	0.505	0.648	-0.765	1.775	FOS CL	0.977	0.004	0.967	0.984
					FOS OP	0.986	0.009	0.953	0.996

Tadpole Stage Length

The observed tadpole stage length in the sites which had estimates for both mesocosms was not consistent. For one site the open treatment had a longer stage length, one site had a longer stage in the closed treatment, and the stages were the same length in another site (Table 8). There was no estimate for the closed canopy treatments at HCR and FCR so the open treatment estimate was taken to be the site estimate.

The top performing model for tadpole stage length suggested tadpole period varied with site only, though the model where tadpole period varied with site and canopy treatment (additive model) was very similar ($\Delta AIC = 0.33$). The no effect model, and the canopy treatment only effect model performed worse ($\Delta AIC = 42.205$ and 34.354 respectively). Although the site only model and the additive model had approximately equivalent AIC scores, the site only model was chosen because stage length did not appear to differ significantly with treatment in the additive model ($z = -1.291$, $P = 0.197$). Because there was little support that stage length differed between treatments, the estimates of tadpole period for each site were averaged across canopy treatments to obtain site estimates.

Table 8. Estimates of the average number of days of the tadpole period for each mesocosm and the overall average between the two treatments. Estimates for HCR and FCR are taken from open treatments only.

Site	Open	Closed	Average days
DYL	106	93	99.5
REF	56	56	56
HCR	48	-	48
FCR	40	-	40
FOS	56	70	63

Population Growth Rates

Because tadpole survival estimates differed between canopy cover treatment only at HCR and DYL, these sites were the only ones used in the matrix analysis. At both sites, the difference in λ associated with tadpole survivorship between treatments corresponded to a 30% yearly decline for the open treatments, and a stable or nearly stable population growth for the closed treatments (Table 9, Figure 4). The elasticity analysis indicated that population growth rates are most sensitive to changes in adult survival with an elasticity value of 0.554, and less sensitive to changes in the combined early stages survival with an elasticity value of 0.148.

Table 9. Matrix modeling results for stable stage population growth rates (λ). Treatment = Doyle open, Doyle closed, Hills Creek open, Hills Creek closed. E_m = average eggs per mass from counts across all sites divided in half assuming a 1:1 sex ratio, H = average egg hatch rate across all treatments and sites, S_h = recruitment into tadpole population calculated as [0.0064/0.23227], S_d = estimated tadpole daily survival from mark-recapture analysis, n = tadpole stage length (days). M_s = metamorph survival, J_s = juvenile survival, A_s = adult survival rates, and F_b = proportion of adult females reproductively active from Licht (1974). 95% LCL, UCL = lower and upper confidence limits.

Treatment	E_m	H	S_h	S_d (LCL , UCL)	n	M_s	$J1_s$	$J2_s$	A_s	F_b	λ (LCL , UCL)
DYL OP	258.5	0.918	0.027	0.934 (0.912 , 0.952)	99.5	0.52	0.686	0.686	0.686	1	0.690 (0.686 , 0.713)
DYL CL	258.5	0.918	0.027	0.981 (0.956 , 0.992)	99.5	0.52	0.686	0.686	0.686	1	0.971 (0.725 , 1.228)
HCR OP	258.5	0.918	0.027	0.871 (0.790 , 0.925)	48	0.52	0.686	0.686	0.686	1	0.691 (0.686 , 0.760)
HCR CL	258.5	0.918	0.027	0.962 (0.951 , 0.971)	48	0.52	0.686	0.686	0.686	1	0.980 (0.891 , 1.072)

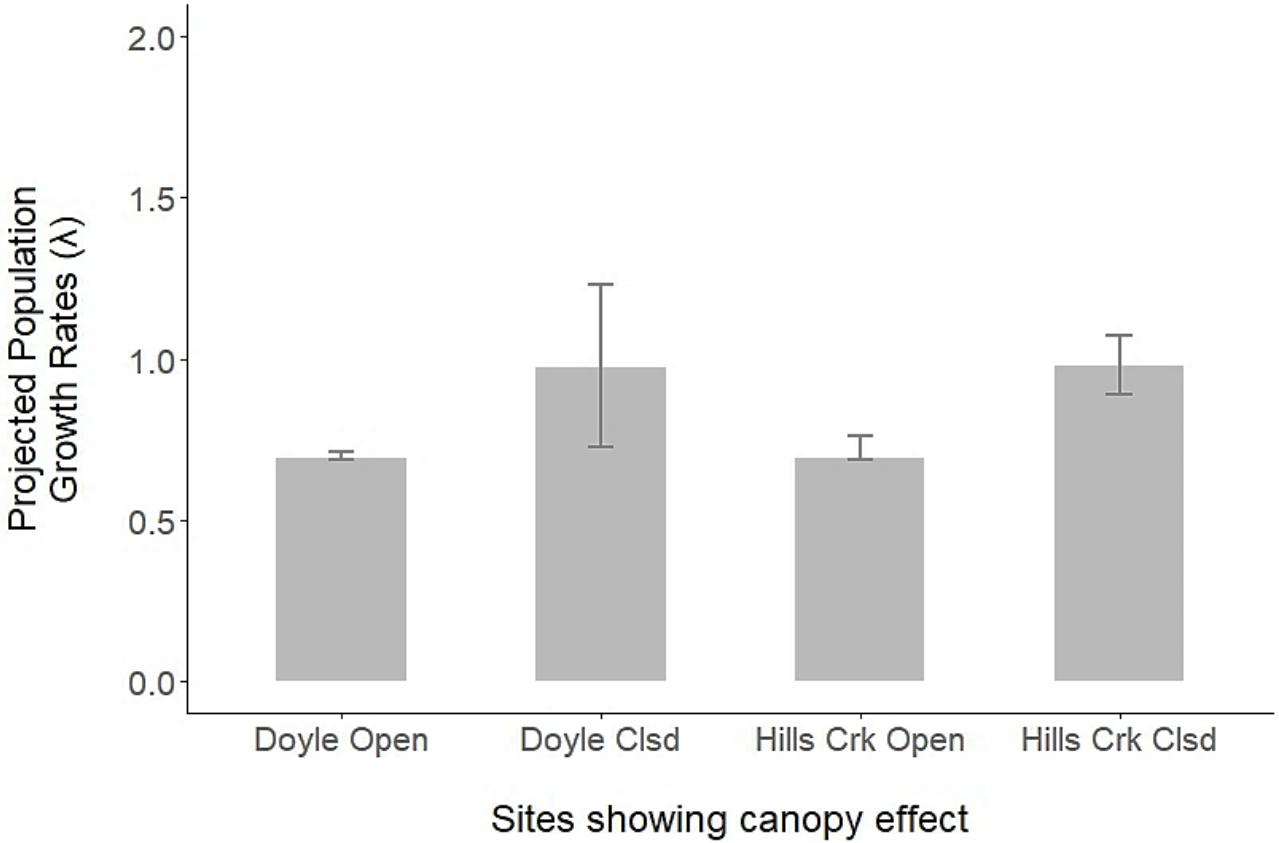


Figure 4. Projected population growth rates (λ) associated with tadpole survivorship in open and close mesocosms at sites DYL and HCR. Bar values are λ calculated from the point estimates of tadpole stage survivorship (S_d^n) for each treatment. Error bars are values for λ calculated from the LCL and UCL of tadpole stage survival for each treatment.

DISCUSSION

In this study, canopy cover appeared to be an important characteristic for some populations. As animals developed from egg to tadpole, the influence of canopy cover became more influential, where there was no effect on egg hatch success but large differences in tadpole survival between treatments for some populations. Despite early stage survival demonstrating lower elasticity, I found that variation in tadpole survival associated with canopy cover can impact population growth rates. Canopy alterations to influence tadpole survival may also be more efficient than managing habitats for juvenile or adult survival because tadpoles occur in higher densities and it may be easier to affect a greater number of animals. However, because not all populations of northern red-legged tadpoles appear to respond to canopy cover the same, a general knowledge of breeding sites accompanied with small scaled canopy manipulation experiment is advisable prior to site-wide alterations.

Canopy Cover Effects

The strength of the canopy cover effect on some vital rates may be more pronounced between entire systems which vary in cover amounts, than between areas of different cover amounts within systems. For example, previous studies which demonstrated a canopy cover effect on vital rates had contrasted ponds of mostly open or closed canopies (Werner and Glennemeier 1999, and Thurgate and Pechmann 2007). This study, however, contrasted vital rates associated with canopy cover amounts

between areas within breeding sites having a mosaic of cover. In breeding sites with a canopy mosaic there may be no barriers preventing the water body from mixing across the different canopy cover microenvironments. This mixing could lead to a more homogenous aquatic environment across the entire breeding site. So even though aquatic conditions can influence egg vital rates (Licht 1971, Humpesch and Elliott 1980, and Seymour et al. 2000), and that these conditions can vary between open and closed canopy ponds (Werner and Glennemeier 1999), mixing across treatments in the current research could have devalued the canopy influence on egg hatch success. Mixing across treatments may also explain why there were no differences in tadpole stage length between treatments, even though other research showed time to metamorphosis did appear to differ between open and closed canopy ponds (Thurgate and Pechmann 2007).

Despite the dissimilarities in study designs, and whether or not site-level water mixing affected hatch success or tadpole stage length, the current research and that of Werner and Glennemeier (1999) and Thurgate and Pechmann (2007) all suggest canopy cover can influence tadpole survival. The direction of the canopy effect in Werner and Glennemeier (1999) and Thurgate and Pechmann (2007) was different than this study, where those authors showed lower tadpole survivorship in closed systems and this work showed lower tadpole survivorship in open canopy treatments.

Of the five sites evaluated for tadpole survival, two showed a detectable canopy cover effect. Both sites had significantly lower survival estimates for the open canopy treatment than the closed. There could be several reasons why canopy cover influenced tadpole survival in some sites but not others. One reason could include local to adaptation

to closed canopy systems. If tadpoles adapted to generally closed canopy systems have higher tolerances to closed canopy environments than tadpoles from open canopy systems, and if tolerances to canopy cover are unidirectionally plastic, this could explain why only two sites showed a canopy effect and the similar responses seen in the two sites. Unidirectional plasticity refers to the ability for individuals within a population to successfully adjust to environmental conditions in one direction across a gradient or range, but not the other. For example, Natterjack toads (*Bufo calamita*) from populations adapted to more saline environments performed as well as toads native to freshwater when moved to freshwater environments, but also had higher tolerances for more saline environments (Gomez-Mestre and Tejedo 2003). However, in the current study neither of the sites with lower survival in the open treatments were closed canopy systems, suggesting unidirectional plasticity along a canopy gradient does not explain why canopy cover affected tadpoles at these sites but not others.

A different mechanism which may explain the shared response between DYL and HCR to canopy cover treatments on tadpole survival could include predation rates associated with canopy cover specific to these two sites. Because tadpoles are easier to visually identify in contrast the surrounding environment in sunnier areas than in shaded areas, predation rates may have been higher in the open mesocosm treatments at DYL and HCR. This may be particularly applicable if the suite of predators at these two sites tend to locate prey items through visual cues rather and olfactory or other sensory cues. However, because predator species richness and diversity were not measured in this study

this possibility is speculative for the sites in this study, though it does present an interesting line of inquiry which may be pursued in future research.

Another reason that only two sites showed canopy effects could be that there was an interaction either between latitude and elevation with canopy, or between climate variables associated with latitude and elevation with canopy. If the effect of canopy was dependent on latitude or elevation and if the two sites shared similar latitudes or elevations, this could signal an interaction. And because climate can be strongly associated with latitude and elevation, a positive correlation with canopy effects and latitude or elevation of sites with canopy effects could indicate an indirect interaction between climate and canopy.

An interaction between canopy cover and latitude or elevation, or climate associated with latitude or elevation does not appear to be responsible for the similar responses in tadpole survival at these sites. The two sites were separated in latitude by nearly 500 km, and there was another site at nearly the same latitude as the northern site that did not show a canopy effect. A large separation in latitude between sites which demonstrated canopy effects, in addition to almost no separation in latitude with another site which did not have a canopy effect, suggests there was not an interaction of canopy with latitude or latitude associated climates conditions.

A canopy by elevation interaction also does not appear to be responsible for the similar canopy effects. Of the two sites with canopy effects, one was low elevation coastal at 102 m elevation, and the other site was an interior mountain foothill site at 384 m elevation. There was a third site which had an even lower elevation (3 m) and closer to

the coastline, but did not show a canopy effect. This would suggest elevation or an elevation associated climate characteristic was not interacting with canopy to drive tadpole survival rates. Some other characteristic or combination of characteristics common to both sites which had a canopy effect could explain the similar responses to the treatments but remains to be discovered.

It may be possible that canopy effects on tadpole survival are not detectable until the differences are large enough. Sites DYL and HCR had two of the three largest differences in canopy cover during the survey period. During the tadpole period specifically, the two sites had the two largest differences in canopy cover. That these two sites showed larger differences in canopy cover, as well as the only sites demonstrating canopy effects on tadpole survival could reflect some threshold effect of canopy differences and tadpole survival for each site. This possibility provides additional intriguing avenues of research.

Climate plays a crucial role in driving vital rates and population dynamics for a variety of amphibian species (Pounds et al. 1999, Grafe et al. 2004, Daszak et al. 2005, McCaffery and Maxell 2010, Todd et al. 2010). That mean air temperature could not explain the different canopy effects might reflect that air temperatures do not accurately represent the effects climate may have on this species or life stage. Tadpoles exist exclusively in the aquatic environment and direct measurements of air temperature may not translate into analogous measurements of water temperatures or to other factors important to tadpole survival. The complex interaction of climate, environment, and hydrology is most likely not as easily summarized as: differences in air temperatures

equal similar differences in aquatic conditions. It may also be that temperature ranges, or average daily temperature minimums or maximums could better represent the effects of air temperature on tadpole survival.

Population Growth Rates

The contribution of early life stages to population growth can be small relative to the contribution from later life stages for iteroparous species. This has been well documented for a variety of species (Heppell et al. 1996, Crooks et al. 1998, Enneson and Litzgus 2008, Morris et al. 2011). Vital rates with relatively high variation have less influence on population growth compared to vital rates with lower variation (Pfister 1998, Saether and Bakke 2000). The elasticity analysis in this study is consistent with these observations, where the combined fecundity and early stage survival rate had a lower relative influence on λ than adult survival. However, this does not mean vital rates with low elasticities or high variation do not have the ability to impact population growth. The results from the matrix projections in this study suggest that although managing adult survival will have greater impacts on population growth rates compared to similar changes in tadpole survival, it may be less practical to manage these later stage vital rates. These results appear to agree with others which suggest early stage vital rates can have an important role in driving population dynamics (Gallard et al. 1998, Govindarjulu et al. 2005, and Sergio et al. 2011).

Population growth rates of northern red-legged frogs may be more effectively and efficiently managed by influencing tadpole survival than by targeting juvenile or adult

survival. In Govindarjulu et al. (2005), the authors conclude managing for metamorph survival provided the greatest impact on λ, and that metamorphs were caught more easily than juveniles or adults due to their higher densities. Like bullfrog metamorphs in Govindarjulu et al. (2005), northern red-legged frog tadpoles are concentrated in higher densities than juveniles or adults. Managing for tadpole survival at breeding sites may then be able to affect a greater overall number of animals compared to managing surrounding upland habitats for juvenile or adult survival.

CONCLUSIONS

For northern red-legged frogs, maintaining appropriate canopy cover levels can increase tadpole survival and influence population trajectories. But the influence on canopy cover on tadpole survival, and thus its effectiveness as a management tool, varies from site to site. When conservation strategies such as habitat management are applied similarly across different populations or life stages, they are likely to have different results. Strategies may have to be adaptable in how they are applied to populations or stages to produce the desired effects.

LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 in Petrov, B.N., and F. Csaki, (eds.) Second International Symposium on Information Theory. Akademiai Kiado, Budapest.

Anholt, B.R., S. Negovetic, and C. Som. 1998. Methods for anaesthetizing and marking larval anurans. Herpetological Review 29:153–154.

Arnason, A.N. 1973. The Estimation of Population Size, Migration Rates and Survival in a Stratified Population. Researches on Population Ecology 15(2):1-8.

Burnham, K. P., and D.R. Anderson. 2002 . Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Second Edition, Springer-Verlag, New York City, New York, USA.

California Department of Fish and Wildlife, Natural Diversity Database. October 2017. Special Animals List. Periodic publication. 65.

Caswell, H. 2000. Matrix Population Models: Construction, Analysis and Interpretation, Second Edition. Sinauer, Sunderland, Massachusetts, USA.

Crooks, K.R., M.A. Sanjayan, and D.F. Doak. 1998. New Insights on Cheetah Conservation though Demographic Modeling. Conservation Biology 12(4):889-895

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128:231–240.

Daszak, P., D.E. Scott, A.M. Kilpatrick, C. Faggioni, J.W. Gibbons, and D. Porter. 2005. Amphibian Population Declines at Savannah River Site are Linked to Climate, not Chytridiomycosis. Ecology 86:332-3237.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The Relative Contribution of Demographic Parameters to Population Growth Rate. Ecology 67(5):1427-1431.

Enneson, J.J., and J.D. Litzgus. 2008. Using Long-term Data and a Stage-classified Matrix to Assess Conservation Strategies for an Endangered Turtle (*Clemmys guttata*). Biological Conservation 141(6):1560-1568.

Fox J., and S. Weisberg. (2011). An {R} Companion to Applied Regression. Second Edition. Sage, Thousand Oaks, California, USA

Francesco Ficetola, G., and F. De Bernardi. 2004. Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. Biological Conservation 119:219–230.

Gallard J., M. Festa-Bianchet, and N.G. Yoccoz. 1998. Population Dynamics of Large Herbivores: Variable Recruitment with Constant Adult Survival. Trends in Ecology and Evolution 13:58-63.

Gomez-Mestre, I., and M. Tejedo. 2004. Contrasting Patterns of Quantitative and Neutral Genetic Variation in Locally Adapted Populations of the Natterjack Toad, *Bufo calamita*. Evolution 58(10): 2343-2352.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 183–190.

Govindarajulu, P., R. Altwegg, and B.R. Anholdt. 2005. Matrix Model Investigation of Invasive Speceis Control: Bullfrogs on Vancouver Island. Ecological Applications 15: 2161-2170.

Grafe, T.U., S.K. Kaminsky, J.H. Bitz, H. Lüssow, and K.E. Linsenmair. 2004. Demographic Dynamics of the Afro-tropical Pig-nosed Frog, *Hemisus marmoratus*: Effects of Climate and Predation on Survival and Recruitment. Oecologia 141:40-46.

Grant, E. H. C. 2008. Visual Implant Elastomer Mark Retention through Metamorphosis in Amphibian Larvae. Journal of Wildlife Management 72:1247–1252.

Heppell, S.S., L.B. Crowder, and D.T. Crouse. 1996. Models to Evaluate Headstarting as a Management Tool for Long-lived Turtles. Ecological Applications 6(2):556-565.

Humpesch, U.H., and J.M. Elliott. 1980. Effect of Temperature on the Hatching Time of Eggs of Three *Rhithrogena spp.* (Ephemeroptera) from Austrian Streams and an English Stream and River. Journal of Animal Ecology 49:643-661.

Laake, J.L. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Lefkovitch, L.P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21(1):1-18.

Licht, L.E. 1971. Breeding Habits and Embryonic Thermal Requirements of the Frogs, Rana aurora aurora and Rana pretiosa pretiosa, in the Pacific Northwest. Ecology 52(1):116-124.

Licht, L.E. 1974. Survival of Embryos, Tadpoles, and Adults of the Frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* Sympatic in Southwestern British Columbia. Canadian Journal of Zoology 52:613-627.

McCaffery R.M., and B.A. Maxell. 2010. Decreased Winter Severity Increases Viability of a Montane Frog Population. Proceedings of the National Academy of Sciences 107:8644-8649.

McCallum, M.L. 2007. Amphibian Decline or Extinction? Current Declines Dwarf Background Extinction Rate. Journal of Herpetology 41:483-491.

Morris Jr., J.A., K.W Shertzer, and J.A. Rice. 2011. A Stage-based Matrix Population Model of Invasive Lionfish with Implications for Control. Biological Invasions 13:7-12.

Oregon Conservation Strategy. 2016. Oregon Department of Fish and Wildlife, Salem, Oregon.

Pfister, C.A. 1998. Patterns of Variance in Stage-structured Populations: Evolutionary Predictions and Ecological Implications. Proceedings of the National Academy of Science of the United States of America 95(1): 213-218.

Piha, H., M. Luoto, and J. Merilä. 2007. Amphibian Occurrence is Influenced by Current and Historic Landscape Characteristics. Ecological Applications 17:2298-2309.

Porej, D., M. Micacchion, and T. E. Hetherington. 2004. Core Terrestrial Habitat for Conservation of Local Populations of Salamanders and Wood Frogs in Agricultural Landscapes. Biological Conservation 120:399–409.

Pounds, J.A., M.P.L. Fogden, and J.H. Campbell. 1999. Biological Response to Climate Change on a Tropical Mountain. Nature 398: 611-615.

Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M.P.L. Fogden, P.N Foster, E. La Marca, K.L. Masters, A. Merina-Viteri, R. Puschendorf, S.R. Ron, A. Sanchez-Azofeifa, C.J. Still, and B.E. Young. 2006. Widespread Amphibian Extinctions from Epidemic Disease Driven by Global Warming. Nature 439:161-167.

PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 27 January 2017.

R core team. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/

Saether, B., and Ø. Bakke. 2000. Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. Ecology 81(3):642-653.

Schwarz, C., J. Schweigert, and A. Arnason. (1993). Estimating Migration Rates Using Tag-Recovery Data. Biometrics 49(1), 177-193.

Sergio, F., G. Tavecchia, J. Blas, L. Lopez, A. Tanferna, and F. Hiraldo. 2011. Variation in Age-structured Vital Rates of a Long-lived Raptor: Implications for Population Growth. Basic and Applied Ecology 12:107-115.

Seymour, R.S., J.D. Roberts, N.J. Mitchell and A.J. Blaylock. 2000. Influence of Environmental Oxygen on Development and Hatching of Aquatic Eggs of the Australian Frog, *Crinia georgiana*. Physiological and Biochemical Zoology 73:501-507.

Scott, E. 2005. A phylogeny of ranid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data. Cladistics 21:507–574.

Stebbins, R.C. 1951. Amphibians of Western North America. University of California Press. 539 pp.

Storm, R.M. 1960. Notes on the Breeding Biology of the Red-Legged Frog (*Rana aurora aurora*). Herpetologica 16(4):251-259.

Stuart, S. N. 2004. Status and Trends of Amphibian Declines and Extinctions Worldwide. Science 306:1783–1786.

Thurgate, N. Y., and J. H. K. Pechmann. 2007. Canopy Closure, Competition, and the Endangered Dusky Gopher Frog. Journal of Wildlife Management 71:1845–1852.

Todd, B.D., D.E. Scott, J.H.K. Pechmann, and J.W. Gibbons. 2010. Climate Change Correlates with Rapid Delays and Advancements in Reproductive Timing in an Amphibian Community. Proceedings of the Royal Society of London B: Biological Sciences 278:2191-2197.

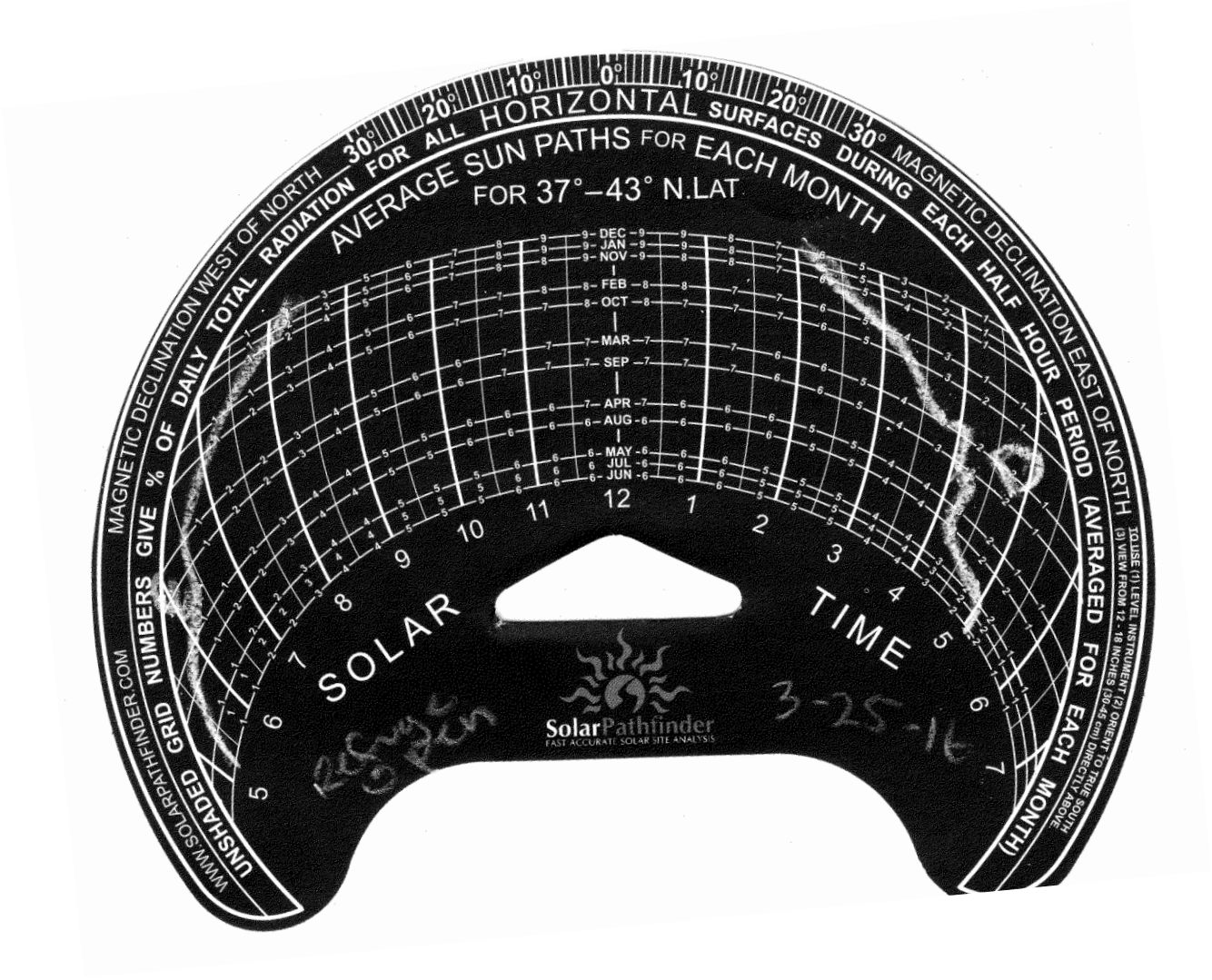
Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York City, New York, USA.

Werner, E. E., and K. S. Glennemeier. 1999. Influence of Forest Canopy Cover on the Breeding Pond Distributions of Several Amphibian Species. Copeia 1999:1-12.

White, G.C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement, 120-138.

Williams, B. K., T. A. G. Rittenhouse, and R. D. Semlitsch. 2008. Leaf litter input mediates tadpole performance across forest canopy treatments. Oecologia 155:377–384.

APPENDIX A



Appendix A: Example of Solar Pathfinder template used to estimate monthly solar exposure. Above template was used at REF field site in the open mesocosm treatment. Templates are one-time use and were catalogued by date, location, and treatment type.

The template sheet is segregated by twelve lines traversing the sheet laterally, approximating the daily pathway of the sun through the horizon for each month. Each month-specific daily pathway is further delineated into quadrants which represent

variable amounts of percent cover. Once a tracing is complete, all of the quadrants within each month-specific daily-pathway which are inside the trace outline are summed to give an estimate of total percent cover for each month. For instance, tracing the reflection of canopy at a field site and adding the percent values of the quadrants within the trace outline, a site in the northern hemisphere may have 40 percent canopy cover during December but only five percent cover in July. Template sheets are specific to the range of latitude where the measurements are taken.

APPENDIX B

Appendix B. Model results from the general model evaluated with the early and late entry datasets (Tables 10 and 11). Survival (S) was estimated for each mesocosm, and recapture probability was estimated for each mesocosm and fit as a function of total daily catch. Transition probabilities were fixed to 0. The reported betas (β) are the untransformed parameter estimates, SE are the standard errors, and LCL and UCL are the lower and upper confidence limits. Estimates are the real transformed (derived) survival parameter estimates from the model output.

Table 10. Results from the general model evaluated with the early entry dataset.

Untransformed Betas					**Real (transformed) parameter estimates**				
Mesocosm	**β**	**SE**	**LCL**	**UCL**	**Mesocosm**	**Estimate (S)**	**SE**	**LCL**	**UCL**
DYL CL	15.253	1125.801	-2191.316	2221.823	DYL CL	1.000	0.000	1.000	1.000
DYL OP	3.550	0.300	2.961	4.138	DYL OP	0.972	0.008	0.951	0.984
REF CL	0.170	0.423	-0.660	1.000	REF CL	0.976	0.007	0.958	0.987
REF OP	0.927	0.843	-0.725	2.578	REF OP	0.989	0.009	0.949	0.998
HCR CL	-0.281	0.333	-0.933	0.372	HCR CL	0.963	0.005	0.952	0.972
HCR OP	-1.633	0.426	-2.468	-0.798	HCR OP	0.872	0.034	0.790	0.925
FCR CL	-0.216	1.232	-2.631	2.199	FCR CL	0.966	0.040	0.729	0.997
FCR OP	-0.169	1.029	-2.185	1.848	FCR OP	0.967	0.031	0.810	0.995
FOS CL	0.320	0.366	-0.398	1.038	FOS CL	0.980	0.004	0.969	0.986
FOS OP	0.793	0.754	-0.685	2.271	FOS OP	0.987	0.009	0.952	0.997

Table 11. Results from the general model evaluated with the late entry dataset.

Untransformed Betas					Real (transformed) parameter estimates				
Mesocosm	**β**	**SE**	**LCL**	**UCL**	**Mesocosm**	**Estimate (S)**	**SE**	**LCL**	**UCL**
DYL CL	1.300	0.475	0.369	2.231	DYL CL	0.981	0.008	0.956	0.992
DYL OP	2.652	0.161	2.337	2.967	DYL OP	0.934	0.010	0.912	0.951
REF CL	0.973	0.317	0.351	1.595	REF CL	0.974	0.007	0.956	0.985
REF OP	1.548	0.627	0.318	2.777	REF OP	0.985	0.009	0.953	0.995
HCR CL	0.589	0.216	0.165	1.012	HCR CL	0.962	0.005	0.951	0.971
HCR OP	-0.735	0.342	-1.406	-0.064	HCR OP	0.872	0.034	0.790	0.925
FCR CL	0.681	1.206	-1.681	3.044	FCR CL	0.966	0.040	0.729	0.997
FCR OP	1.263	2.017	-2.691	5.217	FCR OP	0.980	0.039	0.493	1.000
FOS CL	1.078	0.244	0.600	1.557	FOS CL	0.986	0.009	0.953	0.996
FOS OP	1.583	0.642	0.325	2.841	FOS OP	0.977	0.004	0.967	0.984