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Forest mediated light regime linked to amphibian distribution and performance

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Abstract The vegetation in and around the basins of ephemeral wetlands can greatly affect light environments for aquatic species such as amphibians. We used hemispherical photographs to quantify the light environment in terms of the global site factor (GSF), the proportion of available solar radiation that actually strikes the wetland. We compared GSF to the distribution and performance of two amphibian species (*Pseudacris crucifer* and *Rana sylvatica*) within 17 ephemeral wetlands in northeastern Connecticut, USA. We found that *P. crucifer* is restricted to lighter wetlands (GSF >0.34) and that its abundance is proportional to GSF. By contrast, *R. sylvatica* is found across the light gradient and its abundance is unrelated to GSF. For both species, GSF is a strong predictor of larval developmental rate. In addition, *P. crucifer* growth rate is higher in lighter wetlands. Through thermal effects, changes in resources, or other influences, light appears to be an important predictor of the distribution and performance of amphibians. Because the structure of canopies can change rapidly, and because amphibians can be strongly impacted by these changes, vegetation mediated effects on wetland light environments may be critical to understanding the dynamics of amphibian populations within forested biomes.

Keywords Amphibian · Development · Distribution · Global site factor · Growth

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Introduction

Amphibians resident in small freshwater wetlands have become a model system for ecologists (Wilbur 1997; Werner 1998; Morin 1999). Despite this attention, important aspects of the mechanisms underlying the distribution and abundance of natural populations remain poorly understood (Wellborn et al. 1996; Skelly 1997, 2001; Alford 1999; Skelly and Kiesecker 2001). Recently, long-term surveys have uncovered dramatic changes in the distribution of amphibian species over time. While some of these dynamics have occurred in the context of population declines and species extinction (reviewed by Alford and Richards 1999), it appears that even healthy amphibian populations can undergo rapid changes (Sjogren-Gulve 1994; Skelly et al. 1999; Carlson and Edenhamn 2000). Preliminary evidence suggests that some observed changes in amphibian distributions could result from alterations in the vegetation canopy above small wetlands (Skelly et al. 1999, 2002; Werner and Glennemeier 1999).

The light environments of nonpermanent wetlands are apt to be particularly susceptible to the effects of vegetation. Because they tend to be relatively small, the crowns of trees and other vegetation can overtop ephemeral wetlands. Because they are often shallow, many nonpermanent wetlands can support rooted vegetation within their basins. Where succession, fire, timber harvest, beaver (*Castor canadensis*), or other disturbances result in temporal changes in vegetation structure, corresponding changes in light environment may be expected (Skelly et al. 1999; Skelly and Freidenburg 2000). Ecologists studying the role of gap formation in terrestrial forests and other systems have shown that the timing, size, and spatial distribution of such dynamics can have an overriding effect on the distribution of species (e.g., Paine and Levin 1981; Whitmore 1989; Pacala et al. 1996). The purpose of this study is to evaluate the relationship between vegetation and amphibians. We hypothesize that relationships among vegetation, solar radiation, temperature, and other factors are likely to have

strong effects on the present day distribution and performance of amphibians across a light gradient.

We used hemispherical photographs of the canopy cover to quantify the light regime over 17 temporary ponds in Connecticut, USA. This technique has been largely developed by plant ecologists who have long recognized the importance of solar radiation and the need for a method with which to analyze it at relatively fine scales and over long time periods (Evans and Coombe 1959; Anderson 1964). We used 3 years worth of survey and sampling data to evaluate what effect this factor has on the distribution, abundance, and performance of two amphibian species: wood frogs (*Rana sylvatica*) and spring peepers (*Pseudacris crucifer*).

Materials and methods

This study was conducted at the 3,800-ha Yale-Myers Forest in northeastern Connecticut, USA. Timber harvesting, as well as the activities of beaver (*Castor canadensis*), have promoted the development of a diversity of light environments within wetlands at the Yale-Myers Forest. The 17 ephemeral wetlands used in this study range from heavily shaded to relatively open. Maximum surface areas range from 40 to 5,200 m² and maximum depths were between 25 and 250 cm. They were selected for study during 1998 or earlier because they were known amphibian-breeding sites and were nonpermanent.

We quantified the light environment at each wetland in terms of the global site factor (GSF) (Anderson 1964). This ratio estimates the amount of light that actually strikes a point over the amount of light that would strike the same point if there were no overhead obstructions. The GSF changes depending both on the length of time considered and the time of year. We estimated GSF using hemispherical photographs of the forest canopy. With such photographs, it is possible to estimate the amount of diffuse and direct beam radiation that would strike the photograph point during a given time interval (Evans and Coombe 1959; Anderson 1964). This method has been used by plant ecologists for many years, and estimates of photon flux based on hemispherical photographs have been shown to closely correspond to average direct sensor measurements (Chazdon and Field 1987; Becker et al. 1989; Rich et al. 1993). We analyzed the photographs and estimated GSF with Hemiview (Delta-T 2001). Necessary parameters for this program were estimated from the 1960–1990 data in the National Solar Radiation Database (2001) for Hartford, Connecticut (approximately 40 km from the study site).

Photograph points were laid out in a grid pattern with 5-m intervals bounded by the high water mark of the wetlands in 1999. Two photographs were taken at each point. “Leaf-on” photographs were taken during the summer of 1999 and “leaf-off” photographs were taken during the winters of 1999 and 2000. We used these two sets of photographs to estimate the average GSF from April to August, the embryonic and larval periods of our focal species at this site. As leaf emergence at the study site typically occurs during mid-May, we based our calculations on leaf-off photographs prior to and leaf-on photographs after 15 May. The average GSF for a wetland thus estimated is referred to simply as GSF in the remainder of this paper.

We measured natural patterns of distribution, abundance, and performance of two amphibian species in each of the 17 wetlands: wood frogs (*Rana sylvatica*) and spring peepers (*Pseudacris crucifer*). These species are the most common anurans in nonpermanent wetlands at Yale-Myers Forest. From 1998 to 2000, every wetland was visited in March or April and at least three more times during discrete sampling periods between early May and early July (I: first half of May; II: second half of May; III: first half of June; IV: first half of July). Sampling intervals usually lasted 2 days or less and never lasted more than 1 week. During March and April

wetlands were visually inspected for eggs. During May through July sampling visits, depth was measured, wetlands were visually inspected for adult and larval amphibians and eggs, and timed continuous dip-net sampling (between 5 and 15 person minutes depending on surface area) was conducted throughout the wetland. Up to 20 amphibian larvae of each of the focal species were collected and stored in 70% EtOH. The larvae were later measured (snout-vent length, SVL), and staged (Gosner 1960) under a dissecting scope.

We used logistic regression to determine the relationship between GSF and the presence-absence distribution of spring peepers and wood frogs. A species was considered present if eggs or larvae were ever found in a wetland between 1998 and 2000. Linear regression was used to relate larval density of each species to GSF. Density was measured as the number of larvae encountered per person-minute averaged across the three dip-net sampling rounds (I, II and III). In addition, we analyzed the relationship between GSF and larval performance. For each sampling period during which a species was present in at least three wetlands, we related GSF to the average body size (mm SVL) and developmental stage (Gosner stage, Gosner 1960) of the larvae from a given wetland using linear regression. Results from 2000 are presented here; results from prior years were comparable. Finally, we used multiple linear regression to determine whether the relationship between size and developmental stage varied with GSF. In these regressions, the response variables were the average sizes of tadpoles from each developmental stage from each wetland. Predictor variables were GSF and Gosner stage. A significant effect of GSF in this regression suggests that tadpoles at a given Gosner stage vary in size in a manner that is correlated with GSF.

Water temperature was measured in 11 of the study wetlands using a Hobo temperature logger suspended 10 cm below the surface at the site of maximum wetland depth. Temperature was recorded every hour during the month of April. Temperature is probably lower during this month than at any other time during the larval period and is thus probably more important at this time as a developmental constraint. In addition, the embryos and larvae are less developed during this month and are thus less able to compensate for pond temperature variation by seeking out different spots within the pond (L.K. Freidenburg, unpublished data). To estimate the association between water temperature and light environment we calculated a regression of GSF against the average April temperature from each of the wetlands for which we had such data.

Results

Wood frogs were present in each of the 17 wetlands, thus their distribution was independent of GSF. By contrast, distribution of spring peepers was strongly correlated with wetland light environment (logistic regression: $df=1$, $\chi^2=5.83$, $P=0.016$). These frogs were found in most of the high light wetlands and in none of the darkest wetlands ($GSF < 0.34$).

The density of wood frog larvae was unrelated to GSF (Fig. 1a; linear regression: $R^2=0.001$, $MS=0.06$, $F_{1,15}=0.02$, $P=0.889$) while density of spring peeper larvae was positively related to GSF (Fig. 1b; linear regression: $R^2=0.44$, $MS=1.89$, $F_{1,15}=11.98$, $P=0.003$). The increase in spring peeper density with increasing GSF persisted when the analysis was restricted to the eight wetlands with nonzero densities (linear regression: $R^2=0.60$, $MS=1.62$, $F_{1,6}=9.12$, $P=0.023$).

Larval developmental stage of both species tended to be more advanced on a given date within lighter wetlands (Table 1, Fig. 2). The relationship between GSF and developmental stage was small or insignificant during

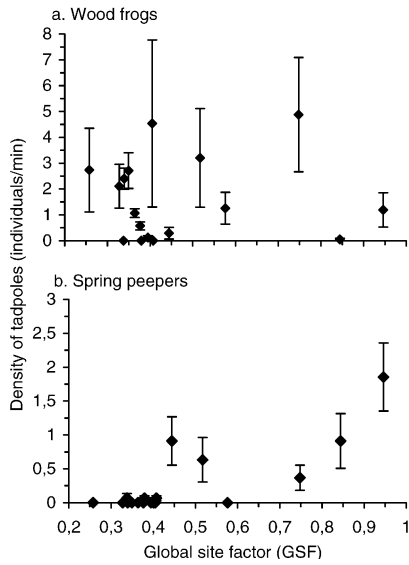


Fig. 1 Density of **a** wood frog and **b** spring peeper larvae across 17 wetlands as a function of light level. Light level is indexed as global site factor (*GSF*). Larval density is estimated as the number of tadpoles encountered per person minute while dip-netting. Each point represents an average calculated across visits during up to 3 years. The *bars* represent 1 SE

Table 1 Results from least squares regression of average tadpole size and developmental stage as a function of light environment (indexed by global site factor, *GSF*). Responses for wood frogs and spring peepers were collected during 2000 while sampling 17 wetlands at the Yale-Myers Forest in northeastern Connecticut. There were three sampling periods: early May (I), late May (II) and early June (III)

Species	Response	Period	<i>N</i>	Slope	<i>R</i> ²	<i>P</i>
Spring Peepers	Gosner stage	I	3	-0.20	0.11	0.789
		II	6	4.38	0.52	0.107
		III	8	13.90	0.78	0.003
	Body size	I	3	-1.05	0.87	0.239
		II	6	5.02	0.57	0.082
		III	8	9.94	0.62	0.020
Wood Frogs	Gosner stage	I	15	3.23	0.56	0.001
		II	14	5.40	0.55	0.107
		III	13	11.48	0.56	0.003
	Body size	I	15	2.65	0.33	0.025
		II	14	3.10	0.12	0.227
		III	13	1.93	0.02	0.685

early sampling and became strong and significant by early June (Table 1, Fig. 2).

Body size of spring peepers tended to show a pattern similar to that observed for development: a strong positive relationship between body size and *GSF* became evident as the season progressed (Table 1, Fig.2). This was not the case for wood frogs. While there was some evidence of a positive relationship between light and body size for wood frogs early in the season, this relationship tended to disappear as the season progressed.

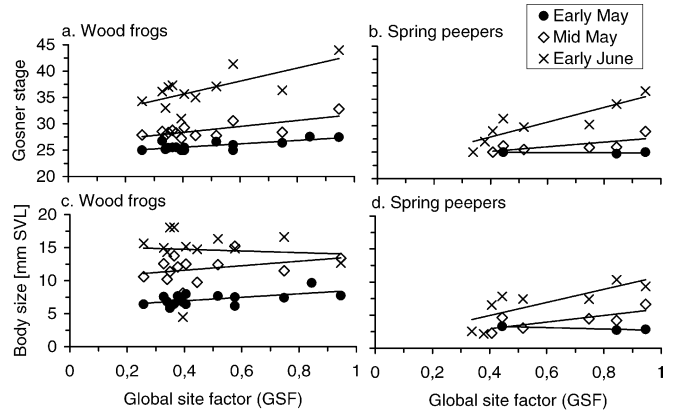


Fig. 2 Performance of wood frogs (**a, c**) and spring peepers (**b, d**) during 2000 as a function of light level within a wetland (indexed as global site factor, *GSF*). Performance was measured as the average Gosner (Gosner 1960) developmental stage (**a, b**), or body size (**c, d**). Samples were collected during three sampling periods: early May (*filled circles*), mid May (*hollow diamonds*), and early June (*crosses*). Lines of best fit from least squares regression are presented for each sampling period (Table 1). The standard error for average body size (mm SVL) and average Gosner stage was generally less than 5% of the mean

Multiple linear regression showed that wood frog larvae at a given stage of development tended to be larger in darker wetlands (1998: slope = -3.038, SE=0.819, $t_{82} = -3.7071$, $P < 0.001$. 1999: slope = -1.288, SE=0.587, $t_{99} = -2.19$, $P = 0.031$. 2000: slope = -1.387, SE=0.5062, $t_{64} = -2.740$, $P = 0.008$). There was no significant relationship between *GSF* and size of spring peepers at a given stage of development (1998: slope = -1.854, SE=1.354, $t_{7} = -1.3688$, $P = 0.2134$. 1999: slope = -414, SE=0.4942, $t_{19} = -0.838$, $P = 0.4125$. 2000: slope = -0.351, SE=0.583, $t_{29} = -0.602$, $P = 0.552$).

Among the 11 wetlands in which water temperature was measured (April 2000), wetlands with higher *GSF* tended to be warmer (linear regression: $MS = 2.26$, $F_{1,9} = 6.43$, $R^2 = 0.35$, $P = 0.032$).

Discussion

Incoming solar radiation is apt to be particularly variable in ephemeral wetlands. Tree crowns often extend entirely across smaller wetlands and some species such as red maple (*Acer rubrum*) and buttonbush (*Cephalanthus occidentalis*) can root within shallow basins. As a result, the light environments in our darkest wetlands are comparable to those found in the understory of mature forests in the northeastern United States (Canham et al. 1994; Finzi and Canham 2000).

This gradient in light among wetlands created by variation in vegetation structure is strongly associated with the distribution and performance of amphibian species. In the case of one species, spring peepers, we identified a light boundary ($GSF = 0.34$) below which the species was consistently absent. In those wetlands in which spring

peepers were present, their density was proportional to GSF (Fig. 1b). Despite their reliance on forested terrestrial environments after metamorphosis (Delzell 1958), spring peepers appear to be excluded from wetlands under heavy forest cover during embryonic and larval phases. Given that closed-canopy forests grow throughout much of the range of this species, this means spring peepers necessarily depend on wetlands that are too large to be overtopped by tree crowns, where shoreline vegetation has recently been disturbed, or where a higher light environment is maintained through some other means.

What prevents spring peepers from using heavily shaded wetlands? Spring peeper larvae grow and develop more slowly in darker wetlands. During June, when spring peepers in the lightest wetlands were nearing metamorphosis, conspecifics in the darker wetlands were still in early stages of development (Fig. 2b). We documented up to three and fourfold differences in body length during late season. Field transplant experiments have shown similar decreases in growth and development in low light environments (Werner and Glennemeier 1999; Skelly et al. 2002). Such reduced performance may lead to an increased likelihood of larval mortality from drying events in nonpermanent wetlands (Skelly 1995).

While reduced growth and development could explain the restricted distribution of spring peepers as well as decreased density in darker wetlands, amphibians also are known to be selective in their choice of oviposition sites (Hopey and Petranka 1994; Resetarits and Wilbur 1989; Resetarits and Wilbur 1991; Kiesecker and Skelly 2000). The results of a pilot experiment in which the canopy was removed from a heavily shaded wetland at the Yale-Myers Forest are consistent with such an effect. Spring peeper larvae were absent from this wetland during the 3 years prior to canopy removal and have been present during each of 3 years since (D.K. Skelly, unpublished data). While darker wetlands may act as demographic sinks for spring peepers, it also is possible that adults avoid placing their offspring in these environments.

Unlike spring peepers, wood frogs breed in wetlands across the light gradient and their larval density was not significantly related to GSF (Fig. 1a). Neither was there any indication that light was related to wood frog growth patterns (Fig. 2c). While wood frogs seem able to maintain relatively dense populations of rapidly growing larvae even in heavily shaded wetlands, their development rate was correlated with GSF (Fig. 2a). Thus, for both species there is a performance cost associated with living in shaded wetlands.

Solar radiation could affect amphibian performance through a variety of mechanisms. Light affects the composition and abundance of the primary producers in aquatic ecosystems (Feminella et al. 1989; Wetzel 2001). Periphyton is an important food source for tadpoles (Kupferberg et al. 1994; Hill et al. 1995) and can be less abundant and less diverse in shaded wetlands (Skelly et al. 2002). In addition, there is evidence that spring peepers and wood frogs are less able to assimilate organic matter available in benthic substrates from shaded wetlands (Skelly and Golon, unpublished data).

The performance patterns we observed also are consistent with the effects of temperature on ectotherms. In this study, darker wetlands tended to be colder. Controlled temperature laboratory experiments show that both growth and development rates of amphibian larvae can be limited by temperature (e.g., Smith-Gill and Berven 1979; Berven and Gill 1983). Even when provided abundant, high quality food resources, modest decreases in ambient temperature can cause large reductions in growth and development of amphibians (Newman 1998). These reductions are typically asymmetric; for a given decrease in temperature, larvae will suffer greater reductions in development rate versus growth rate (Ray 1960; Smith-Gill and Berven 1979). Consequently, larvae sampled from colder environments tend to be larger at a given developmental stage compared with conspecifics from warmer environments. The asymmetry of temperature effects is widely reported in ectotherms but the mechanisms remain debated (Atkinson 1994, 1995; Van der Have and de Jong 1996). Whatever the reason, the existence of this asymmetric pattern among wood frogs is strongly suggestive of an impact of temperature on growth and development patterns. Its absence among spring peepers suggests that this species may respond differently to temperature change, that it is not temperature limited in its performance, or that its restriction to relatively lighter wetlands precluded observation of the asymmetric temperature effect.

The links established here between wetland light environment and amphibian performance and distribution are particularly meaningful in the context of vegetation dynamics. The forest cover on the Yale-Myers Forest and central New England has changed dramatically over the last 300 years. After settlement reduced the forest cover in some parts of New England to as low as 20% by the middle of the eighteenth century, many farms were abandoned and forests allowed to regenerate. Today, as in pre-settlement times, forest covers more than 90% of the Yale-Myers Forest and central New England (Meyer and Plusnin 1945; Foster 1992; P.M.S. Ashton, unpublished data). Disturbances from such things as timber harvest, beaver and fire can also cause the canopy above wetlands to change rapidly (Skelly et al. 1999; Skelly and Freidenburg 2000). When allowed to regrow, forest can encroach and overtop a small wetland within a few decades or less (Skelly et al. 1999). This study suggests amphibians may undergo changes in distribution, abundance and performance as a result of such changes in vegetation.

The ability of wood frogs to persist in spite of canopy closure could be related to their ability to maintain relatively rapid growth and development across different light environments. There also is some evidence that this species may evolve rapidly in response to thermal changes that accompany change in canopy (Skelly and Freidenburg 2000). Regardless of origin, the persistence of wood frogs across the light gradient means that this species is able to utilize a much higher fraction of ephemeral wetlands in our study area than spring peepers. The distribution of spring peepers appears to be at least

partly determined by the pattern of recent disturbance around smaller wetlands (e.g., Paine and Levin 1981; Pacala et al. 1996; Batzer et al. 2000).

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