Using the Phenology of Pond-Breeding Amphibians to Develop Conservation Strategies

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Abstract: *Researchers suggest that regulatory agencies interested in protecting pond-breeding amphibians should consider wetland isolation, wetland size, and pond hydroperiod (total number of days pond is flooded annually) when modifying existing wetland regulations. Another criterion that has received less attention is the effect of the timing of inundation on the reproductive success of pond-breeding amphibians. Over 3 years, we monitored the timing of movements of adult and recently metamorphosed anurans and caudates at seven small, isolated wetlands in southern Rhode Island. Based on dates of immigration for adults and emigration for metamorphs, we concluded that different species of amphibians require ponds to be flooded for 125 days to at least 580 days. For species that breed primarily in seasonally flooded ponds, 95% of metamorphs had emigrated from breeding ponds by 31 July in only two species (* Rana sylvatica *and* Ambystoma opacum*), whereas species using semipermanent ponds required inundation until 18 November. Our results suggest that in most years ponds must be inundated for 4–9 months, with water in ponds from March through August, for successful reproduction of the majority of pond-breeding amphibians in Rhode Island. We recommend that biologists gather data on amphibian movement phenology in other regions to help regulators and managers develop relevant legislation to protect the habitat of pond-breeding amphibians.*

Uso de la Fenología de Anfibios que se Reproducen en Estanques para Desarrollar Estrategias de Conservación

Resumen: *Los investigadores sugieren que las agencias reguladoras interesadas en la protección de anfibios que se reproducen en estanques deberían tomar en consideración el aislamiento de los humedales, el tamaño del humedal y el hidroperíodo del estanque (número total de días del año que el estanque está inundado) para modificar las regulaciones existentes de humedales. Otro criterio que ha recibido menor atención es el efecto del tiempo de ocurrencia de la inundación sobre el éxito reproductivo de los anfibios que se reproducen en estanques. Monitoreamos por más de tres años los tiempos de los movimientos de anuros y acudados adultos y recién metamorfoseados en siete humedales pequeños y aislados ubicados al sur de Rhode Island. En base a los datos de inmigración para adultos y emigración para metamorfos, concluimos que diferentes especies de anfibios requieren que los estanques estén inundados por 125 días hasta por lo menos 580 días. Para las especies que se reproducen principalmente en estanques inundados estacionalmente, el 95% de los metamorfos habían emigrado de los estanques de reproducción para el 31 de Julio (* Rana silvatica *y* Ambystoma opacum*), mientras que las especies que emplearon estanques semipermanentes requirieron de la inundación hasta el 18 de Noviembre. Nuestros resultados sugieren que en la mayoría de los años los estanques usados por anfibios reproductores deben estar inundados por 4-9 meses, con agua en los estanques desde Marzo y hasta Agosto para que se de una reproducción exitosa para la mayoría de las especies de anfibios que se reproducen en estanques en Rhode Island. recomendamos a los biólogos que reúnan datos sobre la fenología de movimientos de anfibios en otras regiones para ayudar a los reguladores y administradores a desarrollar una legislación relevante que proteja el hábitat de anfibios que se reproducen en estanques.*

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Introduction

There is considerable interest among biologists to modify existing state and federal wetland regulations in the United States because those regulations often do not adequately protect the habitat of many species of pond-breeding amphibians (Semlitsch & Bodie 1998; Gibbs 2000; Semlitsch 2000; Snodgrass et al. 2000*a*). If a wetland is going to be filled or drained, wetland size is one of the primary characteristics used by government agencies to determine whether to permit the alteration (Kaiser 1998). Semlitsch and Bodie (1998) recently proposed that wetlands as small as 0.2 ha should be protected, because small ponds may be critical to amphibian metapopulations. There can be a weak relationship between wetland size and amphibian species richness, however, so Snodgrass et al. (2000*a*) suggest that pond hydroperiod—the number of days a pond is inundated with surface water—should also be an important criterion in wetland protection programs. For example, three states in New England (Massachusetts, New Hampshire, and Connecticut) regulate filling of isolated depressions that contain surface water for at least 2 continuous months in the spring or summer (Colburn 1995; Donahue 1995; Tappan 1997). We believe that the current debate, which has focused primarily on wetland size and pond hydroperiod, has not considered the movement phenology of amphibians as an important criterion in assessment of the effectiveness of current wetlands regulations.

Numerous amphibian species require ponds as breeding habitat, in which adults mate and oviposit and larvae develop until they metamorphose into a terrestrial stage (Conant & Collins 1991). The duration of the larval period to metamorphosis is highly variable among species and can fluctuate within a species as a function of different densities of competitors and predators (Wilbur 1972, 1980). For example, Wilbur (1972) found that the larval period for spotted salamanders (*Ambystoma maculatum*) ranged from 91 to 122 days in the presence of different densities of potential competitors. The timing of pond drying also can affect the length of the larval period of some amphibian species (Semlitsch 1987; Wilbur 1987; Semlitsch & Wilbur 1988; Skelly 1996).

Amphibian species richness and productivity in breeding ponds are positively correlated with hydroperiod in experimental settings (Wilbur 1987; Rowe & Dunson 1995) and in natural populations (Pechmann et al. 1989; Semlitsch et al. 1996; Snodgrass et al. 2000*b*). The importance of hydroperiod in a natural population was shown by Semlitsch et al. (1996), who monitored a pond in South Carolina over 16 years which was inundated an average of 170 days annually (range 3–391 days). They found that years with short hydroperiods ($\leq$100 days) resulted in total reproductive failure, whereas years with long hydroperiods ($>$200 days) tended to have the greatest diversity and productivity.

We believe that timing of inundation is another important characteristic of amphibian breeding sites. It is critical that ponds are flooded at the appropriate time of year to meet the life-history requirements of amphibian species that could potentially breed at the site (Semlitsch 1985; Pechmann et al. 1989). Because many species often breed at the same pond, one strategy amphibians use to avoid competition and predation pressure is temporal segregation in use of breeding ponds (Blair 1961; Wilbur 1980, 1987).

Few studies have quantified the movement phenology of pond-breeding amphibians, including information on both the timing of immigration by adults and emergence by metamorphs (but see Murphy 1963; Shoop 1974; Semlitsch 1985; Petranka & Thomas 1995; Paton et al. 2000). Usually only qualitative information on seasonal variation in movements is available for most parts of North America (Wright & Wright 1949; Klemens 1993; Semlitsch et al. 1996). Some states certify ponds as critical breeding habitat based on the presence of obligate vernal-pool species, such as wood frog (*Rana sylvatica*) and spotted salamanders (e.g., Massachusetts; Colburn 1995). But until regulators know the migration phenology of obligate and facultative vernal-pool amphibians, it is difficult to decide when to conduct surveys to determine whether a species occurs at a particular pond. In addition, regulators need to know the timing of the hydroperiod for successful reproduction by amphibians. Ponds that dry up by May could provide vital breeding habitat for some species of amphibians in the southeastern United States, whereas in southern New England ponds may need to have surface water until at least July.

We quantified the movement phenology of three species of caudates and seven species of anurans throughout the year from 1997 to 1999 in southern Rhode Island. The objectives of our research were to (1) determine interspecific variation in the migration phenology of adult pond-breeding amphibian species in southern Rhode Island, (2) assess interspecific variation in emigration phenology by metamorphs from breeding ponds, and (3) quantify the timing and duration of inundation necessary to maintain species of pond-breeding amphibians in southern Rhode Island.

Methods

Study Area

We conducted fieldwork at seven isolated ponds within a 284-km^2 region of Washington County in southern Rhode Island. Hydroperiods at the ponds we monitored ranged from seasonally flooded (ponds contained surface water for extended periods during the growing season, but dried up before the end of the growing season in most years) to semipermanently flooded (ponds in most years contained surface water throughout the entire growing season but not necessarily all year; Cowardin et al. 1979). Regionally, those ponds that are not permanently flooded are referred to as vernal pools. Ponds ranged in size from 0.003 to 0.15 ha (Crouch 1999). All ponds were surrounded primarily by broad-leaved deciduous forests, dominated by red maple (*Acer rubrum*) at edges of ponds, with a variety of oaks (*Quercus* spp.) and white pine (*Pinus strobus*) in adjacent uplands. Annual precipitation in the region is approximately 123 cm, with seasonally flooded ponds usually having surface water from November into June or July (Golet et al. 1993).

Amphibian Movements

We used a drift fence with pitfall traps (hereafter arrays) to monitor amphibian movements at ponds (Gibbons & Semlitsch 1982). We completely encircled seven ponds with drift fences 2–5 m above the high-water line. We constructed drift fences from 1-m-tall black nylon silt fencing. We manufactured pitfall traps, 15 cm in diameter and 33 cm deep, from metal cans taped together end to end. Pitfall traps had a plastic funnel placed at the entrance to minimize escape rates. We placed pitfall traps at 10-m intervals on the interior and exterior of the drift fence. Arrays had an average of 24.8 pitfall traps (range 8–48).

Based on prior research (Klemens 1993), we attempted to encompass the entire period when amphibians might migrate across the landscape. We opened arrays in late February (mean, 26 February; range, 12 February–27 March), depending on snow conditions, and closed arrays in early November (mean, 1 November; range, 30 September–29 November). Therefore, arrays were open for an average of 228 days annually. We monitored arrays at three ponds in 1997, six ponds in 1998, and three ponds in 1999. We monitored two ponds for only 1 year, four ponds in 2 consecutive years, and one pond for 3 consecutive years. We checked traps daily, starting at approximately 0600 hours, with trapping sessions taking 30 minutes to 6 hours to complete depending on capture rates. We processed all captured animals in the field and released them on the opposite side of the fence from the original capture location. We recorded the spe-

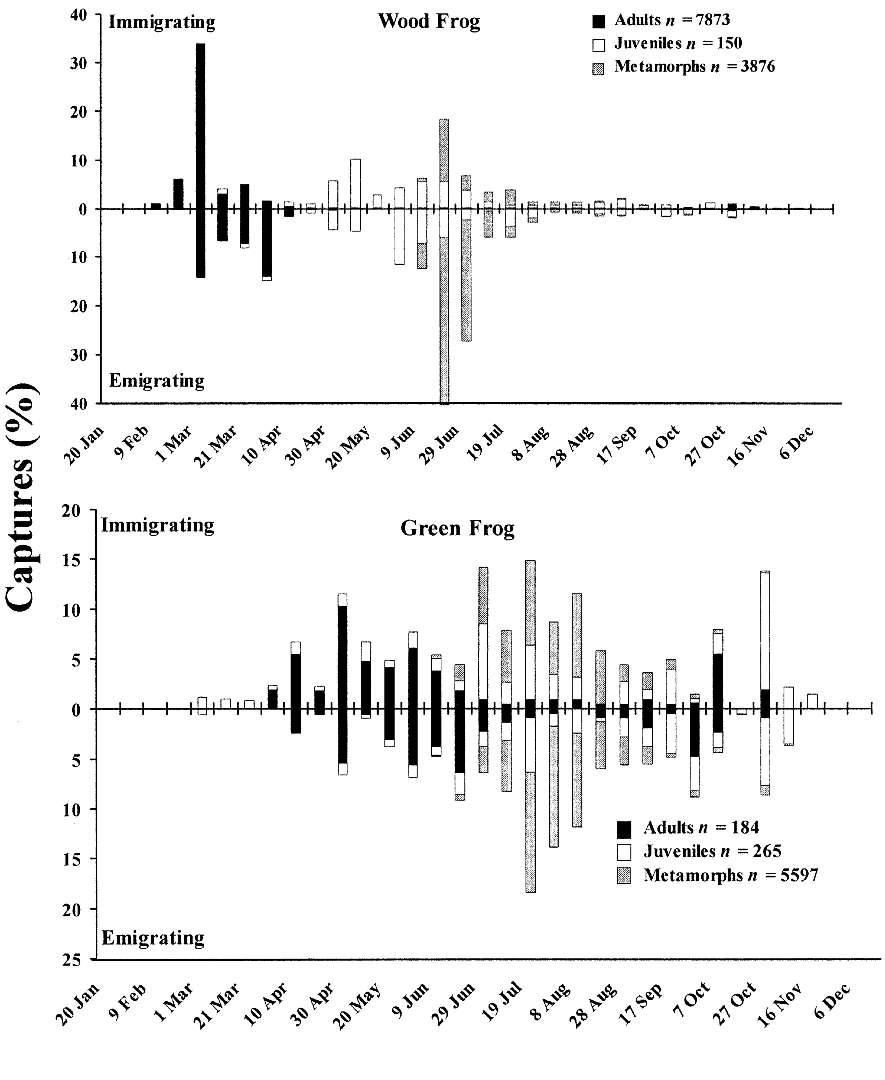

Figure 1. Movement phenology of wood frogs, green frogs, American toads, and pickerel frogs at breeding ponds in southern Rhode Island. Shown is the percentage of individuals captured per 100 trap nights within 10-day time periods for each of three age cohorts.

cies, age (adult, juvenile, and metamorph [i.e., recently emerged tadpole or larvae]), gender, trap number and location (interior or exterior of array), and Julian date (1-365) for each individual captured.

Analysis

To compare movement chronologies among species, we first calculated captures per 100 trap nights (hereafter, capture rates) for each site. Each night that an individual pitfall trap was opened was classified as 1 trap night. We calculated immigration chronologies of adults based only on captures on the exterior of arrays, from the date when arrays were first opened until 1 July, because we assumed that adults captured after 1 July were simply dispersing (Klemens 1993). The only exception was adult marbled salamanders (*Ambystoma opacum*): immigration chronology for this fall breeding species was based on captures from 1 August to when arrays were closed in mid-November (Klemens 1993). Metamorph emigration chronology was based on capture rates on the interior of arrays from 1 June to when arrays were closed. Inspection of normality plots for movement chronologies for both adults and metamorphs indicated that data were normally distributed.

To investigate the temporal patterns of adult and metamorph migration, we used ordination methods to quantify interspecific differences in movement chronologies. We used canonical correspondence analysis (Program CANOCO 4; ter Braak & Smilauer 1998), with a species' relative abundance as the main matrix and Julian date as the constraining environmental variable, because the relationship between a species' relative abundance and Julian date was unimodal. We tested the significance of Julian date in accounting for variation among species abundance with a Monte Carlo randomization test with a time-series permutation restriction. The postulated unimodal relationship of the probability of presence of a species and the Julian date was plotted with CANODRAW and CANOPOST (ter Braak & Smilauer 1998).

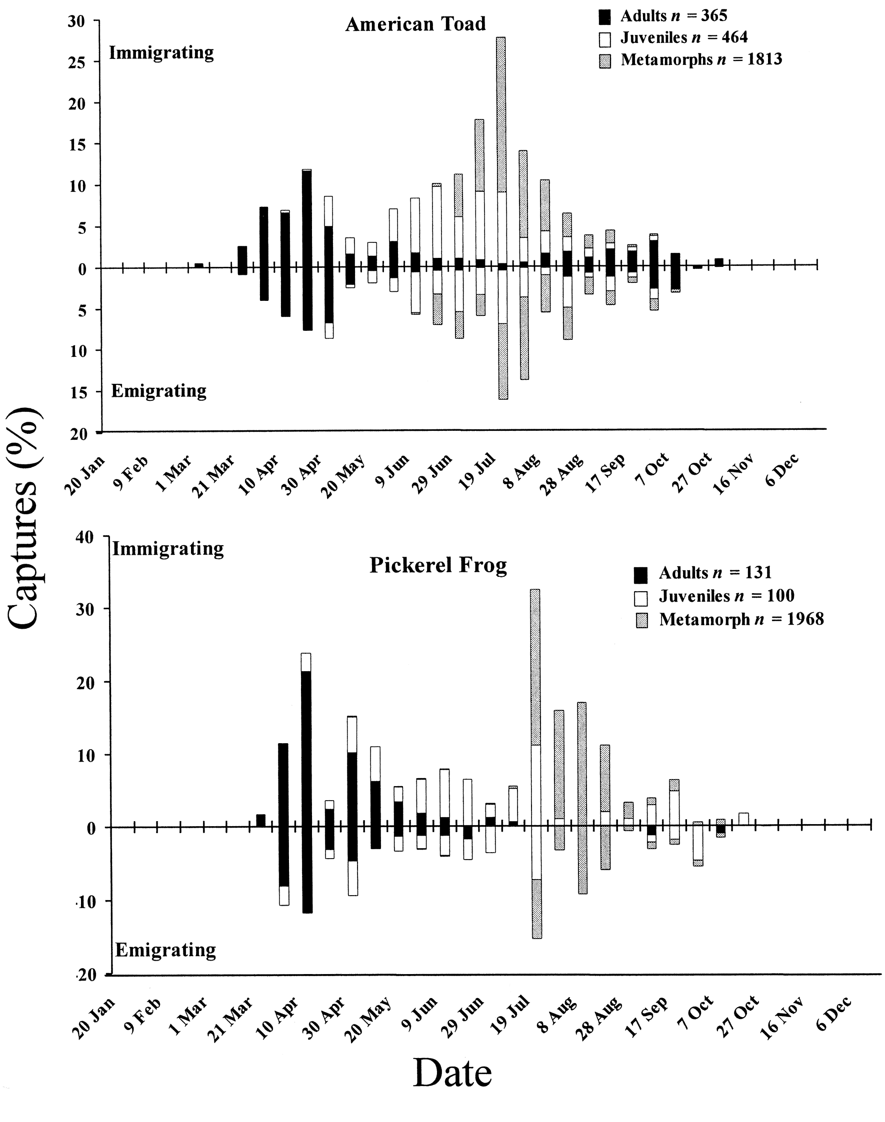

Figure 1. Continued.

We determined the amount of time each species used breeding ponds based on two measures. First, for each year at each pond, we calculated the cumulative proportion of adults that immigrated to breeding ponds and the cumulative proportion of metamorphs that emigrated from breeding ponds based on capture rates. We calculated peak immigration periods by adults for each species based on the number of days between the fifth and ninety-fifth percentiles from the cumulative estimates. We used a similar analysis to quantify peak emigration periods for metamorphs. We then calculated the maximum length of time that each species used breeding ponds based on the difference between the ninety-fifth percentile of mean peak metamorph emigration and the fifth percentile of mean peak adult immigration. By eliminating outliers, we believe that this method encompasses the primary movement period for each species.

We also calculated a minimum estimate of duration in ponds for each species based on the number of days between the median dates when adults immigrated and median dates when metamorphs emigrated. For both estimates (maximum and minimum), we assumed that green frogs (*Rana clamitans*) and bullfrogs (*R. catesbeiana*) overwintered for 1 year in southern Rhode Island (Martof 1956; Collins 1979), although some populations of green frogs are capable of undergoing metamorphosis within the same breeding season and some bullfrog tadpoles overwinter for 2 years before undergoing metamorphosis (Viparina & Just 1975; Klemens 1993). For the purposes of this analysis, either strategy requires a pond with standing water throughout the year. Adult marbled salamanders immigrate to dry basins in the fall, and female marbled salamanders remain with eggs until ponds are flooded, which in southern Rhode Island is usually in early November (Doty 1978; Klemens 1993). Therefore, we assumed for this analysis that marbled salamanders required water in ponds from 1 November until metamorphs emigrated from breeding ponds.

Results

We documented 29,933 captures in 79,306 trap nights (37.7/100 trap nights): 12,050 adults (15.2/100), 1,338 juveniles (1.7/100), and 16,545 metamorphs (20.8/100). We captured 6 species at all seven ponds: green frogs (7.6/100), pickerel frogs (*Rana palustris*, 2.8/100), bullfrogs (*R. catesbeiana*, >0.01/100), wood frogs (15.0/100), spring peepers (*Pseudacris crucifer*, 2.2/100), and spotted salamanders (1.4/100). American toads (*Bufo americanus*, 3.8/100) and gray treefrog (*Hyla versicolor*, 0.2/100) were detected at six ponds, red-spotted newts (*Notophthalmus viridescens*, 2.0/100) were at five ponds, and marbled salamanders (*Ambystoma opacum*, 6.5/100) were at only three ponds.

We captured anurans and caudates from early February to mid-December in southern Rhode Island (Figs. 1–3). Peak immigration for adults of nine species occurred from early March through late May, whereas the primary metamorph emigration period occurred from early June through late October. Juvenile frogs tended to be most active in the intervening months between peak adult movements and metamorph emigration, whereas the few juvenile caudates we documented occurred simultaneously with adults.

There was significant interspecific variation in immigration phenology among adults (F ratio = 76.01, p = 0.002), with the first canonical correspondence axis (Julian date) accounting for 32% of variation in the relative abundance matrix of a species (Fig. 4). Based on species-response curves for adults, we detected three or four peak periods when adults were immigrating to ponds (Fig. 4). Wood frogs were the first to immigrate, from late February through mid-March (Fig. 1), followed by spotted salamanders (Fig. 3) and red-spotted newts (Fig. 3) from mid March to mid April. Most species—spring peeper, pickerel frogs, American toads, green frogs, and gray treefrogs (Figs. 1 & 2)—immigrated during April and May. The marbled salamander was the only species to breed during the fall, with peak immigration occurring in late August (Fig. 3). Peak adult immigration for all species averaged 56.7 ± 5.5 (SE) days, with immigration periods ranging from 36 days for adult marbled salamanders to 79 days for bullfrogs (Table 1).

We also detected significant interspecific differences in the emigration phenology of metamorphs (F ratio = 45.19, p = 0.008), with the Julian date accounting for 24% of the variation in the relative-abundance matrix (Fig. 4). Based on species-response curves for metamorphs, there were three to four peak time periods when young amphibians left ponds (Fig. 4). The first two species to initiate emigration were marbled salamanders and wood frogs, with individuals leaving during mid-June through July (Table 1). Only marbled salamanders and wood frogs had 95% of metamorphs emerge from breeding ponds by the end of July. The second peak consisted of the two arboreal species, spring peepers and gray treefrogs, with most individuals emigrating from ponds during July. Metamorphs of five species, the green frog, American toad, pickerel frog, spotted salamander, and bullfrog, had a relatively protracted emigration period from June through September. The last species to emigrate from ponds was the red-spotted newt, with peak emigration from mid-September through mid-November. Peak emigration took an average of 59.9 ± 19.0 days for metamorphs of all species. The earliest metamorphs to depart, marbled salamanders and wood frogs, had relatively short peak-emigration periods (39 and 32 days, respectively; Table 1). In contrast, American toads took 91 days for emigration of 95% of individuals from breeding ponds. Most species needed standing

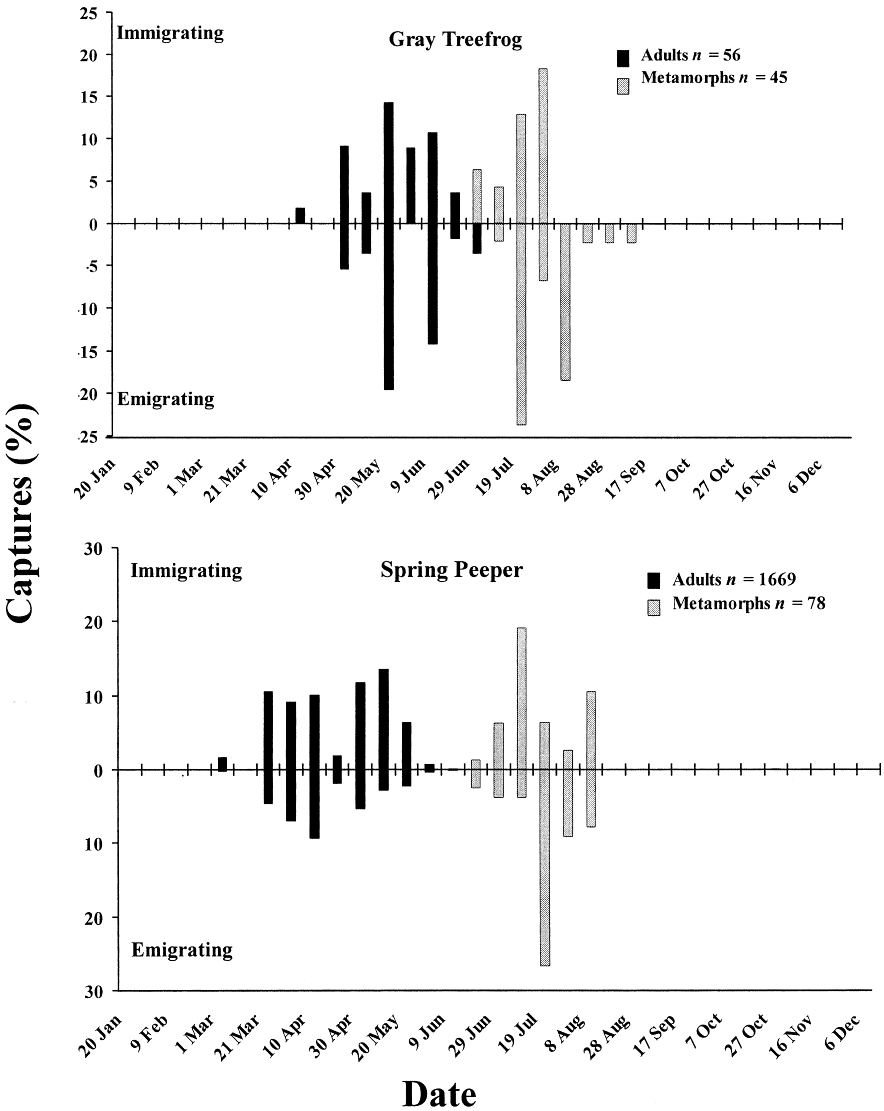

Figure 2. Movement phenology of spring peepers and gray treefrogs at breeding ponds in southern Rhode Island. Shown is the percentage of individuals captured per 100 trap nights within 10-day time periods for each of three age cohorts.

water in breeding ponds until early August for successful emigration of 50% of metamorphs.

We estimated that the maximum length of time amphibians were in breeding ponds averaged 258.8 ± 163.2 days (range, 125–580 days; Table 1) in southern Rhode Island. Of the species capable of producing metamorphs within 1 year—all species except green frog and bullfrog—the maximum estimate of duration in ponds was a mean of 184.8 ± 53.1 days (Table 1). We assumed that water needed to be in a pond only after 50% of adults had immigrated and until 50% of metamorphs had emigrated; thus, minimum estimates averaged 197.2 ± 150.6 days (range, 66 days [gray treefrog] to 488 days [bullfrog]; Table 1).

Discussion

The movement phenology of pond-breeding amphibians in southern Rhode Island exhibited significant temporal variation among species, both for immigration of adults and emigration of metamorphs. We expected this result because qualitative estimates of movement chronology document temporal segregation among species (e.g., Klemens 1993). In addition, the seasonal differences in movements of adult anurans can be inferred from seasonal variation in levels of calling activity (Blair 1961; Varhegyi et al. 1998). Less is known about the movement dynamics of recently metamorphosed individuals in natural populations.

Based on the movement chronology of adults and metamorphs during this study, we estimate that amphibian species in southern Rhode Island require breeding hydroperiods ranging from 125 to over 580 days for successful production of 95% of metamorphs. We define *breeding hydroperiod* as the number of days when amphibians are actively breeding or larvae are developing in an inundated wetland, whereas *pond hydroperiod* is the number of days the wetland is inundated with sur-

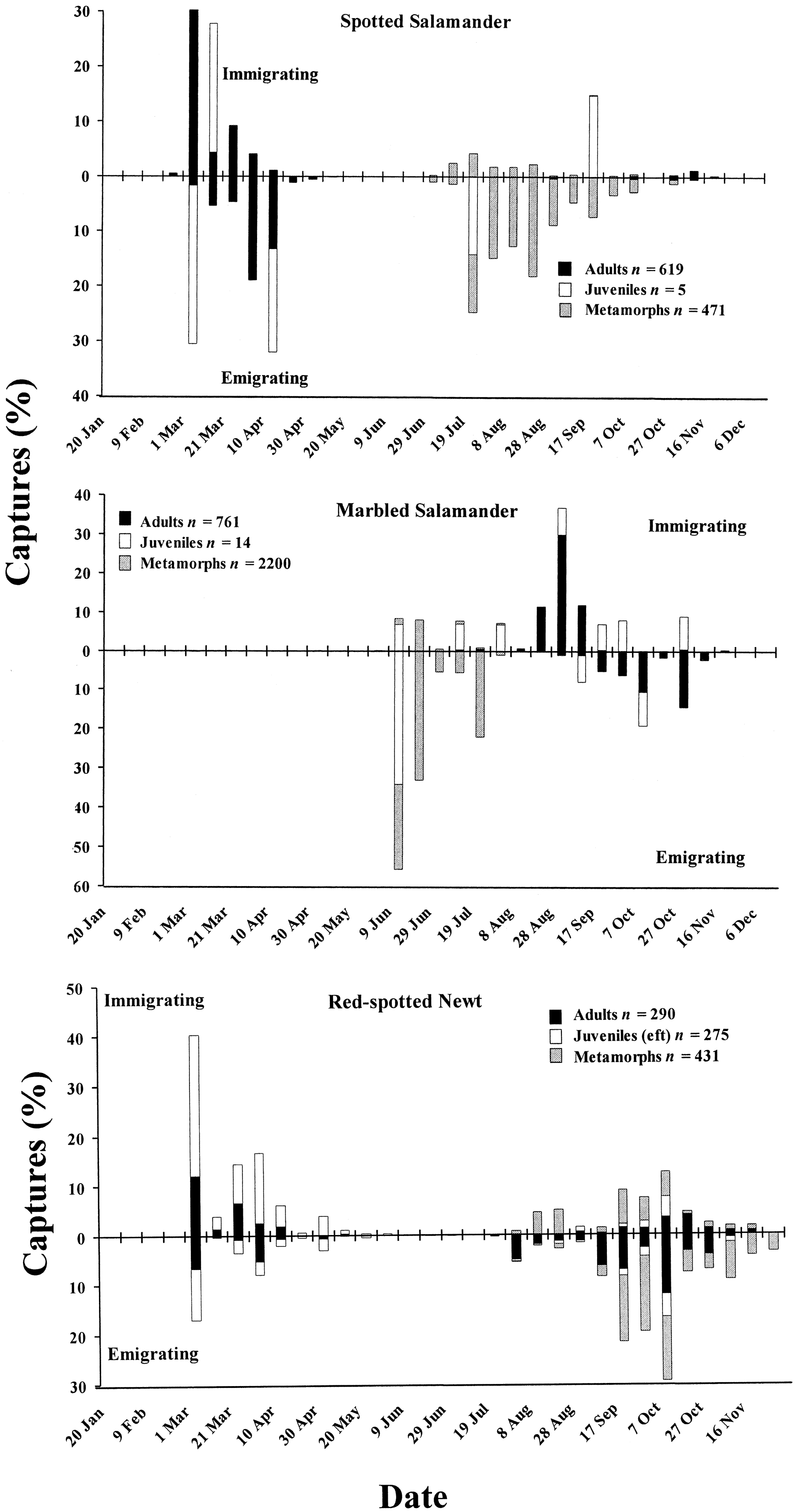

Figure 3. Movement phenology of spotted salamanders, marbled salamanders, and red-spotted newt at breeding ponds in southern Rhode Island. Shown is the percentage of individuals captured per 100 trap nights within 10-day time periods for each of three age cohorts.

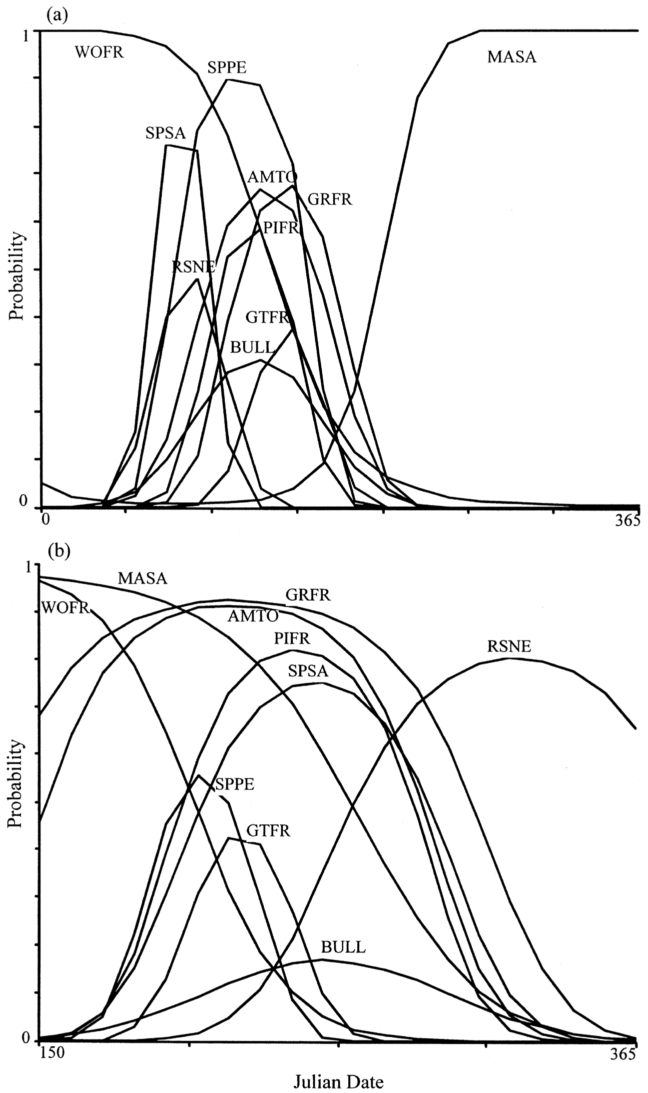

Figure 4. Interspecific variation in movement phenology of pond-breeding amphibians based on canonical correspondence models for (a) adults and (b) metamorphs in southern Rhode Island (AMTO, American toad; BULL, bullfrog; GRFR, green frog; GTFR, gray treefrog; MASA, marbled salamander; PIFR, pickerel frog; RSNE, red-spotted newt; SPSA, spotted salamander; SPPE, spring peeper; WOFR, wood frog).

face water. The breeding hydroperiod averaged 150 days (range, 125–174) for five species of anurans and 243 days (range, 211–264) for three species of caudates, based on 95% of metamorphs emigrating from breeding ponds. Several states in New England regulate isolated depressions with a pond hydroperiod that is a minimum of 2 continuous months in the spring or summer (Colburn 1995; Donahue 1995; Tappan 1997). Based on our study, the pond hydroperiod should be 4–9 continuous months to meet the habitat requirements for most pond-breeding amphibians in Rhode Island. Ephemeral wetlands inundated for only 2 months may be critical habitat for some invertebrates (e.g., fairy shrimp [*Eubranchipus* spp.]), but their hydroperiods are too brief to provide breeding habitat that will successfully produce metamorphs for any amphibians in southern New England.

The relationship between hydroperiod and amphibian productivity that we documented in New England agrees with data from the southeastern United States. Snodgrass et al. (2000*a*, 2000*b*) documented similar relationships at a series of wetland depressions in South Carolina: wetlands with hydroperiods ranging from 240 to 300 days per year had the greatest species richness. Permanent wetlands tended to have lower species richness because of the presence of fish predators, whereas ponds with relatively short hydroperiods had fewer, more specialized species uniquely adapted to wetlands that are more ephemeral. Semlitsch et al. (1996) recorded greater reproductive success at a single wetland in years when the hydroperiod was >200 days.

In drought years, ponds tend to evaporate early in the summer, perhaps by early June. Therefore, those species with the earliest emigration by metamorphs tend to be most successful. Some species of anurans may be capable of producing some metamorphs in a relatively short time, yet it is the date of pond drying that is critical under drought conditions. In an experimental setting, Wilbur (1987) documented that American toads, diploid gray treefrogs (*Hyla chrysoscelis*), and eastern spadefoot toads (*Scaphiopus holbrooki*) are capable of undergoing metamorphosis in <50 days. We found that tetraploid gray treefrogs and spring peepers both have the potential to produce significant numbers in ponds with a breeding hydroperiod of <100 days. We did not document natural populations of American toads or gray treefrogs undergoing metamorphosis as rapidly as Wilbur found in warmer conditions in North Carolina, but Wilbur (1987) did not include the duration of mating, oviposition, and hatching, which could add several days or weeks to his time estimates.

Although the length of the hydroperiod is critical to successful metamorphosis of most larval amphibians (Semlitsch & Wilbur 1988; Pechmann et al. 1989; Snodgrass et al. 2000*a*, 2000*b*), we also documented the importance of the timing of the hydroperiod. Generally, ponds fill early enough for all amphibian species in southern New England, except in very dry winters or when the previous year was extremely dry, so the feature critical to reproduction in these species is the date of the drawdown. In our study, only wood frogs and marbled salamanders had 50% emigration by metamorphs before 1 July. Wood frogs were the only species to occur in all seven ponds that we monitored, whereas marbled salamanders were detected in only three ponds. One potential explanation is that the breeding-hydroperiod requirements are more restrictive for marbled salamanders. These salamanders bred only in ponds that

Table 1. Cumulative percentiles of timing of amphibian adult immigration to ponds, metamorph emigration from ponds, and two estimates of duration in breeding ponds in southern Rhode Island.

	Adult immigration			*Metamorph emigration*			*Days in pond*	
Species	*5%*	*50%*	*95%*	*5%*	*50%*	*95%*	*minimum*[a]	*maximum*[b]
Gray treefrog	1 May	27 May	28 Jun	15 Jul	1 Aug	3 Sep	66	125
Spring peeper	25 Mar	2 May	27 May	27 Jun	22 Jul	10 Aug	81	138
Wood frog	26 Feb	9 Mar	4 Apr	18 Jun	29 Jun	20 Jul	112	144
Pickerel frog	1 Apr	1 May	2 Jun	22 Jul	12 Aug	16 Sep	103	168
American toad	31 Mar	23 Apr	13 Jun	22 Jun	31 Jul	21 Sep	99	174
Spotted salamander	1 Mar	16 Mar	8 Apr	21 Jul	18 Aug	28 Sep	155	211
Red-spotted newt	8 Mar	26 Mar	18 Apr	13 Sep	2 Oct	18 Nov	190	255
Marbled salamander	3 Aug	26 Aug	8 Sep	14 Jun	27 Jun	23 Jul	238	264
Green frog	2 Apr	21 May	19 Jun	4 Jul	5 Aug	13 Sep	441[c]	529[c]
Bullfrog	28 Mar	14 Apr	15 Jun	9 Aug	15 Aug	29 Oct	488[c]	580[c]

[a]*Equals fiftieth percentile for metamorph emigration minus fiftieth percentile for adult immigration.*
[b]*Equals ninety-fifth percentile for metamorph emigration minus fifth percentile for adult immigration.*
[c]*Assumes that species overwinters for one winter.*

filled in early November and remained flooded for over 250 days, which allowed larvae to overwinter and undergo metamorphosis. In contrast, wood frogs needed ponds that filled by early March and remained flooded for about 115 days. Three other widespread anurans, the gray treefrog, spring peeper, and American toad, needed water in ponds until 1 August. Finally, red-spotted newts, which were locally abundant (Klemens 1993), required ponds with a relatively long hydroperiod because efts did not emerge often until mid-November. Only two species of amphibians in southern New England, green frogs and bullfrogs, generally need permanent ponds for successful reproduction because, both overwinter for 1-2 years before initiating metamorphosis (Viparina & Just 1975; Berven et al. 1979).

Semlitsch and Wilbur (1988) suggest that the larvae of pond-breeding amphibians exhibit at least two life-history strategies in response to variation in pond hydroperiods. Some species initiate metamorphosis after a minimum number of days and variable size, or a minimum size and a variable number of days. Based on the duration of peak emigration by metamorphs during our research in southern Rhode Island, three species—the marbled salamander, wood frog, and spring peeper—appear to fit this category, because most individuals emerged from ponds relatively rapidly (<40 days). Eastern spadefoot toads also probably use this strategy because of their ephemeral habitats (Klemens 1993), although none bred at the ponds we monitored. Synchronized breeding and rapid emergence by metamorph wood frogs may also be adaptations that minimize tadpole predation and cannibalism (Petranka & Thomas 1995).

The larvae of most amphibian species in southern Rhode Island appear to exhibit an alternative strategy, which maximizes the amount of time they use breeding ponds when possible. These species appear capable of assessing the length of hydroperiod in a given year and extending or shortening their time in the pond before undergoing metamorphosis. Species that adopted this strategy— the American toad, bullfrog, green frog, pickerel frog, gray treefrog, spotted salamander, and red-spotted newt—had prolonged peak-emigration periods of >40 days. The primary adaptive value to larvae that remain in aquatic environments for extended time periods, if a longer pond hydroperiod exists, is that it allows more individuals to reach the minimal size threshold to initiate metamorphosis and permits some individuals to increase their size before emerging from ponds (Shoop 1974; Semlitsch & Wilbur 1988; Rowe & Dunson 1995). Available evidence suggests that timing of size at metamorphosis does not directly affect survival but does strongly influence other fitness traits, such as size and age of reproduction and survival to first reproduction (Shoop 1974; Smith 1987; Semlitsch et al. 1988; Berven 1990; Beck & Congdon 1999).

Hydroperiod and the timing of inundation is a function of the quantity, frequency, and types of hydrologic inputs and outputs to and from a wetland basin over the course of the year (Novitzki 1989). In Rhode Island, mean monthly precipitation is relatively constant, ranging from 8 to 12 cm throughout the year, whereas evapotranspiration rates fluctuate from 17 cm in July to near 0 cm during the dormant season (Golet et al. 1993). Monthly evapotranspiration rates are constant among years. Within a year, pond levels are determined by seasonal variations in evapotranspiration rates, whereas inter-year differences in pond levels are the result of annual variations in precipitation (Golet et al. 1993). Therefore, there is some spatial autocorrelation in the time of pond filling, because many wetlands in the region tend to fill at approximately the same time. In this case, there can be a strong correlation between hydroperiod and timing of inundation; for example, wetlands that dry early in the summer will be inundated only during spring months and will have a relatively short hydroperiod, whereas wetlands that dry during late summer or fall, or not at all, will be inundated throughout the spring and summer and have longer hydroperiods. Recharge rates can vary dramatically among individual ponds and different wetland systems, however, which are influenced to a great degree by the nature of the surficial geologic deposits that underlie the basin and the basin's position on the landscape (Pyle 1998).

Land-use regulators interested in protecting pond-breeding amphibians should consider wetland size, pond isolation (Semlitsch & Bodie 1998), and pond hydroperiod (Snodgrass et al. 2000*a*), but also should consider the timing of wetland drawdown and life-history requirements of individual species. Because the pond hydroperiod may vary considerably among years and many amphibian species are long-lived, ponds that have suitable breeding hydroperiods in even a minority of years should be considered important habitat. In southern New England, ponds used as breeding sites for amphibians should, at a minimum, have surface water from early March until early July to be considered suitable habitat for some species of pond-breeding amphibians, suitable habitat being defined as that from which at least 50% of metamorphs emerged. Only two species, the wood frog and marbled salamander, produced terrestrial metamorphs from ponds that dried earlier. Available evidence suggests, however, that protecting ponds with the potential for inundation through August in some years will be much more effective in maintaining the long-term stability of amphibian populations, especially in drought years (Pechmann et al. 1989; Snodgrass et al. 2000*a*). We concur with Snodgrass et al. (2000*a*) that, to maximize the probablility maintaining pond-breeding amphibian populations, regulatory agencies should strive to maintain a diversity of wetlands with varying hydroperiods and minimal nearest-neighbor distances among wetlands (Semlitsch & Bodie 1998; Gibbs 2000). We hope the data we present here will be useful to regulators attempting to develop regulations to protect pond-breeding amphibians in southern New England. In addition, we hope biologists will gather similar data in other regions of North America, because movement phenologies vary by latitude; therefore, regulations designed to protect pond-breeding amphibians will have to be developed at a regional scale.

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