Ontogenetic and interspecific variation in timing of movement and responses to climatic factors during migrations by pond-breeding amphibians

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Abstract: Pond-breeding amphibians from temperate regions undertake overland migrations to reproduce in aquatic habitats. In turn, their offspring metamorphose and emigrate to upland, terrestrial habitats. We examined the diel patterns and daily variability of migrations of adult and juvenile amphibians in response to climatic cues. Of the eight species (*Ambystoma talpoideum* (Holbrook, 1838), *Ambystoma tigrinum* (Green, 1825), *Bufo terrestris* (Bonnaterre, 1789), *Hyla gratiosa* LeConte, 1856, *Pseudacris crucifer* (Wied-Neuwid, 1838), *Pseudacris ornata* (Holbrook, 1836), *Rana sphenocephala* Cope, 1886, and *Scaphiopus holbrookii* (Harlan, 1935)) that we observed, all migrated almost exclusively at night except for the recently metamorphosed *B. terrestris*, which frequently migrated diurnally (>50% of captures). Additionally, we correlated daily captures of adult and juvenile *A. talpoideum*, *A. tigrinum*, *B. terrestris*, and *R. sphenocephala* to maximum and minimum daily temperatures, number of previous days without rain, total rainfall during the previous 24 h, and interactions of these variables. Rain was often the most important predictor of amphibian movements. However, species differed in their response to climatic factors, with some species and age classes being more dependent on rain for migrations than others. Rapid changes in regional weather patterns may affect species' migrations differently, possibly altering arrival times of reproductive adults or affecting the likelihood of successful migrations.

Résumé : Les amphibiens des régions tempérées qui se reproduisent dans les étangs entreprennent des migrations terrestres afin d'aller pondre dans les habitats aquatiques. À leur tour, leurs rejetons se métamorphosent et migrent vers des habitats terrestres plus en altitude. Nous examinons les patrons diurnes et la variabilité journalière des migrations des amphibiens adultes et des jeunes en réaction aux signaux climatiques. Les huit espèces observées (*Ambystoma talpoideum* (Holbrook, 1838), *Ambystoma tigrinum* (Green, 1825), *Bufo terrestris* (Bonnaterre, 1789), *Hyla gratiosa* LeConte, 1856, *Pseudacris crucifer* (Wied-Neuwid, 1838), *Pseudacris ornata* (Holbrook, 1836), *Rana sphenocephala* Cope, 1886 et *Scaphiopus holbrookii* (Harlan, 1935)) migrent toutes presque exclusivement la nuit, à l'exception des *B. terrestris* fraîchement métamorphosés, qui migrent souvent (>50 % des captures) en plein jour. Il y a, de plus, une corrélation entre les captures d'adultes et de jeunes d'*A. talpoideum*, d'*A. tigrinum*, de *B. terrestris* et de *R. sphenocephala*, d'une part, et, d'autre part, les températures journalières minimales et maximales, le nombre de jours antérieurs sans pluie, les précipitations totales durant les 24 h précédentes et les interactions entre ces variables. La pluie est souvent la meilleure variable prédictive des captures d'amphibiens. Cependant, les espèces diffèrent dans leur réaction aux facteurs climatiques et certaines espèces et certaines classes d'âge sont plus dépendantes de la pluie pour leur migration que d'autres. Les variations rapides des patrons climatiques régionaux peuvent affecter les migrations des diverses espèces de façon différente, probablement en modifiant le moment d'arrivée des adultes reproducteurs et en affectant la probabilité des migrations réussies.

[Traduit par la Rédaction]

Introduction

Many animals migrate in response to changes in climate or resource availability. This well-documented phenomenon is widespread across animal taxa. For example, many birds undergo seasonal migrations that coincide with latitudinal shifts in food availability (Alerstam 1990), and wildebeest and zebra migrate thousands of kilometres as water resources become scarce (Wolanski and Gereta 2001). Other animals undergo significant breeding migrations (e.g., Pacific salmon, Groot and Margolis 1991; blue whales, Calambokidis and Steiger 1997). Many populations of amphibians in temperate regions undertake mass yearly migrations from terrestrial habitats to breed in ephemeral wetlands where their aquatic offspring develop (Duellman and Trueb 1986). In turn, aquatic larvae eventually undergo metamorphosis and return to terrestrial habitats through mass emigrations.

Amphibians are characterized by having highly permeable skin, a trait that predisposes them to rapid evaporative water loss (Shoemaker et al. 1992). Consequently, the availability of water and risk of desiccation can constrain species distributions and activity patterns (Gibbons and Bennett 1974; Kam and Chen 2000). For pond-breeding adult amphibians and recently metamorphosed juveniles that undertake overland migrations, migratory activity may be highly dependent upon adequate climatic factors to mitigate the risk of desiccation. Breeding migrations and the emigration of recently metamorphosed juveniles from wetlands have been corre-

lated to daily rainfall for many species (e.g., Anderson 1967; Semlitsch 1981, 1985; Sexton et al. 1990; Greenberg and Tanner 2004, 2005), and the seasonal phenology of amphibian reproductive migrations is also well-documented for populations of many species (e.g., Beebee 1995; Semlitsch et al. 1996; Paton et al. 2000; Gibbs and Briesch 2001). However, the timing of migration varies among species (Paton et al. 2000), among years (Gibbons and Semlitsch 1991), and with latitude within a single species (Brandon and Bremer 1967; Morin 1983). Thus, to appropriately contrast species' migratory responses to climatic factors, multiple species must be compared from a single geographic location during the same year.

Interspecific differences in physiological tolerance and resistance to desiccation may contribute to differences among species in migratory responses to climatic factors. Furthermore, current global climate models predict changes in regional climates, with some areas receiving more rainfall and other areas becoming increasingly arid (National Assessment Synthesis Team 2001). Although reductions in total rainfall can affect the persistence of pond-breeding amphibian populations owing to changes in pond hydroperiods and subsequent larval mortality (Semlitsch and Wilbur 1988; Carey and Alexander 2003; Daszak et al. 2005), changes in the frequency and duration of rainfall could potentially decrease the likelihood of successful overland migration for some species. Furthermore, changes in the timing of rainfall may alter arrival times of immigrating, reproductive adults, resulting in changes in the competitive interactions among aquatic larvae. Therefore, to evaluate future impacts of climate change, we must understand how climatic factors affect patterns of overland migration in a diverse assemblage of amphibians.

Predation is another factor that can influence the migratory movements of amphibians. Adult temperate amphibians migrate largely at night, a behavior that is often attributed to predator avoidance (Harrison 1985; Semlitsch and Pechmann 1985; Pechmann and Semlitsch 1986). Diurnal species are often those that produce toxic compounds and display aposematic coloration, traits that offer predator resistance (e.g., *Notophthalmus viridescens* (Rafinesque, 1820); Semlitsch and Pechmann 1985). However, the extent of diurnality that exists in migrations of recently metamorphosed amphibians as they leave their natal wetlands remains unclear. For newly metamorphosed amphibians, the need to abandon their larval habitat in search of new prey or to escape intraspecific competition may outweigh the costs of migrating during suboptimal conditions, prompting juvenile amphibians to emigrate by day as well as by night. Conversely, the greater surface area to volume ratio of juveniles compared with those of adults may lead to juveniles being more nocturnal than adults in their movements to avoid desiccation.

Our primary goal in this study is not to characterize the seasonal phenology of amphibian migrations, but instead to simultaneously examine the variation in daily movements of migrating animals in response to climatic factors for several species at a single wetland. Our capture of over 400 000 amphibians during a single year (Gibbons et al. 2006) allowed us to address the following four questions. First, are there interspecific or ontogenetic differences in diel patterns of migratory activity? Second, does daily variation in amphibian migrations correspond with identifiable climatic factors? Third, are there interspecific or ontogenetic differences in which climatic variables predict migratory activity? And finally, are diurnal amphibian movements more dependent on rain than are nocturnal movements?

Methods

Study site

Ellenton Bay is an isolated Carolina bay wetland located on the US Department of Energy's Savannah River Site in Aiken, South Carolina. It is subject to periodic droughts but generally holds water year-round and does not contain fish. During particularly wet years, the bay covers an area of approximately 10 ha and is dominated by shallow water (<1 m deep) and relatively uniform distributions of emergent grasses (predominantly the genus *Panicum* L.), water lilies (*Nymphaea odorata* Ait.), and water-shields (*Brasenia schreberi* Gmel.). The margin of Ellenton Bay is forested predominantly with loblolly and slash pine (genus *Pinus* L.); however, the wetland itself is entirely free of canopy cover and receives direct sunlight. A previous study has described the high abundances and diversity of amphibians at this wetland (Gibbons et al. 2006). For further details of the study site, see Gibbons et al. (2006).

Data collection

We completely encircled Ellenton Bay with a terrestrial drift fence and monitored it daily from 1 February 2003 to 10 February 2004. We constructed the drift fence of aluminum flashing (1230 m long, 40 cm high) and buried it several centimetres into the soil (Gibbons and Semlitsch 1982). We placed 164 paired traps, spaced every 15 m along the fence, with half of the traps on each side of the fence so that we could categorize animals as entering or leaving the bay (Gibbons and Semlitsch 1982). The paired traps included 19-l pitfall traps (plastic buckets, $n = 82$), 2.3-l pitfall traps (metal coffee cans, $n = 42$), and wooden box funnel traps ($n = 40$) that were similar to those used in other studies (Himes 2000; Zappalorti and Torocco 2002). We describe additional details of our collection methods in Gibbons et al. (2006).

We checked the pitfall and funnel traps every morning after sunrise between 0600 and 0900. We checked the traps again in early evening just before sunset (1700–2000) from 19 May 2003 to 31 September 2003. This allowed us to characterize diel movement patterns of adults and recently metamorphosed emigrating amphibians. We recorded captures of all amphibians and reptiles but did not record the sexes of adult amphibians. We recorded daily rainfall with a rain gauge located away from the canopy, maximum and minimum daily air temperatures in the shade at approximately 2 m above the ground, and water depth at the center of the bay.

Statistical analyses

We used the χ^2 test of independence (Sokal and Rohlf 1995) to determine (*i*) if recently metamorphosed amphibians were more likely than adults to move during the day and (*ii*) if diurnal amphibian movements were more restricted to

Table 1. Sample sizes of animals captured during periods when the traps were checked twice daily and results of χ^2 tests to determine if adults are more likely to move at night than recently metamorphosed individuals.

	Sample size			
	Juvenile	Adult	χ^2	p
Ambystoma talpoideum	6 527	372	3.49	0.062
Ambystoma tigrinum	1 212	25	0.00	0.958
Bufo terrestris	65 002	1450	1026.68	<0.001*
Hyla gratiosa	373	56	6.69	0.011
Pseudacris crucifer	127	9	0.22	0.637
Pseudacris ornata	127	38	1.18	0.277
Rana sphenocephala	210 152	638	1.04	0.307
Scaphiopus holbrookii	63	16	1.21	0.272

Note: For the proportion of animals moving at night see Fig. 1.
*Statistically significant after correcting for multiple comparisons using the sequential Bonferroni method.

rain than were nocturnal movements. For some species, we observed fewer than five adults moving during the day. In these cases, we employed Yates' correction for small expected values (Sokal and Rohlf 1995). In addition to reporting p values for the χ^2 tests, we also indicate which results remain significant at $\alpha = 0.05$ after controlling for family-wise error rates using the sequential Bonferroni method.

Construction of regression models

Amphibian species differ in the seasonal timing of their migrations. Thus, to accurately evaluate the climatic factors contributing to the daily movement of a particular species and age class, we excluded seasonal portions of the data that were obviously irrelevant to the particular case in question. For example, to investigate the daily movements of recently metamorphosed *Rana sphenocephala* Cope, 1886, we only analyzed days from the first capture of an emigrating recently metamorphosed individual to the last capture and excluded all other days.

We chose to examine the influence of four climatic variables on the daily movement patterns of amphibians. These included total amount of rainfall in the past 24 h (R$_{AIN}$), maximum daily temperature (T$_{MAX}$), minimum daily temperature (T$_{MIN}$), and the number of preceding days without rainfall (D$_{AYS}$N$_O$R$_{AIN}$). We also included the interaction terms R$_{AIN}$ × T$_{MAX}$, R$_{AIN}$ × T$_{MIN}$, R$_{AIN}$ × D$_{AYS}$N$_O$R$_{AIN}$, T$_{MAX}$ × D$_{AYS}$N$_O$R$_{AIN}$, and T$_{MIN}$ × D$_{AYS}$N$_O$R$_{AIN}$. Our dependent response variable in the models was the number of animals captured each day. Wetland depth can affect the timing of metamorphosis and subsequent emigration by juvenile amphibians (Semlitsch and Wilbur 1988; Leips et al. 2000). However, the wetland in our study continued filling until well after the juvenile amphibians had emigrated. Thus, we did not include bay depth as a predictor variable.

We rank-transformed both the independent and dependent data prior to regression to avoid violating assumptions of normality that resulted from overdispersion in our data. Ties within a rank were assigned a mean rank. Rank transformation is comparable with robust regression and is favorable over regression on log-transformed data (Iman and Conover 1979; for discussion see Semlitsch 1985). Other models such as the zero-inflated negative binomial (ZINB) can be used to model nontransformed data. However, both ZINB models

and classical linear regression models assume that the error terms in the regression model are independent (Durbin and Watson 1950). Time-series data such as daily counts of amphibian captures often suffer from serial autocorrelation, a problem that violates the assumption of independence. Specifically, amphibian captures tend to be tightly clustered over multiple days and are separated by clusters of days with no captures (Durbin–Watson d test; $p < 0.05$ for all models). No ZINB model that appropriately accounts for serial autocorrelation has been formally introduced (Dan Hall, personal communication). Thus, we constructed all possible AR1 (autoregression with a time lag of one step) models using the ranked data and interaction terms and identified the model that best predicted amphibian movements using Akaike's information criterion (AIC; Akaike 1976). Additionally, we constructed AR1 autoregression models for each species and cohort using R$_{AIN}$ as the sole predictor of animal captures. "R$_{AIN}$ only" models allowed us to compare the variance in migratory response to rainfall among species and demographics in the absence of other factors. We created AR1 autoregression models using the PROC AUTOREG option in SAS® version 9 (SAS Institute Inc. 2000).

Results

Diel movement patterns

We captured over 400 000 individuals from 24 amphibian species and had sufficiently high captures during the period for which we monitored the drift fence twice daily to analyze diel activity patterns for two salamander species and six anuran species: the mole salamander (*Ambystoma talpoideum* (Holbrook, 1838)), eastern tiger salamander (*Ambystoma tigrinum* (Green, 1825)), southern toad (*Bufo terrestris* (Bonnaterre, 1789)), barking treefrog (*Hyla gratiosa* LeConte, 1856), spring peeper (*Pseudacris crucifer* (Wied-Neuwid, 1838)), ornate chorus frog (*Pseudacris ornata* (Holbrook, 1836)), southern leopard frog (*R. sphenocephala*), and eastern spadefoot toad (*Scaphiopus holbrookii* (Harlan 1935); Table 1). Generally, these species moved exclusively at night (Fig. 1). The one notable exception occurred in recently metamorphosed *B. terrestris*, which exhibited significantly greater diurnality than adults ($p < 0.001$; Fig. 1, Table 1).

Fig. 1. Proportion of adult and metamorphosed amphibians that moved at night. Recently metamorphosed *B. terrestris* exhibited significantly greater diurnality than adults ($p < 0.001$); intraspecific comparisons were nonsignificant for all other species. Sample sizes are provided in Table 1.
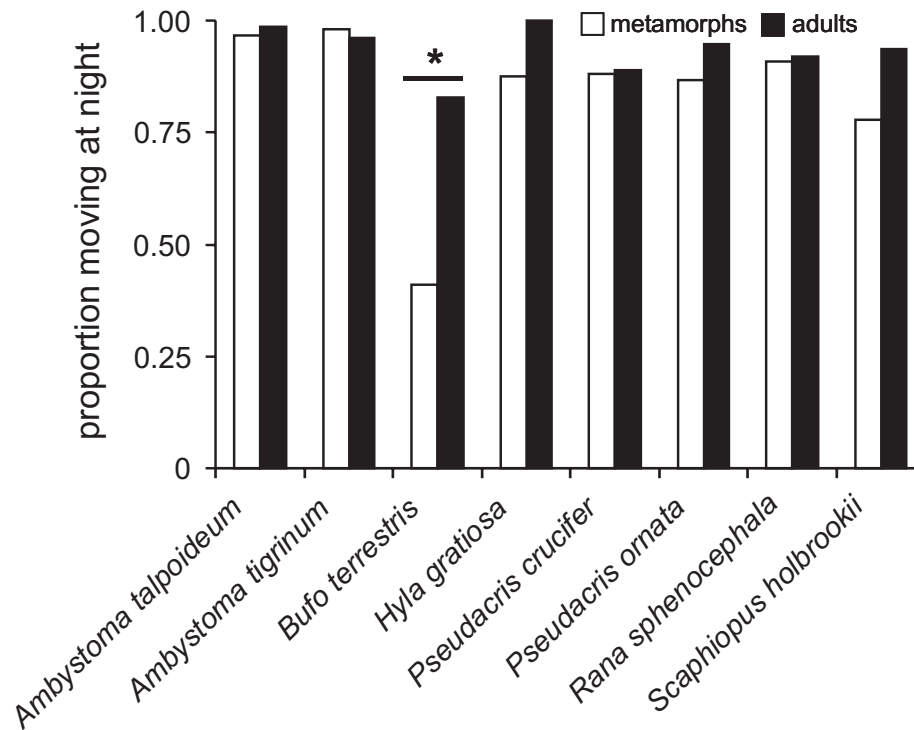

Table 2. Autoregression models (AR1) correlating amphibian captures to climatic factors are shown.

	Cohort	Best model	R^2 Total	Rain
Ambystoma talpoideum	Metamorphs	$y = 78.44 + 0.469R_{AIN} - 0.002R_{AIN} \times T_{MAX} + 0.001R_{AIN} \times D_{AYS}N_{O}R_{AIN}$	0.545	0.526
	Adults	$y = 49.35 + 0.572R_{AIN}$	0.404	0.404
Ambystoma tigrinum	Metamorphs	$y = 0.68 + 0.719R_{AIN} + 0.243D_{AYS}N_{O}R_{AIN}$	0.954	0.613
	Adults	$y = 56.44 + 0.004R_{AIN} \times T_{MIN} - 0.002T_{MAX} \times D_{AYS}N_{O}R_{AIN}$	0.367	0.317
Bufo terrestris	Metamorphs day	$y = 44.73 + 0.244R_{AIN} + 0.002T_{MIN} \times D_{AYS}N_{O}R_{AIN}$	0.230	0.210
	Metamorphs night	$y = 51.26 + 0.244R_{AIN}$	0.208	0.208
	Adults	$y = 95.87 + 0.153R_{AIN} + 0.001T_{MAX} \times D_{AYS}N_{O}R_{AIN}$	0.560	0.549
Rana sphenocephala	Metamorphs	$y = 106.38 + 0.321R_{AIN}$	0.777	0.777
	Adults	$y = 67.91 + 0.425R_{AIN} + 0.268T_{MIN} - 0.001R_{AIN} \times T_{MAX}$	0.380	0.353

Note: All data were rank-transformed. The most parsimonious models were determined using AIC and are provided. See text for description of climatic factors and interaction terms used as predictor variables. R^2 values from the best overall model and from models using R_{AIN} as the sole predictor for animal captures are provided.

Diel movement patterns did not differ significantly between recently metamorphosed juveniles and adults for any other species after controlling for family-wise statistical error (Fig. 1, Table 1).

Climatic factors contributing to daily variation of amphibian movements

We had sufficient captures to analyze the role of climatic factors in the movements of two salamander species and two anuran species: *A. talpoideum*, *A. tigrinum*, *B. terrestris*, and *R. sphenocephala*. R_{AIN} was selected as an important predictor for amphibian captures in eight of the nine regression models (Table 2). For many species, R_{AIN} was not the only predictor variable included in the favored model. Minimum daily temperature, the number of preceding days without rain, and some interaction variables also predicted the magnitude of amphibian movements (Table 2, Figs. 2, 3). Overall, autoregression models (AR1) on the ranked data explained 21%–95% of the variance in captures (Table 2). In "R_{AIN} only" AR1 regression models, R_{AIN} accounted for 21%–78% of the total variance in animal movements and recently metamorphosed juveniles were often more correlated with rainfall than adults except in the case of *B. terrestris* (Table 2). R_{AIN} was poorly correlated with movements of recently metamorphosed *B. terrestris*; however, a greater proportion of daytime movements occurred on days with rain than did nighttime movements (79% versus 63%; $\chi^2 = 507.87$, $p < 0.001$; Fig. 3). For other species, the majority of nighttime movements occurred on days with rain (71%–97%).

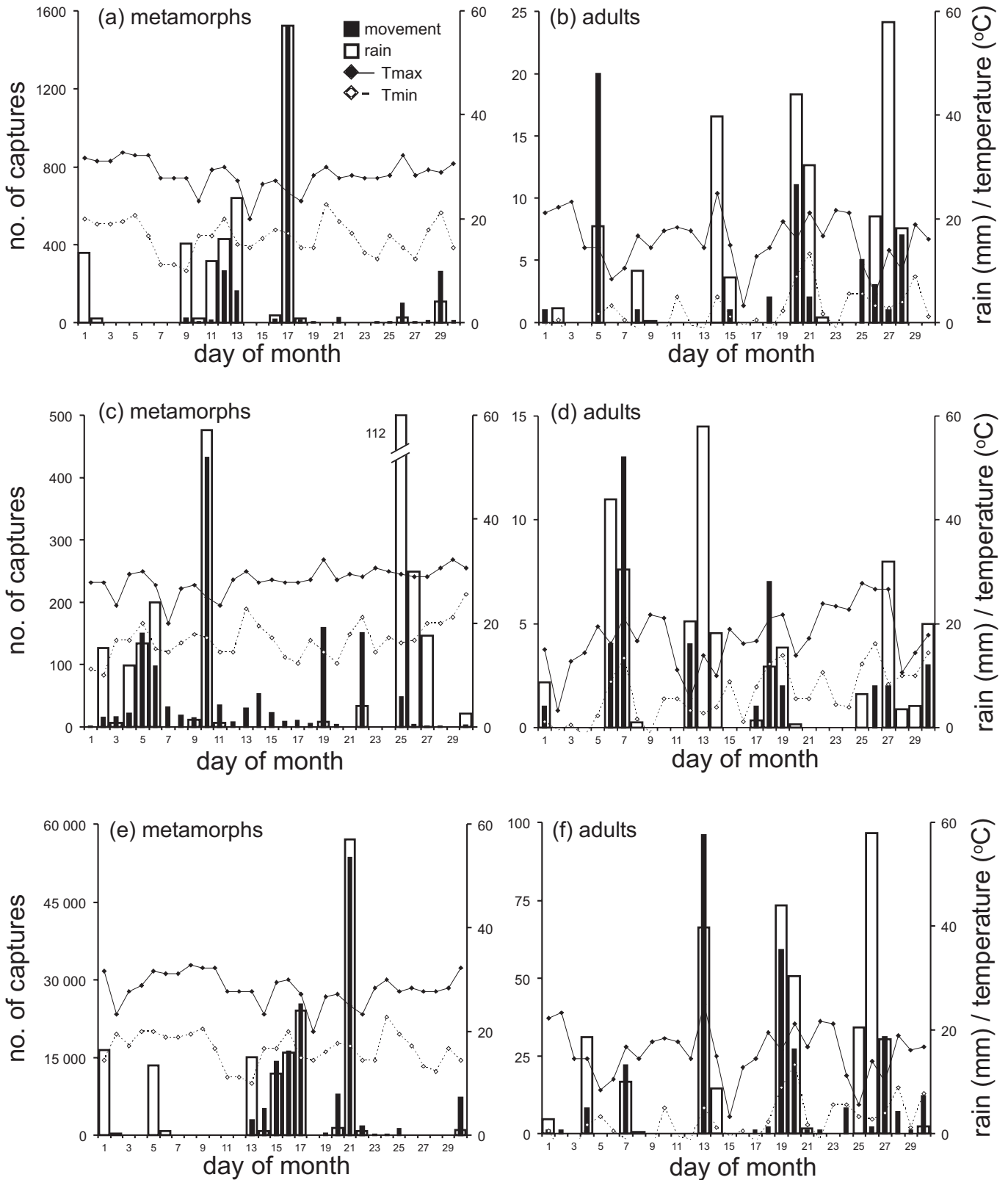**Fig. 2.** Representative examples over a 30-day period of the correlations between climatic factors and daily movements for metamorphs and adults of *A. talpoideum* (*a*, *b*), *A. tigrinum* (*c*, *d*), and *R. sphenocephala* (*e*, *f*). The number of captures per day is identified by the solid bars (left *y* axis) and the corresponding rainfall per day is identified by the open bars (right *y* axis). The maximum and minimum daily temperatures are shown here as solid and broken lines, respectively (right *y* axis). Examples do not encompass the exact same 30-day period for each species and age class. Note the differences in scale for the left *y* axes.

Fig. 3. Representative examples over a 30-day period of the correlations between climatic factors and movements of *B. terrestris* metamorphs captured moving during the day (*a*), metamorphs captured moving at night (*b*), and adults (*c*). Significantly more daytime movements occurred on days with rain than did nighttime movements ($p < 0.001$). The number of captures per day is identified by solid bars (left *y* axis) and the corresponding rainfall per day is identified by open bars (right *y* axis). The maximum and minimum daily temperatures are shown here as solid and broken lines, respectively (right *y* axis). Examples in (*a*) and (*b*) encompass the same 30-day period. Note the differences in scale for the left *y* axes.
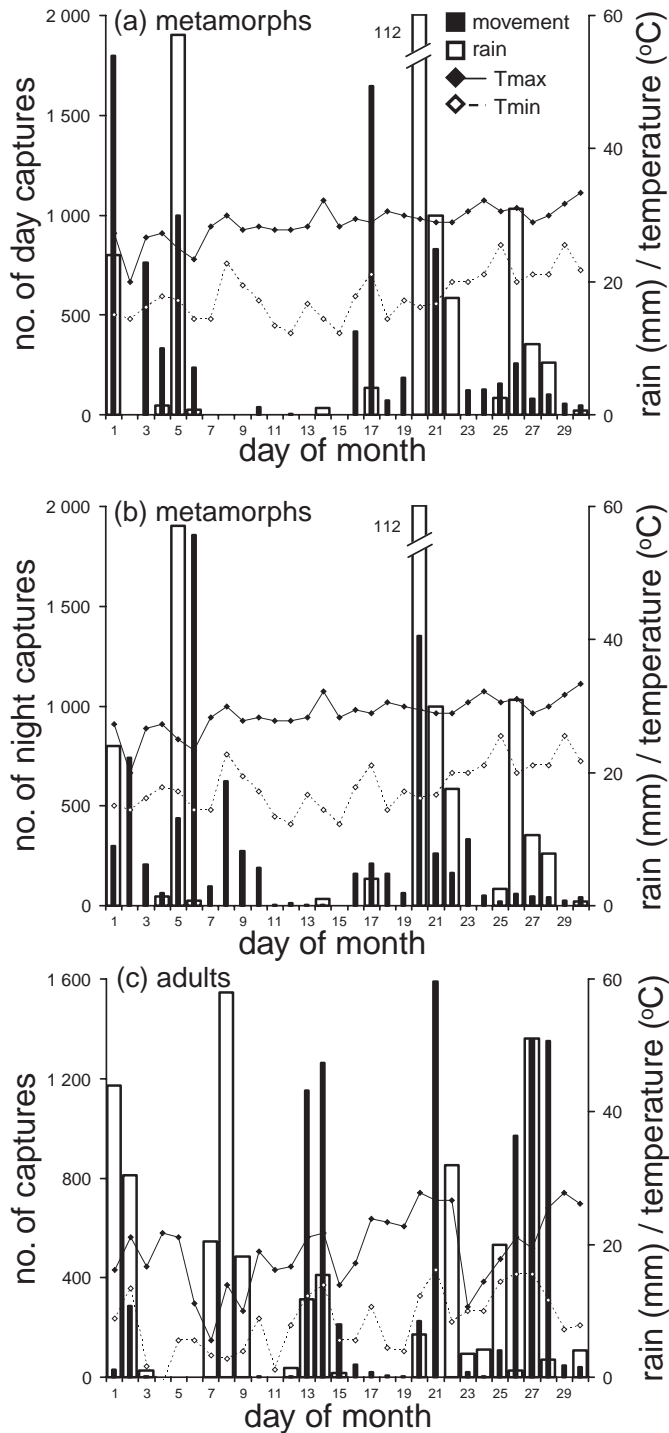
Discussion

The results of the diel portion of this study accord closely with previous observations of temperate, pond-breeding amphibians and suggest that amphibian migrations are largely nocturnal (Noble 1931; Hurlbert 1969; Williams 1973). For example, Pechmann and Semlitsch (1986) found that the four anuran species they observed (i.e., *P. crucifer*, *Pseudacris nigrita* (LeConte, 1825), *P. ornata*, and *R. sphenocephala*) were nocturnal in their migratory movements. Additionally, Semlitsch and Pechmann (1985) reported that four of the five salamander species they observed (i.e., *A. talpoideum*, *Ambystoma opacum* (Gravenhorst, 1807), *A. tigrinum*, and *Eurycea quadridigitata* (Holbrook, 1842)) were also highly nocturnal in their migrations. The observations in the previous studies were made during adult breeding migrations and our observations of recently metamorphosed juveniles extend the generality of these findings. Because juvenile amphibians are smaller than adults and because they have concordantly greater surface area to volume ratios (Spight 1968), they likely face greater desiccation risks during diurnal migrations. Thus, it may have been reasonable to expect juveniles to be less likely to migrate during the day than adults. However, this was often not the case; juveniles usually exhibited more diurnal migratory movements than adults, although these results were only statistically significant for *B. terrestris*.

Amphibians are highly dependent on adequate moisture to maintain water balance (Jørgensen 1997; Hillyard 1999). Desiccation risk is presumably lower during, and immediately following, rainfall, and many studies have correlated amphibian migrations with heavy rains (e.g., Semlitsch 1985; Semlitsch and Pechmann 1985; Greenberg and Tanner 2004; Greenberg and Tanner 2005). Our results further support this generalization and indicate that total daily rainfall is often the most important climatic factor influencing the magnitude of amphibian movements. However, some groups were less dependent on rainfall for migration than others. For example, the number of migrating recently metamorphosed *B. terrestris* was poorly correlated with rainfall. The ability of *B. terrestris* to move across a broader range of environmental conditions is likely related to their higher tolerance of body water loss compared with other species observed in this study (Thorson and Svihla 1943). Interestingly, even in recently metamorphosed *B. terrestris*, diurnal movements occurred more frequently on rainy days than did nocturnal movements (Table 2, see also Figs. 3*a*, 3*b*), possibly the result of the desiccating conditions produced by high daytime temperatures (Moore and Sievert 2001). Absence of rain was also an important predictor for amphibian migrations. For example, following prolonged dry spells, even small amounts of rain were enough to elicit migratory responses for recently metamorphosed *A. talpoideum* (e.g., see days 19 and 22 in Fig. 2*c*); this phenomenon has also been reported for *B. quercicus* (Greenberg and Tanner 2005). Except in *B. terrestris*, the magnitude of movements by recently metamorphosed amphibians was more highly correlated to rain than it was among adults, as evidenced by the "RAIN only" regression models.

Although desiccation risk is lower at night than in the daytime, previous research has shown that many amphibians

migrate at night even when suitable rainfall and temperatures are available during daytime periods (Semlitsch and Pechmann 1985; Pechmann and Semlitsch 1986). Although this does not preclude desiccation risk from having contributed to the historic evolution of these behaviors, it does suggest that predation from diurnal predators may also explain nocturnal migrations. This explanation is supported, in part, because species that are resistant to predation migrate both during the day and at night. In one study, *N. viridescens* migrated during both day and night, a pattern that the authors attributed to the highly toxic skin secretions and aposematic coloration (Semlitsch and Pechmann 1985). In our study, only recently metamorphosed juvenile *B. terrestris* exhibited a high degree of diurnality. *Bufo terrestris* possess granular parotoid glands that produce bufotoxins which make them unpalatable to predators (Hutchinson and Savitzky 2004) and may account for their ability to migrate diurnally. Despite this, adult *B. terrestris* did not migrate diurnally. We also did not observe diurnal movements in *S. holbrookii*, despite several previous accounts (e.g., Neill 1957) and our own observations of diurnal migrations in these toads at other wetlands. However, the lack of diurnal movements in *S. holbrookii* may be a result of the poor recruitment observed at Ellenton Bay during the course of the current study.

Pond-breeding amphibians undertake significant overland migrations both as adults and as recently metamorphosed juveniles. While some researchers have suggested that these migrations occur predominantly at night to minimize the risk of predation, maintaining appropriate water balance remains critical for amphibians, and migrating at night is one method for reducing desiccation risk. Additionally, our results support the generalization that amphibian migrations are intimately associated with rain. However, our findings also demonstrate that there can be considerable variation among species in their migratory responses to climatic factors. We propose that species differ in their diel migratory patterns and responses to climatic factors, at least in part, because of differences in physiological tolerance, risk of desiccation, and risk of predation. As a result, future changes in climate and regional weather patterns may have important species-specific consequences for amphibians that rely on suitable climatic factors to successfully complete their breeding and juvenile migrations.

Acknowledgments

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