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Evaluating the Effects of Anthropogenic Stressors on Source-Sink Dynamics in Pond-Breeding Amphibians

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Abstract: *Although interwetland dispersal is thought to play an important role in regional persistence of pond-breeding amphibians, few researchers have modeled amphibian metapopulation or source-sink dynamics. Results of recent modeling studies suggest anthropogenic stressors, such as pollution, can negatively affect density and population viability of amphibians breeding in isolated wetlands. Presumably population declines also result in reduced dispersal to surrounding (often uncontaminated) habitats, potentially affecting dynamics of nearby populations. We used our data on the effects of mercury (Hg) on the American toad (*Bufo americanus*) as a case study in modeling the effects of anthropogenic stressors on landscape-scale amphibian dynamics. We created a structured metapopulation model to investigate regional dynamics of American toads and to evaluate the degree to which detrimental effects of Hg contamination on individual populations can disrupt interpopulation dynamics. Dispersal from typical American toad populations supported nearby populations that would otherwise have been extirpated over long time scales. Through support of such sink populations, dispersal between wetland-associated subpopulations substantially increased overall productivity of wetland networks, but this effect declined with increasing interwetland distance and decreasing wetland size. Contamination with Hg substantially reduced productivity of wetland-associated subpopulations and impaired the ability of populations to support nearby sinks within relevant spatial scales. Our results add to the understanding of regional dynamics of pond-breeding amphibians, the wide-reaching negative effects of environmental contaminants, and the potential for restoration or remediation of degraded habitats.*

Keywords: *Bufo americanus*, dispersal, landscape ecology, mercury, metapopulations, pollution, population modeling, stochasticity

Evaluación de los Efectos de Estresantes Antropogénicos sobre la Dinámica Fuente-Vertedero en Anfibios que se Reproducen en Charcas

Resumen: *Aunque se piensa que la dispersión entre humedales juega un papel importante en la persistencia regional anfibios que se reproducen en charcas, pocos investigadores han modelado la dinámica de metapoblaciones o fuente-vertedero de anfibios. Resultados de estudios recientes sugieren que los estresantes antropogénicos como la contaminación pueden afectar negativamente a la densidad y viabilidad poblacional de anfibios que se reproducen en humedales aislados. Las declinaciones poblacionales presumiblemente también resultan en la reducción de la dispersión hacia hábitats circunvecinos (a menudo no contaminados), afectando potencialmente la dinámica de poblaciones cercanas. Utilizamos nuestros datos sobre los efectos de mercurio (Hg) sobre el sapo (*Bufo americanus*) como un estudio de caso para modelar los efectos de estresantes antropogénicos sobre la dinámica de anfibios a nivel de paisaje. Creamos un modelo de metapoblación estructurada para investigar la dinámica regional de sapos y para evaluar el grado en que los efectos perjudiciales de la contaminación por mercurio sobre poblaciones individuales puede alterar la dinámica interpoblacional. La dispersión desde poblaciones típicas de sapos soportó a poblaciones cercanas que de otra manera hubieran sido extirpadas en el largo plazo. Mediante soporte a tales poblaciones vertedero, la dispersión entre subpoblaciones asociadas a humedales incrementó sustancialmente la productividad total de las redes de humedales, pero este efecto declinó con el incremento de la distancia entre humedales y el decremento del tamaño del humedal. La contaminación por mercurio redujo sustancialmente la productividad*

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de subpoblaciones asociadas con humedales y limitó la capacidad de las poblaciones para soportar a vertederos cercanos en escalas espaciales relevantes. Nuestros resultados contribuyen al entendimiento de la dinámica regional de anfibios que se reproducen en charcas, de los efectos negativos de gran alcance de los contaminantes ambientales y del potencial de restauración o remediación de hábitats degradados.

Palabras Clave: *Bufo americanus*, contaminación, contaminación por mercurio, dispersión, ecología del paisaje, estocasticidad, metapoblaciones, modelos poblacionales

Introduction

Metapopulation theory has revolutionized the way conservation biologists view species and habitat management at regional scales. Classically, the metapopulation concept recognizes the potential for stochastic processes to cause extirpation of populations in patches of otherwise high-quality habitat and highlights the essential role of dispersal (permanent, unidirectional movement of individuals from one subpopulation to another) in maintaining viability of species in heterogeneous landscapes (Levins 1969, 1970; Hanski 1999). Subsequently, Pulliam (1988) recognized that variation in patch quality could result in source-sink dynamics, wherein dispersal from large source populations can support nearby sink populations in patches that are too small or resource poor to be viable over long periods in the absence of immigration. Basic understanding of metapopulation and source-sink dynamics heralded productive research aimed at understanding how anthropogenic activities can disrupt metapopulation dynamics through alteration of natural dispersal patterns (McCullough 1996).

Amphibians provide excellent models for evaluating the extent to which localized anthropogenic activities can affect species viability at regional or metapopulation scales. Pond-breeding amphibians have long been thought to conform well to the pond-as-patch case of a classic metapopulation, in which interwetland dispersal is necessary to buffer against periodic extinction of subpopulations due to stochastic processes (Marsh & Trenham 2001). Despite debate about the validity of these traditional assumptions (Marsh & Trenham 2001; Smith & Green 2005), theoretical and empirical work confirms that interwetland dispersal can play an important role in the persistence of amphibians at regional scales (e.g., Gill 1978; Sjogren 1991; Halley et al. 1996). Recently it has been shown how habitat alteration or other anthropogenic activities can affect dispersal among wetland-associated subpopulations. For example, Semlitsch and Bodie (1998) and Gibbs (1993) demonstrated that loss of small isolated wetlands would dramatically increase interwetland distances and thus decrease dispersal rates and reduce viability of metapopulations of wetland-associated species. Likewise, habitat alteration may hinder dispersal of amphibians, either through increased resistance of landscapes to movement or behavioral avoidance of altered habitats (e.g., deMaynadier & Hunter 1999; Rothermel & Semlitsch 2002; Rothermel 2004). However, few researchers have evaluated how loss of emigrants from areas degraded by anthropogenic activities may affect the viability of amphibian populations in the surrounding landscape.

Environmental pollution is a suspected contributor to the global decline of amphibians (Alford 2010), and results of numerous laboratory studies show the sensitivity of amphibian embryos and larvae to a wide array of environmental contaminants (Sparling 2010). Although few researchers have attempted to translate experimentally derived individual-level effects of environmental contaminants to population dynamics, 3 recent models show that contaminant exposure can affect the viability of amphibian populations (Karraker et al. 2008; Salice et al. 2011; Willson et al. 2012). Presumably, such population declines also result in reduced dispersal. However, no one has examined the extent to which loss of emigrants due to environmental contamination affects amphibian populations in the surrounding uncontaminated landscape.

We used our data on the effects of mercury (Hg), a widespread heavy-metal contaminant known to have adverse effects on wildlife, on a common pond-breeding amphibian as a case study in modeling the effects of anthropogenic stressors on landscape-scale amphibian dynamics. Previously, we used a series of field surveys along the floodplain of the historically Hg-contaminated South River, Virginia (U.S.A.), and longitudinal laboratory and mesocosm experiments to comprehensively evaluate the effects of Hg contamination on American toads (*Bufo americanus*). We then used population models to demonstrate that exposure to high levels of Hg reduced population sizes and elevated extinction probability of populations in stochastic environments (Willson et al. 2012).

Here, we extend our previous research to evaluate regional dynamics when amphibian subpopulations centered on breeding wetlands are linked by interwetland dispersal. Specifically, we created a stochastic, structured metapopulation model by linking individual models for American toad subpopulations that varied stochastically in response to empirically derived precipitation data for our study site. We then used this model to evaluate conditions under which small wetlands act as population sinks (i.e., populations that are only viable over long periods if they are supplemented by immigrants from surrounding source populations); the contribution of sink populations to landscape-scale amphibian productivity (i.e., biomass production); how contamination of the source wetland with Hg affects that wetland's productivity and ability to support nearby sinks populations; and how simulated contamination of wetlands within a real multiwetland network affects the viability of subpopulations and overall productivity of the network.

Methods

American Toad Demographic Population Model

Previously, we developed a stochastic stage-based matrix population model for American toads in the floodplain of South River (Willson et al. 2012). Briefly, our model, which we based on the general amphibian population model proposed by Vonesh and De la Cruz (2002), included 4 age classes and was regulated by density-dependant larval interactions, which are important drivers of population dynamics in pond-breeding amphibians, including American toads (Brockelman 1969; Wilbur 1977; Vonesh & De la Cruz 2002). Despite the importance of larval density dependence, population dynamics of pond-breeding amphibians are stereotypically erratic, due largely to annual variation in recruitment driven by environmental stochasticity, particularly precipitation (Pechmann et al. 1991; Semlitsch et al. 1996). We incorporated the effects of environmental stochasticity on recruitment by varying the size of the breeding habitat and probability of catastrophic reproductive failure on the basis of annual spring precipitation data for the region. Thus, at each (yearly) time step, initial larval density was determined by the number of breeding females, female fecundity, and embryonic survival divided by the size (circumference) of the larval habitat, which varied stochastically with precipitation (Willson et al. 2012).

In our previous model, we considered an isolated American toad population breeding within an ephemeral wetland with a mean circumference of 100 m, which is representative of those present at our study site. We obtained yearly cumulative spring (March–June) rainfall data for the Central Mountains region of Virginia from the National Oceanic and Atmospheric Administration National Climatic Data Center (www.ncdc.noaa.gov) for the years 1895–2010. For each yearly projection, we drew randomly from the pool of precipitation values and set a breeding-pool circumference of 100 m at the mean spring precipitation value (36.25 cm). Around that mean, we assumed a direct correlation between precipitation and breeding pool size, up to a maximum circumference of 200 m (twice the average) at the maximum rainfall value of 57.71 cm.

In addition, we linked the probability of catastrophic reproductive failure due to pond drying to precipitation by fixing larval survival at zero in the 15% of years with

Table 1. Parameter values used to model American toad (*Bufo americanus*) population dynamics under reference (no Hg effects) and contaminated (exposed to high levels of Hg through both maternal transfer and larval diet) conditions.[a]

Parameter	*Reference value*	*Effect of Hg*[b]
Clutch size	6731	NE
Embryonic survival	0.70	−20%
Maximum larval survival	0.59	−50%[c]
First-year juvenile survival	0.2	NE
Second- & third-year juvenile survival	0.2	
Adult survival	0.6	
Proportion mature at age 3 years	0.5	−7%
Density-dependent coefficient	0.007	
Density-dependent exponent	1	

[a] *For a complete discussion of model parameterization and experiments used to derive effects of Hg see Willson et al. (2012).*
[b] *Situations where Hg treatments did not differ from reference treatments are denoted NE and blank cells represent effects that were not evaluated experimentally.*
[c] *At metamorphic climax under limited food rations (Bergeron et al. 2011*b*; Todd et al. 2011*b*); only imposed at high larval density (>150/m shoreline) (Willson et al. 2012).*

the lowest cumulative spring rainfall. The location of our study site in a river floodplain necessitated consideration of additional catastrophic reproductive failure due to flooding. Floods can result in substantial surface flow within the floodplain that can wash out amphibian breeding pools and likely kill or displace larvae far downstream in areas inhabited by fish and other predators. We considered catastrophic reproductive failure due to flooding by fixing larval survival at zero in the 7.5% of years with the highest cumulative spring rainfall (Willson et al. 2012). We parameterized the model with demographic data from our own studies of American toads and the literature (Table 1). For detailed descriptions of the population model and parameterization see Willson et al. (2012).

Modeling Source-Sink Dynamics

Here, we extend our previous work by evaluating the effects of Hg contamination on regional dynamics of American toads in multiwetland networks. We addressed this objective by creating a structured metapopulation model (Akcakaya 2000) in which models for discrete populations centered on breeding wetlands are linked via interpopulation dispersal of newly metamorphosed individuals (Gill 1978; Breden 1987; Semlitsch 2008). Following Breden (1987) and Halley et al. (1996), we defined dispersal (I_t) from one (source) wetland to another wetland with a negative exponential function,

$$I_t(r, M_t) = \alpha M_t \times \exp\left(-\frac{r}{D}\right), \quad (1)$$

where r is the distance between 2 wetlands, M_t is the number of newly metamorphosed individuals produced at the source wetland in year t, D is the characteristic dispersal radius, and α is the rate of exponential decay. On the basis of field data for the closely related and ecologically similar Fowler's toad (*Bufo fowleri*) (Reading et al. 1991) and common toad (*Bufo bufo*), we used Halley et al.'s (1996) parameterization of this function ($\alpha = 0.26$, $D = 700$ m). We assume individuals dispersing to other wetlands originated from the pool of animals that would not have survived to return to their natal wetland as breeders. Thus we did not subtract them from the surviving pool of year-old individuals at their natal wetland.

Our approach to modeling the effects of environmental stochasticity on the basis of empirical precipitation data (Willson et al. 2012) allowed us to mechanistically link stochastic population dynamics of multiple wetlands such that populations fluctuated in synchrony. At each time step, we used the randomly drawn spring precipitation value to determine the size of each wetland and its probability of drying, resulting in catastrophic reproductive failure of amphibians breeding there. Specifically, for each wetland we adjusted the linear correlation between precipitation and wetland size described above such that the mean breeding-pool circumference occurred at the mean spring precipitation value (36.25 cm). Thus, wetlands exhibited the same correlation between precipitation and size, but were centered on different mean values of circumference. However, we maintained the same threshold for drying (57-m circumference) for all wetlands so that smaller wetlands exhibited a greater probability of drying than larger wetlands.

Incorporating Effects of Hg Contamination

Mercury is an environmental contaminant of global concern due to its ubiquity, toxicity, and ability to bioaccumulate in wildlife (Mason et al. 1996; Fitzgerald et al. 1998). Previously, we used a pluralistic combination of field surveys and factorial laboratory, mesocosm, and terrestrial enclosure experiments to systematically evaluate the individual and interactive effects of exposure to environmentally relevant concentrations of maternal and larval dietary Hg throughout the life cycle of the American toad (Bergeron et al. 2010*a*, 2010*b*, 2011*a*, 2011*b*; Todd et al. 2011*a*, 2011*b*, 2012). Using theoretical models to evaluate the population-level consequences of these effects, we found that only combined exposure to high levels of Hg through both maternal transfer and larval diet resulted in substantial population-level effects (Willson et al. 2012). Thus, here we focused on the effects of exposure to high levels of Hg in both the aquatic (larval) and terrestrial (adult) stages. These effects, as they bear on parameters used to model toad population dynamics in this study, are summarized in Table 1 and are discussed in detail in Willson et al. (2012).

Analyses

We conducted a set of simulations aimed at evaluating source-sink dynamics in American toads and the effects of Hg contamination on the persistence of population sinks within the landscape. Initially, we considered a theoretical 2-wetland source-sink system linked by dispersal of newly metamorphosed toads. The source wetland was defined as an ephemeral breeding pool with a mean shoreline length of 100 m, typical American toad breeding habitat at our study site (Willson et al. 2012). We systematically varied the size (circumference) of the smaller sink wetland and its distance from the source wetland (r) while holding other parameters constant and monitored probability of extinction after 200 years and mean annual production of newly metamorphosed individuals (summed across both wetlands). We set a minimum viable population size for reproduction at 10 adults (Willson et al. 2012), below which no reproduction occurred, and rounded the number of individuals in each age class down to the next lowest integer at the end of each time step. We ran 500 simulations for each parameter combination, beginning with an initial population vector representing the equilibrium values for each age class in an average-sized population (circumference = 100 m). We repeated this process under 3 scenarios: neither wetland contaminated with Hg and no dispersal between wetlands, neither wetland contaminated with Hg and dispersal between wetlands, and source wetland contaminated with Hg and dispersal between wetlands. In the contaminated simulation, we adjusted parameters on the basis of all observed effects of exposure to high maternal and dietary Hg (Table 1).

Next, we applied our theoretical approach to a real network of 6 isolated ephemeral wetlands (Fig. 1) in a predominantly forested region of our study site within the South River floodplain, just northeast of Crimora, Virginia (17S, 0691485E, 4228486N). We used aerial photographs (taken 31 January 2007) to measure the perimeter of the inundated portion of each wetland and the distance between each wetland pair within the network (Fig. 1). We evaluated extinction probabilities for each wetland in the network over 200 years and mean total annual production of newly metamorphosed toads by the network under the following scenarios: no wetlands contaminated and no dispersal between wetlands; no wetlands contaminated and wetlands linked by dispersal of newly metamorphosed toads; each wetland within the network individually contaminated with high levels of Hg and the remaining 5 wetlands not contaminated; and all 6 wetlands within the network contaminated with high levels of Hg. As in previous simulations, we set a minimum viable population size for reproduction at 10 adult individuals and rounded the number of individuals in each age class down to the next lowest integer at the end of each time step. We ran 5000 simulations for

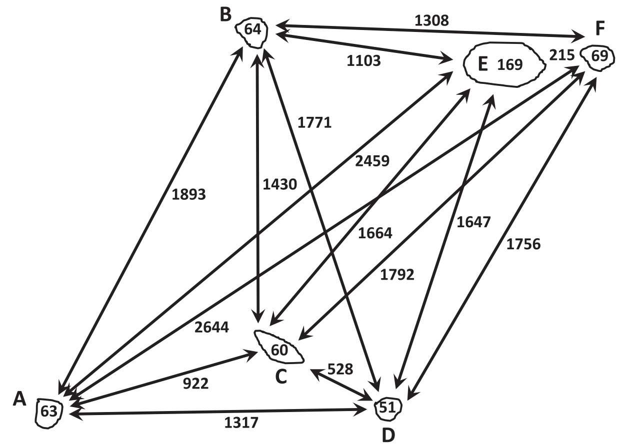

Figure 1. Schematic illustrating the size and spatial arrangement of wetlands within the wetland network used to explore the consequences of Hg contamination on landscape-scale dynamics of American toad (Bufo americanus) *populations (enclosed polygons, wetlands A–F; numbers within polygons, size [circumference in meters] of wetland; numbers along arrows, distances between wetlands [meters]). The wetland network was located along the floodplain of the historically Hg-contaminated South River (northeast of Crimora, Virginia [U.S.A.]). To ease visualization, the schematic is not drawn perfectly to scale (i.e., wetlands are enlarged and some spatial locations are slightly shifted to ease labeling). Arrows represent bidirectional permanent dispersal among wetlands, not round-trip migration by individuals.*

each scenario, beginning with an initial population vector representing the equilibrium values for each age class in an average-sized population (circumference = 100 m). All models were constructed and run in program R (R Foundation for Statistical Computing, Vienna).

Results

In the absence of interwetland dispersal, persistence of American toad populations was solely dependent on the size of the wetland, a proxy for carrying capacity (Fig. 2a). When wetland circumference was <60 m, populations were subject to nearly 100% probability of extirpation after 200 years. However, allowing dispersal of newly metamorphosed individuals between wetlands greatly enhanced persistence of the smaller population provided the interwetland distance was sufficiently small to allow for frequent recolonization events (Fig. 2b). Thus, when the circumference of the smaller wetland was <60 m and the interwetland distance was <1600 m, the smaller wetland was supported as a sink that required dispersal from the larger source wetland to persist over long time frames.

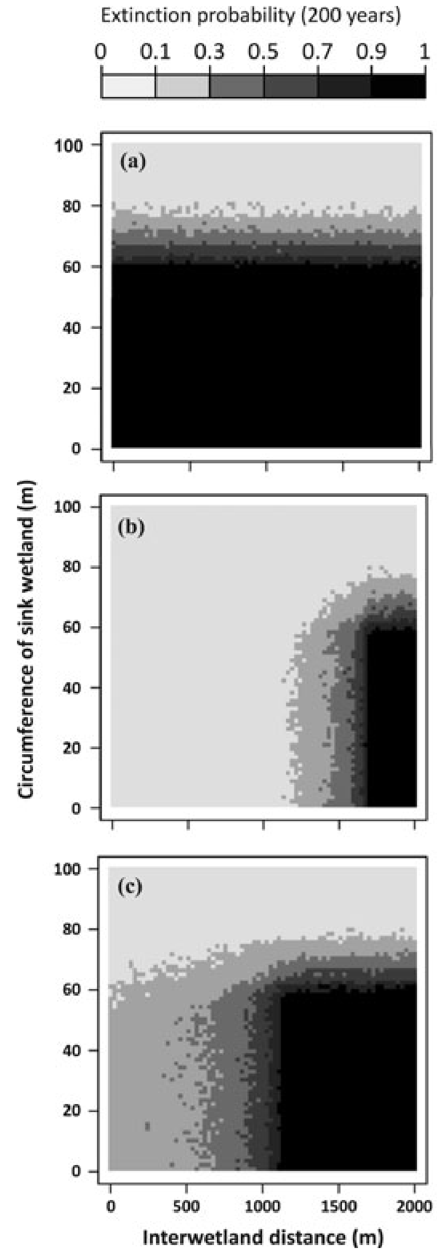

Figure 2. Extinction probability of the smaller (sink) population of American toads (Bufo americanus) *in a 2-population source-sink system centered on breeding wetlands as a function of the size (circumference) of the sink wetland and distance between the 2 wetlands (r). The source wetland represents a typical breeding wetland at our study site (circumference = 100 m) (Willson et al. 2012), and the wetlands are linked by dispersal of newly metamorphosed individuals. Shading represents extinction probability of the sink population after 200 years under 3 scenarios: (a) both wetlands uncontaminated with Hg and no dispersal between wetlands, (b) neither wetland contaminated with Hg and dispersal between wetlands, and (c) source wetland contaminated with Hg and dispersal between wetlands.*

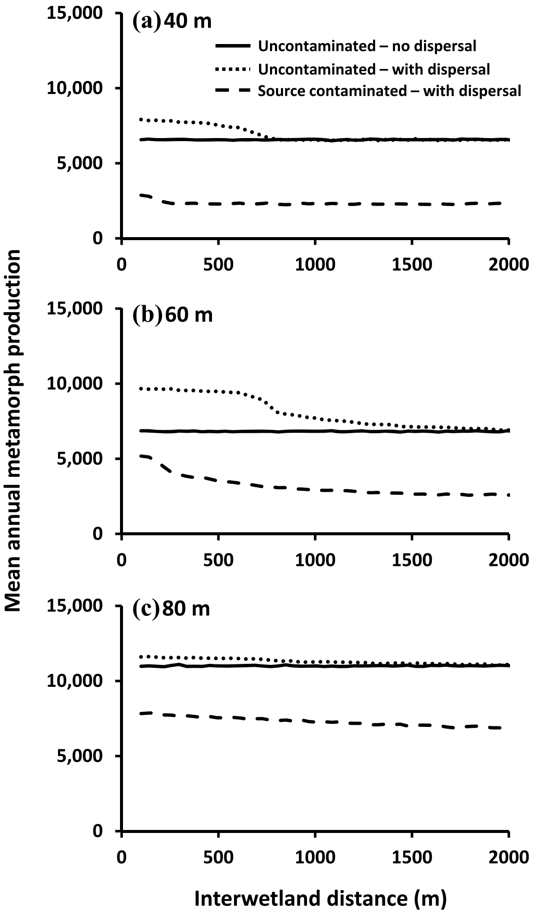

Figure 3. Effects of Hg contamination on productivity of a 2-population source-sink system of American toads (B. americanus) *as a function of the size (a–c [circumference]) of the sink wetland and distance between the 2 wetlands (r). Lines show mean annual production of newly metamorphosed individuals under 3 scenarios: neither wetland contaminated and no dispersal between wetlands, neither wetland contaminated and dispersal between wetlands, and source wetland contaminated and dispersal between wetlands.*

Simulating contamination of the source wetland with high levels of Hg reduced that population's ability to support a smaller sink population (Fig. 2c). Although the sink was still supported when the interwetland distance was small, the threshold distance within which the sink population could be sustained was reduced to approximately 1000 m. Moreover, even below this threshold, the extinction probability of toads inhabiting this wetland was still 20–30% after 200 years.

Allowing dispersal to occur among wetlands increased annual production of newly metamorphosed individuals from the 2-wetland system, but the increase in productivity depended on size of the sink wetland and interwetland distance (Fig. 3). In the absence of Hg contamination, interwetland dispersal increased productivity by approximately 20% and 35% for 40- and 60-m circumference wetlands, respectively, provided interwetland was <800 m (Figs. 3a and b). The increase in productivity was greatest when the sink wetland was of moderate size (60-m circumference). At 80-m circumference, productivity was high and not substantially increased by dispersal (Fig. 3c). Contamination of the source wetland with Hg substantially reduced overall productivity of the 2-wetland network and reduced the distance below which dispersal increased productivity.

In the absence of interwetland dispersal, only the largest wetland (E) in a real spatial configuration of 6 wetlands (Fig. 1) supported a population that was sufficiently large to preclude local extinction over 200 years (Table 2). Conversely, the population inhabiting the smallest wetland (D) exhibited a 100% probability of local extinction without interwetland dispersal. Dynamics of populations in most of the smaller wetlands were strongly affected by their proximity to the largest wetland. For example, although 2 wetlands (A and B) were similar in size, the population in wetland B was relatively resistant to extirpation due to its proximity to the largest wetland. Allowing dispersal between wetlands within the network dramatically decreased probability of extirpation for populations inhabiting all wetlands, such that populations in all but one wetland were at very low (<1%) risk of extirpation. In addition to reducing extinction risk, allowing dispersal between wetlands increased mean annual production of newly metamorphosed individuals from the network by 40% overall (nearly 7000 individuals).

When wetlands were linked by dispersal, simulating contamination of individual wetlands within the network negatively affected the network as a whole, but the magnitude of this effect depended on the size of the contaminated wetland and the proximity to other wetlands (Table 2). Contaminating the most remote wetland (A) had little effect on other wetlands, although it substantially increased extinction risk of toads inhabiting this remote wetland. Conversely, although the largest wetland (E) maintained a viable population under all scenarios, simulating contamination of this wetland increased extinction probability of populations inhabiting 4 of the 5 other wetlands in the network and resulted in a 36% reduction in mean annual production of newly metamorphosed individuals from the network as a whole. Simulating a scenario in which all wetlands within the network were contaminated with high levels of Hg resulted in the most severe effects overall. The population in wetland A was no longer supported as a sink, and populations in wetlands C and E shifted from being highly stable to relatively extinction prone (74% and 62% probability of population extirpation, respectively). Most dramatically, contamination of the entire network reduced mean annual productivity by 68% (16,700 fewer individuals produced annually) relative to the uncontaminated network.

Table 2. Results of model simulations evaluating the consequences of Hg contamination on extinction probabilities and mean total annual production of newly metamorphosed American toads within a real spatial configuration of wetlands.[a]

Wetland(s)[b] contaminated with Hg	*Probability of extinction at 200 years for each wetland (A–F)*						*Total annual metamorph production*	
	A	*B*	*C*	*D*	*E*	*F*	*Mean*	*SD*
None, no dispersal	0.729	0.623	0.929	1	0	0.391	17,466	4,900
None, with dispersal	0.255	0	0.003	0.003	0	0	24,390	4,650
A	0.383	0	0.003	0.003	0	0	22,312	3,292
B	0.485	0	0.004	0.004	0	0	22,095	4,508
C	0.336	0	0.002	0.003	0	0	22,615	3,817
D	0.285	0	0.003	0.003	0	0	23,615	4,170
E	0.563	0.002	0.125	0.129	0	0	15,527	5,102
F	0.340	0.000	0.005	0.006	0	0	21,865	4,696
All	1	0.009	0.740	0.629	0	0	7,691	682

[a] *Wetland network located along the floodplain of the historically Hg-contaminated South River, northeast of Crimora, Virginia (U.S.A.). Sizes and spatial arrangement of wetlands are shown in Fig. 1.*
[b] *Wetland letters correspond to Fig. 1.*

Discussion

Our structured metapopulation model demonstrated that typical American toad populations have the ability to support nearby sink populations that would otherwise decline to extinction and that maintenance of sink populations depends on wetland size and interwetland distance. Allowing dispersal between wetlands increased productivity of wetland networks through support of sink populations in the landscape, but Hg contamination substantially reduced productivity of wetland-associated subpopulations and their ability to support nearby sinks within relevant spatial scales. These results have implications for understanding the dynamics of pond-breeding amphibians, the negative population-level effects of environmental contaminants, and the potential for restoration or remediation of contaminated habitats.

Our results demonstrate that interpopulation dispersal is critical to regional dynamics of pond-breeding amphibians. Modeling metapopulations requires explicit consideration of stochasticity and the degree to which populations respond synchronously to stochastic processes (Hanski et al. 1995; Hanski 1999). Although the role of stochasticity in amphibian population dynamics has been considered (e.g., Halley et al. 1996; Harper et al. 2008; Salice et al. 2011), the issue of synchrony has been largely overlooked (Trenham et al. 2003; Smith & Green 2005). We adopted a habitat-based approach to modeling synchronous stochastic dynamics (Akcakaya 2000) by linking dynamics of subpopulations via shared responses to environmental variation (precipitation). Using this novel theoretical approach, we confirmed that stochasticity and dispersal can play key roles in regional dynamics of American toads and that a combination of wetland size and interwetland distance affect persistence of wetland-associated sub-populations (Halley et al. 1996). Furthermore, we found that toad dynamics conformed more readily to a source-sink framework than to that of a classic metapopulation, at least at spatial scales relevant to our study site. Results of genetic and dispersal studies suggest that amphibians may exhibit metapopulation dynamics at relatively large spatial scales (2–10 km) (Smith & Green 2005). Our results suggest that source-sink processes may be important at smaller scales, especially when dynamics of subpopulations are synchronized in response to environmental variation.

Although our study was designed to evaluate the role of interpopulation dynamics on population viability, it also revealed an important emergent property of amphibian metapopulations—increased productivity. In addition to playing a critical role in maintenance of sink populations, dispersal among wetlands substantially increased the overall productivity, in terms of annual metamorph production, of wetland networks. This finding underscores the contribution of sink habitats to amphibian dynamics. Although these habitats are too small or resource poor to support viable populations over long periods, they contribute substantially to landscape-level productivity and may themselves periodically act as sources under favorable environmental conditions (e.g., years of above-average precipitation). Results of prior studies reveal the importance of conserving interconnected wetland networks to ensure the persistence of amphibian species (Semlitsch 2000, 2003). Our study adds an additional layer of support for landscape-oriented approaches to amphibian conservation because our results suggest that loss of connectivity between wetlands may reduce overall productivity. Thus, maintenance of interconnected wetland networks may be necessary to support the full range of ecosystem services performed by amphibians (Burton & Likens 1975; Davic & Welsh 2004). Furthermore, our results suggest that researchers touting the value of individual wetlands on the grounds of their amphibian productivity (e.g., Gibbons et al. 2006) may be conservative because they do not consider that dispersal from these wetlands can magnify productivity of the surrounding landscape.

Few researchers have evaluated the potential for environmental contamination to affect dynamics of populations outside contaminated habitats (but see Spromberg et al. 1998; Spromberg & Scholz 2011). We demonstrated that in addition to causing localized amphibian population declines or extinctions, environmental Hg contamination has the potential to adversely affect surrounding populations through a reduction in the number of dispersing individuals. For American toads, contamination of a typical breeding wetland reduced the threshold distance below which the population was able to support sink populations in the surrounding landscape from 1600 to 1000 m. This shift equated to a 61% reduction in the area of surrounding habitat in which sink populations could be supported. Moreover, contaminating wetlands resulted in a substantial reduction in amphibian productivity and reduced the effect of dispersal in enhancing regional productivity.

Our results for American toads were driven primarily by lethal interactive effects of maternal and dietary Hg acting at metamorphic climax (Bergeron et al. 2011*b*; Willson et al. 2012), but regional amphibian dynamics may also be negatively affected by sublethal effects of contaminants that reduce interpopulation dispersal. For example, contaminants affect locomotor performance in a variety of organisms, including amphibians (e.g., Bergeron et al. 2011*b*; Bridges 1997; Burke et al. 2010). Although we found no direct effects of Hg on hopping performance of juvenile American toads, exposure to maternal Hg reduces juvenile body size (Todd et al. 2011*b*, 2012). Because body size is a primary driver of locomotor performance and stamina (John-Alder & Morin 1990; Todd et al. 2011*b*), it follows that this sublethal effect could reduce dispersal rates and compromise the ability of affected populations to support nearby sinks. Finally, it is important to consider that adverse effects on amphibian metapopulations may result from interactions of sublethal contaminant effects with other stressors that affect dispersal. For example, dispersal rates already reduced by lethal or sublethal effects of contaminants could be further reduced by habitat alteration (Rothermel & Semlitsch 2002; Rothermel 2004) or dispersal barriers such as roads (Marsh et al. 2005).

Our case study demonstrates that our theoretical findings are directly applicable to real landscapes. Simulated contamination of individual wetlands at our study site generally affected the stability and productivity of nearby wetlands, but the relative importance of individual wetlands depended on their size and isolation (Gibbs 1993). Although this case study demonstrated that effects of contaminants on metapopulations apply to real landscapes, this result depends on the spatial arrangement of wetlands. Other cases could certainly be found in which effects were less pronounced. For example, if the space between wetlands in a landscape is small, interwetland dispersal is likely great enough that degradation of individual wetlands would have little effect on the viability of populations in adjacent wetlands. Conversely, if interwetland distances are sufficiently great to preclude dispersal, wetlands may operate in isolation offering little augmentation to one another. Similarly, the metapopulation-level effects of contaminants on other amphibians may differ from those of American toads due to interspecific variation in dispersal capabilities. Toads (*Bufo* spp.) are highly terrestrial and individuals are capable of occasional extreme long-distance movements (Smith & Green 2005, 2006). Species with more limited dispersal abilities, such as many salamanders, may be expected to show stronger effects at more localized geographic scales than American toads.

Although the negative effects of environmental contaminants on amphibian populations may be more extensive than previously thought, our results also provide insight into potential remediation or mitigation strategies for wetland-associated species. Just as contamination of a wetland can reduce the ability of populations in that wetland to supplement nearby sinks, creation of uncontaminated wetlands can increase the viability of nearby populations in contaminated habitats. Our simulation results suggest that creation or restoration of larger wetlands that are closer to contaminated areas will provide the most benefit to those areas, provided those wetlands exhibit hydrological and ecological conditions suitable for amphibians (e.g., no predatory fish). Due to typically positive correlations among wetland size, hydroperiod, and occupancy of predatory fish, it is likely that in most natural landscapes wetlands of intermediate size that dry periodically harbor the highest amphibian abundances and typically act as source populations (Snodgrass et al. 2000).

In the context of remediation, it is also important to consider which effects of contaminants resulted in population-level effects and under what conditions those effects occurred. For example, population-level effects of Hg were strong only when larvae were exposed to high levels of Hg through both diet and maternal transfer, a condition that would occur only if both aquatic larval habitats (wetlands) and maternal foraging habitats (surrounding uplands) were contaminated (Bergeron et al. 2011*b*; Willson et al. 2012). Thus, our results suggest that if Hg contamination can be reduced within breeding habitats, or if uncontaminated alternative breeding sites can be created nearby, population-level effects of Hg might be reduced, even if adults continue to accumulate Hg in terrestrial habitats and pass it to offspring though maternal transfer (Bergeron et al. 2011*b*; Willson et al. 2012).

The metapopulation concept has provided a useful lens through which to view conservation that highlights the importance of environmental stochasticity, landscape heterogeneity, and dispersal. Considering our studies of the effects of Hg on American toads in a metapopulation context allowed us to draw inferences that are beyond the scope of traditional ecotoxicological studies. Specifically, we used population models to demonstrate that reduced dispersal due to localized environmental contamination can reduce the viability of nearby populations in uncontaminated habitats. Highly integrative studies that include descriptive, experimental, and theoretical approaches are needed to bridge the gap between manipulative laboratory experiments that measure effects of anthropogenic stressors on individual organisms and conservation of populations, species, communities, and ecosystems.

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