Wetlands (2016) 36:731–744
DOI 10.1007/s13157-016-0781-4

ORIGINAL RESEARCH

Different Anuran Species Show Different Relationships to Agricultural Intensity

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Received: 17 November 2015 / Accepted: 20 May 2016 / Published online: 7 June 2016

Abstract Studies on associations between agricultural intensity and anurans have found inconsistent results among species. However, studies vary in their definitions of agricultural intensity and spatial scales of analyses. If differences are real, they might be caused by differences among species' adult or juvenile habitat associations with agricultural intensity, and/or differences in sensitivities to agricultural inputs, e.g., fertilizers. We estimated relative abundances of eight anuran species in 39 ponds located in landscapes of varying agricultural intensity. We measured row crop and cereal grain cover, our measure of agricultural intensity, at multiple spatial extents. We then constructed path models for individual species to determine direction and potential causes of associations with agricultural intensity, measured at the scale of effect of each species. We found highly variable associations with agricultural intensity among anurans. As predicted, much of this variation could be explained by adult habitat amount and larval habitat quality. Overall, our results suggest that agricultural intensity, at least at levels found in eastern Ontario, can affect anurans through multiple pathways and mechanisms, in both positive and negative directions. We therefore suggest that authors use caution if making general statements about the impacts of agricultural intensity on anurans.

Electronic supplementary material The online version of this article (doi:10.1007/s13157-016-0781-4) contains supplementary material, which is available to authorized users.

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Keywords Habitat amount · Habitat quality · Agriculture · Nitrate · Amphibian · Conservation

Introduction

Habitat loss is the primary threat to species globally (Sala et al. 2000) and to anurans (frogs and toads) in particular (Hazell 2003; Cushman 2006). One of the major drivers of habitat loss is agriculture (Wilcove et al. 1998; Venter et al. 2006), which is particularly detrimental to biodiversity at high intensities (e.g. Donald et al. 2006; Le Féon et al. 2010). "Agricultural intensity" can be characterized by high use of fertilizers, herbicides and insecticides, large farm sizes with large crop fields, high livestock densities, and generally high levels of mechanization (Boutin and Jobin 1998; Stoate et al. 2001; Donald et al. 2006; Le Féon et al. 2010). Crop type can often be used to classify the level of agricultural intensity, as some crops (e.g., row crops and cereal grains) are associated with high chemical use and high mechanization (Boutin and Jobin 1998). Thus, the area of a landscape containing crops associated with high agricultural intensity can be used as an index of the agricultural intensity of that landscape.

Associations between agricultural intensity and anurans are generally assumed to be negative (e.g. Beja and Alcazar 2003; Cayuela et al. 2015). However, studies on associations of anurans with agricultural cover (e.g. Bonin et al. 1997a; Knutson et al. 2004) and chemical inputs such as fertilizers (e.g. Hecnar 1995; Smith et al. 2006) have found inconsistent results both among and within species. For instance, among species, all possible associations (positive, negative, or neutral) to both crop cover and nitrate concentrations have been observed (Figs. 1, 2). Similarly, one species, *Lithobates clamitans*, has shown both negative (Knutson et al. 2004) and positive (Gagné and Fahrig 2007) associations with agricultural cover,

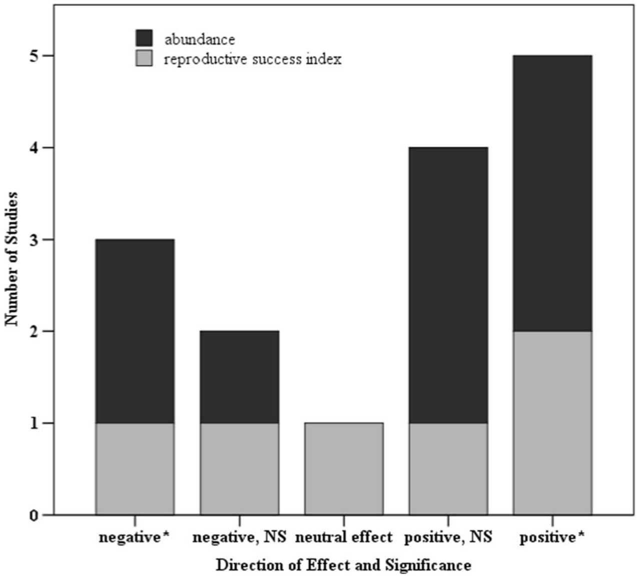

Fig. 1 Landscape-scale studies examining associations between the proportion of the landscape in agricultural production and various amphibian responses. Significant effects are denoted by *. Studies of anuran abundance are indicated by dark gray shading and studies of anuran reproductive success indices are indicated by light gray shading. Data are provided in Online Resource 1

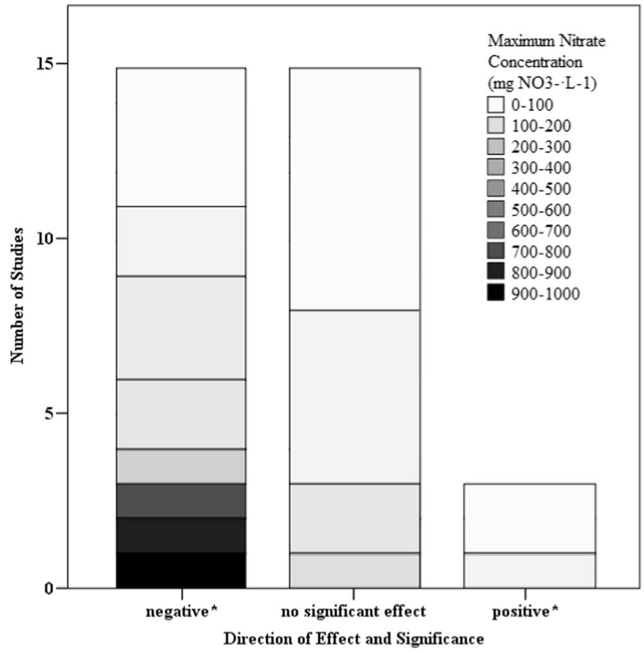

Fig. 2 Laboratory studies on the effects of nitrate on anuran tadpole survivorship and/or growth. Only studies that conducted quantitative analyses were included. Response variables included tadpole relative growth rate, survivorship, or change in mass after a given time. Shading indicates the maximum nitrate concentration used in each study (between 0.8 and 983.5 mg NO3-•L-1). Significant effects are denoted by *. Data are in Online Resource 1

as well as both negative (Hecnar 1995) and positive (Smith et al. 2006) associations with nitrate inputs.

One possible explanation for variation in anuran associations with agricultural intensity is that, in different studies, agricultural intensity may be correlated differently, either negatively or positively, with adult habitat amount. If different studies have different correlations between agriculture intensity and a species' adult habitat, this could cause differences among studies in that species' apparent association with agricultural intensity. For example, if *Lithobates pipiens* abundance is determined primarily by the availability of its adult habitat (open natural and semi-natural areas, including perennial forage crops (Mazerolle 2001)), then in a data set where adult habitat is negatively correlated with row crops or cereal grains, this will result in an apparent negative association with agricultural intensity for this species (assuming it cannot use these high-intensity-agriculture crops for adult habitat). In contrast, where there happens to be a positive correlation between high-intensity-agriculture crops and open natural and semi-natural areas, the apparent association of *L. pipiens* with agricultural intensity may be positive. Similarly, there could be a positive correlation between high-intensity crops and open natural and semi-natural areas, but a negative correlation between these crops and forest. The positive correlation between high-intensity crops and open natural and semi-natural areas could result in an apparent positive association of *L. pipiens* with agricultural intensity, but an apparent negative association of *Hyla versicolor* with agricultural intensity, as *H. versicolor* uses forest for adult habitat (Johnson 2005).

Another possible explanation for among-species variation in anuran associations with agricultural intensity is that agricultural intensity may differentially affect the larval habitats of different species if, for example they have different sensitivities to agrochemicals. For species that are sensitive to a particular agrochemical, we expect lower survivorship in ponds with greater concentrations of that agrochemical. For example, species whose tadpoles rely heavily on algal food resources, such as *H. versicolor*, *Pseudacris crucifer*, and *Pseudacris triseriata* (Whitaker 1971; Hoff et al. 1999; and Quammen and Durtsche 2003, respectively), might benefit from fertilizer inputs if these inputs increase periphyton and phytoplankton growth in agricultural ponds (Bell 2002; Maberly et al. 2002), and this increases tadpole growth (Leibold and Wilbur 1992; Kiffney and Richardson 2001; de Wijer et al. 2003). In contrast, for species that are sensitive to agrochemicals, chemical inputs could reduce larval habitat quality by decreasing survivorship and hatch rates (Bonin et al. 1997b; Relyea 2005; Relyea et al. 2011). For example, fertilizer inputs can be toxic for some embryonic and larval anurans (Hecnar 1995), when resulting nitrate concentrations exceed 5 mg/L (see Online Resource 1).

Variation in associations with agricultural intensity could also be explained by differences among studies in definitions or measures of agricultural intensity, spatial scales used in landscape studies, and chemical exposure dosages used in lab experiments. Some studies measure agricultural intensity using indicator values such as livestock density and chemical inputs (e.g. Le Féon et al. 2010), whereas others include yield values and numbers of tractors per unit area (e.g. Donald et al. 2006). Different aspects of agricultural intensity may affect a species in different ways. For instance, tillage and the use of machinery and insecticides may reduce the abundance of *Cydinae* burrowing bugs (Chapin and Thomas 2003), but we do not know how increased fertilizer use or increased crop field size might affect them. Similarly, measuring landscape variables, such as row crop and cereal grain cover, over different spatial extents could cause variation in associations. For example, some insects show differing associations with landscape predictors depending on the scale at which the predictor is measured (e.g. Holland et al. 2004; Hirao et al. 2008; Thomson et al. 2010). Finally, different chemical exposure concentrations can have different or even contrasting effects on larval anurans, as seen with *L. clamitans*, which showed increased growth in nitrate-nitrogen concentrations of 5 mg/L (Smith et al. 2006), but has a median lethal concentration of 144 mg/L in laboratory tests (Hecnar 1995).

Here we address the questions: do different anuran species associate differently with agricultural intensity and, if so, what could be driving these differences? We surveyed anurans in agricultural ponds, and we defined agricultural intensity as the proportion of the landscape surrounding the pond that is covered by row crops or cereal grains. We then measured agricultural intensity at multiple spatial extents. We selected the ponds to represent a wide range of percent cover of these high-intensity-agriculture crops in the surrounding landscapes. We also measured the nitrate concentration in ponds as a separate index of agricultural intensity in the surrounding landscapes. Finally, we measured the proportion of the surrounding landscapes in lower-intensity perennial crops and forests, which serve as adult habitat for some anuran species, and wetland area in the surrounding landscapes as a measure of immigration potential.

Based on the arguments above, we tested the following predictions. In landscapes surrounding breeding ponds, if the amount of adult habitat of a given anuran species is negatively correlated with agricultural intensity, we expected a negative relationship of agricultural intensity to the abundance of that species in the ponds. For anuran species whose tadpoles rely more on algal food resources, we expected positive relationships to both agricultural intensity and nitrate, as long as nitrate concentrations are below toxic levels for those species (see Online Resource 1 for documented nitrate effects). For species that are sensitive to nitrate toxicity, we expected negative relationships to both agricultural intensity and nitrate, as long as nitrate concentrations meet or exceed toxic levels for those species.

Methods

Overview

We selected 39 ponds in agricultural areas within eastern Ontario (Fig. 3). In this region, high-intensity-agriculture crops are mainly corn, soy, beans, and cereal grains. Perennial grass, hay fields, and alfalfa/clover fields are common low-intensity perennial crops. Agricultural fields are interspersed with woodlands, wetlands, and small urban areas. To measure agricultural intensity, we calculated the proportion of landscape cover in high-intensity crops within 250, 500, and 1000 m of each of the 39 ponds. We also calculated proportions of forest, perennial crops, and wetlands at the same scales. We measured anuran abundances and a suite of local pond variables in each of the 39 ponds. We used generalized linear models to determine the scale of effect of each landscape predictor (high-intensity crop cover, forest, perennial crops, and wetlands) on the abundance of each species (Elliott et al. 1999). We used correlations to determine the single local pond variable that was most associated with each species. We then conducted path analyses to determine the direction and potential causes of associations between agricultural intensity and the abundance of each species. For each species, the path analysis included five variables: the amounts of high-intensity crop cover, adult habitat (either forest or perennial crops), and wetlands in the landscape (to control for immigration potential); the nitrate concentration; and the best local pond variable for that species.

Site Selection

The overall goal of site selection was to identify a set of potential anuran breeding ponds within agricultural landscapes containing a wide range of high-intensity crop cover. We used three data sources: (i) Ontario's Ministry of Agriculture, Food, and Rural Affairs' Agricultural Resource Inventory for urban areas, forests, and agricultural land use types (Ontario Ministry of Agriculture Food and Rural Affairs 2010), (ii) the Ontario Hydro Network - Waterbody polygon for ponds (Ontario Hydro Network 2011), and (iii) the NRVIS/OLIW Data Management Model For Wetland Unit for wetlands (Land Information Ontario 2010). We used ArcMap 10.1 to conduct all GIS analyses (ESRI, Redlands, CA, USA).

Site selection proceeded as follows. First, we used the OHN waterbody polygon to find ponds in Eastern Ontario that were 20–100 m in diameter and at least 1 km from major water sources. 1688 ponds met this criterion. We considered ponds of 20–100 m diameter because, in this size range, we could expect to find any of the anuran species in our region. Choosing ponds that are distant from other water sources reduced the potential for population spillover effects.

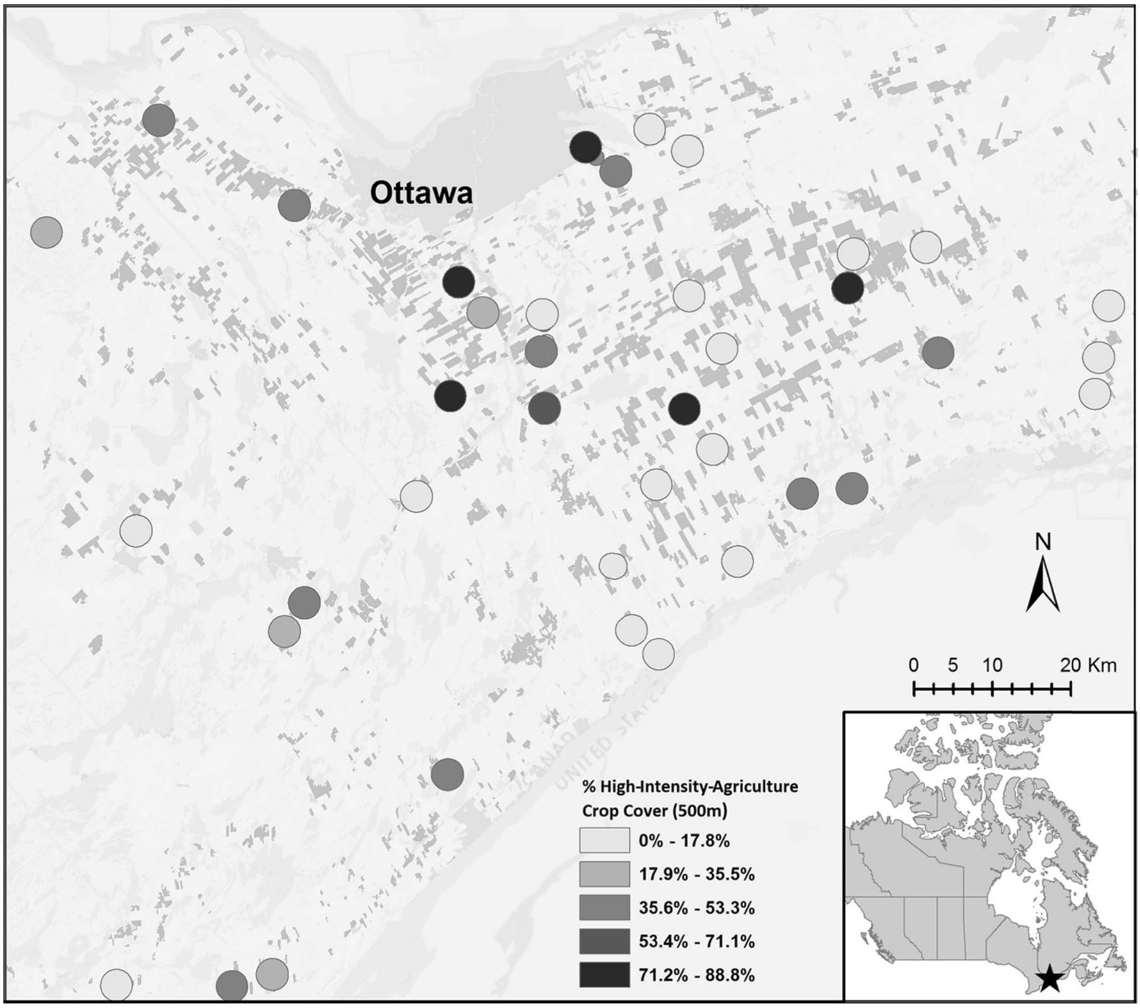

Fig. 3 Distribution of ponds sampled for anurans in eastern Ontario (n = 39). Each pond is represented by a circle with shading indicating percent high-intensity agricultural land cover (row crops and cereal grains) within 500 m of the pond. Areas of high-intensity agricultural land on other parts of the map are shown in the darker shading

We then calculated the proportion of row crop and cereal cover within 500 m of each pond. We chose 500 m for this initial step because it falls in the middle of the known scales at which landscape context affects anurans in our region (Eigenbrod et al. 2008). As we were looking for ponds in landscapes of varying proportions of row crop cover or cereal grains, we removed any ponds in landscapes that did not contain row crops or cereal grains, resulting in 302 landscapes, with high-intensity crop cover ranging from 0.3–92.5 % (mean 18.3 ± 24.4 SD) within 500 m.

From these we removed any ponds in landscapes containing former quarries, extraction pits, livestock pastures, or large urban areas, which may produce chemical inputs other than those associated with crop production. After visual examination of satellite imagery, we also removed ponds that had highly degraded edges (with little vegetation), indicating use by livestock. Ponds used by livestock are rare in this region and are not associated with intense agricultural practices as defined here, so including them could have confounded the interpretation of our results. As we were interested in agriculturally situated ponds, we also removed any that were bordered by more than 50 % trees or forest. This reduced our potential set of ponds to 77. This number was further reduced to 63, after ponds within 2 km of each other were excluded, to reduce spatial autocorrelation and pseudoreplication.

Finally, while obtaining permissions from landowners to sample ponds, we asked them whether the ponds were artificial and whether they were subject to management activities that might influence anurans, such as use for watering holes, fish stocking, or irrigation. These artificial and managed ponds were excluded, giving us a set of 41 candidate ponds. Thus, we began the field season with these 41 sites, but ended with 39, because two ponds were drained during the summer.

Anuran Call Surveys

We took 10-min chorus surveys of anurans at each pond four times from April 15th (when the first *P. crucifer* were heard) until July 29th, 2013, allowing for coverage of all species' breeding seasons. We conducted surveys in a randomized order and waited silently for ten minutes prior to each survey to ensure that our presence did not influence calling behaviour. We used the following classes when recording abundance: 0 (no calls), 1 (distinct calls of separate individuals), 2 (some calls overlap but most individuals can still be identified), and 3 (mostly overlapping calls and continuous calling) (modified from Bishop et al. 1997). Two to four ponds were sampled per night. If a given pond was surveyed first on one night, it was surveyed last in the night during the next round of surveys, to reduce the influence of survey order. We summed the abundance ranks among the four survey dates for each species at each pond to provide an index of relative abundance (Pope et al. 2000).

Local Pond Variables

Prior to each survey, we measured a number of local pond variables. We visually estimated the percent of pond surface covered by open water or floating, emergent, or submerged vegetation, as well as the percent of pond circumference covered by overhanging vegetation (which we considered to be any plant taller than two m). We recorded the following local water parameters, two m from the shore: water temperature, electrical conductivity (an indicator of salinity), and pH, each measured with a Hanna Instrument handheld tester (HI98129) held at the pond surface; pond depth, measured with a weighted measuring tape; and water clarity, measured with a Secchi disk tube and headlamp to provide consistent light, as surveys were conducted in the dark. We also later measured pond area using the OHN waterbody polygon. After all of the surveys were completed, we took water samples to the lab and analyzed them for nitrate concentration, using the cadmium reduction method with a spectrophotometer and NitraVer® 5 Nitrate Reagent Powder Pillows (as per American Public Health Association 1998).

Landscape Variables

Landscape variables—high- and low-intensity agricultural cover, wetlands, and forest—were the proportion of each cover type in the landscape surrounding the pond, at each spatial scale (see below). High-intensity agricultural cover was defined as the proportion of landscape cover in corn, soy, cereal grains, and beans; whereas low-intensity agricultural cover was the proportion in perennial crops (i.e., hay and alfalfa fields). Although fieldwork was conducted in 2013, the polygons used for high and low-intensity crops, forests, and ponds were created in 2010, and the polygon used for wetlands was created in 2011. These were the most recent spatial data available.

Data Analyses

Scales of Effect

We created three nested landscapes, with 250, 500, 1000 m radii, around each pond, to determine the scale at which the association of each landscape predictor with the abundance of each species was strongest (its scale of effect (Wiens 1989)). For each species, these 'scales of effect' were identified for: percent high-intensity crop cover, percent adult habitat cover—either forest or perennial crops, depending on each species' documented adult habitat (see Table 1)—, and percent wetlands. We determined these scales of effect using generalized linear models, with negative binomial distributions to account for over-dispersed abundance data, and log link functions. The scale with the highest absolute β-coefficient value for the association of each landscape predictor with the abundance of each species was considered to be the scale of effect for that predictor on that species.

Local Pond Variable Correlations

We examined correlations between the abundance of each species and local pond predictors: pH, nitrogen concentration, water temperature, conductivity (a measure of salinity), depth, pond area, water clarity, and percent of: overhanging vegetation, open water, submerged vegetation, emergent vegetation, and floating vegetation. We identified the local pond predictor with the highest absolute Pearson correlation (negative or positive) for each species, and included this predictor in later path analyses as a measure of control for local pond effects. We only identified a single local pond variable for a given species to avoid the risk of over-specifying the final models.

Path Analyses

We constructed path models for each species, to determine the direction and potential causes of associations of agricultural intensity with the abundance of each species. The number of estimable paths for each species' path analysis was limited by our sample size (39); to produce reliable results, sample size should be at least five times the number of paths estimated (Petraitis et al. 1996). We estimated six paths for each species. Predictor variables for a given species included nitrate concentration, best local pond predictor for that species, and proportion of the landscape in each of the following: row crop and cereal grain cover, adult habitat for that species, and wetland cover (each at its scale of strongest effect). Adult habitat was either forest or perennial crop cover, depending on the known adult habitat type for that species. Wetland cover was included to control for effects of potential immigration. We chose path analysis so that we could simultaneously model the proportion of high intensity agriculture as both a direct effect

Table 1 Life history characteristics of anurans in eastern Ontario

Species	Larval period	Reference(s)	Larval Diet	Reference(s)	Adult Habitat	Reference(s)	Breeding Site Fidelity	Reference(s)
A. americanus	50–60 days	Wright and Wright 1949	omnivorous (plant material, periphyton, detritus, and dead fish or tadpoles)	Ahlgren and Bowen 1991, Quammen and Durtsche 2003	Open natural and semi-natural areas/ generalist: grasslands, gardens, fields, lawns, barnyards, and forests.	Klemens 1993	Inconsistent breeding site fidelity.	Homan et al. 2010
H. versicolor	45–65 days	Wright 1932	primarily algae and periphyton	Hoff et al. 1999	Forest: trees and vegetated fences, forested areas	Conant and Collins 1998, Johnson 2005	Do not exhibit breeding site fidelity.	Johnson and Semlitsch 2003, Ptacek 1992
L. catesbeianus	a few months to 3 years	Bury and Whelan 1984	algae, aquatic plant material, and some invertebrates	Bury and Whelan 1984	Wetlands and Forest, strongly aquatic: herbaceous wetlands, forested wetlands, vegetated shoals, sluggish backwaters and oxbows, farm ponds, reservoirs, marshes, and still waters, lakes, rivers, creeks, and streams	Storer 1922, Hammerson 1999, Conant and Collins 1991	Consistent breeding site fidelity.	Garcia et al. 2012
L. clamitans	about 3 months to 2 years	Collins 1993, Pauley and Lannoo 2005	primarily on algae, but also crustaceans and fungi	Werner and McPeek 1994	Wetlands and Open natural and semi-natural areas, semi-aquatic: shorelines of lakes and of ponds, bogs, fens, marshes, swamps, and streams.	Collins 1993	Consistent breeding site fidelity.	Oldham 1967
L. pipiens	about 50–70 days	Lannoo 1996	algae, plant material, detritus, invertebrates, and other vertebrates (including other tadpoles)	McAllister et al. 1999	Open natural and semi-natural areas: typically grassy areas, meadows, or fields but can include other sites such as peat bogs and perennial forage crops	Merrell 1977, Mazerolle 2001, Guerry and Hunter 2002	Consistent breeding site fidelity.	Dole 1965a, Dole 1965b
L. sylvaticus	65–130 days	Redmer 2002	detritus, plant material, periphyton, may also cannibalize conspecifics and prey upon other aquatic animals	Petranka and Thomas 1995, Quammen and Durtsche 2003	Wetlands and Forest: willow thickets, wet meadows, bogs, and temperate forests (both coniferous and deciduous)	Conant and Collins 1998, Redmer 2002	Consistent breeding site fidelity.	Vasconcelos and Calhoun 2004, Homan et al. 2010, Berven and Grudzien 1990.
P. crucifer	about 3 months	Wright and Wright 1949	primarily algae and periphyton	Quammen and Durtsche 2003	Wetlands and Forest: lowland marshes, wetlands, sphagnum bogs and cattail Wetlands and Forest: wetlands, ponds, pools, and ditches in and near woods	Wright and Wright 1949	Appear to exhibit site fidelity.	Werner et al. 2009.
P. triseriata	40–90 days	Whiting 2004	primarily algae	Whitaker 1971	Wetlands and Forest: damp meadows, marshes, forest edges, bottomland swamps, and temporary ponds.	Gibbs et al. 2007	Appear to exhibit site fidelity.	Conant and Collins 1991.

Table 2 Pearson correlations for landscape predictors (measured as percent cover) in 250, 500 and 1000 m - radius landscapes. $p < 0.05$ is denoted by * and $p < 0.01$ by **. Low-intensity agricultural cover consisted of perennial crops (hay and alfalfa) whereas high-intensity agricultural cover consisted of row crops (corn, soy, and beans) and cereal grains. $n = 39$ landscapes

Cover Type	High-Intensity Crop	Low-Intensity Crop	Wetland
250 m - Radius Landscapes			
Low-Intensity Crop	−0.536**		
Wetland	−0.248	0.289	
Forest	−0.173	−0.122	0.169
500 m - Radius Landscapes			
Low-Intensity Crop	−0.584**		
Wetland	−0.215	0.136	
Forest	−0.191	−0.168	0.304
1000 m - Radius Landscapes			
Low-Intensity Crop	−0.378*		
Wetland	−0.14	−0.12	
Forest	−0.292	−0.306	0.395*

and as an indirect effect via nitrate concentration. We used SPSS version 22.0.0 for all statistical analyses (IBM, Meadville, PA, USA).

Results and Discussion

We found eight of 10 anuran species that occur in eastern Ontario (Online Resource 2; *Lithobates palustris* and *Lithobates septentrionalis* were not found). Ponds had on average 3.95 species, with each having at least one species and none having more than six.

The range of high-intensity crop cover in the landscapes was 0.2–100 % (mean 42.2 ± 30.1 SD) within 250 m of the ponds, 0.3–88.8 % (mean 30.6 ± 25.7 SD) within 500 m of the ponds and 3.6–85.2 % (mean 24.6 ± 19.4 SD) within 1000 m.

Landscape predictor correlations are in Table 2. All correlations among the landscape predictors were lower than |0.6|. As expected, each landscape predictor was highly correlated with itself across all scales, because they are nested variables. Low-intensity and high-intensity-agriculture crop cover were significantly negatively correlated at all three scales (r between −0.38 and −0.54) and wetland and forest cover were significantly positively correlated at the 1000 m-radius scale ($r = 0.40$).

The range in values of nitrate concentrations among ponds was 0.43–4.94 mg/L (mean 1.09 ± 0.80 SD). Correlations between nitrate concentration and other pond variables were low (all less than |0.3|; Table 3).

Correlations among the local pond predictors are provided in Table 3. Moderate negative correlations were found between pond depth and water clarity and between pond depth and emergent vegetation cover.

Table 3 Pearson correlations among local pond variables in 39 sample ponds in the agricultural region of eastern Ontario. Water temperature, electrical conductivity (an indicator of salinity), and pH, were measured two m from the shore with a Hanna Instrument handheld tester (HI98129) held at the pond surface. Pond depth was measured with a weighted measuring tape. Water clarity was measured with a Secchi disk tube. Percent of pond surface covered by open water or floating, emergent, or submerged vegetation, as well as the percent of pond circumference covered by overhanging vegetation (considered to be any plant taller than two metres) was visually estimated. $p < 0.05$ denoted by *, $p < 0.01$ by **

Pond Variables	Water Temp.	pH	Elect. Cond.	Depth	Water Clarity	Overh. Veg.	Pond Area	% Emerg. Veg. Cover	% Float. Veg. Cover
pH	.117								
Conductivity	.208	−.293							
Depth	.003	.150	−.207						
Water Clarity	−.080	−.162	.050	−.387*					
Overhanging Vegetation	−.056	−.150	−.201	−.231	.040				
Pond Area	.093	−.123	.083	−.072	.055	−.096			
% Emer. Veg. Cover	.007	−.285	.148	−.365*	.048	.299	−.212		
% Float. Veg. Cover	.123	−.128	.144	−.003	.107	−.038	−.023	−.011	
Nitrate Conc. (mg/L)	−.080	.062	−.087	.264	−.149	.039	.140	−.037	−.138

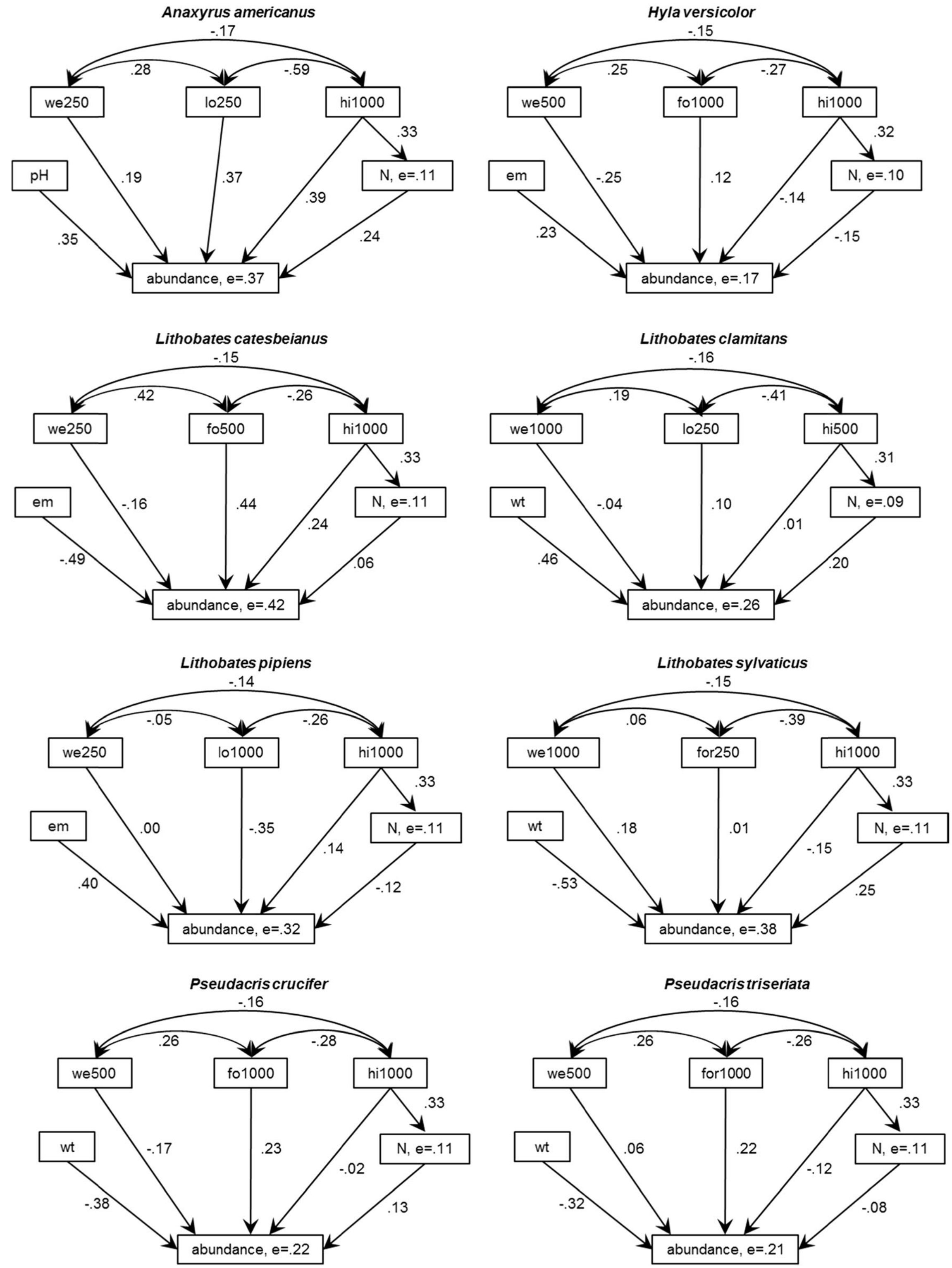

Fig. 4 Path analyses assessing the direction and potential causes of associations of agricultural intensity with the abundance of anurans in the agricultural region of eastern Ontario. Each path analysis included five variables: nitrate concentration (N), the best local pond variable for that species (positive or negative; % emergent vegetation pond cover (em), water temperature (wt), or pH), and the proportion of the landscapes in each of the following: high-intensity row crop and cereal grain cover (hi), adult habitat for that species (forest (fo) or low-intensity perennial crop cover (lo)), and wetland cover (we)). The scales (250, 500, or 1000 m radius) at which each landscape association was strongest with each species are displayed with each cover type (e.g. we500 indicates that the association with wetlands was strongest at 500 m). Error terms (residual variance) for abundance and nitrate are denoted by 'e'

Table 4 Pearson correlations between anuran abundance and local pond predictors in 39 sample ponds in the agricultural region of eastern Ontario. Bold indicates the highest absolute Pearson correlation value for each species. $p < 0.05$ denoted by (*), $p < 0.01$ by (**)

Pond Variables	*Anaxyrus americanus*	*Hyla versicolor*	*Lithobates catesbeianus*	*Lithobates clamitans*	*Lithobates pipiens*	*Lithobates sylvaticus*	*Pseudacris crucifer*	*Pseudacris triseriata*
Water Temperature	.324*	.036	−.115	**.447****	−.023	**−.552****	**−.440****	**−.348***
pH	**.407***	.056	.267	−.048	−.007	−.327*	−.210	.140
Conductivity	−.003	−.109	.076	.057	.082	.070	−.158	−.330*
Depth	.063	.024	.123	−.065	−.121	−.040	−.261	−.057
Water Clarity	−.132	.039	.020	.064	.242	.093	.314	.016
Pond Area	.393*	−.044	.098	.271	−.175	.224	.082	−.034
Overhanging Veg.	.008	−.002	−.276	−.105	−.022	.226	−.038	−.188
% Emerg. Veg. Cover	−.047	**.264**	**−.449****	−.051	**.338***	.172	.342*	.040
% Float. Veg. Cover	.024	.211	−.064	.073	−.092	.064	.063	.029

In the path analyses (Fig. 4), we included only the single strongest local pond predictor (positive or negative) for each species (Table 4) because the number of estimable paths was limited by our sample size. The local variables included in the path analyses were: water temperature for *Lithobates clamitans*, *Lithobates sylvaticus*, *Pseudacris crucifer*, and *Pseudacris triseriata*; pH for *Anaxyrus americanus*; and % emergent vegetation for *Hyla versicolor*, *Lithobates catesbeianus*, and *Lithobates pipiens*.

Species Associations with Agricultural Intensity

Overall, our results indicate that different species do associate differently with agricultural intensification. The path analyses for the eight anuran species revealed both negative and positive associations with both high-intensity crop cover and nitrate concentration (see Fig. 4 and Table 5). For example, *A. americanus* was positively associated with both high-intensity-agriculture crop cover and nitrate concentration, *H. versicolor* was negatively associated with both high-intensity crop cover and nitrate concentration, and *L. pipiens* and *L. sylvaticus* showed opposite and opposing associations with high-intensity crop cover and nitrate concentration.

That different species associate differently with agricultural intensification is generally consistent with the literature (Figs. 1, 2). The fact that we found these differences among species within a single study, with a consistent definition of agricultural intensity and empirically identified scales of effect, indicates that differences among species are real, and not just a result of differences in definitions and scales among studies. Interestingly, negative associations with high-intensity crop cover were generally weaker than positive associations.

What Drives the Differences among Anuran Species in their Associations with Agricultural Intensity?

Overall, our results suggest that differences among species are likely related to correlations between agricultural intensity and

Table 5 Path analysis model fit indices and path coefficients. Several goodness of fit measures were included to assess the overall fit of each model, with bold indicating a "good fit". Measures included: the X^2 "badness of fit" measure (if $p < 0.05$, the model was a bad fit (Hair et al. 2006)), the comparative fit index (if CFI ≥ 0.90, the model was a good fit (Bentler 1990)), the Tucker-Lewis index (if TLI > 0.95, the model was a good fit (Bollen 1989)), and root mean square error (if RMSEA ≤0.07, the model was a good fit (Hu and Bentler 1999))

Species	High Intensity Crop Cover Path Coefficient	Nitrate Conc. Path Coefficient	Model X^2, df, p	Model Fit Indices		
				CFI	TLI	RMSEA
A. americanus	0.39	0.24	**6.33, 6, 0.39**	**0.96**	0.86	**0.038**
H. versicolor	−0.14	−0.15	**2.64, 6, 0.85**	**-**	−5.08	**0**
L. catesbeianus	0.24	0.06	**5.65, 6, 0.46**	**1.0**	**1.08**	**0**
L. clamitans	0.01	0.20	**3.7, 6, 0.62**	-	−3.87	**0**
L. pipiens	0.14	−0.12	**3.54, 6, 0.68**	**1.0**	**10.44**	**0**
L. sylvaticus	−0.15	0.25	**11.15, 6, 0.08**	0.7	−0.05	0.15
P. crucifer	−0.02	0.13	**5.83, 6, 0.44**	**1.0**	**1.109**	**0**
P. triseriata	−0.12	−0.08	**5.82, 6, 0.44**	**1.0**	**1.195**	**0**

adult habitat amount (negative or positive) and to the effects of agricultural intensity on larval habitat quality. In several previous studies, the correlations between agricultural intensity and anuran adult habitat were not accounted for (e.g. Bonin et al. 1997a; Babbitt et al. 2009). In our study we attempted to account for these correlations by including adult habitat amount as a predictor variable in the path analyses. However, some studies indicate that path analysis only partly controls for such correlations (Bentler and Chou 1987; O'Rourke et al. 2013), so it remains possible that some of the relationships we found between anurans and agricultural intensity could be due to residual correlations with adult habitat amount.

Anaxyrus americanus showed positive associations with both high-intensity-agriculture crop cover and nitrate. *A. americanus* was more positively associated with high-intensity crops than any of the other species in our study. It is likely that agricultural cover (both low and high intensity crops) can function as adult habitat for this species. The known habitat for *A. americanus* includes semi-natural gardens and grasslands (Klemens 1993), and our results suggest it may also include row crops and cereal grains. We are uncertain as to the cause of the positive association of nitrate concentration with *A. americanus*. It may have been due to the slight positive correlation between high-intensity crop cover and nitrate concentration ($r = 0.31$ at 500 m), although the path analysis is meant to account for such correlations to a certain degree (Bentler and Chou 1987; O'Rourke et al. 2013; Donyavi et al. 2015). It also may have been due to a potential positive association between nitrate and the larval habitat quality of this species, but we believe this to be less likely because *A. americanus* has a relatively short larval period of only 50–60 days (Wright and Wright 1949).

Lithobates pipiens also showed a positive association with high-intensity crop cover, likely also because it can use crop fields as adult habitat. The known habitat for *L. pipiens* is open natural and semi-natural habitats, such as perennial crops (Merrell 1977; Mazerolle 2001; Guerry and Hunter 2002), but our results suggested a stronger relationship of this species to high-intensity crops than to perennial crops. In fact, it had a negative association with perennial crop cover, which was unexpected based on its known habitat associations (see Table 1). Unlike *A. americanus*, *L. pipiens* had a negative association with nitrate concentration, perhaps due to decreased larval habitat quality; *L. pipiens* is known to be sensitive to nitrate toxicity (Hecnar 1995). The weaker positive association of *L. pipiens* with high-intensity crop cover, when compared to *A. americanus*, could be explained by the negative effect of nitrate concentration on this species, combined with the positive correlations between high-intensity crop cover and nitrate ($r = 0.33$).

A third species, *Lithobates catesbeianus*, also had a positive association with high-intensity crop cover. However, this was likely not due to an association with adult habitat, because this species is strongly aquatic (Conant and Collins 1975). We speculate that the apparent positive association of high-intensity crop cover with this species was due to its slight negative correlation with emergent vegetation cover in ponds ($r = -0.25$ at 500 m), and the negative correlation between emergent vegetation cover and *L. catesbeianus* abundance ($r = -0.45$). However, we note that overall, the path analysis for this species is confusing, because it shows a negative association with wetland cover, which is unexpected based on known habitat associations for this species (see Table 1).

Three species (*Hyla versicolor*, *Lithobates sylvaticus*, and *Pseudacris triseriata*) were negatively associated with high-intensity crop cover. It is tempting to interpret these relationships as caused by negative (though weak) correlations between high-intensity crop cover and their adult habitat (forest cover; $r = -0.17$, -0.19, and -0.29, within 250, 500 and 1000 m of the wetlands, respectively). However, path analyses should account for such correlations to a certain degree (Bentler and Chou 1987; O'Rourke et al. 2013; Donyavi et al. 2015). Therefore, it is possible that high-intensity crop cover has a direct negative effect on the abundance of these species, independent of the effects of decreased adult habitat amount. We speculate that this negative effect could be related to agrochemical use. Although *H. versicolor* is not sensitive to nitrate toxicity (Boone and Bridges-Britton 2006), it can be sensitive to other agrochemicals used in Ontario (Ontario Ministry of Agriculture Food and Rural Affairs 2016). One such agrochemical is glyphosate, a broad-spectrum herbicide that is highly toxic to this species and to amphibians in general (Relyea 2005). In our study, *H. versicolor* also had a negative association with nitrate concentration, but we suspect that this was related to the use of other agrochemicals. In contrast, *L. sylvaticus* showed a positive association with nitrate. This species is not susceptible to nitrate toxicity in concentrations lower than 50 mg/L ammonium nitrate (see Online Resource 1), so we speculate that this positive association was due to increased algal abundance (for larval food).

The two remaining species—*Lithobates clamitans* and *Pseudacris crucifer*—also had positive associations with nitrate. We suspect that the positive associations were also due to increased larval food. *L. clamitans* is not susceptible to nitrate toxicity in concentrations lower than 44 mg/L nitrate (Online Resource 1), whereas the nitrate susceptibility of *P. crucifer* has not been tested.

Overall, our results confirm that different anurans associate very differently with agricultural intensity. High-intensity-agriculture crop cover is negatively related to adult habitat for some species and positively for others. Nitrate can improve larval habitat for some species but reduces larval habitat quality for others either directly or through a correlation with other agrochemicals.

Study Limitations and Caveats

Pesticide use might be considered a more direct index of agricultural intensity than fertilizer use. Unfortunately we were not able to assess pesticide levels in our ponds because we lacked necessary resources to do so. We note, however, that ponds with higher pesticide inputs typically also have higher fertilizer inputs (Geiger et al. 2010) and both are associated with row crop and cereal grain agriculture (Boutin and Jobin 1998).

Although we aimed to only survey ponds without fish, we could not conclusively rule out fish presence. Fish presence in anuran breeding ponds can be associated with decreased anuran species richness (Hecnar and M'Closkey 1997), increased nitrate concentrations (Torras et al. 2000; Figueredo and Giani 2005) and decreased algal biomass (Torras et al. 2000). Therefore, it is possible that the presence of fish in some our study ponds may have confounded results.

We acknowledge that our sample size was low (39) and, although it may seem that the number of predictors was large, only five were used in the path analysis for each species. Only one local pond variable was used in each path analysis for each species and the predictor representing amount of adult habitat in the landscape was pre-selected according to known habitat relationships for each species. Although multiple scales were examined for each landscape variable for each species, in the path analyses we only used a single scale of measurement for each landscape variable for each species.

Our abundance surveys were likely influenced by both weather variability and breeding phenology of each species. We attempted to minimize this variability by summing the abundance ranks across the four sampling dates for each species. Another way to reduce this variability is to use the maximum abundance rank observed on a single sample date, for each species, on the assumption that this date represents our best combination of weather and timing relative to breeding for that species. We re-ran the path analyses using maximum abundance ranks. The direction of the relationships between agricultural intensity and abundance of each species did not differ from our original path analyses, and differences in relationship strength were small (see Online Resource 3).

Our ponds had nitrate levels ranging between 0.43 and 4.94 mg/L, whereas watersheds throughout North America can have levels ranging from <1 to 100 mg/L (Rouse et al. 1999). As our ponds had nitrate concentrations on the low end of the range, we cannot extrapolate our conclusions to ponds with very high nitrate concentrations. This is important because the effects of nitrate on anurans vary with concentration, as seen in laboratory studies (Fig. 2).

We used the abundance of adult males during the breeding season as an index of relative population sizes. We implicitly assumed that this measure incorporates the effects of agricultural intensity throughout the life stages leading to adulthood. Agricultural intensity can influence anurans at many life stages, including through egg mortality (Vonesh and De la Cruz 2002), tadpole mortality (Peltzer et al. 2008), and adult reproductive success (Babbitt et al. 2009). It is only reasonable to assume that our index of relative abundance integrates these effects if calling males tend to call at or near the ponds where they developed and emerged (Berven and Grudzien 1990). This has been shown for *L. sylvaticus*, *L. pipiens*, *L. catesbeianus*, and *L. clamitans* (see Table 1).

We also note that laboratory studies on the effects of nitrate on anurans are generally only conducted on tadpoles (see Online Resource 1). It is unclear how the survival, behaviour, reproductive success, or breeding habitat selection of adult anurans may be affected by nitrate concentration in breeding ponds.

Our study occurred within the agricultural region of eastern Ontario, with its particular anuran species and agricultural practices. Associations with agricultural intensity may differ in other regions with different anuran species, regulations, and/or crops. For instance, in areas that ineffectively regulate pesticide use (see Ecobichon 2001; Schreinemachers and Tipraqsa 2012), we may expect to find stronger negative associations with agricultural intensity than in areas where buffer zone regulation significantly reduces wetland contamination (Dunn et al. 2011). However, we hypothesize our general conclusion that different anuran species associate differently with agricultural intensity likely holds across regions, as long as the different species present have different adult and larval habitat requirements and different sensitivities to agrochemicals.

Implications

Our results call into question extrapolations that are sometimes made about associations of anurans with agricultural intensity. As we found marked differences among anuran species in their associations with both nitrate and high-intensity-agriculture crop cover, studies on single anuran species should not be extrapolated to other anurans (Tárano and Fuenmayor 2013). Our results also suggest that extrapolating from laboratory nitrate effects to nitrate effects in the field is problematic (Joern and Hoagland 1996; Sih et al. 2004), particularly when nitrate concentrations in the field are much lower than those used in lab tests. Many of the species included in our study associated positively with nitrate, but negatively in laboratory studies using higher concentrations (see Online Resource 1).

Overall, our results suggest that agricultural intensity is not strongly associated with anuran abundance in our region. Negative associations with high-intensity-agriculture crop cover are generally weaker than positive associations. Ponds with higher concentrations of nitrate do not appear to be associated with decreased anuran abundance, at least at the levels present in our area. On the other hand, our results confirm that habitat loss due to agriculture has a significant effect on anurans, particularly for species that rely on forests for adult habitat, such as *P. triseriata*, *H. versicolor*, and *L. sylvaticus*. However, our results suggest that some species (e.g. *A. americanus*) can use high-intensity-agriculture crops as adult habitat; for these species, agriculture does not necessarily constitute 'habitat loss'.

The term 'agricultural intensity' is used inconsistently in the ecological literature, referring to anything from quantities of insecticide sprayed to sizes of crop fields. In light of this, we suggest that the term be more narrowly defined to promote consistent, ecologically relevant, use in the literature. We suggest that habitat effects should be described as habitat effects, whereas associations with 'agricultural intensity' should refer to associations with increased chemical usage (i.e. for a particular crop type), independent of the effects of habitat loss.

Agricultural intensity can affect anurans through several different pathways and mechanisms. These impacts can influence anuran habitat and abundance in both positive and negative directions. We therefore suggest that authors use caution if making general statements about the impacts of agricultural intensity on anurans.

Acknowledgments We thank Gabriel Blouin-Demers, Sara Collins, Steven Cooke, Susie Crowe, Jude Girard, Tom Hotte, Amanda Martin, Sandra Martins de Freitas, and Liv Monck-Whipp for ideas and comments on previous drafts. Chris Love was an invaluable field assistant. Two anonymous reviewers provided helpful comments on an earlier version. This work was supported by a Natural Sciences and Engineering Council of Canada grant to LF.

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