

Variation in tiger salamander density within prairie potholes affects aquatic bird foraging behaviour

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Abstract: Through competitive asymmetry, coexisting fish populations can alter aquatic bird distributions and reduce the reproductive success of their offspring. Gray tiger salamanders (*Ambystoma mavortium diaboli* Dunn, 1940) may function similarly in fishless prairie potholes. To test the hypothesis that tiger salamanders compete with aquatic birds (including ducks, grebes, and American Coot (*Fulica americana* J.F. Gmelin, 1789)) for prey resources during the breeding season, 16 potholes were divided into halves by an impermeable plastic barrier and tiger salamander densities were increased or decreased on opposite sides of the barrier. From late May until early July, aquatic invertebrates were sampled from both sides of the divider and the foraging activities of birds were observed. Invertebrate samples revealed that densities of most macroinvertebrate taxa were lower in the halves of potholes with relatively higher densities of tiger salamanders. On average, bird occupancy was evenly distributed on either side of the divider. In contrast, birds spent 65% more time foraging where tiger salamander densities were low (71.2% of total time observed) than where they were high (46.2% of total time observed). The birds most responsive to differences in tiger salamander density and food availability were dabbling ducks, followed by American Coot and diving ducks. This ranking corresponds to the degree of dietary overlap documented between tiger salamanders and aquatic bird assemblages in the study area.

Résumé : Par le moyen de l'asymétrie compétitive, les populations de poissons présentes dans les milieux aquatiques peuvent modifier les répartitions des oiseaux aquatiques et réduire le succès reproductif de leur progéniture. Les salamandres tigrées de Gray (*Ambystoma mavortium diaboli* Dunn, 1940) peuvent avoir le même effet dans les mares des prairies sans poissons. Afin de vérifier l'hypothèse selon laquelle les salamandres tigrées font compétition aux oiseaux aquatiques (en particulier, les canards, les grèbes et les foulques d'Amérique (*Fulica americana* J.F. Gmelin, 1789)) pour les ressources de proies durant la saison de reproduction, 16 mares ont été divisées en deux par une barrière de plastique imperméable; la densité des salamandres tigrées a été augmentée ou réduite de part et d'autre de la barrière. De la fin mai jusqu'au début de juillet, les invertébrés aquatiques ont été échantillonnés des deux côtés de la barrière et les activités de recherche de nourriture des oiseaux aquatiques ont été notées. L'échantillonnage des invertébrés montre que la densité de la plupart des taxons de macroinvertébrés est plus faible dans les moitiés des mares qui contiennent le nombre relatif plus grand de salamandres tigrées. En moyenne, les oiseaux occupent de façon égale les deux côtés de la barrière. En revanche, les oiseaux passent 65 % plus de temps à chercher leur nourriture là où les densités de salamandres tigrées sont faibles (71,2 % du temps total d'observation) par comparaison aux sites où leur densité est élevée (46,2 % du temps total d'observation). Les oiseaux qui réagissent le plus aux différences de densité des salamandres et de disponibilité de nourriture sont, dans l'ordre, les canards barboteurs, les foulques d'Amérique et les canards plongeurs. Cet ordre correspond au degré connu de recoupement des régimes alimentaires entre les salamandres tigrées et les divers peuplements d'oiseaux aquatiques de la région.

[Traduit par la Rédaction]

Introduction

Asymmetric exploitative competition has been shown to occur between coexisting but distantly related taxa, particularly in variable environments (Reichman 1979; Ricklefs 1990). Estimates of interaction strengths in communities suggest that the intensity of competitive interactions between distantly related taxa rivals that of closely related taxa (Englund et al. 1992; Barnes 2003). The consequences of this indirect effect through common prey resources may lead to resource limitation in the disadvantaged taxa. Although

resource limitation is routinely cited as an important determinant of community structure (Wiens 1989), the actual demonstration of resource limitation directly in animal populations under natural conditions is difficult (Myers and Rothman 1995; Sjöberg et al. 2000). The interaction between individual behaviour and population dynamics suggests that behavioural activities of animals may be indicative of relative resource quality or quantity (Haemig 1994; Fryxell and Lundberg 1997; Nummi et al. 2000). Given the choice, consumers should be attracted to foraging habitats with relatively higher resource availability.

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Prairie potholes are seasonally productive palustrine environments that support migratory aquatic birds (including ducks, grebes, and American Coot (*Fulica americana* J.F. Gmelin, 1789)) and, depending on hydrologic conditions, gray tiger salamanders (*Ambystoma mavortium diaboli* Dunn, 1940; herewithin, also simply as tiger salamanders). These consumers exhibit substantial dietary overlap (Benoy et al. 2002) and tiger salamanders have been shown to affect trophic interactions between aquatic birds, invertebrates, and phytoplankton standing crop through compensatory predation (Benoy 2002). Within potholes, tiger salamanders, like fathead minnow (*Pimephales promelas* Rafinesque, 1820), are generally thought to out compete dabbling and diving ducks (Anatidae) and American Coot for common prey (Hanson and Riggs 1995; Bouffard and Hanson 1997). This suggests that potholes containing tiger salamander populations may be marginal for breeding birds.

During the breeding season, most migratory aquatic birds, especially females, augment their diets during the nesting and laying stages with higher proportions of aquatic invertebrates (~80% of total diet; Krapu and Reinecke 1992). Similarly, for the first few weeks post hatch, duckling, American Coot chick, and grebe chick diets are almost entirely composed of aquatic invertebrates (Driver 1988; Sedinger 1992). Birds can readily discriminate between foraging habitats of contrasting resource profitability (Weller 1999). Furthermore, the foraging behaviours of aquatic birds are easily observable and have been successfully used as indicators of resource limitation in Black Duck (*Anas rubripes* Brewster, 1902) and Mallard (*Anas platyrhynchos* L., 1758) ducklings (Hunter et al. 1983; Nummi et al. 2000). Concurrent with nesting activities and brood rearing, tiger salamander eggs hatch into larvae that can reach densities in the thousands per hectare (Deutschman and Peterka 1988; Carlson and Berry 1990). Thus, the potential for indirect interactions between aquatic birds and tiger salamanders through prey resources may be greatest during this period of the breeding season.

For this study, I manipulated aquatic invertebrate availability within a series of prairie potholes through the systematic reduction or addition of tiger salamanders. I recorded aquatic bird behavioural activities according to high or low tiger salamander densities on either side of impermeable barriers used to split potholes in half. First, I predicted that birds in halves with relatively low tiger salamander density would spend a greater proportion of time foraging than birds in halves with high tiger salamander density. As a corollary to this prediction, the bird species that differ most in their time allocated to foraging should be those that have the greatest diet overlap with tiger salamanders, such as dabbling ducks. Second, I predicted that the observed effects in foraging time would vary with the difference in tiger salamander density between manipulations among potholes. Aquatic invertebrates were also sampled periodically during the course of the experiment to provide an independent estimate of the effects of variation in tiger salamander density on resource availability. This combination of experimental manipulation and behavioural observation under natural conditions provided complementary lines of evidence to address the hypothesis that aquatic birds are sensitive to resource levels during the breeding season.

Methods

Study area

Pothole experiments were carried out southwest of Minnedosa, Manitoba, Canada (50°16'N, 99°50'W), near the northeastern edge of the Prairie Pothole Region (PPR) during the spring and summer of 2000. Sixteen potholes were randomly selected from a pool of semi-permanent potholes that were constrained by the morphometric criteria that they be symmetric, no deeper than 125 cm, and no larger than 0.6 ha. Study potholes were evenly spread out over a 16-km² area and no two potholes were immediately adjacent to one another. Potholes in this area rarely disappear even though water levels can fluctuate widely within a season. Except during spring thaw and periods of exceptionally heavy or sustained rainfall, most potholes exist in isolated drainage basins with low drainage to surface water area ratios. Heavy rainfall that occurred towards the end of the study was likely responsible for the presence of several fathead minnows collected in one pothole on one occasion. Although a few fish species, such as fathead minnow and brook stickleback (*Culaea inconstans* (Kirtland, 1840)) occur in this portion of the PPR, their occupancy rate across potholes is low because of the combined effects of isolation and depleted dissolved oxygen concentrations causing summerkill and winterkill. Tiger salamanders, in contrast, are adapted to these types of hydrologically variable and isolated aquatic habitats (Wissinger et al. 1999). Geomorphologic and biogeochemical features of this landscape and its associated biotic communities are described in detail in Benoy (2002).

Tiger salamander manipulations

From early May until early August, potholes were bisected by floating dividers of 5 cm × 10 cm boards that extended from shore to shore. Polyethylene plastic sheeting was attached to the boards and draped to the sediment-water interface to divide the potholes in half. The sheeting was anchored with lead line that was duct-taped to the bottom. An extra 20–30 cm of sheeting was allowed to hang from the boards in case water levels fluctuated (i.e., increased) or in case the dividers shifted position and the sheeting billowed. The dividers traversed zones of emergent vegetation near the shoreline and continued upland to beyond the edge of the water.

Once the pothole dividers were in place, two types of traps were used to test for the presence of tiger salamanders on either side of the dividers in all of the potholes: (1) standardized aluminum minnow traps and (2) salamander traps that resemble drift nets (Mushet et al. 1997). Both trap types have openings approximately 2.5 cm wide and sample passively over 24-h periods. Upon determination of the presence of tiger salamanders in a particular pothole, trapping effort was concentrated on one randomly selected side of the divider (designated as low tiger salamander density (LTSD)). Any live tiger salamanders that were collected were simply transferred to the other side (designated as high tiger salamander density (HTSD)). Dead tiger salamanders were discarded. If no tiger salamanders were trapped in a particular pothole, then individuals were imported from potholes outside of the study area and added to one side of the divider. Five minnow traps and one salamander trap were set for

each trapping effort. The trapping effort for all potholes (i.e., potholes with existing populations of tiger salamanders and source potholes outside of the study area) was the same and independent of pothole area: twice per week for 3 weeks or a total of 6 salamander trap days and 30 minnow trap days per pothole. Tiger salamander densities were corrected for pothole area and expressed in units per hectare. All tiger salamander life stages (i.e., larval, neotenic, and adult) were included in the manipulation. Thus, paired contrasts of high and low (or absent) densities of tiger salamanders were established within each pothole.

Upon completion of the study in early August, final densities of tiger salamanders on each side of the divider were estimated using the same trapping effort as before observations. Any tiger salamanders trapped during this period were exported to another pothole outside of the study area to avoid the possibility of double-counting and artificially increasing density estimates.

The University of Guelph Animal Care Committee, on behalf of the Canadian Council on Animal Care, approved tiger salamander manipulations for this study. Permits for this research included WSP00010 (Wildlife Branch, Manitoba Conservation, Winnipeg) and CWS00-M015 (Canadian Wildlife Service, Environmental Conservation Branch, Winnipeg).

Aquatic invertebrate sampling

In mid-May, following cessation of tiger salamander manipulations and during bird foraging observations, aquatic invertebrates were sampled on either side of the divider on six occasions to characterize the effects of contrasting tiger salamander densities on resource availability. Ten samples (five on each side of the divider) were collected at approximately weekly intervals at each pothole for a total of six sampling rotations, which bracketed the period when birds were observed. Invertebrates were sampled using 3.8-L activity or "funnel" traps, based on the design of Murkin et al. (1983). The traps were accessed by canoe to minimize disturbance to the sediments and benthic communities. Activity traps are time-integrated sampling devices that are suspended in the water column over 24-h periods. Consequently, benthic invertebrates (e.g., Gastropoda) tend to be underrepresented. Given that tiger salamander densities were manipulated within basically symmetrical potholes, this sampling bias should not affect comparisons of relative differences in invertebrate densities.

Retrieved activity traps were poured through a 180- μ m net and preserved in 70% ethanol. Invertebrate samples were passed through a 1-mm sieve before processing. Although microinvertebrates, especially small zooplankton such as Bosminidae and Rotifera, are important components of pothole food webs, they compose a very small fraction, by aggregate volume, of waterfowl diets (Krapu and Reinecke 1992). The invertebrates, and a small number of tadpoles and larval tiger salamanders also collected in the activity traps, remaining in each sample were identified using Merritt and Cummins (1996), Thorp and Covich (1991), and Preston (1982), and were counted.

Aquatic bird observations

Starting in late May, after tiger salamander densities were manipulated within potholes and the first round of inverte-

brate sampling was completed, observations of aquatic bird activity budgets were performed using a spotting scope (Bushnell Spacemaster). Behavioural observations were not conducted on the same days of subsequent invertebrate sampling. Each observation period lasted for 2 h and they generally occurred either in the early morning or in the early evening to coincide with times of the day when feeding was most intense. At 10-min intervals, the number of adult birds on either side of the divider was recorded, as well as the species, sex (ducks only), and the specific behavioural activity of each bird. Of the several activities identified, only occurrences of foraging (diving, tipping, dabbling, etc.), relative to all other activities, were considered relevant to this study. Locations of individual birds were monitored throughout each 2-h period so that every bird observed had a separate record. Each pothole was observed on either three or four occasions, once every 7–10 days.

Statistical analyses

All statistical analyses were performed using SAS[®] version 8.01 (SAS Institute Inc. 1999). Univariate normality was assessed using the Shapiro–Wilk statistic W and homoscedasticity was assessed using Bartlett's test. Variables that violated assumptions of parametric tests were $\log(x + 1)$ -transformed. Statistical significance was set at $\alpha = 0.05$.

To test for differences in invertebrate densities between halves of potholes with HTSD and LTSD, randomized complete block mixed-model analysis of variance (ANOVA) with two treatment (fixed) factors was used. Predictor variables included pothole side (the first fixed factor; HTSD or LTSD side of the divider) and sampling rotation (the second fixed factor; 1–6). This model is analogous to a two factor repeated measure experimental design where the treatment factors are considered the within-subject factors (Zar 1996). Least squared means were used to compare invertebrate densities. Modified error terms for testing specific statistical hypotheses are listed in table captions, as use of residual error terms for mixed-model ANOVA is inappropriate.

Randomized complete block two-way ANOVA was used to determine if the tiger salamander manipulations affected the proportion of time that birds allocated to foraging. The predictor variable included in the statistical model was side (HTSD or LTSD side of the divider). The dependent variable, percent foraging time, was defined as foraging time divided by total time observed. For each bird, the total number of foraging observations during a 2-h period (0–12, based on 10-min observation intervals) was divided by the duration of time that the bird was observed on a particular side of the divider (always greater than or equal to time spent foraging). For birds that occupied only one half of a pothole during an observation period, percent foraging time was entered as 0 for the other half. The paired design of the experiment was factored into the statistical model by inclusion of the variable "pothole", the blocking term. Two-way ANOVA without interaction is preferable to t test for paired comparisons for this data structure, as the contribution of the blocking factor can be estimated (Sokal and Rohlf 1995). ANOVA analyses were performed on all groups of birds (i.e., dabbling and diving ducks, female and male ducks, American Coot, and grebes), and on individual species where the total number of birds observed on a pothole was greater than 10.

Table 1. Summary statistics and results of statistical analyses for the invertebrate responses to the tiger salamander (*Ambystoma tigrinum*) manipulations (HTSD, high tiger salamander density; LTSD, low tiger salamander density).

	Densities*		Side [†]		Rotation [†]		Side × rotation [†]	
	HTSD side	LTSD side	$F_{[1,15]}$	<i>P</i>	$F_{[5,55]}$	<i>P</i>	$F_{[5,55]}$	<i>P</i>
Macroinvertebrates	407.1±25.2	541.3±41.3	86.80	<0.0001	3.90	0.0043	0.90	0.4860
Gastropoda	6.3±1.7	6.6±1.4	0.36	0.5627	7.41	<0.0001	1.03	0.4115
Diptera	128.3±22.8	169.2±44.3	7.57	0.0189	7.11	<0.0001	0.46	0.8020
Coleoptera	47.8±4.9	80.9±9.7	19.08	0.0011	3.07	0.0163	0.34	0.8886
Hemiptera	49.6±12.2	56.1±9.4	5.52	0.0385	3.84	0.0047	1.02	0.4164
Odonata	7.7±1.6	11.6±2.5	5.35	0.0411	2.17	0.0708	1.51	0.2022
Amphipoda	128.8±32.7	205.4±60.7	8.30	0.0149	3.12	0.0149	0.89	0.4920
Ephemeroptera	2.5±0.8	5.4±2.8	0.61	0.4510	8.16	<0.0001	0.26	0.9341
Trichoptera	2.9±1.4	15.2±9.9	5.30	0.0418	4.15	0.0029	1.69	0.1517
Hydracarina	20.3±3.0	16.5±1.6	0.38	0.5518	3.15	0.0144	0.63	0.6800
Zooplankton	1751.8±318.7	3245.7±892.9	4.78	0.0513	0.06	0.9980	0.30	0.9104
Cladocera	1284.6±318.0	2765.4±855.0	5.12	0.0449	0.60	0.7019	0.57	0.7211
Copepoda	467.3±98.8	428.3±83.8	3.44	0.0905	3.27	0.0117	0.12	0.9864

Note: Because the statistic is a mixed model ANOVA, residual error terms were replaced by appropriate error terms to test for effects: side × pothole for the “side” effect, rotation × pothole for the “rotation” effect, and side × rotation × pothole for the “side × rotation” effect. Values in boldfaced type are statistically significant ($P < 0.05$).

*Macroinvertebrate and zooplankton densities are untransformed least squared means (±SE) across all sampling rotations from mid-May until early July.

[†]Macroinvertebrate and zooplankton densities were $\log(x + 1)$ -transformed prior to statistical analysis.

Although known quantities of tiger salamanders were removed from and added to either side of the pothole dividers, the a priori tiger salamander densities for most potholes were unknown; the exception being LTSD sides of potholes where tiger salamanders were never found throughout the duration of the experiment. For this reason, only estimates of final tiger salamander densities after bird observations were complete were used in the statistical analyses involving tiger salamanders.

To ascertain if there was a predictable relationship between the percentage of time that birds spent foraging on either side of the divider and the range of variation in tiger salamander densities among potholes, a tiger salamander “effect size” was estimated for each pothole. This variable was calculated by log transforming the quotient of the average number of tiger salamanders trapped on the HTSD and LTSD sides of the divider in each pothole following completion of the bird observations. Average numbers of tiger salamanders from each pothole were increased by one to facilitate division involving potholes with zero tiger salamanders on LTSD sides. Curvilinear regression was used to relate average percent foraging times of birds to tiger salamander effect size, as the relationships for the HTSD and LTSD sides are bounded by 0 and 100, respectively.

Results

Tiger salamander manipulations

Four of the 16 potholes in the study did not initially contain tiger salamanders. For these potholes, an average of 770.0 tiger salamanders·ha⁻¹ (SE = 132.5) were added to the HTSD side. For the other 12 potholes, the total number of tiger salamanders trapped in the LTSD sides of potholes and transferred to the HTSD sides ranged from 27.3 to 2458.1·ha⁻¹ (mean = 566.4·ha⁻¹, SE = 246.8·ha⁻¹).

At the conclusion of the experiment, only two of the four potholes initially without tiger salamanders had LTSD sides

that were still absent of tiger salamanders. Inventories of tiger salamanders revealed that, across all 16 potholes, there were 2.5 times as many total tiger salamanders in the HTSD side than in the LTSD side (one-way ANOVA, $F_{[1,31]} = 4.472$, $P = 0.044$). On average, 231.7 tiger salamanders·ha⁻¹ (SE = 57.3·ha⁻¹) were trapped in the HTSD sides of potholes compared with 91.8·ha⁻¹ in the LTSD sides (SE = 23.4·ha⁻¹).

Aquatic invertebrate responses

Overall, there were 33% fewer macroinvertebrates on the HTSD sides of the potholes than on the LTSD sides (Table 1). Of the nine macroinvertebrate groups identified, six had densities that were significantly greater on the LTSD sides than on the HTSD sides, which included the groups with the highest densities (Diptera, Coleoptera, Hemiptera, and Amphipoda) comprising over 90% of the total number of macroinvertebrates. Within the zooplankton group, only Cladocera had significantly higher densities on the LTSD sides of the potholes.

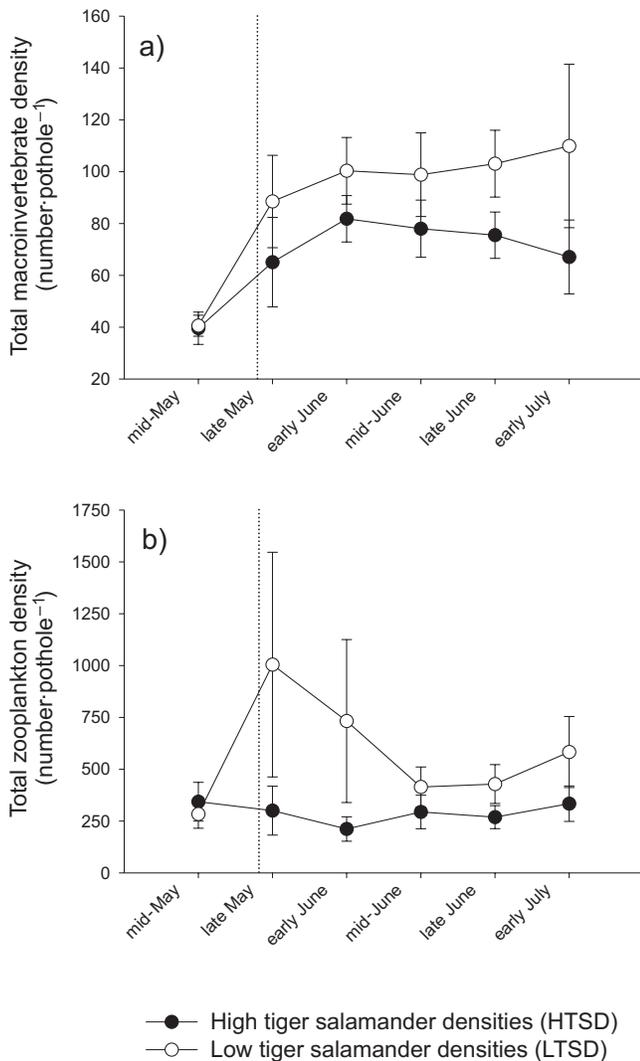
During bird observations, all macroinvertebrate taxonomic groups except Odonata and only Copepoda within the zooplankton group significantly varied over time (Table 1, Fig. 1). No interactions between pothole side and variation over time were observed for any of the invertebrate taxa.

Aquatic bird observations

During the 5-week observational period, 446 birds were observed over a total of 116 h (mean = 7.25 h·pothole⁻¹). The most commonly observed birds were American Coot (27.3%), followed by Blue-winged Teal (*Anas discors* L., 1766) (23.5%), Northern Shoveler (*Anas clypeata* L., 1758) (10.3%), and Mallard (8.7%) (Table 2). Dabbling ducks as a guild composed over half of all the birds observed (52.5%) and they were almost 4 times as numerous as the diving duck guild (14.6%).

When averaged over observation periods and across potholes, the birds were evenly distributed on either side of the

Fig. 1. Time series plots of macroinvertebrate (a) and zooplankton (b) densities on the HTSD and LTSD sides of the pothole dividers before and during bird observations. Error bars are \pm SE. The vertical dotted lines indicate when bird observations were initiated.



divider (HTSD = 37.7%; LTSD = 36.5%; ANOVA, $F_{[1,98]} = 0.13$, $P = 0.7229$). I observed 25.8% of the birds “loafing” on the pothole dividers, and they were mostly dabbling ducks. No statistically significant differences between HTSD and LTSD sides of potholes were obtained for any of the groups of birds: dabbling ducks (ANOVA, $F_{[1,88]} = 0.32$, $P = 0.5765$), diving ducks (ANOVA, $F_{[1,31]} = 1.51$, $P = 0.2339$), American Coot (ANOVA, $F_{[1,53]} = 0.00$, $P = 0.9704$), and grebes (ANOVA, $F_{[1,19]} = 1.25$, $P = 0.2832$) (Fig. 2). When grouped into sexes, the distribution of male ducks also did not differ on either side of the divider (ANOVA, $F_{[1,63]} = 1.08$, $P = 0.3061$). However, 50% more female ducks were observed on the LTSD side than on the HTSD side, although this did not translate into a significant difference (ANOVA, $F_{[1,39]} = 2.61$, $P = 0.1154$). Similarly, individual species, for which there were a total number of birds observed greater than 10, were also distributed evenly

on either side of the pothole dividers as indicated by their distribution along the 1:1 line in Fig. 3a.

In contrast, most birds spent significantly more time foraging in the halves of potholes with lower tiger salamander densities. When combined, all birds spent an average of 71.2% of their time foraging on the LTSD side of the pothole and only 46.2% on the HTSD side. Observed foraging rates were relatively unchanged from survey to survey. All groups of birds, except grebes, spent significantly more time engaged in feeding activities on the LTSD side of the divider than on the HTSD side (Table 2). Dabbling ducks foraged for more than two-thirds of their total time on the LTSD side of the divider (mean = 71.1%) compared with less than one-third of their time on the HTSD side (mean = 31.4%). Diving ducks also foraged more on the LTSD side of the divider (mean = 68.0%) than on the HTSD side (mean = 40.1%), but not to the same extent as dabbling ducks. When all of the duck species were grouped, females spent 75.7% of their time foraging on the LTSD side of the divider and 40.8% of their time foraging on the HTSD side, compared with 67.0% and 34.2% for males, respectively.

Of the seven species observed with greater than 10 individuals, four spent significantly more time foraging in the halves of potholes with relatively fewer tiger salamanders; the rest had P values < 0.1 (Table 2). The species with the greatest contrast in the amount of time spent foraging on the LTSD side of the divider compared with the HTSD side was Gadwall (*Anas strepera* L., 1758) (3.1), followed by Red-head (*Aythya americana* (Eyton, 1838)) (2.7), Blue-winged Teal (2.1), Northern Shoveler (1.7), Ruddy (*Oxyura jamaicensis* (J.F. Gmelin, 1789)) (1.5), and American Coot (1.4) (Fig. 3b).

The blocking term “pothole” was not significant for any of the aquatic bird response variables (Table 2), which indicated that variation among the experimental potholes did not account for observed variation in percent foraging times as a function of the tiger salamander manipulations.

Following completion of the bird observations, tiger salamander effect sizes ranged from almost 47.93 in a pothole that was absent of tiger salamanders on the LTSD side to 0.92 in a pothole that had a slightly greater number of tiger salamanders trapped on the LTSD than on the HTSD side (mean = 7.39, SE = 3.23). When regressed against tiger salamander effect size, significant relationships were obtained for percentage of time spent foraging on the LTSD side of the divider (Fig. 4; $F_{[1,15]} = 6.0206$, $R^2 = 0.334$, $P = 0.0304$) and the HTSD side of the divider ($F_{[1,15]} = 5.2849$, $R^2 = 0.306$, $P = 0.0403$).

Discussion

The importance of indirect effects in determining community structure has been investigated for several decades (Schoener 1993; Wootton 1994). Exploitative competition, whereby organisms interact through a common resource, is perhaps the most familiar indirect effect and it has garnered much attention as a hypothesis to explain asymmetric relationships between fish and waterfowl (Eadie and Keast 1982; Hunter et al. 1986; Winfield and Winfield 1994). For this experiment, I took advantage of the apparent indirect ef-

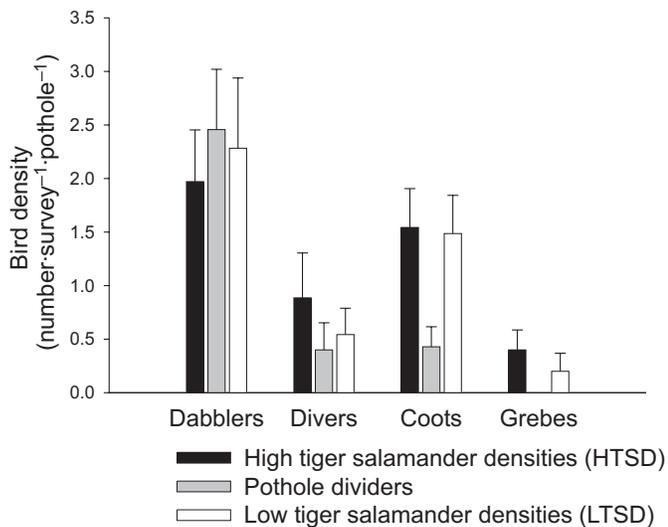
Table 2. ANOVA of bird foraging times across potholes by tiger salamander treatment or side (HTSD or LTSD side of the divider) broken down by guild, by sex, and by species in cases where the total number of individuals observed was greater than and equal to 10 (not including birds observed on the divider).

	Abbreviation	Pothole			Side		
		df	F	P	df	F	P
All birds		15, 31	0.32	0.9755	1, 31	13.16	0.0031
Dabbling ducks		13, 29	0.88	0.5891	1, 29	16.22	0.0007
Blue-winged Teal (<i>Anas discors</i>)	BWTE	11, 23	2.15	0.1199	1, 23	9.23	0.0125
Gadwall (<i>Anas strepera</i>)	GADW	6, 13	0.97	0.5144	1, 13	10.62	0.0173
Mallard (<i>Anas platyrhynchos</i>)	MALL	8, 17	3.76	0.1520	1, 17	6.61	0.0824
Northern Shoveler (<i>Anas clypeata</i>)	NSHO	9, 19	0.60	0.7703	1, 19	6.02	0.0365
Diving ducks		9, 21	0.90	0.5914	1, 21	5.84	0.0312
Redhead (<i>Aythya americana</i>)	REDH	5, 13	0.72	0.7071	1, 13	5.17	0.0634
Ruddy (<i>Oxyura jamaicensis</i>)	RUDU	7, 15	0.91	0.6714	1, 15	4.04	0.0793
Female ducks		12, 27	0.57	0.8134	1, 27	9.36	0.0156
Male ducks		13, 29	0.76	0.6838	1, 29	8.06	0.0149
American Coot (<i>Fulica americana</i>)	AMCO	11, 25	0.98	0.5145	1, 25	10.05	0.0091
Grebes*	GREB	6, 13	1.83	0.2395	1, 13	0.69	0.4385

Note: Pothole is the blocking factor that accounts for the paired structure of the field design. Standard residuals were used as the error term for all analyses.

*Horned (*Podiceps auritus*) and Pied-billed (*Podilymbus podiceps*) Grebes were combined.

Fig. 2. Mean (+SE) number of birds observed on the HTSD and LTSD sides of the pothole and on the pothole dividers.



fect of tiger salamanders on breeding aquatic birds through invertebrate resources that was observed in earlier studies (Benoy 2002; Benoy et al. 2002). Within potholes, birds skewed their foraging time budgets towards areas with lower tiger salamander density, and the effects were most pronounced for those species that have the greatest dietary overlap with tiger salamanders (Benoy et al. 2002). Although foraging is not synonymous with ingestion (Nummi et al. 2000), the relationship obtained between increased aquatic invertebrate densities in the presence of lower tiger salamander densities and greater foraging strongly supports the hypothesis that invertebrate intake by aquatic birds was also greater.

To test for the effects of variation in tiger salamander density on waterfowl distribution within potholes and foraging behaviour, the critical effect was the contrast in tiger sala-

mander density on either side of the divider within each pothole. The total number of individuals added to the HTSD side in advance of the bird foraging observations ranged from about 400 to 4000·ha⁻¹. Tiger salamander densities in the thousands per hectare were mostly composed of larvae and they are comparable to the range reported for wetlands in North Dakota (Wiedenheft 1983; Deutschman and Peterka 1988). Final estimates of tiger salamander densities averaged just less than 100·ha⁻¹ on the LTSD side of the divider to just over 200·ha⁻¹ on the HTSD side, a reduction of approximately an order of magnitude from the beginning until the end of the study (early May until mid-July). High densities of larvae tend to experience high rates of mortality, and by the time the remaining larvae reach a sexually mature state, as adults, densities have dropped substantially (Deutschman and Peterka 1988). Thus, my estimates of tiger salamander densities before and after the bird observations are comparable to those reported in the literature for population densities in unmanipulated prairie lakes.

Although tiger salamanders and fathead minnow appear to be functionally similar consumers in prairie potholes with respect to their effects on food-web structure, there are potentially important differences between their spatial dynamics and their life-history strategies that may affect their interactions with migratory aquatic birds. The simple presence or absence of fathead minnow is strongly related to invertebrate resources (Hanson and Riggs 1995; Zimmer et al. 2000), whereas significant relationships between tiger salamanders and invertebrate resources only occur at relatively moderate or high tiger salamander densities (Benoy 2002). Except periods of atypical snowmelt and rainfall, the distribution of minnow species across the PPR is well established; fish populations persist in prairie potholes and lakes that are relatively permanent. In these aquatic systems, invertebrate community structure and species composition is continuously affected by the presence of fish. In contrast, semi-permanent and seasonal wetlands that are inhospitable to

Fig. 3. Plots of bird species for which there were greater than 10 individuals according to (a) the mean (\pm SE) number of birds observed on the high tiger salamander density (HTSD) and low tiger salamander density (LTSD) sides of the pothole dividers, and (b) the mean (\pm SE) percentage of the total time spent foraging on the HTSD and LTSD sides of the pothole dividers. The diagonal dotted line in both plots is the 1:1 line. Abbreviation codes for each of the species are included in Table 2.

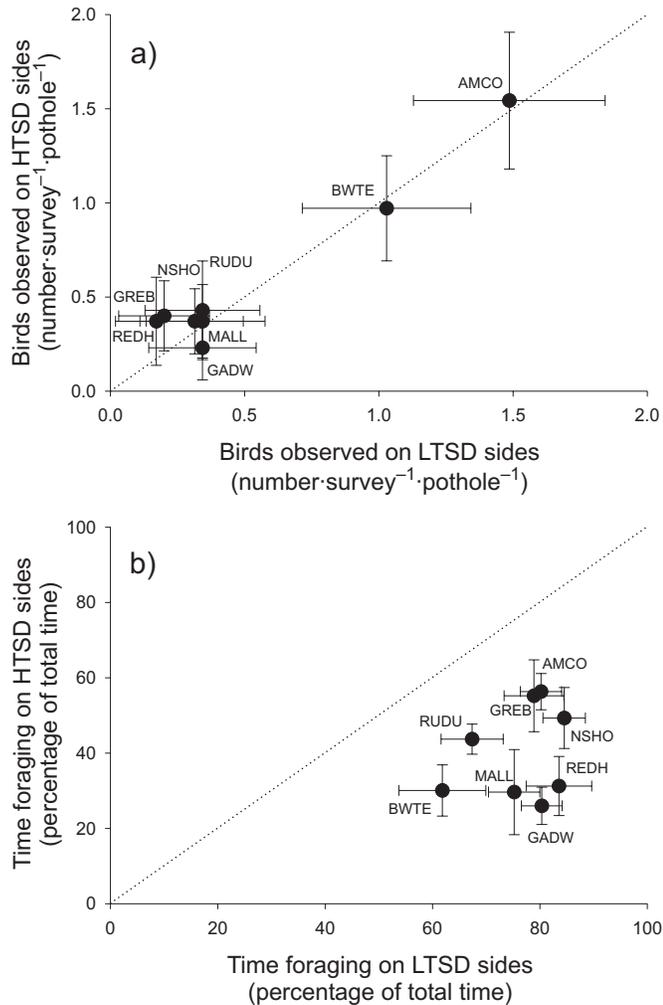
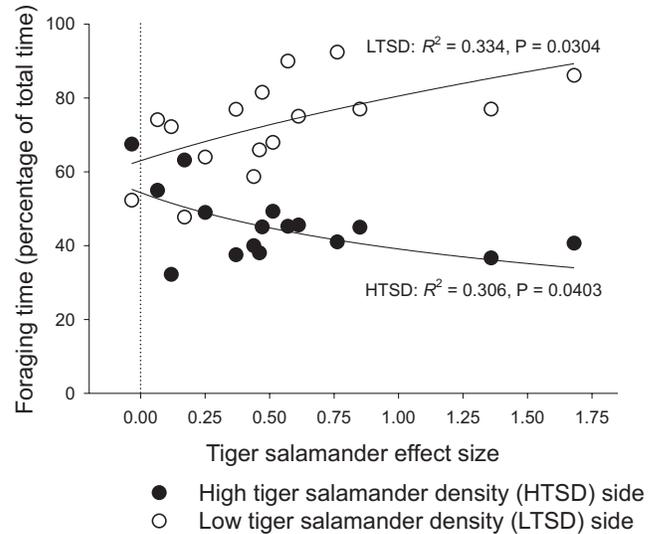


Fig. 4. Relationships between mean foraging times (percentage of total time) for birds on either side of the pothole dividers and tiger salamander effect size (logarithm of the quotient between final estimates of tiger salamander densities on the HTSD and LTSD sides of the potholes). Regression output is based on the power function $y = a(1 + x)^b$. The vertical dotted line indicates no effect size, i.e., equal densities of tiger salamanders.



fish may or may not contain tiger salamanders, depending on the spatial distribution of tiger salamanders across the region and their associated metapopulation dynamics (Marsh and Trenham 2001). Thus, the invertebrate communities that inhabit these aquatic systems may only infrequently coexist with tiger salamanders. Migratory aquatic birds may be able to more readily discriminate among potholes that have reduced invertebrate availability owing to the presence of fish populations than tiger salamander populations. An implication of this hypothesis for understanding resource limitation is that breeding birds may attempt to fledge offspring from potholes that have suboptimal resource availability as a result of competition with tiger salamanders that were not detected or present during nesting.

When tiger salamanders and aquatic birds do coexist, the likelihood of significant indirect interaction is high. Tiger salamanders are generalist consumers and broad diet overlap

exists between both larval and adult tiger salamanders and ducks (Benoy et al. 2002). All of the invertebrate taxa with densities that significantly differed according to the tiger salamander manipulations also ranked highly in the lists of shared prey types between tiger salamanders and aquatic birds (i.e., Diptera, Coleoptera, Hemiptera, Amphipoda, and Cladocera). Furthermore, dabbling ducks have higher diet overlap with tiger salamanders than diving ducks. Results of this study indicate that dabbling ducks altered their activity budgets to spend relatively more time foraging on the LTSD side of the divider than did diving ducks. Interestingly, two of the species that skewed their foraging locations most towards the LTSD side of the divider, Gadwall and Northern Shoveler (dabbling duck species), also had the highest specific prey type overlap with tiger salamanders (Benoy et al. 2002). Overall, these behavioural patterns are similar to those obtained by Kaminski and Prince (1981), who found that the percent occurrence of foraging by dabbling ducks was positively correlated with mean invertebrate abundance.

While male ducks showed no preference for occupying LTSD or HTSD sides of the divider, females spent 50% more time on the LTSD side. Females also spent proportionately more time foraging on both sides of the divider than males did. Prelaying and laying female ducks have higher demands for invertebrate prey than males (Krapu and Reinecke 1992), and other studies involving activity budgets of ducks have also shown that females preferentially forage where invertebrate abundances are relatively higher and for longer periods of time (Kaminski and Prince 1981; Krapu and Reinecke 1992).

In contrast, Horned (*Podiceps auritus* L., 1758) and Pied-billed (*Podilymbus podiceps* (L., 1758)) grebes did not significantly alter activity budgets in relation to tiger salamander densities. Grebes might not respond to differences

induced by tiger salamanders to the prey resource base for at least two reasons. First, grebe diets (especially those of Pied-billed Grebes) can include amphibian larvae, so their relationship with tiger salamanders may more properly be described as intraguild predation (Polis and Holt 1992). Second, tiger salamanders are gape-limited, constraining access to larger invertebrates that may otherwise be potentially available to grebes (Zaret 1980). The strength of the American Coot response to contrasting tiger salamander densities was intermediate to those of ducks and grebes. Adult American Coots are primarily herbivorous relative to the other birds observed in this study, except during the breeding season when aquatic insects and molluscs are incorporated into the diet (Driver 1988; Alisauskas and Arnold 1994). Therefore, although increased tiger salamander densities may have reduced invertebrate availability, the consequences of this reduction were less important for American Coots than for dabbling ducks as a guild.

For all aquatic bird species, behavioural observations of foraging activity budgets of adult birds were used to specifically estimate relative resource availability. The evidence presented here, that birds preferentially foraged in habitats with higher densities of prey resources as a function of tiger salamander density, is consistent with the hypothesis that tiger salamanders can cause resource limitation in coexisting aquatic birds. To more explicitly link the potential influence of tiger salamanders on avian population dynamics, behavioural observations of individuals, supplemented by measurements of changes in body mass, should be conducted at the brood stage (Hill et al. 1987; Sjöberg et al. 2000). Cox et al. (1998) showed that Mallard duckling survivorship was positively related to body mass (and invertebrate availability) during the first 2 weeks post hatch. This suggests that mortality rates may be greater for ducklings, and aquatic bird offspring in general, that have high dietary overlap with tiger salamanders.

The determination of resource limitation in migratory aquatic birds has proven to be a challenge. Traditional approaches to the problem, involving ecophysiological analyses and bioenergetic modeling, have more recently been supplemented by manipulative field experiments. Such studies offer a powerful tool for testing hypotheses of community structure, provided that appropriate controls and adequate replication are in place (Raffaelli and Moller 2000). Although unequivocal evidence of resource limitation was not obtained using this experimental strategy, the results obtained indicate that behavioural observations are useful for identifying resource availability. The overall conclusions of this study are (i) tiger salamanders are capable of reducing aquatic invertebrate densities in prairie potholes; (ii) tiger salamanders, especially at relatively high densities, indirectly interact with coexisting aquatic birds through exploitation of common prey; and (iii) avian activity budgets are sensitive to variation in food supply.

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