PRIMARY RESEARCH PAPER

# Variation in prey-specific consumption rates and patterns of field co-occurrence for two larval predaceous diving beetles

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Received: 14 December 2012/Revised: 6 June 2013/Accepted: 8 June 2013 © Springer Science+Business Media Dordrecht 2013

**Abstract** Freshwater predatory insects can exert strong effects on prey, although how multiple similar predators may coexist is not well understood. Larval predaceous diving beetles are often numerically and taxonomically abundant predators in lentic systems, but the proximate mechanisms that explain their high abundance remain unknown. Field surveys were conducted twice in June in ponds in Alberta, Canada to assess the associations between larvae of two genera (*Graphoderus, Rhantus*), their spatial locations, and correlations with potential prey. Both larvae were common and positively correlated within wetlands although neither varied with pond depth nor distance from edge. Laboratory trials indicated that *Graphoderus*, *rus* consumed more prey (corixids) at the surface,

**Electronic supplementary material** The online version of this article (doi:10.1007/s10750-013-1595-5) contains supplementary material, which is available to authorized users.

Handling editor: B. Oertli

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Present Address: D. A. Yee (⊠) Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, MS 39406, USA e-mail: donald.yee@usm.edu whereas *Rhantus* killed benthic prey (chironomids) and corixids at an equal rate; damselflies were the least consumed prey. Predation also varied with depth, with both larvae feeding at higher rates in the shallowest environments compared to *Graphoderus* at an intermediate depth. Predator–prey correlations from ponds were mostly congruent with predation trials; *Graphoderus* was positively correlated with corixids, *Rhantus* was positively correlated with corixids and chironomids; beetles were uncorrelated with damselflies. Reliance on different prey in different microhabitats may be an important mechanism for the maintenance of high abundance of dytiscid larvae.

**Keywords** Aquatic habitat  $\cdot$  Niche  $\cdot$  Ponds  $\cdot$  Predator  $\cdot$  Water beetles

### Introduction

Predation is one of the central structuring mechanisms of ecosystems (Holt & Polis, 1997; Sih et al., 1998), and its effects have been shown to resonate across populations and communities (e.g., Sih et al., 1985), often through complex trophic cascades and indirect effects (Duffy, 2003; Bruno & Cardinale, 2008). Besides the interest in predation as a purely scientific pursuit, predators also can provide critical ecosystem services through suppression of pest populations (Wilby & Thomas, 2002; Cardinale et al., 2003; Letourneau et al., 2009). A long-standing approach to the study of predation was to assume that predator diversity could be summarized as a single trophic level (Fretwell, 1987). Similarly, when this trophic level was considered, often only a single predator or a series of single predators were examined (Sih et al., 1998). Recently, the characterization of predation has been expanded to include the diversity of predators and the diversity of their potential interactions (e.g., Polis, 1991; Sih et al., 1998; Rosenheim, 1998; Schmitz, 2007; Letourneau et al., 2009). Although considerably more complicated to disentangle, examination of these multiple predator–prey systems (Ives et al., 2005) has yielded many new insights and testable predications that are not apparent from single predator situations (Sih et al., 1998).

An important step for understanding multi-predator systems is in identifying the mechanisms that may drive community patterns of related predators, especially when these predators compete for prey, or prey on one another. Broadly speaking, coexistence of consumers is often explained via niche differentiation or character displacement (Schluter & McPhail, 1992; Pritchard & Schluter, 2001; Resetarits, 2001), but for generalist predators, these explanations are often insufficient to explain coexistence, as many are habitat generalists that often use overlapping resources (e.g., predaceous diving beetles, Lundkvist et al., 2003; Rundle et al., 2003; Yee et al., 2009). The identification of functional characteristics for predators (e.g., behavioral attributes such as hunting mode and habitat domain, Schmitz, 2005) is a relatively recent topic for understanding the coexistence of multiple predators. In general, predator hunting modes can be classified into sit-and-wait (ambush predator maintains a fixed position for prolonged periods of time), sit-and-pursue (ambush predator may follow or pounce on prey from a fixed position that may change periodically), and active (predators aggressively seek out prey from non-fixed positions), with habitat domain incorporating both microhabitat choice and the spatial extent of movement by a predator (Schmitz, 2005). Such behavioral differences could be considered a form of character displacement (Brown & Wilson, 1956), although if predators show regimented feeding patterns or behaviors (e.g., dytiscid larvae, Galewski, 1971) it would be an open question if character displacement could be considered an explanation for coexistence. Although the identification of such aspects of predators is important for understanding consumptive and non-consumptive effects on prey (reviewed in Preisser et al., 2007), evaluating how habitat domain and hunting mode affect patterns of prey consumption is an important step for fully understanding the coexistence of multiple predatory species (Schmitz, 2005).

Aquatic beetles in the family Dytiscidae (i.e., predaceous diving beetles) represent a group of predators whose community patterns remain unresolved (Vamosi & Vamosi, 2007). Many dytiscid species are widely distributed generalist predators that commonly coexist in relatively high densities, and also appear to occupy similar or overlapping niches within aquatic habitats (Zimmerman, 1959; Nilsson & Söderberg, 1996; Larson et al., 2000), which suggests perhaps a minor role for niche differentiation. Instead, dytiscid coexistence may be more directly affected by competitive intra- and interspecific interactions (Zimmerman, 1959; Juliano & Lawton, 1990a, b; Schneider & Frost, 1996; Kehl & Dettner, 2003; Hart & Marshall, 2009), dispersal behaviors (Kehl & Dettner, 2003; Yee et al., 2009), habitat isolation and dominant predator presence (Wohlfahrt & Vamosi, 2011), or a combination of these mechanisms. Recent studies have identified potential niche differentiation in some larval dytiscids (Culler & Lamp, 2009; Yee, 2010), so this mechanism remains a possibility for explaining patterns of coexistence in nature.

Dytiscids are cosmopolitan and abundant predators in isolated freshwater aquatic habitats (Larson et al., 2000) and are often the dominant predator in fishless environments (Batzer & Wissinger, 1996). This family is the most diverse among aquatic beetles ( $\sim 4,000$ species), and predatory adults and larvae simultaneously occur in a variety of aquatic habitats, with adult beetles linking such habitats via flight (Larson et al., 2000). Dytiscids prey on a variety of aquatic invertebrates (Arts et al., 1981; Deding, 1988; Kehl & Dettner, 2003; Lundkvist et al., 2003; Aditya et al., 2006) and vertebrates (Formanowicz & Bobka, 1989; Tate & Hershey, 2003); adults and larvae also engage in interspecies and intraguild predation (IGP) and cannibalism (Deding, 1988; Nilsson & Söderström, 1988; Hicks, 1994; Larson et al., 2000; Kehl & Dettner, 2003; Vamosi & Vamosi, 2007; Culler & Lamp, 2009; Yee, 2010). Beyond proximate mechanisms that may explain co-occurrence patterns of dytiscids, several factors have been examined to explain community patterns of dytiscids, including water permanence (Jeffries, 2005), habitat shading and vegetation complexity (Binckley & Resetarits, 2009; Yee, 2010), and water quality parameters such as salinity and acidity (Alarie & Leclair, 1988; Arnott et al., 2006). These examinations often do not address specific interactions between predators, nor have studies examined specific habitat associations or experimentally addressed differences in prey consumption to understand co-occurrence patterns.

We focused our attention on two common larvae dytiscid taxa found in fishless agricultural ponds in Alberta, Canada (Yee, personal observation): Graphoderus and Rhantus. Identification keys for larval dytiscid do not exist for most genera, but based on past work from these same ponds larvae were likely G. occidentalis (Horn) and R. sericans (Sharp) (Yee et al., 2009; Yee, 2010) or R. bionatuatus (Harris) (Online Resource 1), although we refer to them by their genus throughout this study. Recent work on these taxa has shown that these dytiscids are voracious predators, larvae display significant differences in hunting mode with some overlap in habitat domain (Graphoderus feed near the surface, Rhantus feed in the middle and near the bottom of the water column), and that these differences appear to influence the level of predation among and within genera (Yee, 2010). Our aims in the study were to (1) examine the relationships between spatial habitat parameters (depth and distance from shore) and abundance of larval Graphoderus and Rhantus, (2) determine the spatial associations between beetle genera and with beetles and potential prey, and (3) quantify prey consumption rates of these common dytiscids in the laboratory. These aims would allow us to test the hypothesis that high beetle abundance in ponds results, in part, from different spatial associations of, and different patterns of prey consumption for, these beetles.

# Methods

## Field sampling

Ponds were located approximately 20 km north of Strathmore, AB, Canada in agricultural prairies (51°18'17"N, 113°28'15"W) (Yee et al., 2009). This fenced site (1.6 km<sup>2</sup>) contained approximately 35 ponds that varied in size and permanence. The dominant aquatic vegetation in all temporary ponds consisted of Nuttall's salt meadow grass [*Puccinellia nuttalliana* (JA Schultes) AS Hitchc.]. From all ponds, we haphazardly selected 12 unconnected semi-

permanent or temporary ponds with the criteria that they were fishless. Ponds varied in size from 187 to 7,549 m<sup>2</sup> (mean 1,772  $\pm$  608 m<sup>2</sup>) with a maximums sampled depth of 33 cm during the period of study. Distance between neighboring ponds was between 10 and 85 m. Other ponds used in this area during the same time did not vary in significant ways in water chemistry values (Yee et al., 2009). All ponds were surveyed on 7–8 June 2007 but because of drying only 11 ponds were surveyed on 27–28 June (hereafter early vs. late June, respectively). As the active season for invertebrates in ponds in this area begins in May and ends with most ponds drying out by early August (Silver & Vamosi, 2012), our samples occurred during the mid-point of the active season.

We sampled each pond at three locations, with each location equidistant from one another so that locations formed a triangle. At each location, we took three replicate 0.16 m<sup>2</sup> samples that varied in depth and distance from the edge. This approach resulted in nine total samples per pond. At each location, the first sample was positioned at the pond edge, with the next two successive samples moving toward the center of the pond. For each sample, we carefully placed a rigid plastic bottomless tub (49  $\times$  33 cm opening) into the water column until it met the pond bottom with the longest side perpendicular to the pond edge. Thus, each successive sample was 33 cm further from the pond edge. Because placement and sampling tended to disturb the pond environment, we located subsequent samples approximately 1 m along the pond margin from the previous sample. Depth (cm) was recorded using a meter stick halfway along the longest side of the tub. Six successive sweeps (3 away and 3 toward the researcher) within the tub were made using an aquatic D-net (500  $\mu$ m). All invertebrates were then placed in 70% alcohol and returned to the laboratory for enumeration and identification.

Larval dytiscids were identified to genus (Larson et al., 2000) based on morphological differences. Adult dytiscids and mosquitoes were identified to species based on Larson et al. (2000) and Rempel (1950), respectively. Other potential prey taxa were identified to genus or family based on Clifford (1991).

## Feeding trials

All dytiscids (2nd and 3rd instars) and prey items were collected from two fishless ponds near Cochrane, AB

(51°09'041"N, 114°28'18"W). After capture, dytiscids were placed into individual plastic 100-ml cups with deionized water (DI) and fed a variety of living prey (e.g., chironomids, *Daphnia* sp.) ad libitum. All invertebrates were housed in environmental chambers set at 20°C on a 14:10 light:dark cycle (typical summer conditions). Beetles were kept in these chambers for 1–3 days before being starved 24 h prior to feeding trials.

The experimental setup consisted of clear plastic containers that varied in size to produce four depths (7, 11, 15, and 20 cm) at a constant volume of 1 l of DI water. Depths were chosen to reflect the common depths encountered during field sampling (84% of field samples were at depths between 7 and 20 cm). We used a constant density (total length of plant stems/ volume) of aquatic plants [common water Milfoil, *Myriophyllum sibiricum* (Fern.) collected from Strathmore ponds] across depth treatment levels. Plants were suspended upside down and attached via their stems into slots in cardboard lids at equal distances from each other and container walls.

We added ten individuals of one of three prey types [either chironomids (Tribe Chironomini), corixids, or damselflies (Lestes sp., Enallagma civile)] to each container prior to adding a single starved Graphoderus or Rhantus larvae. These prey represented the 1st, 2nd, and 4th most common non-beetle invertebrates collected during sampling (chironomids, corixids, damselflies). These species also displayed distinct microhabitat associations (chironomids found at the bottom, damselflies found perching on plants or near the bottom, corixids found near or at the surface) and were of different sizes (damselflies > corixids > chironomids). Based on past work (Yee, 2010), handling times for mosquito larvae prey were different between these predators (Graphoderus ate prey within ~4 min, where *Rhantus* took ~9 min). Containers were placed in an environmental chamber (as above) and after 4 h we counted the number of prey eaten. Because larval dytiscids consume prey by piercing with hollow mandibles, it was relatively easy to differentiate acts of predation versus natural mortality. We also established prey-only treatments (hereafter, controls) for each depth by prey treatment combination to quantify the frequency of predation by prey on themselves and to record natural mortality. Beetles and prey were used only once. In total, we conducted nine replicates of each predator (Graphoderus or *Rhantus*), depth (7, 11, 15, and 20 cm), and prey type (chironomids, corixids, or damselflies) combination across a series of individual runs for a total of 216 experimental units. Owing to logistic constraints, we could not conduct all treatment level combinations during each run, although each run contained each predator, all depths, and all prey types.

# Statistical analyses

We analyzed associations between the two most common beetle larvae and pond attributes using a mixed model analysis of covariance (ANCOVA) with pond as a random block term, sample depth (cm) as a covariate, distance from pond edge as a factor with three levels, and beetle abundance as the dependent variable. We ran ANCOVA for each beetle genus at each sampling period (early and late June), separately. To link abundance patterns of predators and prey, we also conducted partial correlation analyses between the two common beetle predators and three of the most common prey (chironomids, corixids, or damselflies) in early and late June, separately, with pond and pond depth as partial correlations. Partial correlations were used to control for variation in predators and prey abundances among ponds and across depths. Because of the number of tests, we used a Bonferroni correction to control for experimental-wise error rate (i.e.,  $\alpha = 0.005$ ).

Mean consumption of prey was analyzed using three-way analysis of variance (ANOVA) with predator taxa, depth, and prey type as independent variables, and arcsine square root transformed proportion prey eaten as the dependant variable. This transformation was conducted to meet assumptions of ANOVA. We performed follow-up Tukey tests using a Bonferroni correction to control for experimental-wise error rates. All analyses were preformed in SAS (2004).

## Results

# Field sampling

Ponds yielded over 17,000 invertebrates (Online Resource 1) representing 62 unique taxonomic affiliations. Dytiscid larvae were one of the most common groups of aquatic invertebrates collected during both sampling periods, accounting for 25.4% of all individuals; dytiscid adults constituted only 2.0% of all individuals. Other common groups included chironomids (40.1%), corixids (9.2%), hydrophilid larvae and adults (approximately 4.9 and 6.1%, respectively), clam shrimp (5.2%), and damselflies (3.2%). There were general differences in abundance between time periods for some groups (e.g., chironomids accounted for <1% of individuals in early June, but 54.0% in late June).

For Graphoderus, we found no effect of depth (early June,  $F_{1.91} = 0.59$ , P = 0.444; late June  $F_{1.83} = 0.82, P = 0.369$ , distance to the pond edge (early June,  $F_{2,91} = 0.26$ , P = 0.775; late June  $F_{2.83} = 0.78$ , P = 0.462), or their interaction (early June,  $F_{2,91} = 0.64$ , P = 0.527; late June  $F_{2,83} =$ 0.47, P = 0.627). A similar outcome was determined for Rhantus, wherein we found no effect of depth (early June,  $F_{1,91} = 0.08$ , P = 0.784; late June  $F_{1.83} = 2.70, P = 0.105$ , distance to the pond edge (early June,  $F_{2,91} = 0.46$ , P = 0.633; late June  $F_{2,83} = 1.06, P = 0.350$ , or their interaction (early June,  $F_{2.91} = 0.35$ , P = 0.705; late June  $F_{2.83} =$ 0.54, P = 0.582). Thus, the abundance of beetles did not vary significantly with increasing depth or with distance from the pond edge during either sampling period.

Partial correlations of predators and common prey in ponds were often significant and generally positive. Abundance of *Graphoderus* and *Rhantus* in ponds was significantly correlated in early (r = +0.600, P < 0.001) but not late June (r = +0.10, P = 0.314). *Graphoderus* were significantly correlated with corixids in early (r = +0.255, P < 0.001) and late June (r = +0.470, P < 0.001), with *Rhantus* also displaying several significant correlations with prey, including corixids in early June (r = +0.532, P < 0.001) and chironomids (r = +0.315, P = 0.002) in late June. Other correlations between predators and prey were not significant.

#### Feeding trials

In none of the control treatments in the laboratory did we observe predation or mortality, and thus we assumed that prey died due to the activities of beetle larvae. In the prey and predator containers, we detected a species  $\times$  prey type interaction (Table 1). Based on mean separation, *Graphoderus* at significantly more corixids compared to other prey types, with *Rhantus* eating a similar proportion of corixids

**Table 1** Results of three-way analysis of variance on predation rates for different predator species (*Graphoderus*, *Rhantus*) and prey types (chironomids, corixids, damselflies) across depths

	df	F	P value
Species (S)	1,192	3.15	0.078
Depth (D)	3,192	3.90	0.010
Prey (P)	2,192	63.18	< 0.001
$S \times P$	2,192	8.68	< 0.001
$D \times P$	6,192	0.97	0.447
$S \times D$	3,192	2.35	0.074
$S \times D \times P$	6,192	0.89	0.501

and chironomids (Fig. 1). Predation by both predators on damselflies was significantly lower than other prey types except predation of chironomids by *Graphoderus* (Fig. 1). We also identified a single significant effect of depth and a marginally significant interaction between depth and species (Table 1). *Graphoderus* and *Rhantus* consumed significantly more prey at 7 cm compared to *Graphoderus* at 11 cm, with other depths resulting in intermediate prey consumption (Fig. 2).

### Discussion

In many ecological studies, niche differentiation or character displacement is important mechanisms invoked to explain coexistence patterns (Schluter & McPhail, 1992; Pritchard & Schluter, 2001; Resetarits, 2001; Pfennig & Murphy, 2003). Habitat generalists, such as dytiscids, often possess overlapping habitat requirements and consequently use similar resources (Lundkvist et al., 2002; Rundle et al., 2003; Yee et al., 2009). Therefore, niche differentiation is likely insufficient to explain coexistence of generalist predators. Correspondingly, we found no specific associations with beetle larvae and habitat parameters in the field, although there were strong links between the types of prey consumed more frequently in the laboratory and the associations between beetle larvae and those prey in natural ponds. These results lend some support to our hypothesis that high beetle abundance in ponds is a result of differences in prey consumption among predators, whereas different spatial associations, at least at the scale considered, do not appear to be important for abundance patterns of predators. We



Fig. 1 Mean ( $\pm$ SE) percent predation of different beetle species on three types of common prey from laboratory trials. The *same letters* shared by means indicate no significant differences after correcting for multiple comparisons



Fig. 2 Mean ( $\pm$ SE) percent predation of different beetle species across depths from laboratory trials. The *same letters* shared by means indicate no significant differences after correcting for multiple comparisons

note that other mechanisms may also lead to the patterns we observed between predator and prey, including similarities in oviposition preferences of adults and associations to similar environmental parameters, and thus we caution that these findings represent correlations, and do not reflect causation. Differences in life-history parameters (e.g., growth rates) may affect co-occurrence patterns, although little of this information exists for larvae dytiscids (Larson et al., 2000). Furthermore, our findings do not support functional equivalency for these predators even though the genera used were of similar size and appear to share some aspects of habitat domain (Yee, 2010). As noted elsewhere (Chalcraft & Resetarits, 2003; Resetarits & Chalcraft, 2007), the functional equivalency of predatory groups is often less than their functional diversity, and this fact may make it difficult to assess a priori if morphologically similar congeners are likely to show similar effects on communities of prey.

The association between any species and its habitat depends not only on the specific ecological requirements, but includes interactions with coexisting species, such as competition and predation (Polis & Holt, 1992). Predation is often a major structuring mechanism of ecosystems (Holt & Polis, 1997; Sih et al., 1998), and differences in functional characteristics of predaceous species can be a main factor leading to coexistence of multiple predators (Schmitz, 2005). Important functional characteristics include behavioral attributes such as specific hunting mode and habitat domain (Schmitz, 2005). Several authors have noted that predator functional roles vary among dytiscid larvae (Formanowicz, 1987; Formanowicz & Bobka, 1989; Culler & Lamp, 2009; Michel & Adams, 2009). Recently, Culler & Lamp (2009) examined selective predation by dytiscid beetles in the genus Agabus. They found no differences in prey consumption rates for different prey types in nochoice tests. In contrast, differences in prey consumption rates were evident when predators had a choice of prey types, revealing occurrences of selective predation. Our study design did not allow us to explore prey selectively by predators, but it seems likely that particular aspects of behavior noted elsewhere could lead to prey preferences. Specifically, Yee (2010) assessed habitat domain and hunting mode for the same beetle genera examined here and showed that Graphoderus was an active, open-water hunter, whereas Rhantus showed a mixture of sit-and-wait and active hunting modes. In addition, Graphoderus was more likely to be found near the top of containers, with Rhantus found in the middle or near the bottom (Yee, 2010). Thus, because of some differences in habitat use we may expect them to differentially exploit prey types that also exist in different areas of the habitat. We do note that our field sampling design did not allow us to quantify the differential spatial associations of these larvae, and thus it remains a possibility that such a mechanism could be operating in natural ponds to explain predator coexistence.

Microhabitat use by predators and prey may help to explain patterns of prey consumption noted in our trials. Both predators consumed corixids at a high rate, and this prey type is known to be an active swimmer found near the bottom of the water column but must occasionally surface for air (Merritt et al., 2008). Thus, some aspects of the habitat domain of both predators may overlap with the prey's habitat use to explain consumption patterns (both species are found in the middle or top of containers, Yee, 2010). Indeed, of all prey types considered only corixids displayed high activity levels in the presence of beetles, and this may help further explain the overall high consumption rates for this type of prey (Fig. 1). In contrast to corixids, the chironomids we used were often found in sediments (personal observation), and although we did not use a substrate in our experimental trials, these prey were still located on the bottom of containers. Their location would have increased their encounters with Rhantus compared to Graphoderus, the latter being consistently found near the tops of containers (Yee, 2010). As predators themselves, damselfly larvae engage in a variety of behaviors (Merritt et al., 2008) although the species used in this study seem to be found near the bottom and often cling to vegetation (Miura & Takahashi, 1988; Stoks & McPeek, 2003). When damselflies were primarily using plants as a perch, this may have offered them a refuge from predation not exploited by other prey. The results presented here corroborate past work showing low predation on damselflies by these predators (Yee, 2010). Overall, the frequency of predation on different prey types does seem to overlap with the known hunting mode and habitat domains for these predators, and may represent a mechanism facilitating coexistence of these predators in nature (Schmitz, 2005).

In addition to the effects of predation, IGP (predators that share prey and also consume one another) may also be an important factor influencing the distributions of species in communities (Polis et al., 1989; Polis & Holt, 1992). This interaction is likely among dytiscids, as they exhibit high densities in ponds, high spatial and temporal overlap among species within ponds, and apparent generalist feeding among species (Nilsson & Söderström, 1988; Larson et al., 2000; Vamosi & Vamosi, 2007). Indeed, a recent multi-species comparison by Yee (2010) revealed predation among several dytiscid genera including Graphoderus and Rhantus. The results showed that Graphoderus was a poor predator on members of its own genus but was more successful preying on Rhantus. Thus, coexistence patterns of these generalist predators may not only be modulated by prey type specific consumption rates on heterospecific prey, but also by differing consumption rates for conspecifics relative to consumption of other generalist predators. Future studies should investigate the effects of specific consumption rates via predation and IGP on the coexistence of generalists in more detail.

In summary, dytiscid abundance in the field was not associated with pond depth or distance from edge at the tested spatial scale. However, prey consumption rates significantly varied with water depth. The openwater predator Graphoderus consumed significantly more prey that showed active swimming behavior close to the water surface (i.e., corixids), whereas the ambush predator Rhantus preyed at an equal rate on active (i.e., corixids) and on substrate-associated prey (i.e., chironomids). Correlations with predators and prey from ponds were congruent with results from predation trials in the laboratory. Thus, results of prey consumption trials in this experiment likely reflect differences in the spatial locations of predators and prey. The results of this study highlight the importance of considering different prey types and prey-specific links to different microhabitats, when coexistence patterns of habitat generalists are evaluated. Preyspecific consumption rates and associated differences in hunting mode may be an important mechanism for the maintenance of high predator diversity in nature.

Acknowledgments We thank S. Taylor for assistance in the field and in the laboratory and the Reinhardt Family and J. Brunen (Ducks Unlimited, Alberta, Canada) for providing access to the field site. This project was supported by funds from an Alberta Ingenuity New Faculty Award (#20060362) and an Natural Sciences and Engineering Research Council of Canada Discovery Grant (RGP283114) to S.M.V.

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