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NICHE OVERLAP AND THE POTENTIAL FOR COMPETITION AND INTRAGUILD PREDATION BETWEEN SIZE-STRUCTURED POPULATIONS[1]

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Abstract. Many populations are heterogeneous collections of different sizes or stages of conspecifics. Existing overlap indices do not account for the size-/stage-structured nature of these populations. In this paper I present new overlap indices that use information about the sizes of individuals that co-occur in time and space to predict the potential for interactions in size-structured guilds. An index of the opportunity for competition (IOC) calculates the frequency with which similar size classes of two species encounter each other, whereas an index of the opportunity for intraguild predation (IOP) calculates the frequency of encounters among disparate size classes of the same two species.

To illustrate that these indices are more appropriate for size-structured populations than conventional indices, I calculated overlap, IOP, and IOC for all species pairs in a diverse assemblage of dragonfly larvae. The new indices revealed size-specific patterns of overlap that were not detected by the conventional index, including that (1) some species with high overlap values should interact mainly as competitors, others mainly as intraguild predators, and many as both competitors and predators, (2) subtle differences in phenology and/or size-specific shifts in habitat distribution can lead to the potential for asymmetric interspecific interactions, (3) some species with low pairwise IOP and IOC values are nonetheless vulnerable to the effects of diffuse competition or intraguild predation, (4) seasonal segregation reduces competitive overlap but at the same time increases the opportunity for intraguild predation. The indices are general in form and should be useful for analyzing distributional data for any size-structured assemblage in which the type and intensity of interaction varies as a function of relative size.

Key words: cannibalism; competition; guilds; intraguild predation; niche overlap; odonates; overlap indices; size-structured populations.

INTRODUCTION

Indices that summarize patterns of resource overlap (food, habitat, etc.) are often used to generate testable hypotheses about the population- and community-level effects of interspecific interactions. The indices most frequently used by ecologists assume that individuals within a population are ecologically identical and therefore overlap to the same degree with individuals of another species (Colwell and Fuentes 1975, Hurlbert 1978, Abrams 1980, Linton et al. 1980, Slobodchikoff and Schulz 1980, Loman 1986, Lu et al. 1989). While this assumption might be reasonable for birds and mammals (but see Łomnicki 1988), it has become increasingly obvious that it is not for many fish, amphibians, and freshwater, marine, and terrestrial invertebrates. Populations of these organisms are often heterogeneous collections of individuals that differ considerably in size and/or life stage, and are said to be highly size- or stage-structured (see reviews by Wilbur 1980, Polis 1984, 1988, Werner and Gilliam 1984, Ebenman and Persson 1988). The ontogenetic size and/or stage changes that occur in these taxa are accompanied by shifts in diet and/or habitat to the extent that different individuals within the same population can differ in resource use by as much or more than that observed between different species of birds and mammals (Keast 1977, Polis 1984, Ebenman 1987, Mittelbach et al. 1988, Muotka 1990). Existing overlap indices do not account for this within-population variation in resource use, and thus, provide an inadequate summary of the potential for competition in many guilds.

Existing indices also do not address the potential for "intraguild predation" (sensu Polis and McCormick 1987) in assemblages in which potential competitors also prey on each other. Recent reviews document that many species concurrently interact as competitors and intraguild predators, and that this complex pattern of interspecific interaction plays an important role in the organization of many communities (Werner and Gilliam 1984, Wilbur 1984, 1988, Sih et al. 1985, Polis 1988, Polis et al. 1989). Information about the potential for intraguild competition and predation is important for designing manipulative experiments between these types of species because both interactions can simultaneously affect the response variables (e.g., survival, growth) typically used to interpret those ex-

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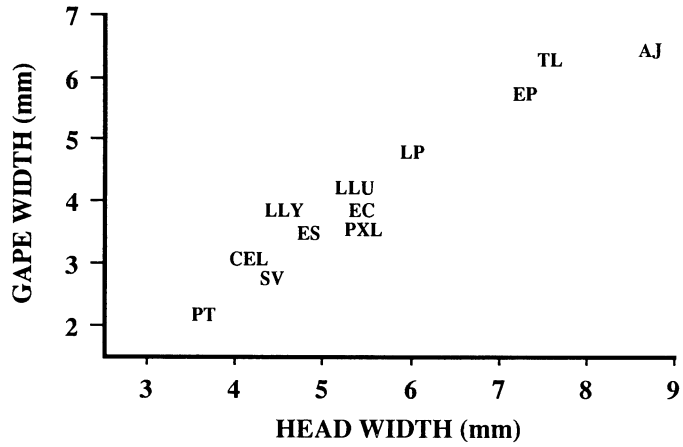


FIG. 1. Interspecific size variation among 12 species of larval dragonflies. Head and gape (labium) widths are for the final instar of each species. Size data for the numerous smaller instars of each species are given in Appendix 1. The abbreviations here are also used in Tables 1–3: PT = *Perithemis tenera,* LLY = *Libellula lydia,* LLU = *Libellula luctuosa,* TL = *Tramea lacerata,* EC = *Epitheca cynosura,* ES = *Erythemis simplicicollis,* SV = *Sympetrum vicinum,* AJ = *Anax junius,* LP = *Libellula pulchella,* PXL = *Pachydiplax longipennis,* EP = *Epitheca princeps,* CEL = *Celithemis elisa.*

periments (Benke 1978, Bradley 1983, Morin 1983, Reichert and Cady 1983, Johnson et al. 1985, Cortwright 1989, Van Buskirk 1989, Wissinger 1989*b*, Hurd and Eisenberg 1990, Spiller and Schoener 1990).

The purpose of this paper is to introduce overlap indices that use information about size variation within populations to summarize the potential for competition and predation in size-structured guilds. The index developed for inferring the opportunity for exploitative competition calculates the frequency with which similarly sized individuals of two species overlap in time and space, whereas the index of the opportunity for intraguild predation calculates the overlap frequency of disparately sized individuals. I assume that the purpose of using such indices is not to prove that particular functional relationships exist between species, but rather to uncover patterns that suggest which of the many possible interactions in a multispecies assemblage should be most profitable to explore experimentally (Hurlbert 1978, Abrams 1980, Lawlor 1980, Mac Nally 1983).

To illustrate the utility of the indices, I use them to summarize the potential for population interactions in a species-rich assemblage of pond-dwelling dragonfly larvae. Inferring the potential for interspecific interaction in this assemblage from field data alone was difficult because of the bewildering array of size combinations that co-occur in time and space (see Appendices 1 and 2). This particular assemblage is complexly size structured because: (1) individuals increase dramatically in size during the 10–15 stages (instars) of larval development, (2) species differ in size at a given instar (see Fig. 1), (3) many different instars of each species are present at any point in time as a result of asynchronous development and/or overlap between generations (Wissinger 1988*b*; Appendix 1), and (4) habitat use among species and among instars within a species varies ontogenetically and seasonally (Wissinger 1988*c*; Appendix 2).

The indices developed in this paper can be used for any assemblage of size-structured populations for which there is information about the distribution and abundance of size (year or stage) classes, and for which there is some general information about the relationship between body size and prey size (e.g., as in Paine 1963, Allan et al. 1987, Polis and McCormick 1987). In the case of dragonflies, individuals tend to choose prey based mainly on size, rather than taxon (Thompson 1978*a*, *b* and references therein). Similarly sized individuals of different species tend to converge on the same abundant prey (Pritchard 1964, Merrill and Johnson 1984 and references therein). When resources are limiting, the intensity of competition between two dragonfly species should depend to a large extent on how frequently larvae that are similar in size overlap in time and space (Crowley and Johnson 1982). In contrast, encounters between disparate sizes of larvae are more likely to result in intraguild predation (Robinson and Wellborn 1987, Van Buskirk 1988, 1989, Wissinger 1988*a*, 1989*b*). This size-specific shift in interaction is not unique to dragonflies. In general, similar size classes of competing predators are more likely to overlap in diet than disparate size classes, which are more likely to interact as predator and prey (Polis et al. 1989).

METHODS

*Spatiotemporal overlap—Hurlbert's index (*L*)*

To set a standard for comparison, spatiotemporal habitat overlap between species was calculated in the conventional manner using Hurlbert's (1978) index "*L*." Results obtained using Schoener's (1970) index of similarity and MacArthur and Levins' (1967) com-

petition coefficient produced qualitatively similar conclusions about the patterns of interspecific overlap in this assemblage (S. A. Wissinger, *unpublished data*). I chose Hurlbert's index because it (1) considers the relative abundance of resource categories, (2) can be interpreted to indicate encounter frequencies in time and space, and (3) was easily modified to consider size-specific overlap.

Briefly (also see Appendix 3), Hurlbert's index L expresses the degree to which interspecific overlap (O) differs from that expected (O_e) when two species use resources according to resource abundance, or

$$L_{ij} = O/O_e = \sum_k p_{ik}p_{jk}/p_k, \qquad (1)$$

where p_{ik} and p_{jk} are the proportional abundances of the i^{th} and j^{th} species in the k^{th} resource category, respectively, and p_k is the proportional abundance of the k^{th} resource category. Although biomass data can be used to estimate abundance (e.g., Crowley and Johnson 1982), I used densities to emphasize the probability of encounters between individuals.

When $i = j$, index L can be interpreted as the degree of intraspecific resource specialization (reciprocal of niche breadth; see Hurlbert 1978, Crowley and Johnson 1982). For interspecific comparisons, $L_{ij} = 1$ when both species use resources according to resource abundance, and 0 when species do not share any resource categories. When both species disproportionately use the same resource categories, $L_{ij} > 1$ (e.g., when $L_{ij} = 2$, species i and j co-occur 2 times more than expected if both were distributed according to resource abundance).

I calculate all indices using the 36 (9 dates × 4 spatial habitats) "resource" categories from which the field data were collected (Wissinger 1988*c*; Appendix 2). The separate calculation of spatial overlap by averaging across dates, or temporal overlap by averaging across spatial categories is potentially misleading because of species-specific seasonal shifts in spatial distribution (Wissinger 1988*c*; see also May 1975).

The relative abundances of habitat categories used in the index (p_k's) are proportional to the areas of the different habitats. Resources were not weighted according to their use by all species because such inferences about "resource availability" weaken the interpretation of the index (S. Hurlbert, *personal communication*). If temporal and/or spatial distributions of species have been influenced by biotic interactions, then using those distributions to infer the availability of resources is circular, even when the two species being indexed are excluded from the weightings (as in Colwell and Futuyma 1971, Crowley and Johnson 1982). In the absence of information on consumer–resource interactions, it was inappropriate to calculate competition coefficients from ratios of inter- to intraspecific overlap (see Abrams 1980, Lawlor 1980).

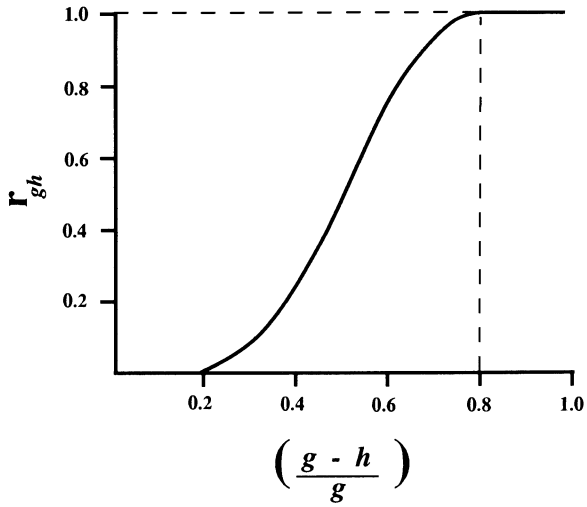


FIG. 2. Plot of the predation function used for calculating the index of the opportunity for predation (IOP). The function relates proportional differences in predator gape (labium) width (g) and prey head width (h) to the proportion of interactions between individuals of those sizes that are likely to result in predation (r_{gh}).

Size-specific overlap indices

Like Hurlbert's index L, these indices also consider the frequency of interspecific encounter, but differ in that all encounters are not of equal relevance to competition and intraguild predation, as will be the case when there is size variation within populations. The indices calculate the frequency with which different size combinations encounter each other in time and space, and weight each encounter according to relative size.

1. *Index of the opportunity for predation (IOP).*— The coefficient (r_{gh}) used to weight encounters in the predation index assumes that the likelihood of predation increases as individual size differences increase. The particular function used in this analysis is based on laboratory data for predation rates between a variety of larval dragonflies including *Libellula lydia, Libellula luctuosa, Tramea lacerata,* and *Erythemis simplicicollis* (Wissinger 1988*a* and *unpublished data*). Proportional size differences between the gape (labium) width (g) of a large larva, and the head width (h) of a small larva is a good predictor of predation rates for a wide range of instar and species combinations. When $(g - h)/g \leq 0$, $r_{gh} = 0$, i.e., there is minimal predation between similarly sized larvae, and smaller larvae do not prey on larger larvae (Fig. 2). Intraguild predation is likely when $(g - h)/g > 0.20$, and predation rates increase as a function of proportional size differences. When the gape width of one instar is 80% larger than the head width of another (i.e., $[g - h]/g > 0.80$), predation is always likely ($r_{gh} = 1.00$). While the specific function I use here is based on data for dragonfly larvae, it seems likely that the general form of this function will be appropriate for many generalist predators, i.e., there will be a minimum size difference be-

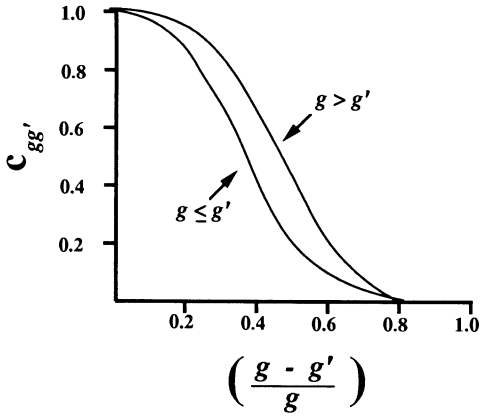


FIG. 3. Plot of the function used for calculating the index of the opportunity for competition (IOC). The function relates proportional size differences in gape (labium width) of two species, g and g', to the likelihood that interactions between individuals of those sizes will be competitive ($c_{gg'}$). For an equivalent size difference in gape, $c_{gg'}$ is larger for the competitive effect of large on small individuals than for the converse.

low which predation is unlikely, and above which predation becomes more likely as sizes become more disparate (e.g., Travis et al. 1985, Polis et al. 1989). For some predators, detection rates may decrease for extremely small prey so that the maximum for this function would be at intermediate size differences (e.g., Allan et al. 1987).

The "index of the opportunity for predation" (IOP) that uses this function differs from Hurlbert's index only in that encounters in time and space are tallied on a size-specific basis, with each encounter weighted by a predation coefficient, in this case, r_{gh}. The index compares the number of potentially predatory encounters O_p to expected encounters O_e, or

$$\mathrm{IOP}_{ij} = O_p/O_e = \sum_g \sum_h \sum_k (p_{igk} p_{jhk} r_{gh})/p_k \qquad (2)$$

where r_{gh} is the potential for predation between the g^{th} instar of predator species i, and the h^{th} instar of prey species j; p_{igk} and p_{jhk} are the proportional abundances of the g^{th} and h^{th} instars of the i^{th} and j^{th} species, respectively, in the k^{th} resource category, and p_k is the proportional abundance of the k^{th} resource category. The index is zero when there is no overlap or when all overlapping larvae are similar in size (i.e., all $r_{gh} = 0$). When all overlapping instar combinations are disparate in size (i.e., all $r_{gh} = 1$), IOP will be the same as Hurlbert's overlap index L. Unlike the situation in conventional overlap analyses, IOP values can be asymmetric, and the index needs to be calculated twice for each pair of species. The derivation of IOP and its algebraic relationship to Hurlbert's index are given in Appendix 3.

2. *Index of the opportunity for competition (IOC).*—The opportunity for exploitative competition can be similarly estimated for size-structured populations by assuming that dietary overlap increases as the difference in gape size decreases. For dragonflies, dietary data from both experimental (Thompson 1978*b*) and field studies (Thompson 1978*a*, Merrill and Johnson 1984 and references therein) suggest that larger larvae use both larger mean prey sizes and a wider array of prey sizes than small larvae. Thus, dietary overlap should be asymmetric with large larvae overlapping more with small larvae than conversely (Wilson 1975, Polis et al. 1989).

The function used as a weighting coefficient for competition, $c_{gg'}$, decreases as the disparity in gape width increases (Fig. 3). When gape widths are identical, the potential for competition is greatest (i.e., $c_{gg'}$ is 1.0); and when they differ by 80% or more, $(g - g'/g > 0.80)$, competition will be minimal (i.e., $c_{gg'}$ is 0). At intermediate size differences, large larvae are assumed to have a greater competitive effect on small larvae than vice versa. I originally compared the results of decreasing convex, concave, linear, and sigmoid functions using the same endpoints and found they had only minor effects on the general conclusions (S. A. Wissinger, *unpublished data*). I chose the sigmoid over a linear function because it preserves the same zero-competition endpoint, but allows for asymmetries at intermediate values.

The index of the opportunity for competition, IOC, differs only from IOP in the way size combinations are weighted, that is,

$$\mathrm{IOC}_{ij} = O_c/O_e = \sum_g \sum_{g'} \sum_k (p_{igk} p_{jg'k} c_{gg'})/p_k, \qquad (3)$$

where $c_{gg'}$ is the potential for competition between the g^{th} and g'^{th} instars of the i^{th} and j^{th} species, respectively. All other notation is the same as in Eq. 2. IOC = 0 when no larvae of two species overlap or when all overlapping larvae are extremely disparate in size (i.e., all $c_{gg'} = 0$). IOC will be the same as Hurlbert's L when all overlapping larvae are similar in size. Because different $c_{gg'}$ values are used depending on which species has the size advantage in a particular comparison, the potential for competition can be asymmetric (i.e., IOC_{ij} does not necessarily equal IOC_{ji}).

Data collection

The data analyzed with the indices, and the methods for collecting those data from a small pond in central Indiana are presented in Wissinger (1988*b*). The indices are calculated for the 12 most abundant species in that assemblage during the 1982–1983 generation using mean densities ($n = 6$) for each larval stage (instar) of each species in each of four spatial habitats once a month during the nine ice-free months of the year (total of 36 spatiotemporal habitat categories). Gape (maximum width of labial prementum) and head widths used for the predation and competition coefficients in the IOP and IOC indices, respectively, were based on means ($n = 10$) of measurements taken to

TABLE 1. Spatiotemporal overlap using Hurlbert's L for 12 species in 36 spatiotemporal habitat categories (4 depths × 9 dates). Habitat specialization values are italic on the diagonal. Species (abbreviated as in Fig. 1) are arranged in decreasing order of abundance.

	PT	LLY	LLU	TL	EC	ES	SV	AJ	LP	PXL	EP	CEL
PT	*1.70*	1.22	1.19	1.47	1.37	1.04	0.82	0.99	0.95	1.00	1.39	1.40
LLY		*8.39*	8.13	6.18	5.75	8.81	2.37	6.91	7.20	8.26	4.32	4.69
LLU			*7.96*	5.73	5.38	8.56	2.43	6.56	7.09	7.74	4.10	4.61
TL				*8.52*	6.55	6.12	2.61	7.20	4.85	7.38	5.17	4.48
EC					*7.18*	5.34	2.97	5.44	4.54	6.75	5.23	4.80
ES						*9.63*	2.06	7.39	7.82	8.72	3.99	4.49
SV							*9.52*	3.07	2.49	2.58	2.70	2.29
AJ								*7.68*	6.04	7.92	4.26	3.88
LP									*6.72*	6.96	3.49	4.12
PXL										*9.55*	4.91	4.53
EP											*4.27*	3.93
CEL												*4.59*

the nearest 0.05 mm with a Wild M8 dissecting microscope (Appendix 1).

The four spatial habitats, nearshore shelf (0–0.5 m in depth), slope (0.5–1.0 m in depth), central basin (1.0–1.5 m in depth), and deep trough (>1.5 m in depth) account for 16, 17, 40, and 27% of the total pond area, respectively. A detailed description of the substrate and vegetational characteristics of these habitats, and the rationale for subdividing the pond in this manner is given in Wissinger (1988*c*).

RESULTS AND DISCUSSION

Conventional overlap analysis

The high overlap values for many species pairs in this assemblage indicate they co-occur to a far greater extent than if they were distributed according to habitat abundance (Table 1). Congeners and other morphologically similar species are most convergent in time and space, and there is little evidence for complementarity in the spatial and temporal use of habitats as found in previous studies (Crowley and Johnson 1982, Carchini and Nicolai 1984). The absence of macrohabitat partitioning is perhaps surprising given that congeners are also most similar in their use of microhabitat (e.g., vegetation climbers, bottom sprawlers), foraging mode (e.g., stalkers, ambushers), and diet (Benke and Benke 1975, Johannsson 1978, Nestler 1980, Blois 1985). The overall patterns of overlap among the dragonfly larvae in this study and in Blois (1985) better fit the predictions of the "competitive coexistence principle" (closely related species are expected to be more convergent in habitat use than expected from a random distribution of species) than the predictions of the "competitive exclusion principle" (see Simberloff 1970, den Boer 1986).

The three smallest species in the assemblage, *Perithemis tenera, Sympetrum vicinum,* and *Celithemis elisa,* have the lowest conventional overlap values (Fig. 1, Table 1). The low overlap values for *P. tenera* reflect

TABLE 2. Indices of the opportunity for intraguild predation (IOP) between 12 species of larval dragonflies (abbreviated as in Fig. 1). IOP_{ij} values are for the predatory effects of the i^{th} species (row) on the j^{th} species (column).*

	PT	LLY	LLU	TL	EC	ES	SV	AJ	LP	PXL	EP	CEL	Total as predator	
PT	*0.05*	0.13	0.14	0.10	0.16	0.07	0.07	0.19	0.08	0.09	0.03	0.36	PT	1.4
LLY	0.38	*0.67*	0.49	0.25	0.17	0.44	0.90	0.28	0.36	0.41	0.12	1.55	LLY	5.4
LLU	0.13	0.16	*0.08*	0.17	0.05	0.17	1.21	0.13	0.07	0.23	0.04	1.20	LLU	3.6
TL	0.88	3.52	3.50	*1.36*	2.13	3.63	1.55	1.51	2.52	2.21	1.13	3.23	TL	25.8
EC	0.38	0.35	0.16	0.01	*0.00*	0.16	1.57	0.11	0.14	0.14	0.00	1.54	EC	4.6
ES	0.33	0.88	0.77	0.24	0.21	*0.58*	0.54	0.30	0.55	0.52	0.12	1.43	ES	5.9
SV	0.24	0.71	0.70	0.29	0.65	0.43	*0.01*	0.43	0.37	0.34	0.32	0.76	SV	5.2
AJ	0.21	1.52	1.38	0.65	0.38	1.40	1.50	*0.61*	1.15	1.19	0.26	1.63	AJ	9.6
LP	0.21	0.51	0.48	0.34	0.23	0.47	1.49	0.30	*0.18*	0.56	0.14	1.15	LP	5.9
PXL	0.25	0.83	0.62	0.37	0.27	0.44	0.77	0.48	0.42	*0.48*	0.15	1.40	PXL	6.0
EP	0.79	0.35	0.29	0.67	0.22	0.28	1.62	0.47	0.21	0.29	*0.13*	1.53	EP	6.7
CEL	0.08	0.05	0.05	0.09	0.05	0.04	0.37	0.12	0.00	0.05	0.12	*0.50*	CEL	1.0
	PT	LLY	LLU	TL	EC	ES	SV	AJ	LP	PXL	EP	CEL		
	3.9	9.0	8.6	3.2	4.5	7.5	11.6	4.3	5.9	6.0	2.4	15.8		
	Diffuse predation													

* Row totals predict the overall importance of each species as a predator in the guild, and column totals predict the potential for diffuse intraguild predation on each species. Intraspecific predation (cannibalism) values (italic on diagonal) are not included in row or column totals.

TABLE 3. Indices of the opportunity for competition (IOC) between 12 species of larval dragonflies (abbreviated as in Fig. 1). IOC_{ij} values are for the effects of the i^{th} species (row) on the j^{th} species (column).*

	PT	LLY	LLU	TL	EC	ES	SV	AJ	LP	PXL	EP	CEL	Total as competitor	
PT	*1.42*	0.50	0.71	0.47	0.40	0.51	0.34	0.36	0.41	0.48	0.25	0.77	PT	5.2
LLY	0.59	*6.26*	6.74	3.33	4.83	6.52	0.52	4.00	5.68	6.27	3.41	2.63	LLY	44.5
LLU	0.77	6.48	*7.32*	3.09	4.35	6.59	0.34	3.87	5.95	5.65	3.23	3.09	LLU	43.4
TL	0.49	4.02	3.21	*6.29*	4.45	3.97	1.46	3.23	2.95	4.72	2.79	1.39	TL	32.7
EC	0.51	4.88	4.62	3.79	*7.03*	4.16	0.48	3.98	3.67	5.40	4.39	2.83	EC	38.7
ES	0.57	6.61	6.96	3.30	4.14	*7.12*	0.56	3.91	5.94	6.37	2.92	2.65	ES	43.9
SV	0.28	0.45	1.38	0.49	0.54	0.52	*9.13*	0.40	0.22	0.65	0.24	0.53	SV	5.7
AJ	0.36	4.21	2.75	2.75	3.91	4.13	0.43	*4.53*	3.62	4.35	2.77	2.25	AJ	31.5
LP	0.49	5.54	6.60	2.42	3.49	5.87	0.35	3.32	*5.71*	4.94	2.61	2.38	LP	38.0
PXL	0.50	6.36	6.04	4.20	5.53	6.37	0.72	4.27	5.01	*7.25*	3.78	2.26	PXL	45.0
EP	0.33	3.45	3.40	2.43	4.49	2.95	0.35	2.72	2.62	3.68	*3.71*	2.04	EP	28.5
CEL	0.81	1.45	2.52	1.03	1.54	2.07	0.69	0.88	2.14	1.86	1.85	*2.79*	CEL	16.8
	PT	LLY	LLU	TL	EC	ES	SV	AJ	LP	PXL	EP	CEL		
	5.7	43.9	44.9	27.3	37.7	43.7	50.3	30.9	38.2	44.4	28.2	25.6		
	Diffuse competition													

* Row totals predict the overall importance of each species as a competitor in this guild, and column totals predict the potential for diffuse competition on each species. Intraspecific competition values (italic on diagonal) are not included in row or column totals.

the predominant use of offshore habitats that are rarely utilized by other species (Appendix 2). This is the one species in the assemblage for which the conventional overlap values (Table 1) alone provide enough information for predicting the opportunity for competition and predation (Tables 2 and 3). The low spatial overlap with other species is perhaps not surprising (see also Benke and Benke 1975, Thorp and Diggens 1982, Wissinger 1988*c*), given that *P. tenera* is asymmetrically vulnerable to competitive and predatory interactions with larger species (Morin 1984*a, b*).

The low overlap values of the other two species are the result of temporal segregation, which minimizes the opportunity for competition, but at the same time enhances the opportunity for intraguild predation. In the case of *S. vicinum,* eggs hatch in early spring and larval development occurs during summer. Eggs of most species in the assemblage hatch in early summer with larval development ensuing through the following spring (Wissinger 1988*b*). Because *S. vicinum* larvae are either not present or are different in size from other species, overlap and IOC values are low (Tables 1 and 3). However, *S. vicinum* is vulnerable to intraguild predation because nearly all encounters in spring are between small *S. vicinum* and large instars of other species (see column total in Table 2). A similar scenario explains why *C. elisa* appears to be vulnerable to intraguild predation, despite relatively low conventional overlap (Tables 1 and 2). *C. elisa* breeds later in the summer than most species so that larvae are smaller in size than those of other species. Previous experimental studies provide empirical evidence that this predicted size disadvantage results in ecologically relevant rates of intraguild predation on *Celithemis* (Benke 1978, Benke et al. 1982). In general, although temporal segregation can minimize the potential for competition between size-structured populations, it should also enhance the opportunity for intraguild predation, especially in temperate habitats where complete temporal segregation is unlikely (see also Polis 1988). The potential for intraguild predation on these two species was not obvious from the conventional overlap analysis.

Size-specific overlap—competition, intraguild predation, both?

Although the conventional overlap indices suggest that many species in this assemblage frequently co-occur in time and space, they do not indicate which species will be potential competitors and/or intraguild predators. The IOC and IOP results indicate that some pairs of highly overlapping species are similar in size at the same place and time, and therefore should frequently interact as competitors and rarely as intraguild predators (e.g., *Epitheca cynosura* and *E. princeps*; Table 3). In contrast, other species with high overlap values are frequently disparate in size and therefore likely to interact mainly as intraguild predators and prey (e.g., *Tramea lacerata* on three *Libellula* species; Table 2). Finally, some species with large overlap values are both potential competitors and predators because both similar and disparate sizes of larvae frequently co-occur in time and space (e.g., *T. lacerata* and *Anax junius*; Tables 2 and 3).

Unlike a conventional overlap analysis, IOP and IOC can also predict the potential for asymmetries in competition and predation. For example, the indices predict that *Celithemis elisa,* which is a late-summer breeder, will be at a competitive disadvantage with earlier breeding species (i.e., most $IOC_{ij} < IOC_{ji}$; Table 3). Experimental studies with *C. elisa* provide empirical evidence that this predicted size disadvantage results in asymmetric competitive interactions with other spe-

cies (Johnson et al. 1985). Even subtle asymmetries in size may be ecologically important. For example, the IOP results suggest that the opportunity for *Libellula lydia* predation on *L. luctuosa* should arise twice as often as vice versa (Table 2). *L. lydia* has a 2–3 wk developmental headstart over *L. luctuosa* (Wissinger 1989*a*), and I have shown empirically that this advantage leads to an asymmetry in the intensity of intraguild predation between these two species (Wissinger 1989*b*).

Row totals in the IOP and IOC matrices summarize the predicted overall effects of these species as a predator and competitor in the assemblage, respectively (Tables 2 and 3). Total IOP values suggest that neither body size nor conventional overlap data are sufficient to predict the opportunity for intraguild predation in this assemblage. For example, based only on body size one would predict that *Tramea lacerata, Anax junius,* and *Epitheca princeps* should be similarly dominant as intraguild predators in this assemblage (Fig. 1). However, IOP row totals indicate that these species will have very different predatory impacts on smaller species (Table 2). *E. princeps* total IOP_{ij} values are much lower than those of the other two large species, and a closer look at field data revealed that this is due to an ontogenetic shift in habitat use (sensu Werner and Hall 1988). Small *E. princeps* do overlap frequently with small larvae of other species, but the large and potentially predatory instars of *E. princeps* move to offshore habitats and therefore rarely encounter small instars of other species. Subtle differences in habitat use also explain the twofold difference in total IOP_{ij} values for *T. lacerata* and *A. junius,* despite having similar gape widths and overlap values with other species (Fig. 1, Tables 1 and 2). This type of analysis emphasizes that, although large species of odonates such as *A. junius* will readily consume smaller larvae in experimental arenas (e.g., Robinson and Wellborn 1987), such experiments need to be interpreted in the context of prey encounter rates in nature. The IOP indices suggest that future experiments on intraguild predation among dragonflies should focus on the predatory effects of *Tramea.*

Diffuse intraguild competition and predation

Ecologists studying species-rich assemblages are often impressed with the diffuse effects of competitive and predatory interactions (Pianka 1974, 1980, Levine 1976, Holt 1977, 1985, Lawlor 1979, Davidson 1980, 1985, Vandermeer 1980, Kerfoot and Sih 1987, Polis et al. 1989). The column totals in the IOC and IOP matrices can be used to predict which species in this assemblage are most vulnerable to diffuse competition and intraguild predation. I use "diffuse" in the sense of McArthur (1972), i.e., ". . . the combined effects of many or most members of an assemblage on a particular species" (see also Moen 1989). Column totals in the IOC matrix suggest that the potential for diffuse competition in this assemblage is highest among *Erythemis simplicicollis, Pachydiplax longipennis, Libellula lydia, L. luctuosa,* and *L. pulchella* (Table 3). A caveat for using column totals to infer diffuse effects is that they need to be interpreted in the context of pairwise values. For example, the IOP column totals of *Libellula lydia* and *L. luctuosa* are large mainly because of large pairwise values with two species (*Anax junius* and *Tramea lacerata*; Table 2). In contrast, the large IOP column totals of *Sympetrum vicinum* and *Celithemis elisa* are the sum of many intermediate pairwise values, and, in MacArthur's (1972) sense, these species should be most vulnerable to "diffuse intraguild predation."

Population size-structure and cannibalism

Diagonal values in the IOP matrix predict the potential for cannibalism. The opportunity for cannibalism is minimal for a species such as *Epitheca cynosura,* which develops synchronously and has relatively few size classes present in the population at any one time (compare Fig. 2 and Appendix 1). In contrast, the opportunity for cannibalism is highest in species with the most broadly size-structured populations (e.g., *Libellula lydia, Erythemis simplicicollis, Anax junius*; see Appendix 1). The high cannibalism value for *Tramea lacerata* reflects the presence of two cohorts that have different, but overlapping, phenologies. One cohort arises in June from eggs deposited by immigrating adults, and the other in July and August from resident adults that emerge from the pond (Wissinger 1988*b*). Manipulative experiments with a closely related species suggest cannibalism can play an important role in regulating *Tramea* populations (Van Buskirk 1989).

The low cannibalism value for *E. princeps* was surprising, given that this species requires 2 yr to complete development, and there is extensive overlap between generations. However, in this population, 1st- and 2nd-yr larvae are segregated in different spatial habitats (near and offshore, respectively), so that the opportunity for cannibalism is low. Experimental studies with a closely related species of *Epitheca* suggest that 1st-yr classes of larvae have both reduced survival and foraging rates in the presence of larger conspecifics (Crowley et al. 1987). Although habitat segregation between year classes appears to be common in assemblages of intraguild predators, few experimental studies have tested the hypothesis that this phenomenon is a response to minimize cannibalism (Polis and McCormick 1987).

Utility of the indices

Above I have illustrated why the overlap indices developed in this paper are more appropriate than conventional indices for summarizing the potential for interspecific interactions between size-structured populations. The index that predicts the opportunity for exploitative competition (IOC) should be most appro-

priate for size-structured guilds in which species tend to shift mainly in *prey size* during ontogeny (e.g., rotifers, filter-feeding marine invertebrates, spiders, scorpions, terrestrial and aquatic insects, lizards, salamander larvae, fish) because the function that expresses body size–prey size relationships can be easily approximated from existing dietary or experimental data (Werner and Gilliam 1984, Mittelbach et al. 1988, Polis 1988). More detailed ecological information would be necessary to use the indices for species that exhibit dramatic shifts in habitat or *prey type* during ontogeny (e.g., Wilbur 1984).

Interpretation of the predation index (IOP) will vary among taxa depending on the nature of interactions between disparate size classes. For herbivores, detritivores, or predators (e.g., damselflies, stoneflies) in which large individuals are aggressive towards, but rarely eat smaller individuals, the results of the IOP can be used to predict the potential for interference competition (Baker and Dixon 1986, McPeek and Crowley 1987, Anholt 1990, Johnson 1991, Peckarsky 1991). However, the indices should be most useful for analyzing distributional data from species-rich assemblages of predators (e.g., Paine 1963, Polis and McCormick 1987) that differ in body size, change dramatically in size during ontogeny, and will either prey on or compete with each other depending on which size classes co-occur most frequently.

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APPENDIX 1

TABLE A1. Population size-structure. Numbers of larvae in each instar category are summed from 24 quantitative samples (6 in each of the 4 habitat categories) taken each month.* Final instar = F, penultimate = F − 1, etc. Size data are mean head and gape (labium) widths in millimetres, measured to the nearest 0.05 mm ($n \geq 10$).

Anax junius

Instar	F − 10	F − 9	F − 8	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	1.05	1.35	1.70	2.19	2.75	3.30	4.15	5.05	6.00	7.35	8.90	
Labium	0.50	0.65	0.80	1.05	1.40	1.70	2.30	2.90	3.55	4.45	6.40	Total
May	2							4	12	8	4	30
Jun	14	23	16	12	5				6	5	8	89
Jul	7	4	10	19	28	27	15	9		2	4	125
Aug	10	9	16	11	4	9	5	10	8	4	1	87
Sep				2	1	7	11	10	14	7	8	60
Oct					1		7	8	10	13	6	45
Nov					2	7	8	6	7	9	10	49
Mar					1	1	3	5	6	6	12	34
Apr						3	2	5	9	8	10	37

Celithemis elisa

Instar	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	0.88	1.10	1.44	1.85	2.39	3.00	4.19	
Gape	0.66	0.90	0.95	1.38	1.72	2.28	3.08	Total
Jul	21	19	23					63
Aug	6	7	19	12	10			54
Sep			1	5	10	6	3	25
Oct			1	1	2	7	7	18
Nov		1		5	5	4	3	18
Mar			1	1	5	4	3	14
Apr			1	2	6	2	1	12
May					2	6	2	10
Jun						1	3	4

Epitheca cynosura

Instar	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	1.10	1.30	1.55	1.85	2.20	3.00	3.90	5.45	
Gape	0.90	1.05	1.30	1.40	1.85	2.45	3.00	3.90	Total
Jun	2								2
Jul	66	40	21						127
Aug			11	28	12				51
Sep					1	17	14		32
Oct							14	15	29
Nov							13	16	29
Mar							8	17	25
Apr							3	24	27
May								18	18

TABLE A1. Continued.

Epitheca princeps

Instar	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	1.14	1.33	1.75	2.34	2.98	4.03	5.39	7.29	
Gape	0.95	1.06	1.42	1.81	2.34	3.09	4.19	5.53	Total
Jun						5	5	10	25
Jul	33	20					3	13	69
Aug	2	4	10	17			1	11	45
Sep				1	8	10		10	29
Oct					4	8	6	5	23
Nov				1		1	2	14	18
Mar						4	3	10	17
Apr					1	1	4	12	18
May						2	10	10	22

Erythemis simplicicollis

Instar	F − 8	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	1.10	1.25	1.45	1.75	2.15	2.60	3.15	3.95	4.90	
Gape	0.75	0.85	1.00	1.20	1.50	1.85	2.30	3.00	3.65	Total
Jun	11	2					1	3	5	22
Jul	19	26	13	8	15	8			2	91
Aug	6	19	35	43	22	7	12	6	2	152
Sep	12	9	3	15	17	11	7	5	1	80
Oct	1	5	3	2	7	10	11	5	3	47
Nov	1	1	3	1	3	11	10	6	5	41
Mar				2	6	7	4	5	10	34
Apr				2	3	6	6	2	4	23
May						1	3	4	3	11

Libellula lydia

Instar	F − 8	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	0.85	1.00	1.15	1.45	1.75	2.20	2.65	3.50	4.50	
Gape	0.70	0.85	1.05	1.30	1.60	2.05	2.50	3.15	3.80	Total
Jun	16	24					2	2	18	62
Jul	84	80	99	19	23	1	3	4	5	318
Aug	68	65	75	96	53	39	22	18		436
Sep	1	6	18	25	27	36	25	18	20	176
Oct		1	5	6	10	14	17	22	36	111
Nov			2	5	11	27	18	11	34	108
Mar				1	4	13	27	19	21	85
Apr				4	7	13	21	14	31	90
May				1	1	5	12	15	20	54

Libellula luctuosa

Instar	F − 8	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	0.90	1.15	1.40	1.65	2.05	2.60	3.30	4.15	5.30	
Gape	0.75	0.85	1.10	1.30	1.80	2.20	2.95	3.40	4.30	Total
Jul	92	48							2	142
Aug	45	71	77	51						244
Sep		3	13	26	24	24	19			109
Oct				3	8	12	25	11		59
Nov				4	5	14	20	14		57
Mar					1	7	25	22		55
Apr					2	6	21	25		54
May							1	18	14	33
Jun								1	12	13

Libellula pulchella

Instar	F − 8	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	0.91	1.10	1.34	1.70	2.16	2.69	3.46	4.51	6.10	
Gape	0.72	0.89	1.14	1.32	1.67	2.14	2.86	3.84	4.90	Total
Jul	8	6	2	2					2	20
Aug	7	9	11	7	2	3				39
Sep			2	4	8	5	5	1		25
Oct					4	4	7	6		21
Nov					3	1	5	5		14
Mar					1	2	4	6		13
Apr					1	2	2	7		12
May							1	3	3	7
Jun								1	2	3

TABLE A1. Continued.

Pachydiplax longipennis

Instar	F − 8	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	0.86	1.09	1.30	1.71	2.07	2.59	3.33	4.34	5.43	
Gape	0.66	0.90	1.01	1.17	1.42	1.76	2.31	2.88	3.62	Total
Jun	9	7				1		3	6	26
Jul	25	27	14	19	7				3	95
Aug		11	11	16	7	8	2	3		58
Sep			2	6	7	4	6	5	2	32
Oct	10	6	1	2		5	8	3	1	36
Nov		6	1	2	2	4	7	4	2	28
Mar			2	1	1	4	5	1	2	16
Apr				1	1	2	8	3	2	17
May					1	2	5	4	4	16

Perithemis tenera

Instar	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	0.60	0.75	1.00	1.40	1.70	2.20	2.80	3.65	
Gape	0.50	0.60	0.70	0.95	1.20	1.50	1.80	2.20	Total
Jul	58	52	10				3	26	149
Aug	40	63	41	37	7	10			198
Sep		3	10	30	26	26	10		105
Oct		3	7	10	13	20	20	23	96
Nov		3	6	20	20	7	24	16	96
Mar				3	17	23	27	20	90
Apr		3	3	6	13	27	14	10	76
May				3	6	17	23	21	70
Jun						3	3	32	38

Sympetrum vicinum

Instar	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	1.05	1.25	1.60	2.00	2.60	3.50	4.45	
Gape	0.80	1.00	1.15	1.40	1.80	2.40	2.90	Total
Mar								0
Apr	61	57						118
May		22	26	29				77
Jun			2	10	17	19	14	62
Jul				7	12	11	11	41
Aug							8	8
Sep								0
Oct								0
Nov								0

Tramea lacerata

Instar	F − 9	F − 8	F − 7	F − 6	F − 5	F − 4	F − 3	F − 2	F − 1	F	
Head	1.10	1.35	1.70	2.20	2.95	3.55	4.35	5.30	6.40	7.55	
Gape	0.90	1.10	1.35	1.80	2.20	2.90	3.55	4.50	5.45	6.30	Total
Jun	91	63	33				1	1	6	11	206
Jul	55	59	56	68	72	17	15	33	11	5	391
Aug	15	12	28	30	36	30	51	30	23	23	278
Sep			4	5	4	9	13	21	18	16	90
Oct				1	2	8	14	12	14	16	67
Nov				2	4	7	11	11	16	4	55
Mar					1	1	2	6	6	5	21
Apr					1	2	2	6	3	5	19
May						1	1	3	6	7	18

* The indices use these instar data on a habitat-specific basis on a given date. The distributions underestimate the size range of larvae actually present in these populations because the smallest instars of each species were difficult to quantify and are not included (see Wissinger 1988*b*).

APPENDIX 2

TABLE A2. Habitat use. Larval dragonfly distributions and abundances used to calculate the overlap values reported in this paper. Values include all instars and are means based on six quantitative samples taken in each depth/date category. (See Wissinger 1988*c* for field methods.)

Date	Depth category (m)				Date	Depth category (m)			
	<0.5	0.5–1.0	1.0–1.5	>1.5		<0.5	0.5–1.0	1.0–1.5	>1.5
Anax junius					*Libellula luctuosa*				
Jul	125	0	0	0	Jul	135	7	0	0
Aug	88	0	0	0	Aug	218	27	0	0
Sep	59	0	0	0	Sep	83	17	0	0
Oct	38	0	0	0	Oct	42	17	0	0
Nov	49	0	0	0	Nov	41	17	0	0
Mar	27	0	0	0	Mar	32	23	0	0
Apr	37	0	0	0	Apr	47	20	0	0
May	29	0	0	0	May	33	0	0	0
Jun	89	0	0	0	Jun	13	0	0	0
Celithemis elisa					*Libellula pulchella*				
Jul	25	13	0	0	Jul	18	0	0	0
Aug	21	27	0	0	Aug	35	3	0	0
Sep	12	17	0	0	Sep	21	3	0	0
Oct	9	13	0	0	Oct	15	7	0	0
Nov	6	13	0	0	Nov	11	3	0	0
Mar	5	10	0	0	Mar	19	0	3	0
Apr	9	3	0	0	Apr	7	0	0	0
May	7	3	0	0	May	5	0	0	0
Jun	3	0	0	0	Jun	22	0	0	0
Epitheca cynosura					*Pachydiplax longipennis*				
Jul	104	23	0	0	Jul	83	0	0	0
Aug	27	23	3	0	Aug	51	0	0	0
Sep	11	27	0	0	Sep	30	0	0	0
Oct	8	27	7	0	Oct	19	0	0	0
Nov	3	23	3	0	Nov	22	0	0	0
Mar	5	17	3	0	Mar	17	0	0	0
Apr	24	3	0	0	Apr	18	0	0	0
May	18	0	0	0	May	16	0	0	0
Jun	8	0	0	0	Jun	11	0	0	0
Epitheca princeps					*Perithemis tenera*				
Jul	53	13	3	0	Jul	27	43	77	3
Aug	17	10	3	0	Aug	39	49	106	7
Sep	9	3	3	0	Sep	0	17	77	11
Oct	7	13	3	0	Oct	0	13	70	8
Nov	4	10	3	0	Nov	0	17	70	10
Mar	1	13	3	0	Mar	0	17	60	13
Apr	11	7	3	0	Apr	0	23	43	10
May	12	7	0	0	May	7	17	37	7
Jun	15	10	3	0	Jun	25	17	3	0
Erythemis simplicicollis					*Sympetrum vicinum*				
Jul	92	0	0	0	Jul	14	27	0	0
Aug	142	0	0	0	Aug	8	0	0	0
Sep	83	0	0	0	Sep	0	0	0	0
Oct	46	0	0	0	Oct	0	0	0	0
Nov	34	0	0	0	Nov	0	0	0	0
Mar	27	0	0	0	Mar	0	0	0	0
Apr	25	0	0	0	Apr	98	20	0	0
May	11	0	0	0	May	43	33	0	0
Jun	9	0	0	0	Jun	23	37	0	0
Libellula lydia					*Tramea lacerata*				
Jul	289	17	0	0	Jul	293	93	0	0
Aug	389	47	0	0	Aug	117	40	3	0
Sep	157	20	0	0	Sep	54	37	0	0
Oct	85	27	0	0	Oct	43	23	0	0
Nov	82	20	10	0	Nov	38	17	0	0
Mar	64	17	3	0	Mar	15	7	0	0
Apr	77	10	3	0	Apr	16	3	0	0
May	51	3	0	0	May	12	7	0	0
Jun	22	0	0	0	Jun	200	3	0	0

APPENDIX 3

Derivation of predation (IOP) and competition (IOC) indices

1. *Relationship to Hurlbert's (1978) overlap index* L.—Hurlbert's (1978) overlap index considers the degree to which interspecific overlap (O) between two species differs from that expected (O_e) when both species use resources in proportion to resource abundance. For each resource category, the frequency of co-occurrence, or overlap ("encounter rate" of Hurlbert) between two species should be proportional to the product of their densities and the size of that category; thus, summing over all categories,

$$O = \sum_k (N_{ik}/A_k)(N_{jk}/A_k)(A_k), \tag{A1}$$

where N_{ik} and N_{jk} are the population sizes of species i and j in the k^{th} resource category and A_k is the size of the k^{th} resource category.

When two species are both distributed in proportion to resource abundance, overlap is proportional to

$$O_e = (N_i/A)\,(N_j/A)(A), \tag{A2}$$

where $N_i = \sum_k N_{ik}$, the total number of species 1; $N_j = \sum_k N_{jk}$, the total number of species 2; and $A = \sum_k A_k$, the total size of the resource. Thus, the degree to which interspecific overlap differs from that expected when both species use resources in proportion to resource abundance, is

$$L_{ij} = O/O_e = \frac{\sum_k (N_{ik}/A_k)(N_{jk}/A_k)(A_k)}{(N_i/A)(N_j/A)(A)} \tag{A3}$$

and

$$L_{ij} = \sum_k (p_{ik})(p_{jk})(p_k), \tag{A4}$$

where $N_{ik}/N_i = p_{ik}$ and $N_{jk}/N_j = p_{jk}$, the proportional abundance of the i^{th} and j^{th} species in the k^{th} resource; and $A_k/A = p_k$, the proportional abundance of the k^{th} resource.

2. *Index of the opportunity for predation (IOP).*—The potential for intraguild predation between two species should depend on the frequency with which individuals that are disparate in size overlap in time and space. This can be calculated by modifying the numerator in Eq. A3 to compare all combinations of size classes that overlap, and then weighting each comparison with a function that relates relative size to the likelihood that an encounter would be predatory. In general, the proportion of encounters between two size classes that result in predation (0–1.0) should increase as the difference in size increases. The particular function used to analyze the data presented in this paper, r_{gh}, is based on size differences between the gape width of the predator and the head width of the prey.

For each resource category k and each size class combination of the i^{th} and j^{th} species, the number of predatory encounters is proportional to the products of the densities of those size classes, the proportion of interactions between those size classes that are predatory, and the size of the resource category. Summing over all size-class combinations and resource categories, the number of potentially predatory encounters between two species is proportional to

$$O_p = \sum_g \sum_h \sum_k (N_{igk}/A_k)(N_{jhk}/A_k)(r_{gh})(A_k), \tag{A5}$$

where N_{igk} and N_{jhk} are the population sizes of the g^{th} and h^{th} size classes of the i^{th} and j^{th} species in the k^{th} resource category; r_{gh} is the proportion (0 to 1.0) of encounters between the g^{th} and h^{th} size classes of the i^{th} and j^{th} species that are potentially predatory; and A_k is the size of the k^{th} resource category.

Following Hurlbert, an index of the opportunity for predation (IOP_{ij}) by the i^{th} species on the j^{th} species compares the frequency with which disparate sizes of two species overlap (O_p) to that expected when all sizes of both species use resources in proportion to resource abundance (O_e), i.e.,

$$\text{IOP}_{ij} = O_p/O_e = \frac{\sum_g \sum_h \sum_k (N_{igk}/A_k)(N_{jhk}/A_k)(r_{gh})(A_k)}{(N_i/A)(N_j/A)(A)}, \tag{A6}$$

which reduces to

$$\text{IOP}_{ij} = \sum_g \sum_h \sum_k (p_{igk}p_{jhk}r_{gh})/p_k, \tag{A7}$$

where r_{gh} is the proportion of encounters between the g^{th} size class of predator species i and the h^{th} size class of prey species j that is likely to be predatory; p_{igk} and p_{jhk} are the proportional abundances of the g^{th} and h^{th} size classes of the i^{th} and j^{th} species, respectively, in the k^{th} resource category; and p_k is the proportional abundance of the k^{th} resource category. IOP will be zero when there is no overlap and when all overlapping individuals are similar in size (i.e., all $r_{gh} = 0$). When all overlapping individuals are disparate in size (i.e., all $r_{gh} = 1$), IOP will be the same as Hurlbert's index L.

3. *Index of the opportunity for competition (IOC).*—The potential for exploitative competition can be predicted in an analogous manner by substituting for r_{gh} with a weighting coefficient that describes the potential for competition as a function of size similarities. The function used for the data analyzed in this paper, $c_{gg'}$, is based on the relative sizes of the gape widths of two individuals. Substituting $c_{gg'}$ for r_{gh} in Eq. A5, and summing over all size-class combinations and resource categories, the number of encounters between two species that are potentially competitive, O_c, will be

$$O_c = \sum_g \sum_{g'} \sum_k (N_{igk}/A_k)(N_{jg'k}/A_k)(c_{gg'})(A_k), \tag{A8}$$

where N_{igk} and $N_{jg'k}$ are the population sizes of the g^{th} and g'^{th} size classes of the i^{th} and j^{th} species in the k^{th} resource category; $c_{gg'}$ is the proportion (0 to 1.0) of encounters between the g^{th} and g'^{th} size classes of the i^{th} and j^{th} species that are potentially competitive; and A_k is the size of the k^{th} resource category.

An index of the opportunity for competition (IOC_{ij}) for the competitive effects of the i^{th} species on the j^{th} species compares the frequency with which similar size classes of two species overlap (O_c), to that expected when all sizes of both species use resources in proportion to resource abundance,

$$\text{IOC}_{ij} = O_c/O_e = \frac{\sum_g \sum_{g'} \sum_k (N_{igk}/A_k)(N_{jg'k}/A_k)(c_{gg'})(A_k)}{(N_i/A)(N_j/A)(A)}, \tag{A9}$$

which reduces to

$$\text{IOC}_{ij} = \sum_g \sum_{g'} \sum_k (p_{igk}p_{jg'k}c_{gg'})/p_k, \tag{A10}$$

where $c_{gg'}$ is the proportion (0 to 1.0) of encounters between the g^{th} and g'^{th} size classes of the i^{th} and j^{th} species that are potentially competitive; p_{igk} and $p_{jg'k}$ are the proportional abundances of the g^{th} and g'^{th} size classes of the i^{th} and j^{th} species, respectively, in the k^{th} resource category; and p_k is the proportional abundance of the k^{th} resource category. IOC = 0 when no individuals of two species overlap or when all overlapping individuals are extremely disparate in size (i.e., all $c_{gg'} = 0$). IOC will be the same as Hurlbert's L when all overlapping individuals of two species are similar in size (i.e., when all $c_{gg'} = 1$).