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Unexpected Effects of Predators Upon Their Prey: The Case of the American Alligator

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ABSTRACT

Indirect trophic effects play important roles in ecosystem dynamics and can at times oppose and dominate the action of direct feeding linkages. Each predator directly exerts a negative effect upon its prey, but predators may also provide indirect benefits to their prey. In ecosystems, such benefits are effected via indirect trophic pathways that can provide a more than compensating positive influence. The ecosystem of the Big Cypress National Preserve (southwest Florida) appears to contain an unusually high number of such predators—most notably, the American alligator, *Alligator mississippiensis*. The trophic exchanges of carbon among the 68 principal taxa comprising the cypress wetland ecosystem have been quantified during both wet and dry seasons. The network analysis program IMPACTS identified predators that potentially have a positive influence on some of their prey. A total of 64 of these instances were recorded for the wet season and 44 for the dry. Taxa that, on balance, have positive effects upon their prey include fishes, turtles, snakes, birds, and, most significantly, alligators. The feeding habits of alligators benefit a conspicuous number (11) of their prey (invertebrates, frogs, mice, and rats). Further trophic analysis reveals that the predation by alligators on snakes and turtles accounts for most of the trophic benefits bestowed. The actions of alligators in modifying their physical environment has been cited elsewhere as contributing to the maintenance of biotic diversity. It appears that the trophic influence of this species adds further evidence to the important role it plays in the functional ecology of the cypress wetland.

Key words: cypress swamps; ecosystem; indirect interactions; network analysis; predator–prey interaction; *Alligator mississippiensis*.

INTRODUCTION

Fundamental features of population interactions, such as predation and competition have been elucidated by empirical and theoretical investigations of the dynamics between two species (Lotka 1925; Connell 1961; Southern 1970; Thompson 1975; Hairston 1980; May 1981; Grace and Wetzel 1981; Tilman and others 1981; Hassell 1985). Interactions in ecosystems are multiple, however, so that as more dimensions are added, the opportunity could arise for more complex and surprising dynamics. In lacustrine ecosystems, multiple pathways are created that can engender complicated and unexpected effects (Carpenter 1988; DeVries and Stein 1992); substantial modifications in limiting-factor effects can arise (Lane and Levins 1977); the impact of a natural enemy can be profoundly modified so as to challenge the effectiveness of biological control policies (Levins and Shultz 1996); and indirect effects may produce dynamics that defy predictions based on the exploitative ecosystem hypothesis [EEH (Rosemond 1996)].

The most obvious effect of feeding is the negative impact this process exerts upon the host population,

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which by being consumed is diminished both in number and biomass. Indirect effects, however, may lead a predator to benefit its prey. Four-species food-chain models (Abrams 1992) have suggested that adaptive foraging can generate indirect effects of this type. Perturbation experiments conducted on pelagic communities showed that fish predation, usually suppressive, actually increased the abundance of invertebrates (Kerfoot 1987).

Predation, like other interactions, has been invoked as a major determinant in shaping communities and ecosystems (Connell 1975; Sih and others 1985). Indirect positive effects of a predator on its prey have been hypothesized and tested experimentally (Ambrose 1984; Diehl 1995; Sih and Krupa 1996), but in most instances the number of variables considered was not very large. By limiting study only to systems of a few species, one tacitly assumes that effects are not propagated too far in food webs. But there is evidence that this may not be true.

In the Banguela ecosystem food web (Field and others 1991; Abrams and others 1996), for example, the interaction between seal (predator) and hake (prey) is very complicated, and focusing on only a small set of short pathways obscures the net effect of seals upon hakes. Paths of up to length 6 need to be considered in order to establish the net effect. This finding has profound practical implications. The question for the Banguela ecosystem was whether yearly culling of a given quantity of seal biomass permits an increase in the annual yield of hake biomass. The answer could differ if one looked at short versus longer (than length 5) pathways.

Most investigations of species interactions consider effects on population size (either number of individuals or biomass), population growth rate, and individual fitness (Abrams 1987; Arditi and Michalsky 1996). Rarely are population dynamics considered in the context of community structure or on indirect effects within very large food webs, as in the surveys by Schoener (1993) and Menge (1995). When large food webs were investigated, it was for the purpose of finding patterns in the ratio of prey to predators, food-chain length, number of links, and so on (Cohen and others 1989; Schoener 1989).

Ecological management of large ecosystems (DeAngelis and others 1998) requires specific tools, such as simulation models and energy-flow models. The latter have been used to study energy and material circulation in ecosystems (Baird and Ulanowicz 1989; Christian and others 1995; Bondavalli and others 1997), but they trace only the benefit of the prey to the predator, neglecting the negative impact of the predator upon its prey. Ulanowicz and Puccia (1990) provided a quantitative method that overcomes this problem, so that indirect effects generated by negative impacts due to predatory behavior now can be studied as well.

The method developed by Ulanowicz and Puccia (1990) has been applied to a 68-compartment network representing the ecosystem of the cypress wetlands of South Florida (Ulanowicz and others 1997). The study was conducted in the framework of the Across Trophic Levels System Simulation (ATLSS) project, a multiagency effort aimed at understanding South Florida's resources by integrating populations and ecological processes in the context of whole-ecosystem functioning. When IMPACTS was applied to the cypress dataset, the proportion of predators exerting overall positive effects on their prey was higher than in previous cases (Ulanowicz and Puccia 1990). One key omnivore, *Alligator mississippiensis*, imparted overall benefit to 11 of its prey. This finding warrants closer examination, given the importance of this species. Other studies (Craighead 1968; Kushlan 1974; Deitz and Jackson 1979; Kushlan and Kushlan 1980; Norton 1988; Hall and Meier 1993; Mazzotti and Brandt 1994) also indicate that the American alligator plays a special role in ecosystem functioning.

STUDY AREA

The 295,000-ha wetlands of the Big Cypress Natural Preserve (Figure 1) and the adjacent Fakahatchee Strand State Preserve in southwest Florida have been described by the US Forest Service (1996) as a flat, gently sloping limestone plain. In this area, seasonality is marked primarily by variations in water inflow and precipitation, defining a wet season and a dry season. During the rainy season, water flows slowly southward over this plain into the mangrove swamps bordering the Gulf of Mexico. During low-water periods, there may be no discernible flow through the cypress wetlands. In places, the water flow has cut channels into the limestone, allowing deep organic soils to develop. These channels are occupied by tall, dense, elongated swamp forests. The local term for this type swamp is *strand*. Another type is the *dome*, which is a poorly drained to permanently wet depression dominated by cypress (*Taxodium* spp.) (Mitsch and Gosselink 1993).

Cypress swamps do not have a distinct fauna, but share many species with adjacent plant communities. During summer, reptiles and amphibians are the dominant vertebrates (US Forest Service 1996), whereas birds become more abundant in winter. Reptiles and amphibians tolerate the fluctuating water regime and remain active through the cooler seasons.

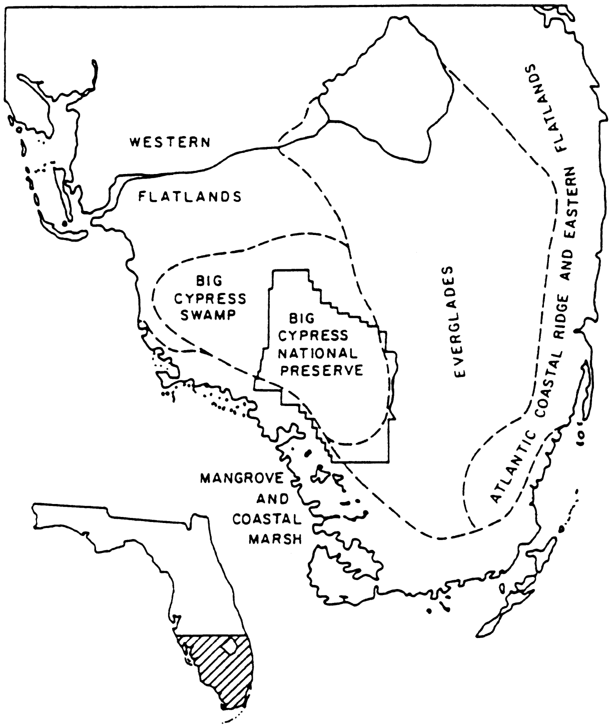


Figure 1. Study area. Modified from Duever and others (1986).

METHODS

The creation of an ecosystem trophic network requires that one know who eats whom and at what rate. Only those organisms with very similar sets of prey and predators should be grouped into the same compartment. Adhering to these criteria was not always possible; when we did not have detailed information for a species, we followed general taxonomic rules lumping species that were taxonomically similar. Species with particular relevance to the goals of ATLSS were retained as separate compartments.

The cypress wetland ecosystem was represented by the 68 separate compartments listed in Table 1 (Duever and others 1986). The stocks and activities of all 68 compartments vary during the course of the year, mostly due to seasonal changes in water level. Hence, the kinetics were depicted in two separate networks—one for the wet, high-water season (June through November) and another for the dry season (December through May), when water levels are relatively low.

The next step involved connecting these compartments to one another via feeding and detrital pathways determined from information on the diets of each taxon and on migrations, advections, primary production, respirations, and harvests. Biomass for each compartment was quantified in units of grams of carbon per square meter (gC m^{-2}) and flows in grams of carbon per square meter per year (gC m^{-2} $year^{-1}$). A complete and detailed description of all sources of data and the accompanying calculations used to estimate the cypress networks can be found on the World Wide Web at www.cbl.umces.edu/~bonda/ALTSS.html.

Ulanowicz collected four principal methods for analyzing quantitative flow networks in a single software package, NETWRK (Ulanowicz and Kay 1991). Unfortunately, NETWRK deals with only the positive contributions of mass flows and does not follow the propagation of the negative effects that accompany predation. Hence, IMPACTS was written to assess the direct and indirect impacts of both the positive and negative effects of heterotrophic predation (Ulanowicz and Puccia 1990). IMPACTS and other software packages for network analysis are available over the Web at www.cbl.umces.edu/~ulan/ntwk/network.html. To illustrate IMPACTS, we focus on a subset of the full 68-compartment network (Figure 2). Both crayfish (*Procambarus alleni*) and turtles (*Chelydra serpentina osceola*, *Sternotherus odoratus*, *Kinosteron baurii*, *Pseudemys nelsoni*, *Deirochelys reticularia chrysea*, and *Apalone ferox*) are prey for alligators. In addition, turtles feed on crayfish.

The positive effect that a prey has upon its predator can be quantified as follows: Let T_{ij} represent the amount (gC m^{-2} $year^{-1}$) of prey i consumed by predator j. Then, $g_{ij} = T_{ij}/\Sigma_k T_{kj}$ will represent the fraction of j's diet comprised by prey i, where k sums over all elements of j's diet. The dietary coefficient, g_{ij}, assigns a weight to each item i in predator j's diet. The negative impact that a predator exerts upon its prey can be quantified as $f_{ij} = T_{ij}/\Sigma_m T_{im}$, where f_{ij} represents the fraction of i's net production that is consumed by predator j, and m sums over all net output (respiration is not included) from compartment i.

The net impact of i upon j will equal the positive contribution from i serving as a prey item for j, minus any detrimental impact that i might have as a predator upon j. Calling this net impact q_{ij}, we see that $q_{ij} = g_{ij} - f_{ji}$. All of the q's can be regarded as components of an n-dimensional matrix (3×3 in this case), called net impact matrix (Q):

$$Q = \begin{bmatrix} 0.00 & 0.33 & 0.14 \\ -0.04 & 0.00 & 0.20 \\ -0.02 & -0.42 & 0.00 \end{bmatrix}$$

Table 1. List of Compartments in the Cypress Wetland Network

No.	Compartment	No.	Compartment	No.	Compartment
1	Living POC	24	Turtles	47	Woodpeckers
2	Living sediment	25	Lizards	48	Passeriformes 1
3	Phytoplankton	26	Snakes	49	Passeriformes 2
4	Floating vegetation	27	Salamanders	50	Opossum
5	Periphyton	28	Large frogs	51	Shrews
6	Macrophytes	29	Medium frogs	52	Bats
7	Epiphytes	30	Small frogs	53	Black bear
8	Understory	31	Salamander larvae	54	Grey fox
9	Vines (leaves)	32	Tadpoles	55	Raccoon
10	Hardwood (leaves)	33	Pelecaniformes	56	Mink
11	Cypress (leaves)	34	Anseriformes	57	Otter
12	Cypress (wood)	35	Vultures	58	Florida panther
13	Hardwood (wood)	36	Kites and hawks	59	Bobcat
14	Roots	37	Galliformes	60	Squirrels
15	Crayfish	38	Egrets	61	Mice and rats
16	Apple snail	39	Great blue heron	62	Rabbits
17	Prawn	40	Other herons	63	White-tailed deer
18	Aquatic invertebrates	41	Wood stork	64	Hog
19	Terrestrial invertebrates	42	White ibis	65	Armadillo
20	Small fish 1	43	Gruiformes	66	Refractory detritus
21	Small fish 2	44	Owls	67	Liable detritus
22	Large fish	45	Caprimulgiformes	68	Vertebrate detritus
23	American alligator	46	Hummingbirds		

Small fish 1, herbivorous and omnivorous small fishes; Small fish 2, primarily carnivorous small fishes; Passeriformes 1, omnivorous passerine; Passeriformes 2, predatory passerine; POC, particulate organic carbon.

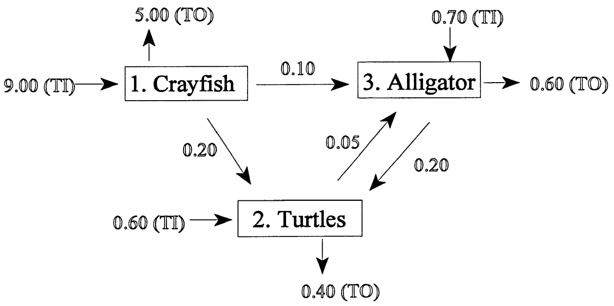


Figure 2. Partial network of cypress wetlands ecosystem, comprising only three compartments. TI, total input to the compartment; TO, total output from the compartment, excluding respiration. All values are gC m^{-2} $year^{-1}$.

In particular, we consider the impact of alligators (3) on crayfish (1). Because crayfish don't feed on alligators, $g_{31} = 0$. The biomass of crayfish taken by alligator divided by the total output from the crayfish compartment yields: $f_{13} = 0.03/(4.7 + 0.1 + 0.2) = 0.02$, so that the net impact of alligator on crayfish becomes $q_{31} = g_{31} - f_{13} = 0.0 - 0.02 = -0.02$. As one might expect, this particular coefficient is negative, because the direct impact of alligator on crayfish is to diminish the stock of the latter. An indirect effect arises from the pathway crayfish → turtles → alligator. In keeping with established practice in input/output analysis, we assume that the overall trophic impact of any concatenation of direct effects is measured by the product of all the *q*'s along that pathway. The indirect effect of alligator on crayfish passing thought turtles thus becomes: $q_{31}indirect = q_{12} \times q_{23} = 0.33 \times 0.20 = 0.066$, and the net impact of alligator on crayfish is the sum of both direct and indirect effects: $q_{31}net = q_{31}direct + q_{31}indirect = -0.02 + 0.066 = 0.046$. Hence, the overall impact of alligator upon crayfish is seen to be positive.

The net impact of any compartment, *i*, upon any other, *j*, will appear as a the *i*-*j*th entry in a matrix that is the sum of all integer powers of the net impact matrix, *Q*. IMPACTS calculates the components of this total impact matrix. To facilitate analysis of systems with many compartments, users may direct IMPACTS to provide a ranked listing of all the total impacts (both direct and indirect) upon any particular (focal) species. Similarly, a ranked listing of the impacts that compartment has upon all other compartments can be reported. These impact coefficients represent the *aggregated* indirect effects between two species. They do not specify which pathways contributed most to those indirect effects. To understand better which pathways played the most significant roles in the overall impact, a separate algorithm, PATHS, was created. PATHS identifies all the predatory concatenations between any two compartments of interest and calculates the relative weights of the indirect impacts that are exerted along each pathway. As the number of such pathways can become very large, PATHS reports only those indirect connections that yield impacts above a given threshold (supplied by the user.)

RESULTS

A large number of positive effects on prey by predators emerged from the analysis of the forested cypress wetland network (Table 2). Whereas Ulanowicz and Puccia (1990) found predator enhancement of prey in only six cases in the network of Chesapeake Bay, 44 instances appeared in the cypress network during the dry season and 64 in the wet season, associated with 22 taxa in the wet-season network, and with 19 in the dry-season model. Compartments 33 (Pelecaniformes), 38 (egrets), 39 (great blue heron), 40 (other herons), and 41 (wood storks) exhibit enhancement only during the wet season, whereas Everglades mink (56) and river otter (57) exhibit enhancement only during the dry period.

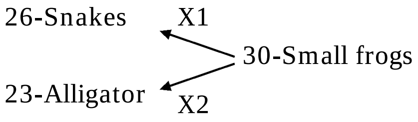
The species that benefits the most prey species is the American alligator. Its feeding habits potentially augment 11 of its prey during the wet season and 9 in the dry. Prey that receive indirect benefit from the alligator include invertebrates (compartments 15, 16, 17, 18, 19), frogs (28, 29, 30), Galliformes (37), and mice and rats (61). Crayfish and salamander larvae are affected positively only during the wet season. The values of net positive impact (NPI) as calculated with IMPACTS are reported in Table 3. Only those values of NPI $> 1\%$ are considered in the following analysis.

Of the full complement of predators that enhance prey, only four give rise to NPIs of > 0.01: small fishes, alligators, turtles, and snakes. Of these more significant benefactors, the American alligator potentially augments the largest number of prey in both wet (7) and dry (6) seasons. Its most positive effects are meted out to small frogs (30) and tadpoles (32) during the wet season. Overall, eight of the instances of significant benefit to prey are more intense during the wet season [(20, 19), (23, 19), (23, 29), (23, 30), (23, 31), (23, 32), (24, 19), and (24, 30)], whereas five are more prominent during the dry period [(23, 18), (23, 37), (23, 61), (26, 16), and (26, 18)].

In interpreting the meaning of the reported positive relationships, we considered not only the NPI, but also the magnitude of *f*, the coefficient of direct negative impact (DNI), of a predator upon its prey. NPI that is not significantly positive could still have a large positive indirect compensation.

A comparison of Tables 3 and 4 shows that most of the actions with significant NPIs (> 0.01) (Table 4) also represent substantial compensations for large DNIs. Apparently, in only two cases [(23,37) and (42, 32), both during the wet season] is there substantial compensation unaccompanied by significant net benefit. Interpretation of net positive benefit is aided by identifying one or a few indirect pathways that account for the bulk of the positive influence. To assist in this task, we employed PATHS, which enumerates all concatenations of feeding transfers connecting any particular predator and prey pair. (Pathways that involve nonfeeding transfers were excluded from the search.) PATHS further quantifies the magnitude of (positive or negative) influence exerted along each pathway and prints out only those concatenations that result in significant (> 0.01) trophic influence. PATHS was applied to all predator–prey couples that yielded either a significant NPI or DNI.

In many instances, very large numbers (> 1000) of predatory concatenations were identified. All routes resulting in a trophic effect of $< 5\%$ of NPI were ignored to focus upon the main actors that create the positive indirect effects (Table 5). The sum of all pathway impacts is also reported in Table 5. It should be emphasized that this value is not equal to the NPI as reported by IMPACTS. This is because PATHS identifies only a subset of all pathways that connect any given couple. (For example, all pathways involving nonpredatory links and other indirect relationships between compartments, such as competition, have not been considered.) For instance, both alligators and snakes feed on small frogs, as depicted in the following graph:



Although there are no direct connections between snakes and alligators, one readily senses that these two taxa compete with each other for small frogs. This fact is borne out by calculations: $q_{23\text{–}26} = q_{23\text{–}30} \times q_{30\text{–}26} = (-f_{23\text{–}30}) \times (g_{30\text{–}23}) < 0$. This negative indirect impact of alligator on snakes, and others like it, are not considered by PATHS. The longest pathways reported in Table 5 have only two intermediates. The probability is that the largest indirect effects are propagated over relatively short pathways (Ulanowicz and Puccia 1990).

Table 2. List of Beneficial Relationships

Wet Season			Dry Season		
No.	Beneficial Predators	Prey	No.	Beneficial Predators	Prey
1	20—Small fish 1	2—Living SED	1	20—Small fish 1	2—Living SED
2		19—Terrestrial invertebrates	2		19—Terrestrial invertebrates
3	21—Small fish 2	1—Living POC	3	21—Small fish 2	1—Living POC
4		2—Living SED	4		2—Living SED
5		3—Phytoplankton	5		3—Phytoplankton
6		5—Periphyton	6		5—Periphyton
7		6—Macrophytes	7		6—Macrophytes
8		7—Epiphytes	8		7—Epiphytes
9		19—Terrestrial invertebrates	9		19—Terrestrial invertebrates
10	22—Large fish	1—Living POC	10	22—Large fish	1—Living POC
11		2—Living SED	11		2—Living SED
12		19—Terrestrial invertebrates	12		18—Aquatic invertebrates
13	23—Alligator	15—Crayfish	13		19—Terrestrial invertebrates
14		16—Apple snail	14	23—Alligator	16—Apple snail
15		17—Prawn	15		17—Prawn
16		18—Aquatic invertebrates	16		18—Aquatic invertebrates
17		19—Terrestrial invertebrates	17		19—Terrestrial invertebrates
18		29—Medium frogs	18		29—Medium frogs
19		30—Small frogs	19		30—Small frogs
20		31—Salamander larvae	20		32—Tadpoles
21		32—Tadpoles	21		37—Galliformes
22		37—Galliformes	22		61—Mice and rats
23		61—Mice and rats	23	24—Turtles	18—Aquatic invertebrates
24	24—Turtles	18—Aquatic invertebrates	24		19—Terrestrial invertebrates
25		19—Terrestrial invertebrates	25	26—Snakes	15—Crayfish
26		30—Small frogs	26		16—Apple snail
27	26—Snakes	15—Crayfish	27		17—Prawn
28		16—Apple snail	28		18—Aquatic invertebrates
29		17—Prawn	29		19—Terrestrial invertebrates
30		18—Aquatic invertebrates	30	27—Salamanders	18—Aquatic invertebrates
31		19—Terrestrial invertebrates	31	28—Large frogs	18—Aquatic invertebrates
32	27—Salamanders	18—Aquatic invertebrates	32	29—Medium frogs	18—Aquatic invertebrates
33		19—Terrestrial invertebrates	33	30—Small frogs	18—Aquatic invertebrates
34	28—Large frogs	18—Aquatic invertebrates	34	36—Kites and hawks	20—Small fish, herb., and omniv.
35		19—Terrestrial invertebrates	35	42—White ibis	20—Small fish, herb., and omniv.
36	29—Medium frogs	18—Aquatic invertebrates	36	43—Griuformes	19—Terrestrial invertebrates
37		19—Terrestrial invertebrates	37	44—Owls	20—Small fish, herb., and omniv.
38	30—Small frogs	18—Aquatic invertebrates	38	54—Gray fox	8—Understory
39		19—Terrestrial invertebrates	39		10—Hardwood wood
40	33—Pelecaniformes	20—Small fish, herb., and omniv.	40	55—Raccoon	20—Small fish, herb., and omniv.
41		21—Small fish, carnivorous	41	56—Mink	20—Small fish, herb., and omniv.
42	36—Kites and hawks	20—Small fish, herb., and omniv.	42	57—Otter	20—Small fish, herb., and omniv.
43	38—Egrets	19—Terrestrial invertebrates	43	65—Armadillo	8—Understory
44	39—Great blue heron	20—Small fish, herb., and omniv.	44		10—Hardwood wood
45		21—Small fish, carnivorous			
46	40—Other herons	19—Terrestrial invertebrates			
47		20—Small fish, herb., and omniv.			
48	41—Wood stork	20—Small fish, herb., and omniv.			
49		21—Small fish, carnivorous			
50	42—White ibis	19—Terrestrial invertebrates			
51		20—Small fish, herb., and omniv.			
52		21—Small fish, carnivorous			
53		29—Medium frogs			
54		30—Small frogs			
55		32—Tadpoles			
56	43—Grinformes	19—Terrestrial invertebrates			
57		20—Small fish, herb., and omniv.			
58		21—Small fish, carnivorous			
59	44—Owls	20—Small fish, herb., and omniv.			
60	54—Gray fox	8—Understory			
61		10—Hardwood wood			
62	55—Raccoon	19—Terrestrial invertebrates			
63	65—Armadillo	8—Understory			
64		10—Hardwood wood			

Table 3. Net Positive Impact (NPI) Coefficient in Wet and in Dry Seasons

No.	Beneficial Predators	Prey	NPI Wet	NPI Dry
1	20— Small fish 1	19—Terrestrial invertebrates	3.12E-02	1.01E-02
2	23—Alligator	18—Aquatic invertebrates	1.78E-02	2.29E-02
3		19—Terrestrial invertebrates	2.22E-02	>0.01
4		29—Medium frogs	3.39E-02	2.09E-02
5		30—Small frogs	1.08E-01	1.52E-02
6		31—Salamander larvae	4.79E-02	—
7		32—Tadpoles	1.40E-01	1.19E-02
8		37—Galliformes	>0.01	1.27E-02
9		61—Mice and rats	6.26E-02	8.78E-02
10	24—Turtles	19—Terrestrial invertebrates	1.25E-02	>0.01
11		30—Small frogs	1.17E-02	—
12	26—Snakes	16—Apple snail	>0.01	1.60E-02
13		18—Aquatic invertebrates	1.28E-02	1.48E-02

The prey are ranked by compartments. Only NPIs of >0.01 are reported.

Table 4. Direct Negative Impact (DNI) Coefficient, in Wet and in Dry Seasons

#	Beneficial Predators	Prey	DNI Wet	DNI Dry
1	20—Small fish 1	19—Terrestrial invertebrates	3.29E-02	1.27E-02
2	23—Alligator	18—Aquatic invertebrates	>0.01	>0.01
3		19—Terrestrial invertebrates	>0.01	>0.01
4		29—Medium frogs	1.26E-01	1.08E-01
5		30—Small frogs	5.94E-02	1.12E-01
6		31—Salamander larvae	1.59E-01	—
7		32—Tadpoles	3.48E-02	1.09E-01
8		37—Galliformes	3.77E-02	2.32E-02
9		61—Mice and rats	2.12E-02	>0.01
10	24—Turtles	19—Terrestrial invertebrates	>0.01	>0.01
11		30—Small frogs	1.63E-02	—
12	26—Snakes	16—Apple snail	>0.01	>0.01
13		18—Aquatic invertebrates	>0.01	>0.01
14	42—White ibis	32—Tadpoles	1.14E-02	—

The prey are ranked by compartments. Only DNIs of >0.01 are reported.

DISCUSSION

A predator can have a significant net positive effect upon its prey in three possible ways (Table 6): (a) the net positive benefit is significant, (b) the direct negative impact is significant, or (c) both NPI and DNI are significant. In the first case, the predator is a marginal one. In the second, the predator exerts a considerable direct negative effect on the prey that is almost exactly compensated for by its positive actions elsewhere. The strongest positive indirect action occurs when both NPI and DNI are significant. Then, the role of the predator *cum* predator is quite obvious, as is also its indirect role as benefactor. Most of the examples in Table 6 belong to the third case, and the alligator is the predator in all but three of those cases. Regarding alligator prey items, three frog compartments receive significant benefit from the reptiles (small frogs, medium frogs, and tadpoles). In all of these cases, the benefits to the frogs derive from the heavy negative impact that alligators have as a predator of snakes (Figure 3). The negative effect of alligators on small frogs during the wet season is $q_{Alligator \rightarrow Small\ frogs} = -0.059$. The indirect effect that alligators have on small frogs because alligators are predators of snakes is, accordingly, $q_{Alligator \rightarrow Small\ frogs} = q_{Alligator \rightarrow Snakes} \times q_{Snakes \rightarrow Small\ frogs} = +0.156$, and the net impact (considering only these two pathways) becomes $q_{Alligator \rightarrow Small\ frogs} = +0.156 + (-0.059) = +0.097$. For the dry season, the net contribution of these two path-

Table 5. All Paths Related to the Beneficial Interactions of Alligators With the Prey Compartments Discussed in the Text

Wet Season				Dry Season			
Beneficial Predators	Prey	Paths	Impacts	Beneficial Predators	Prey	Paths	Impacts
20—Small fish 1	19—Terrestrial invertebrates	1) 19-20-	−3.29E-02	20—Small fish 1	19—Terrestrial invertebrates	1) 19-20-	−1.27E-02
23—Alligator	18—Aquatic invertebrates	1) 18-20-23-	2.14E-02	23—Alligator	18—Aquatic invertebrates	1) 18-20-23-	2.73E-02
		2) 18-21-23-	4.85E-03			2) 18-21-23-	5.70E-03
		3) 18-20-26-23-	−3.10E-03			3) 18-20-26-23-	−2.63E-03
		4) 18-22-23-	1.82E-03			4) 18-22-23-	1.98E-03
		5) 18-23-	−1.05E-03			5) 18-23-	−1.68E-03
	Total		2.39E-02		Total		3.07E-02
	19—Terrestrial invertebrates	1) 19-25-23-	1.03E-02		29—Medium frogs	1) 29-23-	−1.08E-01
		2) 19-20-23-	5.15E-03			2) 29-26-23-	1.06E-01
		3) 19-23-	−1.10E-03			3) 29-24-23-	7.34E-03
	Total		1.44E-02			4) 29-26-27-23-	−4.65E-03
	29—Medium frogs	1) 29-26-23-	1.39E-01			5) 29-26-24-23-	−1.71E-03
		2) 29-23-	−1.26E-01		Total		−1.02E-03
		3) 29-24-23-	4.35E-03		30—Small frogs	1) 30-23-	−1.12E-01
		4) 29-26-27-23-	−2.42E-03			2) 30-26-23-	1.04E-01
		5) 29-26-24-23-	−1.85E-03			3) 30-24-23-	7.61E-03
	Total		1.31E-02			4) 30-26-27-23-	−4.55E-03
	30—Small frogs	1) 30-26-23-	1.56E-01			5) 30-26-24-23-	−1.67E-03
		2) 30-23-	−5.94E-02			6) 30-26-42-23-	−7.87E-04
	Total		9.66E-02		Total		−7.40E-03
	31—Salamander larvae	1) 31-23-	−1.59E-01		32—Tadpoles	1) 32-23-	−1.09E-01
		2) 31-26-23-	1.07E-01			2) 32-26-23-	1.07E-01
		3) 31-27-23-	8.27E-02			3) 32-26-27-23-	−4.69E-03
		4) 31-27-26-23-	−8.31E-03			4) 32-26-24-23-	−1.72E-03
	Total		2.24E-02			5) 32-42-23-	8.56E-04
	32—Tadpoles	1) 32-26-23-	1.34E-01			6) 32-26-42-23-	−8.11E-04
		2) 32-23-	−3.48E-02			7) 32-42-26-23-	−6.50E-04
		3) 32-27-23-	2.98E-02		Total		−9.02E-03
		4) 32-24-23-	1.75E-02		37—Galliformes	1) 37-23-	−2.32E-02
	Total		1.47E-01			2) 37-26-23-	1.76E-02
	37—Galliformes	1) 37-23-	−3.77E-02			3) 37-24-23-	1.62E-02
		2) 37-26-23-	1.84E-02			4) 37-26-27-23-	−7.69E-04
		3) 37-24-23-	1.66E-02		Total		9.83E-03
	Total		−2.70E-03		61—Mice and rats	1) 61-26-23-	8.28E-02
	61—Mice and rats	1) 61-24-23-	4.74E-02			2) 61-24-23-	9.34E-03
		2) 61-26-23-	3.47E-02			3) 61-23-	−5.96E-03
		3) 61-23-	−2.12E-02		Total		8.62E-02
	Total		6.09E-02	26—Snakes	16—Apple snail	1) 16-21-26-	6.83E-03

Table 5. (Continued)

Wet Season				Dry Season			
Beneficial Predators	Prey	Paths	Impacts	Beneficial Predators	Prey	Paths	Impacts
24—Turtles	19—Terrestrial invertebrates	1) 19-24-	−4.33E-03			2) 16-29-26-	5.80E-03
		2) 19-20-24-	9.78E-04			3) 16-26-	−4.24E-03
		3) 19-37-24-	8.83E-04			4) 16-18-26-	2.62E-03
	Total		−2.47E-03			5) 16-22-26-	2.61E-03
	30—Small frogs	1) 30-26-24-	1.66E-02			6) 16-41-26-	2.33E-03
		2) 30-24-	−1.63E-02			7) 16-38-26-	1.92E-03
		3) 30-26-23-24-	−4.61E-03			8) 16-40-26-	1.91E-03
		4) 30-23-24-	1.76E-03			9) 16-42-26-	1.55E-03
	Total		−2.55E-03			10) 16-27-26-	1.43E-03
26—Snakes	18—Aquatic invertebrates	1) 18-20-26-	1.32E-02			11) 16-30-26-	1.10E-03
		2) 18-21-26-	3.03E-03			12) 16-21-22-26-	−9.60E-04
		3) 18-22-26-	9.46E-04		Total		2.29E-02
		4) 18-26-	−9.36E-04		18—Aquatic invertebrates	1) 18-20-26-	1.58E-02
		5) 18-20-23-26-	−7.70E-04			2) 18-21-26-	3.30E-03
	Total		1.55E-02			3) 18-29-26-	1.26E-03
42—White ibis	32—Tadpoles	1) 32-26-42	1.60E-02			4) 18-22-26-	1.15E-03
		2) 32-42-	−1.14E-02			5) 18-26-	−9.90E-04
		3) 32-27-42-	1.96E-03			6) 18-20-28-26-	−9.56E-04
		4) 32-27-26-42-	−3.59E-04			7) 18-20-23-26-	−9.30E-04
	Total		6.20E-03		Total		1.86E-02

Only those paths accounting for >1% of the overall predatory impact are reported.

Table 6. Significant Net Positive Impacts (NPIs) and Direct Negative Impacts (DNIs)

Predator	Prey	Season
Case 1: NPI significant		
Alligator	Terrestrial invertebrates	Wet
Alligator	Mice and rats	Dry
Turtles	Terrestrial invertebrates	Wet
Snakes	Apple snail	Dry
Snakes	Aquatic invertebrates	Wet
Snakes	Aquatic invertebrates	Dry
Case 2: DNI significant		
Alligator	Galliformes	Wet
White ibis	Tadpoles	Wet
Case 3: NPI and DNI significant		
Small fish 1	Terrestrial invertebrates	Wet
Small fish 1	Terrestrial invertebrates	Dry
Alligator	Aquatic invertebrates	Wet
Alligator	Aquatic invertebrates	Dry
Alligator	Medium frogs	Wet
Alligator	Medium frogs	Dry
Alligator	Small frogs	Wet
Alligator	Small frogs	Dry
Alligator	Tadpoles	Wet
Alligator	Tadpoles	Dry
Alligator	Salamander larvae	Wet
Alligator	Galliformes	Dry
Alligator	Mice and rats	Wet
Turtles	Small frogs	Wet

ways is −0.007. Neither of these latter two values exactly equals the overall trophic impacts of alligators on small frogs as calculated by IMPACTS. (They are positive for both seasons.) In either season, however, the path *small frogs → snakes → alligator* is the key route by which alligators benefit their amphibian prey.

The generic pathway *prey → snakes → alligator* also seems pivotal to many of the positive effects that alligators exert on other prey. This is the case for other frog compartments, medium frogs, and tadpoles (Figures 3 and 4) and also for Galliformes, salamander larvae, and small mammals (Figure 4 and Table 5). Snakes also serve as an intermediary for the major beneficial impacts that turtles have on small frogs and that white ibis have on tadpoles.

Turtles serve as the most important intermediary for the positive trophic action of alligators on mice and rats during the wet season (Figure 4). These reptiles also play a strong secondary role as mediators of the benefits that alligators bestow on many of their prey (Table 5). Thus, the positive action of alligators may be attributed to the combined effect of strong predatory and competitive relationships between alligators, turtles, and snakes. Alligators, snakes, and in part also turtles share much the same diet (Table 7), although each predator does so in different proportions and impacts its prey in different ways. Alligators feed more on larger prey (such as snakes and turtles) and relatively less on smaller amphibians (Delany and Abercrombie 1985). As a result, alligators exert a stronger predatory impact on turtles and snakes than on the other common items in their diet. The result is that snakes and turtles benefit only a small number of their prey in comparison to alligators.

The primary intermediaries of the positive action to aquatic invertebrates are fish, both herbivorous (20) and piscivorous (21). Alligators also benefit terrestrial invertebrates (19), but prey only weakly on these organisms, so their presence as “predator” is less definitive.

Seasonality in both the abundance and diet of species appears to change these positive effects of predators on their prey. As we have already described, reptiles and amphibians dominate, in terms of biomass, the cypress swamp vertebrates; in winter, however, birds also become quite abundant, due largely to the suitability of this habitat as a winter nesting ground. (The number of birds present during the rainy season is very small by comparison, so that any predatory impact they may exert in that season is likely to be irrelevant.)

The large numbers of adult birds present in winter exert significant predation pressure. On the other hand, these birds produce eggs and juveniles, which serve as an abundant source of food to many other predators. Another factor that changes trophic activities between wet and dry seasons is the concentration of fauna in small ponds during the dry season. This increases the vulnerability of fish and amphibians.

Although the species are virtually the same in both seasons, the magnitudes of the links between compartments can change dramatically. For example, overall predation on *tadpoles* and *small frogs* is very little during the dry season. The many predators that feed on these compartments during the wet season show virtually no intake during the dry period (the abundance of larval and juvenile frogs falls off markedly during the dry season). Thus, we note how the positive action of alligators on medium frogs remains at almost the same, low level during both seasons. In contrast, the magnitude by which alligators benefit small frogs and tadpoles decreases substantially during the dry period. This

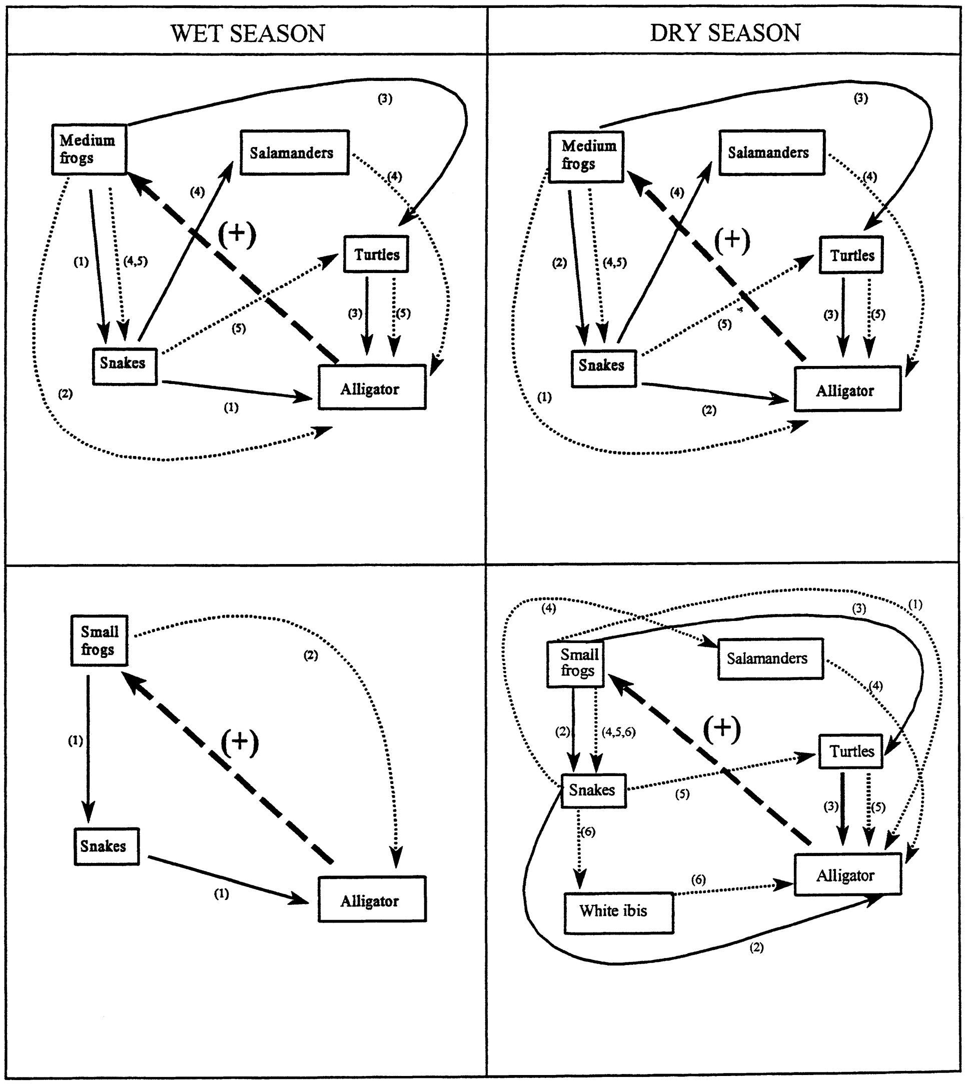


Figure 3. Paths connecting *medium frogs* and *small frogs* compartments to *alligator*. Only paths representing > 1% of the overall predatory impact have been retained. Numbers in brackets refer to the paths reported in Table 5. Dotted lines represent negative links.

drop is also due to the fact that the direct negative impact of alligators on small frogs likewise increases as the wetlands dry up: $q_{Alligator \rightarrow Small\ frogs} = -0.059$ for the wet season and $q_{Alligator \rightarrow Small\ frogs} = -0.112$ for the dry season. Actually, Table 7 reveals how this negative impact of alligators on small frogs is not particularly strong when compared with depredations by snakes. *Small frogs* remain a secondary item in the diet of alligators, comprising around 0.1%–0.4% of total intake. On the other hand, 7.7%–8.9% of a typical alligator's diet consists of snakes, and the latter population depends on small frogs for 2.0%–2.6% of its total diet.

The seasonal changes observed in the magnitude of the beneficial effects that are mediated by snakes can be explained in part by temporal changes in the composition of the alligator's diet. These changes, in turn, are partially induced by the immigration of avian predators at the end of the wet season. As wading bird populations increase in biomass during the dry period, alligators have to share the same prey with a larger pool of predators. In addition, juvenile alligators become abundant during the dry season. Alligator hatching takes place sometime between late July and late August, at the end of the wet season.

American alligators dig and maintain ponds (gator holes) that provide refuge for fishes, frogs, and snakes during the winter dry period (Craighead 1968). Because these species are sources of food for mammals and wintering birds, the effects of alligators extend beyond habitat facilitation. Also, the nest of the American alligator supports commensal reproduction by snakes and turtles (Deitz and Jackson 1979; Kushlan and Kushlan 1980; Hall and Maier 1993), and the adult alligator actively defends its nest and protects the eggs against ovipredation. The economy of the cypress wetland is strongly

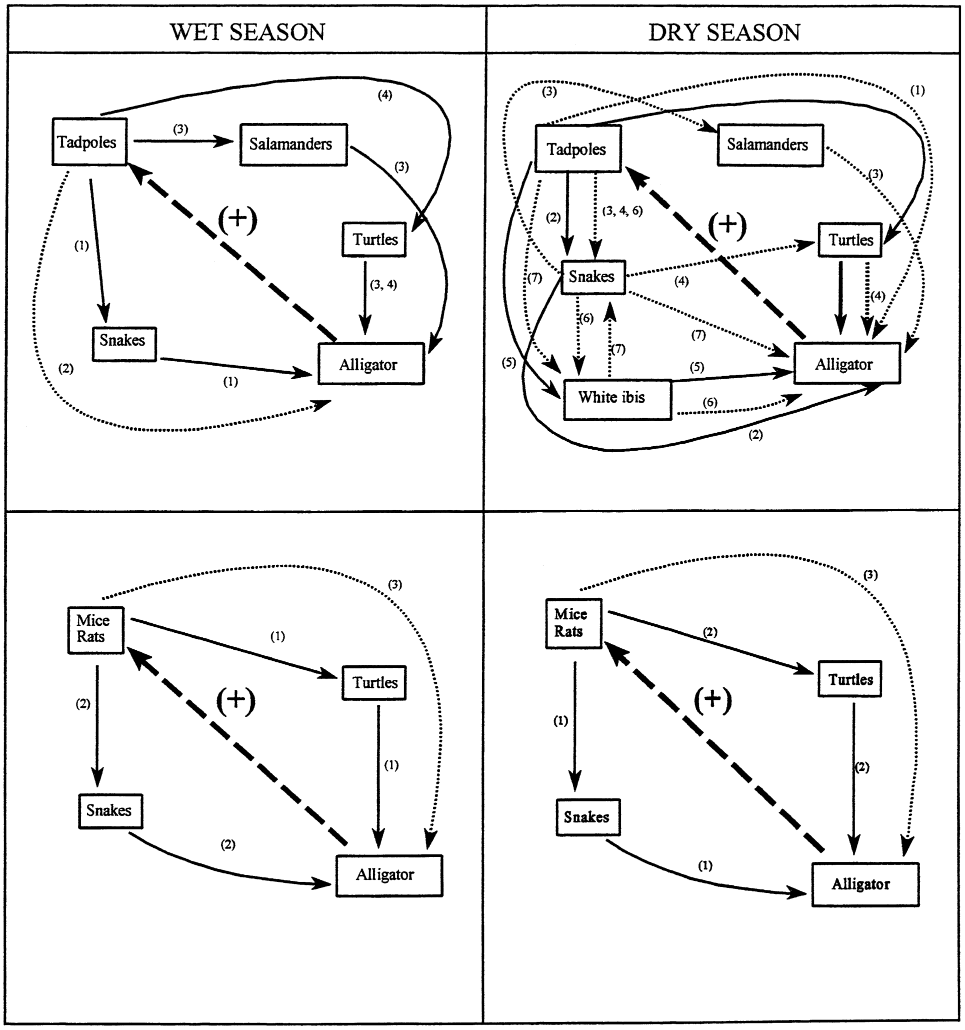


Figure 4. Paths connecting *tadpoles* and *mice and rats* compartments to *alligator*. Only paths representing > 1% of the overall predatory impact have been retained. Numbers in brackets refer to the paths reported in Table 5. Dotted lines represent negative links.

affected by the presence of alligators, which exert rather counterintuitive effects upon energy flow in the ecosystem.

Norton (1988) asserted that the *Alligator mississippiensis* might act as a "keystone" species. According to Paine (1969), keystone predators help to maintain biodiversity by preventing their favorite prey from outcompeting other species. Menge (1995) included this mechanism in his taxonomy of indirect effects. In this study, the positive effects exerted by the American alligator resemble what happens in trophic cascades (sensu Menge 1995) more than keystone predation.

The investigation of the positive effects that *Alligator mississippiensis* exerts upon a large number of its prey in the cypress wetland ecosystem of South Florida has been conducted via a network analysis of the trophic exchanges between system components. Network analysis identified each set of pathways by which the American alligator exerts a counterintuitive effect upon a prey population. The number of paths belonging to any set does not exceed 7, and the maximum length of any individual path is 4. Thus, the positive effects that alligators exert upon certain prey appear in small subsets of the entire network. Because of their relative simplicity, such subsystems seem particularly suited to experimentation and the application of dynamic modeling. Because the number of pathways responsible for the positive effect is not very large, formulating the causal hypotheses required by path analysis becomes easier, and this technique could be invoked to study these subsystems in combination with experiments. From this perspective, network analysis seems complementary rather than mutually exclusive of experimentation, path analysis, and other modeling techniques.

The software package IMPACTS enables one to use network analysis to investigate indirect interactions, because it includes the negative effect that a predator exerts upon its prey in the context of energy flow and illustrates how these negative

Table 7. Diet Composition for the American Alligator, Turtle, and Snake Compartments

	Wet Season			Dry Season		
Diet Compartments	Alligator	Turtles	Snakes	Alligator	Turtles	Snakes
Floating vegetation		10.46			13.73	
Periphyton/macroalgae		18.08			18.93	
Macrophytes		9.71			7.95	
Crayfish	4.83	19.78	6.35	6.68	18.11	5.34
Apple snail	0.48	2.20	0.75	0.28	0.75	0.22
Prawn	3.04	12.46	4.00	4.05	10.98	3.24
Aquatic invertebrates	1.01	4.16	1.38	1.22	3.31	0.97
Terrestrial invertebrates	0.73	3.01	0.96	2.76	7.47	2.20
Small fish 1	47.19	9.29	44.40	45.26	9.29	35.58
Small fish 2	7.08	2.51	6.76	6.14	1.26	4.83
Large fish	4.04	1.59	3.22	4.33	0.89	3.40
Alligator		2.94	5.29		3.05	4.43
Turtles	9.34			9.28		
Lizards	3.50		2.01	3.02		1.66
Snakes	8.91	0.98		7.69	1.02	
Salamanders	6.56	0.93	4.28	4.77	1.02	3.55
Large frogs	0.89		5.04	1.17		8.87
Medium frogs	1.27	0.36	9.07	1.66	0.93	13.39
Small frogs	0.12	0.03	2.04	0.35	0.19	2.64
Salamander larvae	0.11		0.49			0.30
Tadpoles	0.05	0.22	1.31	0.06		0.46
Anseriformes	0.30		0.94			
Galliformes	0.26	0.96	0.84	0.16	0.93	1.01
Egrets	0.06		0.20	0.25		1.55
Great blue heron						0.30
Other herons				0.25		1.57
Wood stork						1.92
White ibis	0.12		0.39	0.23		1.41
Woodpeckers			0.06			0.07
Passeriformes 1		0.04	0.04		0.05	0.05
Passeriformes 2		0.05	0.04		0.04	0.05
Shrews					0.02	0.14
Mice and rats	0.01	0.25	0.14	0.01	0.10	0.87
Rabbits	0.07			0.38		

The diets are expressed as percentages of the overall intake.

actions propagate throughout the system. The algorithm combines the energy-flow approach with loop analysis, a qualitative technique that interprets species interactions by using signed digraphs and differential equations (Ulanowicz and Puccia 1990). IMPACTS is an attempt to communicate across two traditions in ecology in studying the problem of indirect interactions, which is so crucial to our understanding of ecosystem functioning.

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