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Insect predators of mosquitoes of rice fields: portrayal of indirect interactions with alternative prey

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Abstract
The present commentary highlights the likelihood of indirect interactions in rice fields and allied wetlands using the water bugs, odonate larvae and dytiscid beetles as insect predators of mosquito. The biomass and linkage density of the species were used as input to construct the network and estimate the opportunity of intraguild predation (IGP) and apparent competition (AC). It was evident that IGP increased as a function of insect predator body weight (r= + 0.907; P < 0. 05), while an increase in prey biomass decreased its involvement in AC (r = - 0.864; P < 0.05). The interaction between mosquito prey and the predators appears to be affected by the biomass and composition of the species assemblage. Assuming chances of IGP and AC, positive preference for mosquito by the insect predators seems to be an important criterion for effective biological control.

Keywords: Intraguild predation, Apparent competition, Biological control, mosquito, insect predators

1. Introduction

The aquatic community of rice fields and allied wetlands includes different insect predators that consume wide range of prey including mosquitoes. The ability to regulate mosquito population through consumption is a basis for considering predatory insects as biocontrol agent against mosquitoes, evident from mosquito consumption by water bugs [1-6], dytiscid beetles[7-9], and odonate larvae [6, 11] of rice fields and allied wetlands. While use of predatory insects favours sustenance of ecosystem functions and biological integrity of the community, prey selectivity [5, 6, 10, 11] and indirect interactions [6, 12, 13] are important determinants of the efficacy of the mosquito regulation. In rice fields and allied wetlands, coexistence of multiple insect predators with generalist feeding habit increases the possibility of indirect interactions with mosquito as a key prey. Indirect interactions like intraguild predation (IGP) [14] and apparent competition (AC) [15] involve additional species other than the mosquito and the insect predators. Presence of the additional species alters the effects of direct interactions between mosquito and insect predators, eventually affecting the regulation of mosquito populltion. In IGP, a top predator (IG predator) competes and consumes another predator (IG prey), both of which share a common prey (Shared prey, mosquito, in this instance) [14]. Variant forms of IGP exist, depending on the body size and predatory activity of IG predator and IG prey. Apparent competition involves additional prey species, commonly termed the alternative prey, which shares the same predator with the key prey (mosquito, in this instance) [15]. In a prey–predator system, prey consumption by the predator can be considered as a direct effect. Addition of a species in the system, either an erstwhile predator (IG prey for IGP) or a prey (for AC) forms the source of indirect effects that can dampen the direct effect on the existing prey. Consequently, the prey-predator system involving more than two species becomes complex in terms of food web properties. An increase in species number results in a corresponding increase in the number of links and connectance value, and thus increases the complexity of the system. If mosquito consumption by an insect predator is considered as a direct effect, additional predator or an alternative prey would induce indirect effects, thereby altering the regulation of mosquito effectively. Owing to the generalist feeding behavior of the insect predators, IGP and AC are more likely to be factors impeding mosquito regulation in rice fields and allied wetland habitats, with high species diversity [6, 16–19]. Estimation of the possible indirect effects in the species assemblage will enable prediction about the efficacy of

the insect predators in regulating mosquitoes.

Rice fields and allied wetlands host a range of insect predators and prey [20-22] with varying size and length [23-26]. The intensity and outcome of prey–predator interactions depend on several factors including the relative size [24-26] and density of the interacting species and the habitat conditions [2-5, 9-11]. While habitat conditions primarily influence the spatial orientation and encounter rate of the prey and predators [10], the body size and relative abundance influence the prey selection and amount of prey consumed by the predators [10], evident for the prey-predator interactions between water bugs, dytiscid beetles and odonate larvae. Although predatory insects exhibit size and density dependent prey selection, water bugs can attack prey of much bigger size than their own body weight [27, 28]. However, in common instances, the prey of a particular size range is selected by the insect predators following the norms of optimal foraging theory. Predation patterns of insect predators suggest that bodyweight (biomass) can be a predictor of the prey selection, predatory efficiency and pattern and structure of the food web [28-31]. Thus the links between the prey species, i.e. dietary choice, and a particular predator can be portrayed using the body weight as a variable. Dietary choice of a predator reflects the possibilities of IGP and AC within the community. Thus considering the insect assemblage in rice fields, emphasizing body weight as a key parameter and the trophic links of the predators, the possibilities of indirect interactions were estimated against each of the mosquito insect predators. Potential of these insects to be a part of indirect interactions will enable predictions about the regulation of mosquito immature, besides predicting species specific efficiency as biocontrol agent.

2. Materials and methods
2.1 Sampling of rice fields
The rice fields of the University farm house at Tarabag, Burdwan were considered as study sites. Random stratified sampling was employed to collect the insects and mosquitoes from the rice fields under inundated conditions between January and April, and, August to November of 2011, with a cumulative 70 sampling units. Following collection of organisms using insect net fitted with a long handle [32], the specimens were placed in plastic bags, half filled with rice field water, and brought to the laboratory. In the laboratory the specimens were emptied in plastic trays for identification to the genus level following appropriate keys [2-6, 33]. Data on the insect predators and the prey species were recorded [18 -22] from cumulative samples. The wet weight of individual organism was estimated using a pan balance (Citizen, Kolkata, India) to the nearest 0.1 mg. For the analysis only the adult morphs of Coleoptera and Hemiptera (Heteroptera) were considered, while for Odonata larvae, body weight of the maximal size were considered. Information on the prey–predator relation was obtained from existing literature [1-9, 12, 13, 33-38]. The size of the prey species compatible for consumption by the predators was considered, thereby discounting smaller instars of mosquito and chironomid larvae, tubificid worms and bigger sized snails.

The prey and predator species were arranged in a matrix [31, 39-40] where the row elements were the predators (i), and the column elements were prey (j). Links representing trophic relation between prey and predators were scored as a value of 1 and absence of links were assigned a value 0. Thus, a bipartite network of predator and prey species was constructed and analyzed for estimating the connectance C, and linkage density of the predator species (A_i) and prey species (A_j). To predict the possibilities of apparent competition the proportion of links related to coexisting prey species was used as a numerator over the total number of links for a particular prey. Similarly for predicting the possibility of intraguild predation, the links related to non-prey species and the respective predator were used as a numerator over the total number of links (A_i for non-prey species/ A_i). Similarly the clustering coefficient was used to indicate the relative value of the predator in respect to the community assemblage. In all instances a regression equation [41] was constructed using the body weight of the predator species as independent variable against the possibilities of IGP and AC. In view of the hypothesis of the study, the body weight of the predators was used to predict the chances of indirect effects that may influence the mosquito population regulation.

3. Results
A total of 27 species of macroinvertebrates were observed from 52 samples obtained from the rice fields and allied trap ponds. The relative abundance and body weight of the predatory insects and prey varied with the samples (Fig 1a, and b). The species ensemble was composed of fifteen different insect predators and twelve different prey species. The insect predators included the water bugs [(Hemiptera: Heteroptera) *Diplonychus annulatus* (DAN), *D. rusticus* (DRU) (Belostomatidae); *Ranatra filiformis* (RAF) *Ranatra elongata* (RAE), *Laccotrephes* sp. (LAC) (Nepidae); *Anisops* sp. (ANI) (Notonectidae), *Gerris* sp. (GER) (Gerridae)], larvae of dragonfly [(Odonata: Anisoptera) *Brachydiplax* sp. (BRA), *Pantala* sp. (PAN), *Sympetrum* sp. (SYM), *Macromia* sp. (MAC) (Libellulidae); and damselfly (Odonata: Zygoptera) *Ceriagrion* sp. (CER)(Ceriagrionidae)], larvae and adult of dytiscid beetles [(Coleoptera: Dytiscidae) *Cybister* sp. (CYB) and *Acilius* sp. (ACI)(Dytiscidae)] and predatory larvae of the mosquito *Lutzia* sp. [(Diptera: Culicidae) *Lutzia fuscana* (LUT)]. The prey species included the freshwater snails [(Gastropoda: Mesogastropoda) *Lymnaea luteola* (LLU) (Lymnaeidae), *Gyraulus convexiusculus* (GCO), *Indoplanorbis exustus* (IEX) (Planorbidae); *Gabbia orcula* (GOR) (Bithyniidae)], larvae of mayfly [Insecta: Emphemeroptera) *Cloeon* sp. (CLO) and *Baetis* sp. (BAE) (Baetidae)], tubificid worms [(Annelida: Oligochaeta) *Tubifex* sp. (TUB) (Tubificidae)], larvae of chironomid midges (CHI) (Diptera: Chironomidae) and mosquito [(Diptera: Culicidae) *Anopheles* sp. (ANO) and *Culex* sp. (CUL)], the small water bug (Heteroptera) [*Paraplea* sp. (PAR) (Pleidae)] and)- leg stage tadpoles of *Bufo* sp (TAD). Although mosquito, chironomid and tubificid worms were represented by more than one species, for the purpose of network analysis these were grouped together under the broad heads. The mean body weight of the predators ranged from 11 mg (*Lutzia fuscana*) to 267 mg (*Diplonychus annulatus*), while the mean body weight of prey species ranged between 2 mg (larva of *Anopheles* sp.) and 11 mg tadpoles. The log transformed body weight of predators and prey were negatively correlated with abundance (for predators r = - 0.578; for prey r = -0. 245), indicating that bigger species were less abundant in the community. The low values of r for prey and predators could be possibly due to sampling bias, though the snails like *L. luteola* and *G. convexiusculus* remained high in abundance despite their higher body weight. Depending on the instar stages and age the size and body weight of the insect predators and prey varied extensively. For analysis, the smaller instar stages of the

water bugs, dytiscid beetles and odonate larvae were not considered excluding cannibalism.

Analysis of the links among the species showed a connectance (C) of 0.296, and average linkage density of 8 for all species and 14.4 for the predators. The matrix of prey and predator representing the links is shown in Fig 2. A negative correlation (r = - 0.527) was observed for the number of links with the body weight (biomass) of the interacting species (Fig 3a). For the insect predators the number of links increased with the body weight, suggesting that the prey range increased as a function of body weight (Fig 3b).

The proportion of links indicating IGP increased with the body weight of the predators (Fig 4), with *Anisops* and larvae of *Lutzia* sp. yielding a value of 0 to act as IG predator, to almost 0.5 for *D. annulatus*. In a similar way, with the increase in body weight the shared links for apparent competition of the prey decreased (Fig 5), with the tadpoles having a link of 10 and dipteran larvae having a link of 15. Thus the network of predator and prey species weighted by the average body weight suggest that with increase in body weight of prey the number of links are reduced suggesting few predators to share them as prey. While for insect predators, an increase in body weight increased the number of links suggesting their wide dietary choice.
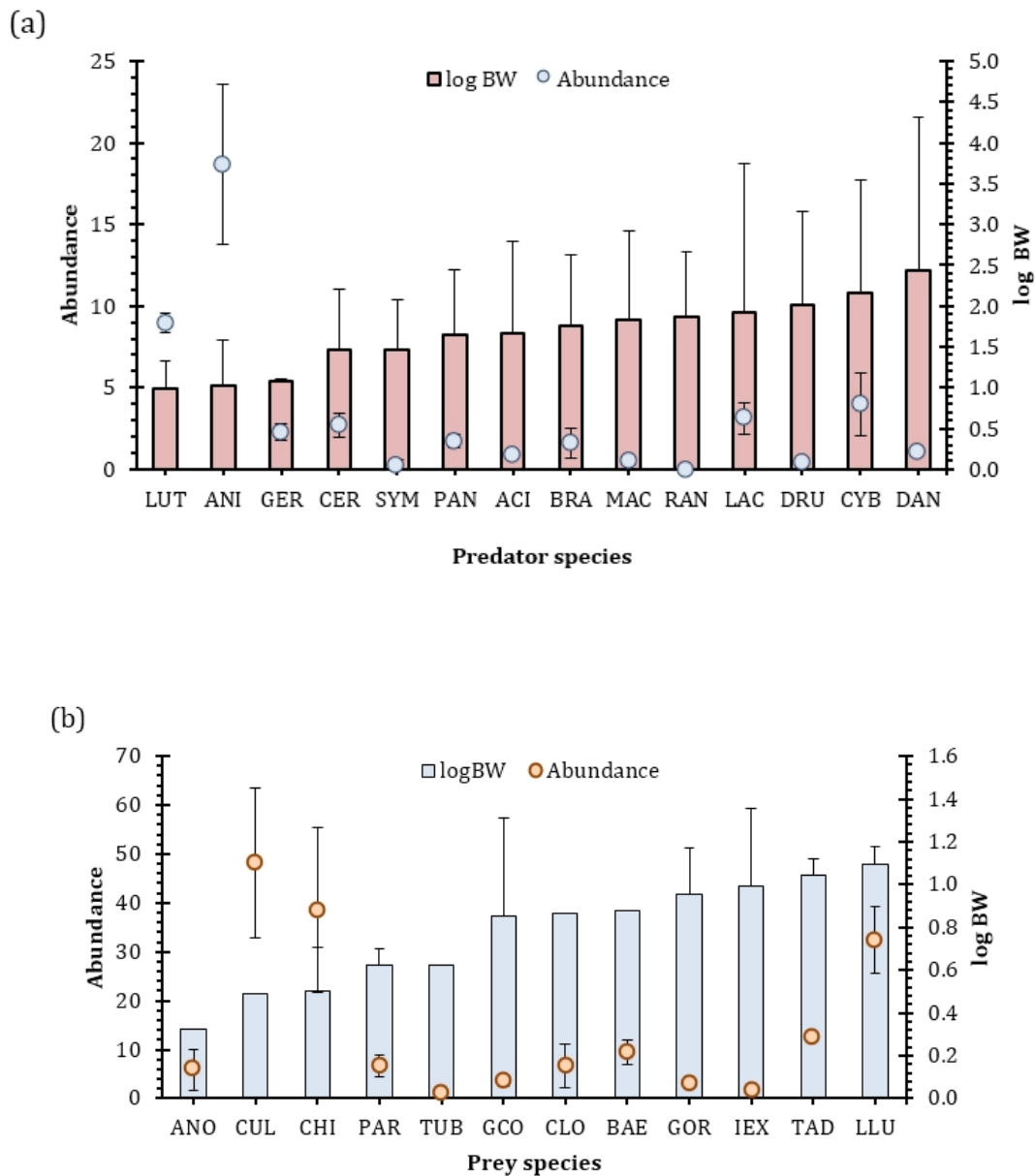

Fig 1: The relative abundance and body weight (log transformed; log BW) of the predatory insects (a) and prey (b) sampled from rice fields of Burdwan, West Bengal India during the study period.

Fig 2: The matrix representing the network of insect predators (row) and prey (column) considered in the study. Each shaded square represents an interaction (link), open squares represent no interaction (link). Cannibalism is excluded, and only adult morphs of Hemiptera, Odonata and Coleoptera are considered. The predators (rows) are arranged in decreasing order of body weight.
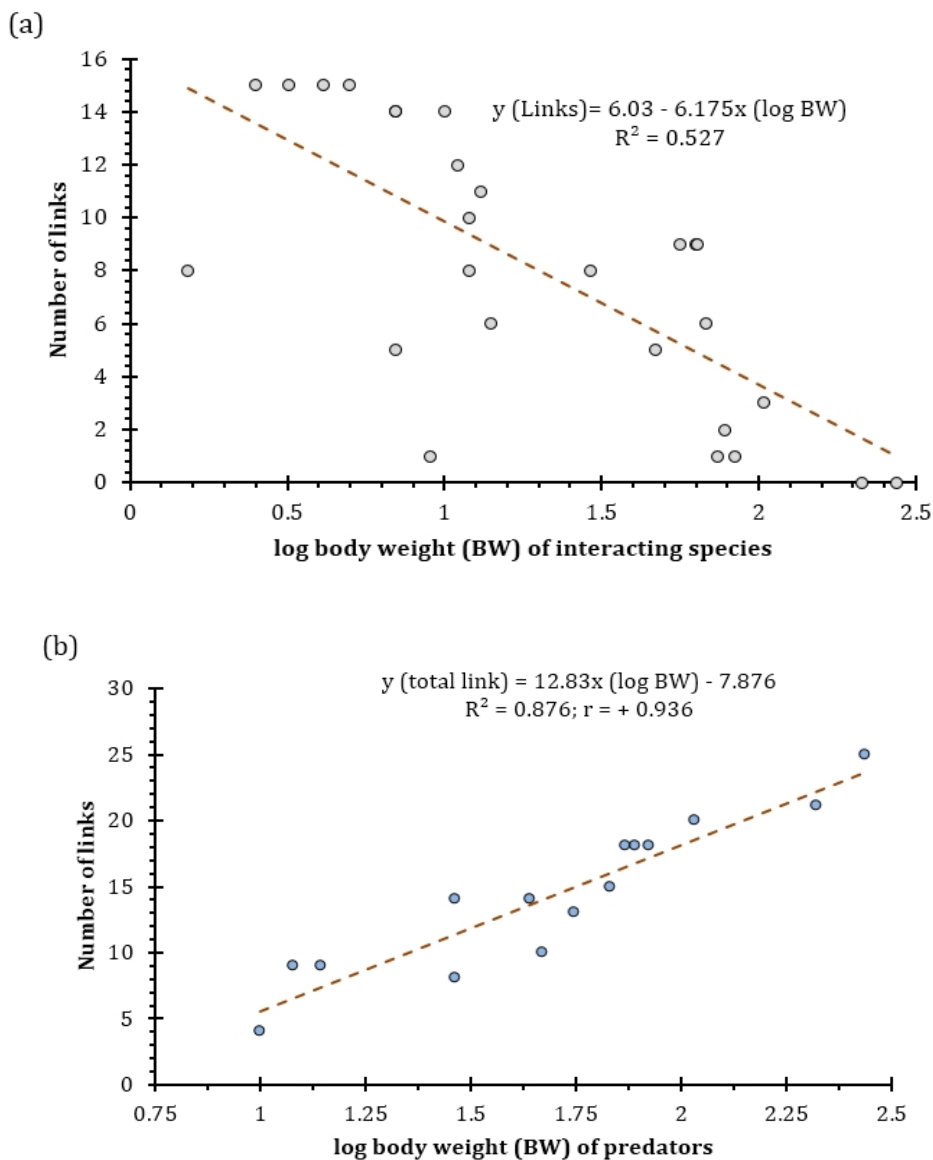

(a)

y (Links)= 6.03 - 6.175x (log BW)
$R^2 = 0.527$

(b)

y (total link) = 12.83x (log BW) - 7.876
$R^2 = 0.876$; r = + 0.936

Fig 3: The relation between the links and the log biomass of predators and prey considered in the study. (a) links of all interacting groups as prey (Cannibalism is ignored while placing the role of predators as prey). (b) links of predator groups only against the prey.
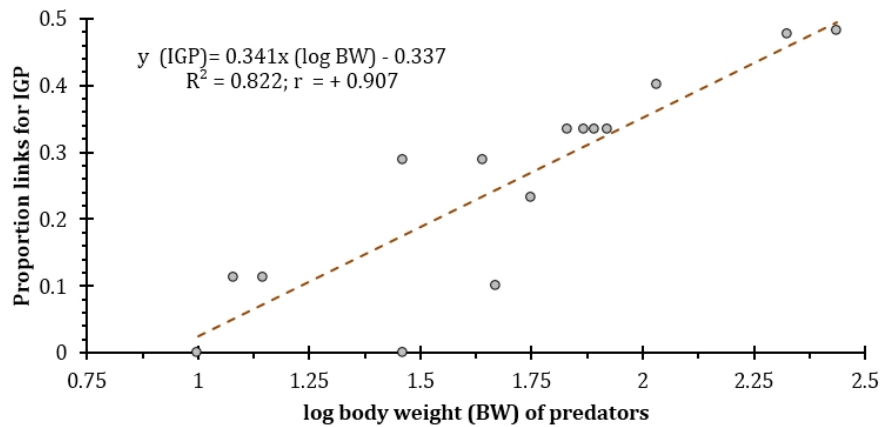
Fig 4: The relation between body weight of predator and the proportional links leading to IGP, based on the fact that a predator of smaller size is vulnerable as prey to a predator of larger size leading to asymmetric IGP.
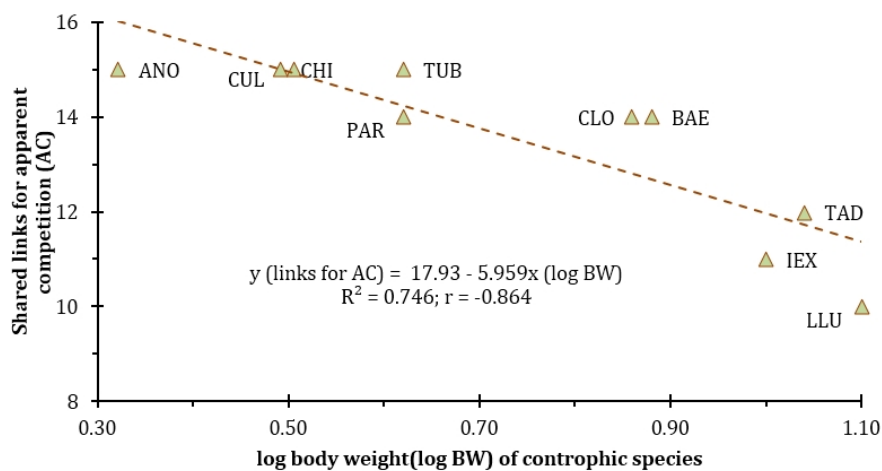

Fig 5: The relation between body weight of the prey species and the shared links for apparent competition, based on the generalist dietary choice of the predators (GOR is excluded due to less number of links).

4. Discussion

In rice fields and allied wetlands multiple predators and prey coexist contributing to the diversity and stability of the aquatic community, evident from several empirical studies [19-23]. Numerical abundance and relative biomass of the constituent species vary in the aquatic habitats thereby influencing the species interactions and shape of the community structure in space and time. In the present context, the variation in relative abundance and biomass of the predators and prey was evident (Fig 1). The prey species were numerically abundant with low biomass in contrast to the predator species, which is in accordance with the observations for size of prey and predators [25, 26]. The number of links of the prey species, the snails, insects, tubificid worms and the tadpoles decreased with the increase in the body weight (Fig 3a), reflecting that prey species with smaller biomass are shared by multiple predators. The predators like *Anisops* sp. and *Gerris* sp. and the larvae of *Lutzia* sp. were comparatively low in biomass with fewer number links to prey groups than the water bugs, dytiscid beetles and odonate larvae. The prey-predator link was an increasing function of the predator biomass (Fig 3b), suggesting that the bigger the predator, the higher is the regulatory effect on the prey ensembles. The observed variation in the linkage density and the biomass of the predators and prey suggests the possibility of indirect interactions like the IGP and AC. In IGP, the biomass of the interacting species can be ordered as IG predator> IG prey and shared prey, which is evident in many instances from terrestrial and aquatic ecosystems. Exceptions to this assumption are known, particularly for waterbugs [27] and host-parasitoid interactions [25, 26], but in the present instance, we excluded such possibilities. On the basis of biomass of the predators and the number of links as indicator of possibility of IGP, a positive correlation was observed. Thus predators with higher body weight are more likely to create an intraguild predation system, using the predators with lower biomass as IG prey. Recent studies on water bugs as predators suggest that predator and prey biomass are positively correlated, though variations are observed since many predators can consume prey of higher biomass [28]. For IGP involving true predators (excluding parasitoids), it is obvious that the body mass of the IG predator is higher than the IG prey and shared prey [14, 15]. On this basis the possibility of IGP is portrayed using the links and the biomass of the prey and predator concerned. It appears that the predators like water bugs and dytiscid beetles are capable of introducing IGP with greater possibility that rest of the insect predators (Fig 4).

The likelihood of apparent competition was portrayed excluding the predators (and cannibalism). As shown in Fig 4b, the chances to be a part of apparent competition decreases

with the increase in prey body weight. In apparent competition, the controphic species exerts a benefit to a target prey species in course of sharing a predator. The present analysis used the number of links to infer about the possibility of a prey species to be included in the apparent competition. Since numerical abundance and prey preference are among other factors that influence the vulnerability of a prey to the predator, the inference may change in circumstance where the numerical abundance and prey preference are considered. If a predator exhibits preference for a bigger sized prey, the prey with smaller body size may benefit out of the interaction. Although the number of predators linked to bigger sized prey was less in the present food web, the possibilities of predation cannot be excluded. However, since many of the prey species (with smaller body weight) exhibited equal links, chances are high that these prey form a part of apparent competition. For effective regulation of the target prey, mosquito for instance, the availability of the alternative prey with similar number of links poses significant concern [12, 13]. Assuming the alternative prey species to be numerically equal, the preference for mosquito will be an important criterion for effective regulation, evident from the studies on waterbugs and odonate larvae [5, 6, 11].

Biological control of mosquitoes using aquatic insect predators is a feasible alternative to avoid the ill-effects of chemicals hampering the ecosystem functions. In order to be effective as biological control agent, the insect predators should exhibit positive selectivity for mosquito over a range of alternative prey including IG prey. Thus on a comparative basis, the tubificid worms, chironomid larvae, may fly larvae bear greater potential than the tadpoles and snails in reducing the vulnerability of mosquito to the insect predators. Indirect interactions like IGP and AC can reduce the effective regulation of mosquito by the insect predators. Analysis of the food web in terms of the characteristic links and body weight of predators enable highlighting the chances of IGP and AC. Applying the network analysis on the species ensemble [25, 39, 40], the relative value of the species in IGP and AC is being highlighted for assessing the levels of regulation. It is evident that the coexistence of the species may be possible through these indirect interactions, though the effective regulation of mosquitoes may not be achieved to a satisfactory level. Simulated studies should be carried out to rank the predator species in terms of the capability for inducing IGP or AC, prior to selection for biological control of mosquitoes. While prey preference and numerical and functional responses have been emphasized for insect predators for mosquito control [5, 6, 10, 11], indirect interactions appear to be equally relevant. Thus field and laboratory assessment of the role of alternative prey in eliciting IGP and AC should be performed to predict the successful operation of biological control of mosquitoes employing generalist insect predators.

5. Acknowledgements

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