

## FLEXIBLE FORAGERS IN FOOD WEBS

# Linking learning adaptation to trophic interactions: a brain size-based approach

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### Summary

1. Given that food web structure potentially affects species coexistence and ecosystem functioning, exploration of the patterns and determinants of the resource–consumer interactions, the building blocks of food webs, should be of particular importance for successful maintenance of biodiversity and ecosystem services.

2. Ecological theory has demonstrated that rapid ‘adaptation’ via learning potentially alters the strength of trophic interaction, and thus, population dynamics. Increasing evidence suggests that learning improves foraging and anti-predator defence behaviours in diverse animal taxa and that cognitive ability is related to population establishment or persistence. However, only a few empirical studies have evaluated the community-level consequences of learning, probably owing to the difficulty in detecting learning-mediated changes at levels higher than the individual and in evaluating the learning ability of individual species.

3. Comparative studies, mostly conducted to identify selection pressures in brain evolution, suggest that brain size is an aggregate proxy for an organism’s learning ability. Therefore, I propose a framework to analyse resource–consumer relationships based on information about the brain size of individual species, which will allow investigation into the effects of learning on food webs.

4. Evidence shows that brain size is related to trophic interactions. Earlier comparative analyses have revealed that diet is correlated with brain size in primates, mammals and insects. My analysis of 623 prey–predator pairs comprising 277 fish species indicates that a larger-brained predator tends to prey on a larger-brained prey; that relative brain size of prey is, on average, larger than that of the predator; and that our understanding of prey–predator pairs is improved by information about brain size.

5. A number of questions remain unanswered. Studies on how brain size is related to trophic interactions are limited to a few animal taxa. The factors leading to brain-related patterns in trophic interactions remain to be addressed. Brain-related patterns with respect to higher level biological organizations, such as whole food webs or chains, and inter-community comparison remain unexplored. Further studies are needed to confirm the general applicability of the hypotheses that relate brain size to trophic interactions and to evaluate the role of learning in shaping biological communities.

**Key-words:** anti-predator defence, cognition, diet choice, food web, foraging adaptation, prey–predator interaction, body size

### Introduction

A flexible change in behaviour or morphology according to the fitness gradient via evolution, learning and phenotypic plasticity (hereafter referred as ‘adaptation’ *sensu* Abrams 2005) is a major feature characterizing organisms. A better

understanding of an organism’s adaptive behaviour is essential for tackling two major questions concerning food web ecology. First, what determines food web structure (e.g. topology, interaction strength distribution), and second, how is population dynamics related to food web structure (de Ruiter, Wolters & Moore 2005). Recent advances in the study of food webs have been made possible by taking advantage of behavioural or evolutionary ecological

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concepts. To answer the first question, behavioural ecologists have tried to understand the pattern of an organism's resource utilization from the viewpoint of adaptive diet choice, resulting in a rich body of work on optimal foraging theory (MacArthur & Pianka 1966; Stephens & Krebs 1986). Optimal foraging theory explains the microscopic pattern of which predator utilizes which prey. When applied to a multi-species system it allows the prediction of some macroscopic features of food webs such as connectance and link distribution within a web (Matsuda & Namba 1991; Beckerman, Petchey & Warren 2006; Petchey *et al.* 2008). With regard to the second question, studies on prey–predator dynamics, with consideration of adaptations in predator and prey species, have explored how behavioural or morphological changes induce temporal or spatial variability in interaction strength thus altering population dynamics (Abrams 2000; Abrams in this volume) and its relation to food web structure (Kondoh 2005).

A major process through which a population or individual improves its behaviour is learning, a cognition-mediated behavioural change induced by experience (Shettleworth 1984). Learning is classified into two groups – individual learning and social learning. While the former is based on choice of an idea from a set of private ideas and is relevant to ‘innovation’ or ‘trial-and-error’, the latter is based on imitation of others (Robert 1990) and forms the core aspect of ‘Machiavellian intelligence’ (Byrne & Whiten 1988). Learning induces behavioural changes in an organism, potentially increasing fitness. Together, individual and social learning allow a new ‘meme’ to arise (individual learning) and extend over a population through imitation (social learning), resulting in a mechanism by which a population flexibly adjusts to a changing environment (Dawkins 1976).

Despite the abundance of available theoretical literature showing that rapid adaptation affects prey–predator interactions, population dynamics and food web structure (Abrams 2000; Bolker *et al.* 2003; Abrams in this volume), empirical studies focusing on the effect of learning on population processes are still limited (Sol & Lefebvre 2000; Sol, Timmermans & Lefebvre 2002; Shultz *et al.* 2005; Sol *et al.* 2005; Drake 2007). Moreover, only a few studies have evaluated the role of learning in structuring biological communities. This is despite the long history of behavioural ecological studies on learning and its potential effects on trophic interactions (Beukema 1968; Ware 1971). On the other hand, evolutionary ecologists have been trying to understand the evolution of cognitive ability, intelligence and learning in relation to the evolution of brain (Jerison 1973; Roth & Dicke 2005).

Here, I review the studies on resource–consumer interaction, learning and its relation to brain structure and, based on this review, propose a possible approach (namely, brain size-based approach) to linking learning to resource–consumer interactions and to food webs. This paper is organized in the following manner. In the next section, I make clear that learning is an essential subject to be studied, or taken into account, to better understand food webs by reviewing behavioural ecological studies on how learning is related to

resource–consumer interactions, the smallest unit of a food web, or the population dynamics of single species. In ‘Brain size as a proxy for learning ability’, based on evolutionary ecological studies of brain, I suggest that brain size can be used as a proxy for cognitive ability. In ‘Relating brain sizes to trophic interactions’, I propose the brain size-based approach, which will allow us to test hypotheses that relate learning to prey–predator interactions, food web structure and dynamics. This approach is then applied to 623 prey–predator pairs comprising 277 fish species with an aim to detect a sign of learning. In Conclusions, I discuss some problems with this approach and propose a course for future study.

### Learning, trophic interaction and population consequences

Learning has a major effect on resource–consumer interactions through multiple mechanisms. Two major ways through which a resource–consumer interaction is modified via learning are improvements in the consumer's foraging behaviour and in the anti-predator behaviour of resource species. Improvements can occur through three different processes, (i) recognition, (ii) handling and (iii) choosing, each of which affects the interaction strength, thus affecting population and community processes, in different ways.

Improvement of foraging behaviour through mechanisms i–iii changes resource–consumer interaction strength as follows. Per-capita interaction strength,  $a_{ij}$ , of consumer  $j$  on resource  $i$  can be given by:

$$a_{ij} = \frac{e_i g_i N_i}{1 + \sum_{k \in \text{Species } j\text{'s potential resource}} e_k g_k h_k N_k} \quad \text{eqn 1}$$

where  $e_k$  is the searching efficiency ( $0 \leq e_k$ ),  $g_k$  is the attacking probability ( $0 \leq g_k \leq 1$ ),  $N_k$  is population density and  $h_k$  is handling time ( $0 \leq h_k$ ). (i) Recognition of resource species  $i$  by consumer  $j$  means that resource  $i$  is included in consumer  $j$ 's potential resource. Resource recognition is the basis of resource–consumer interactions. As a consumer often cannot respond accurately to a novel resource item, improvement of resource recognition is an extremely important process in understanding the ecological consequences of species introduction (Kondoh 2006). For example, a predator reared in a hatchery often shows reduced ability to recognize a natural prey, which is improved by increasing encounter experiences (Beukema 1968; Ware 1971; Reiriz, Nicieza & Braña 1998). (ii) Foraging performance can be improved with experience in diverse taxa (Hughes 1979; Brown & Laland 2003). A predator can improve its capture success or foraging rate for a particular prey item by decreasing the time spent handling or searching (Ehlinger 1989; Croy & Hughes 1991; Reiriz, Nicieza & Braña 1998). This would decrease  $h_k$  or increase  $e_k$ . (iii) Diet choice leads to a change in  $g_k$  in a manner that increases  $\sum_k a_{kj}$  (MacArthur & Pianka 1966; Stephens & Krebs

1986). This is associated with avoidance of non-favourable resources or inclusion of more favourable resources into diet (Vinyard 1982; Barnhisel 1991; Reiriz, Nicieza & Braña 1998). When the quality or quantity of resource temporally changes, a consumer may 'switch' its diet in response. As adaptive switching behaviour requires both discrimination of multiple resource items and 'knowledge' of the relative quantity or quality of those items (Stephens & Krebs 1986), experience is essential for appropriate switching behaviour. Ersbak & Hasse (1983) have shown that a wild brook trout shows greater flexibility in switching to more available prey and higher feeding success than a stocked, naïve brook trout, supporting this view. These improvements in foraging behaviour can occur not only through individual learning but also through social learning (Kieffer & Colgan 1992).

It is not only consumer's learning that alters prey–predator interaction strength. Improvement in prey behaviour via learning also matters. As predation is an important cause of fitness losses, there should be a strong selective pressure for prey behaviours that reduce predation risks (Endler 1986; Lima & Dill 1990). There is accumulating evidence that both social and individual learning are essential for predator avoidance in diverse taxa (Marler 1996; Berger, Swenson & Persson 2001; Bshary, Wickler & Fricke 2002; Brown & Laland 2003). Several studies have demonstrated that 'experienced' individuals, who have been repeatedly exposed to predators, are more likely to survive subsequent encounters with the predators than naïve individuals, through improvement in predator recognition or predator-avoiding behaviour (Olla & Davies 1989; Berejikian 1995; Mirza & Chivers 2000). Furthermore, as predator avoidance is often associated with significant energetic or temporal costs, adjustment of anti-predator behaviour to relative risks of different predators (i.e. a 'choice' of predator to defend against) should be beneficial in case of temporal or spatial variation in predation risks (Harvell 1990; Cresswell 1993). Evidence shows that social learning affects predator avoidance behaviour of prey. A naïve European minnow *Phoxinus phoxinus* that observed another fish being attacked by a predator often invoked an escape response to the predator (Magurran & Higham 1988).

Theory predicts that 'quick adaptation' strongly affects population dynamics, although the actual mechanisms of adaptation are often not specified in mathematical models (Abrams 2000; Kondoh 2003, 2007). Learning, which occurs within a generation, is a possible mechanism that gives rise to quick adaptation. However, empirical studies that have tested the effects of learning on population dynamics are very limited. A few correlational studies have tested whether establishment or persistence is better facilitated in populations of bird species with larger brains (Sol & Lefebvre 2000; Sol, Timmermans & Lefebvre 2002; Shultz *et al.* 2005; Sol *et al.* 2005), a proxy for better cognitive capability (see next section). Shultz *et al.* (2005) analysed the British Common Birds Census (1968–1995) to identify the specific characteristics associated with long-term abundance trends in UK

farmland birds. They found that the population levels of species with relatively smaller brains were more likely to decline. Sol and his colleagues (Sol & Lefebvre 2000; Sol, Timmermans & Lefebvre 2002; Sol *et al.* 2005) analysed the data of human-mediated introduction of birds and concluded that species with larger brain sizes were more successful at establishing themselves in novel environments. Furthermore, this brain effect was attributed to enhanced cognitive abilities, but not to non-cognitive mechanisms such as motor or perceptual abilities (Sol *et al.* 2005). However, the exact behavioural basis of these patterns (e.g. improvement of foraging, predator avoidance or other behaviour) remains unclear.

### Brain size as a proxy for learning ability

Given that learning can affect prey–predator interactions and single-population dynamics, what pattern may arise among prey–predator pairs? Are there any general patterns in cognitive or learning ability at community level? How are species with a better capacity to learn distributed in a food web? An important first step in tackling these questions is to find a convenient 'proxy' for the learning ability of individual species or animal groups. There is no doubt that identification of a proxy for the characteristic of interest provides a powerful tool for food web analysis. For example, recent success in the body size-based approach to food webs has been made possible by a strong link between body size and diverse ecological and physiological entities that lead to many other constraints (Elton 1927; Warren & Lawton 1987; Cohen *et al.* 1993; Woodward *et al.* 2005).

What can be a good proxy for learning ability? Studies on brain provide a potential answer. There is a long history of study on the brain and its evolution, motivated by a desire to understand the origin of human intelligence (Jerison 1973; Allman 2000; Roth & Dicke 2005). As the brain is a metabolically expensive tissue (Aiello & Wheeler 1995; Safi, Seid & Deckmann 2005), there must be an associated benefit that overcomes this energetic cost for large-brained species. So what is the benefit of large brains, or what conditions favour larger brains? This is the exact question that evolutionary ecologists have asked. There have been a number of attempts to identify the most important selection pressure on brain size (reviewed in Dunbar & Shultz 2007; Healy & Rowe 2007). The diverse benefits proposed are classified broadly into two groups, ecological (e.g. diet, habitat complexity, adaptation to novel environments) and social (parental care, group size), which are relevant to individual and social learning respectively.

Environmental, or ecological, hypothesis proposes that large brains evolved because it allowed more flexible and innovative behaviours, and thus, provided more ecological benefits. A relationship between brain size and feeding innovations has been demonstrated across vertebrate taxa (Lefebvre *et al.* 1997; Reader & Laland 2002). Several studies based on statistical association between brain size and variables assumed to be associated with environmental changes have

shown that a large brain is favoured by environmental changes (Lefebvre *et al.* 1997; Reader & Laland 2002; Sol *et al.* 2005), presenting an indirect support to the hypothesis. A larger brain may allow a predator to adapt its foraging behaviour and thus utilize novel prey items or resources that temporally or spatially change their availability (Lefebvre *et al.* 1997; Reader & Laland 2002); or a prey with a larger brain may be more effective in evading predators due to its adaptive anti-predator behaviours such as changing habitat use or behavioural patterns according to a change in the predation risks (Shultz & Dunbar 2006a).

The 'social brain' hypothesis suggests that organisms with superior cognitive ability are more capable of managing social relationships, and thus, are able to solve more problems via social learning or intelligence (Dunbar & Shultz 2007). It has been shown that a larger brain, or a larger specific brain part, is associated with social learning in humming birds (Jarvis *et al.* 2000) and primates (Reader & Laland 2002). Brain (or neocortex) size is correlated with social systems in ungulates (Shultz & Dunbar 2006b), or with social group size, a proxy of social complexity, in primates (Sawaguchi & Kudo 1990; Dunbar 1992, 1998; Barton 1996), carnivores (Dunbar & Bever 1998) and cetaceans (Connor *et al.* 1998; Marino 2002). These patterns seem to imply that social relationships with more individuals are associated with larger brains (but see Emery *et al.* 2007; Shultz & Dunbar 2007, where the maintenance of a long-lasting relationship is considered to be associated with larger brains).

The selection pressures for a larger brain are, however, still controversial. Only with the above-mentioned correlations, we cannot tell whether those proposed variables actually act as a selection pressure or are consequences of evolved large brains. Furthermore, a recent study has found that environmental and social learnings covary (Reader & Laland 2002), suggesting that social and environmental intelligence are not independent of each other and may not be distinguishable (Reader & Laland 2002; Seyfarth & Cheney 2002). Indeed, noting that environmental problems are often solved socially, the social brain hypothesis can be interpreted as having the same root with environmental hypothesis (Dunbar & Shultz 2007). Actually, the established fact that grouping and social interactions among group members provide benefits in foraging and anti-predator behaviour in many animal taxa (Krause & Ruxton 2002) clearly indicates that the cognitive ability to cope with group members should also provide an ecological advantage: a species with a larger brain may be better in hunting or defending against natural enemies in a group. However, these studies certainly suggest that brain size can be used as an aggregate proxy for an organism's learning ability. This is therefore a possible method for describing food webs by using information available on cognitive or learning ability of individual species.

Before introducing studies of a brain-based approach to trophic interactions, it should be noted that there are some drawbacks in considering brain size to be representative of cognitive ability (Roth & Dicke 2005; Healy & Rowe 2007). Healy & Rowe (2007) pointed out two major problems

regarding this. First, given the modularity of function within the brain, what the difference in the whole brain size, which is often used in comparative analysis, represents is unclear. Second, the available data on brain size have been collected by different methods, which may introduce bias falsely leading to significant correlations in comparing data from different sources. In addition, it should also be noted that the animals examined so far to identify ecological or social representatives of brain size are strongly biased in favour of particular animal groups such as primates, some mammals and birds (but see Kotrschal, van Staaden & Huber 1998; Lisney & Collin 2006).

### Relating brain sizes to trophic interactions

Assuming that the brain size represents the cognitive ability of an organism, we can describe food webs (or, prey–predator pairs) using information on the brain size of individual species and analyse the role of cognitive ability in shaping biological communities. Brain size-based analysis is a convenient tool in testing learning effects on prey–predator interactions and population dynamics. In the following section, I have briefly reviewed published studies that relate brain size to trophic interactions, and presented my own analysis to illustrate a possible brain size-based approach to prey–predator pairs.

#### INDIVIDUAL SPECIES

One way to describe trophic relations based on brain size is to relate brain size to the organism's food type. As learning can increase per-capita interaction strength by improving foraging performance (increased searching efficiency,  $e_i$ , and decreased handling time,  $h_i$ , in Eqn 1), a higher learning capability may allow a consumer species to persist with a resource that a consumer with less learning capability cannot persist with. A number of comparative studies have shown that food type is indeed correlated with brain size (Jerison 1973; Eisenberg & Wilson 1978; Clutton-Brock & Harvey 1980; Harvey, Clutton-Brock & Mace 1980; Gittleman 1986; Hutcheon, Kirsch & Garland Jr. 2002; Jones & MacLarnon 2004; Farris & Roberts 2005). Leaf-eating species have smaller brains than fruit-eating or omnivorous species in non-human primates and small mammals (Clutton-Brock & Harvey 1980; Harvey, Clutton-Brock & Mace 1980; Mace, Harvey & Clutton-Brock 1980, 1981), for example, in bats, plant-eaters (e.g. frugivores) generally have larger brains than animal-eaters (insectivores) (Eisenberg & Wilson 1978; Hutcheon, Kirsch & Garland Jr. 2002; Jones & MacLarnon 2004). In mammals, carnivores and omnivores have larger brain sizes than insectivores (Gittleman 1986); brain size is positively correlated with diet breadth in carnivorous beetles (Farris & Roberts 2005). Although the actual causality between diet and brain size is unclear, in terms of comparative study, those patterns were often attributed to cognitive constraints on resource use. For example, considering the pattern that leaf-eating species have smaller brains than fruit-eating species, Harvey, Clutton-Brock & Mace (1980) argued that leaves are more evenly



distributed in space and time, and thus, their utilization requires less learning capability and memory. A larger brain may be necessary to handle a resource that requires more complex foraging strategies or to utilize a wider range of resources that require different handling strategies.

Another way to relate brain size to trophic interactions is to consider how brain size is related to the properties of the prey. Anti-predator behaviour based on a higher cognitive ability of the prey may result in more difficulty in prey finding, capturing (lower  $e_i$  in Eqn 1) and handling (larger  $h_i$ ) for predators (Olla & Davies 1989; Berejikian 1995; Mirza & Chivers 2000; Berger, Swenson & Persson 2001). This implies that the prey's cognitive ability, and thus its brain size, may be correlated with its predation vulnerability. However, few empirical tests are available for validating this prediction. Shultz & Dunbar (2006a) is an exceptional study that examined the relationship between brain size and predation vulnerability. They compared biases in the diet composition of chimpanzees and felids with prey characteristics and found a predator bias to small-brained prey in both predator species in five different tropical forests on two continents. Interestingly, relative brain size was more important than the other contributing factors, i.e. body size and prey group size, in predicting biases in predator diets. However, it was unclear whether this bias was due to predator preference for small-brained prey or unsuccessful attacks on large-brained prey. The mechanism for this pattern has not been identified.

#### PREY-PREDATOR PAIRS

Given that the learning ability of prey and predator improves predator's predation performance and prey's anti-predator behaviours, respectively, the interaction strength between them would be determined as a balance between those opposite forces. In such a case, a pattern may potentially emerge in the relationship between learning or cognitive abilities of prey and its predator (Jerison 1973). However, few studies have systematically explored this relationship. As a first step, I studied predator-prey pairs of fish species known to have considerable cognitive ability (Bshary, Wickler & Fricke 2002). I analysed 623 prey-predator pairs comprising 277 fish species from different communities (Tables S1 and S2, Supporting Information). Species identities in prey-predator pairs were obtained from FishBase (Froese & Pauly 2007), a free-access online data base, and published food web data (Bascompte, Melián & Sala 2005; Brose *et al.* 2005); data on brain sizes ( $B$  [mg]) and body sizes ( $W$  [g]) were obtained from FishBase (Froese & Pauly 2007). When brain sizes or body sizes of multiple individuals were available for a species, the average value was used as a representative.

There was a significant and strong positive correlation between log-scaled body size and brain size ( $r = 0.92$ , d.f. = 277,  $t = 39.4$ ,  $P < 0.001$ ; Fig. 1) in agreement with an earlier study (Jerison 1973). To remove this confounding effect in interspecific comparison of brain size, I used relative brain size ( $\bar{B}$ ), defined as the residuals of a log-log least-squares linear regression of brain size against body size

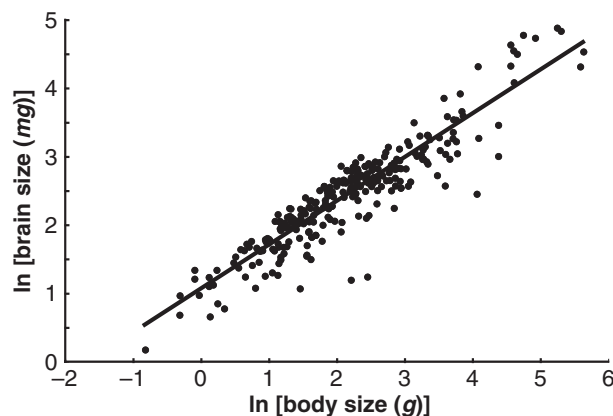


Fig. 1. Relationship between body size and brain size of 277 species.

( $[\ln B] = a [\ln W] + b$ , where  $a = 0.64 \pm 0.02$  SE and  $b = 1.06 \pm 0.04$  SE,  $P < 0.001$  for both  $a$  and  $b$ ,  $R^2 = 0.85$ ), following the standard method used in past comparative studies. Note that usage of this index is based on the assumption that a small absolute residual (not a logarithm) for a small animal is as 'important' as a large residual for a large animal. No significant correlation was observed between body size ( $\ln W$ ) and relative brain size ( $\bar{B}$ ) ( $|r| < 0.001$ , d.f. = 277,  $t = 0.0002$ ,  $P > 0.999$ ).

The first hypothesis tested here relates to the assumption that Jerison (1973) made in arguing that an arms race takes place between predator and prey for brain size. That is, if a prey with a larger relative brain size is more difficult for a predator to find or handle, a predator that utilizes larger-brained prey needs to become more capable of cognition and thus develop a larger relative brain size. Otherwise, the interaction strength becomes too weak for the predator to persist with the prey. Similarly, a prey would require a larger brain to keep the interaction strength low and survive attacks from larger-brained predators. This predicts a positive correlation between relative brain size of prey and predator. My analysis revealed a significant positive correlation between relative brain size of preys and predators ( $r = 0.28$ , d.f. = 621,  $t = 7.14$ ,  $P < 0.001$ ) and that the relative brain

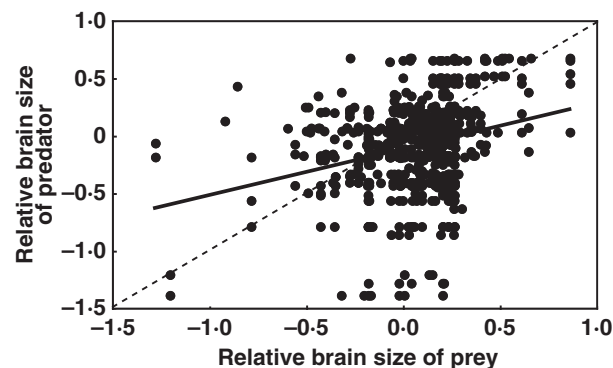


Fig. 2. Relationship between relative brain sizes of 623 prey-predator pairs. The dotted line indicates that  $[\text{prey } \bar{B}] = [\text{predator } \bar{B}]$ .

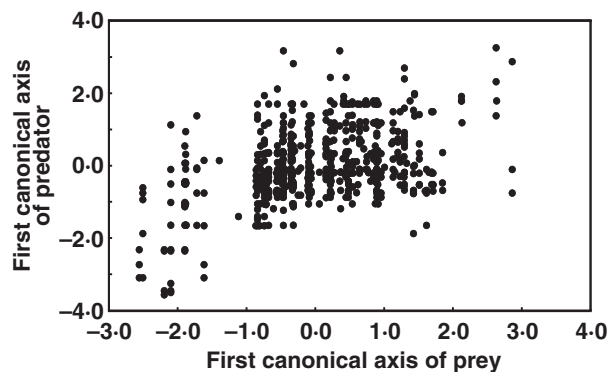
size of the predator increases with increasing relative brain size of prey ( $\bar{B}_{\text{pred}} = a\bar{B}_{\text{prey}} + b$  where  $a = 0.40 \pm 0.06$  SE,  $b = -0.11 \pm 0.02$  SE,  $P < 0.001$  for both  $a$  and  $b$ ) in agreement with the prediction (Fig. 2).

I then compared the relative brain sizes of the predator and its prey. Based on the comparative study of the volumes of endocranial fossil casts of extinct animals, Jerison (1973) found that carnivores always had the larger relative brain size than their prey species and speculated that predators require a larger relative brain size than their prey for a successful hunt. However, the pattern found in my analysis of fish prey–predator pairs was opposite to Jerison’s speculation. The fraction of predator–prey pairs where the relative brain size of the predator is larger than that of the prey was  $214/624 = 34.3\%$  ( $214/594 = 36.0\%$  excluding cannibalisms). The relative brain size of the prey was significantly larger than that of the predator ( $t = 9.05$ , d.f. = 622,  $P < 0.001$ ). The mean difference in  $\bar{B}$  was 0.146, indicating that the relative brain size of the predator was an average of 0.71 times of that of the prey. This may be related to the life-dinner principle (Dawkins & Krebs 1979) that suggests that the prey, which will die if eaten, is under stronger selection pressure than predators, which may survive even if the present hunt is unsuccessful.

It is well known that the body sizes of prey and predator are related (Woodward *et al.* 2005; Brose in this volume). Indeed, a significant positive correlation was observed between prey and predator body sizes ( $r = 0.35$ , d.f. = 621,  $t = 9.34$ ,  $P < 0.001$ ). Given this, does incorporation of relative brain sizes improve our understanding of prey–predator relations? To answer this question, the relationship between prey and predator was analysed by canonical correlation (Manly 1986). This analysis seeks for two linear combinations (canonical axes) constructed of  $[\ln W]$  and  $[\bar{B}]$  ( $a[\ln W] + b\bar{B}$ ) for prey and predator with coefficients ( $a, b$ ) that maximize the correlation between the combinations. By using canonical correlation analysis, we can investigate what relationship exists between prey and predator in terms of  $[\ln W]$  and  $[\bar{B}]$ . The first canonical components, which are best optimized such that the linear correlation between the two canonical axes is maximized, detected by the analysis are  $(0.79[\ln W] + 2.49[\bar{B}])$  and  $(1.03[\ln W] + 0.56[\bar{B}])$  for prey and predator respectively (see Table 1 for standardized coefficients; Fig. 3). The canonical correlation coefficient ( $\sigma$ ) between the first canonical components was 0.43 (Bartlett’s test,  $\chi^2 = 52.8$ ,  $P < 0.001$ ) and higher than the correlation coefficient between body sizes, although the contribution of

**Table 1.** Result of canonical correlation analysis

	Variable	Correlation coefficient ( $r$ )	Canonical coefficient
Prey	Body size	0.77	0.78
	Relative brain size	0.58	0.66
Predator	Body size	0.98	0.95
	Relative brain size	0.16	0.22



**Fig. 3.** The first canonical axes obtained by the canonical correlation analysis.

predator brain size to the predator’s canonical axis was small. This means that prey–predator pairs are better explained by taking relative brain sizes, especially that of the prey, into account. More specifically, a larger predator is expected to utilize a prey species with larger body size and larger relative brain size.

The analysis above suggests a ‘logical model’ that a predator’s body size is related to both body size and relative brain size of prey. Yet, does this model perform better than the model that only takes prey body size or relative brain size into account to explain predator’s body size? To answer this question, I performed stepwise model selection with Akaike’s Information Criterion (AIC). The analysis shows that the best model was that  $[\ln(\text{predator’s body size})] = 2.41 + 0.33 [\ln(\text{prey’s body size})] + 0.82 [\text{prey’s relative brain size}]$  (AIC =  $-220.0$ ; AIC =  $-181.4$  for  $[\ln(\text{predator’s body size})] = a + b [\ln(\text{prey’s body size})]$ ; AIC =  $130.7$  for  $[\ln(\text{predator’s body size})] = a + b [\ln(\text{prey’s relative brain size})]$ ), supporting the view that not only body size but also the relative brain size of the prey plays a role in determining prey–predator pairs.

## Conclusions

Theory suggests that learning adaptations can be a key to understanding trophic interactions. Learning affects foraging and anti-predator behaviours through improvement of recognition, handling and choice. Although all these are important components of trophic interactions and strongly affect prey–predator interactions, population dynamics and community persistence, the role of learning or cognitive ability in these processes has not been well explored. This is partly because of the difficulty in detecting learning-mediated changes at levels higher than the individual and evaluating the learning ability of individual species.

Given the technical difficulty, a possible first step in identifying the role of cognition or learning in higher biological level organizations such as population and community would be to search for patterns in brain size in prey–predator interactions or food webs. It has been found that brain size is associated with diet in mammals, primates and insects (Eisenberg

& Wilson 1978; Clutton-Brock & Harvey 1980; Harvey, Clutton-Brock & Mace 1980; Gittleman 1986; Hutcheon, Kirsch & Garland Jr. 2002; Jones & MacLarnon 2004; Farris & Roberts 2005). Furthermore, although the exact mechanism is still unclear, there is evidence that brain size is correlated with population establishment and persistence (Sol & Lefebvre 2000; Sol, Timmermans & Lefebvre 2002; Shultz *et al.* 2005; Sol *et al.* 2005).

The hypothesis that foraging and defence behaviours are improved by cognition and learning leads to another hypothesis that relates the brain size of a predator to that of its prey. My analysis of prey–predator pairs revealed that a larger-brained predator tends to prey on a larger-brained prey and that the relative brain size of prey species is usually larger than that of the predator. In addition, information on brain size appears to improve the predictability of prey–predator pairs, confirming that brain-sized food web studies are a promising way to narrow the gap between present theory and real food web structure.

A number of unanswered questions remain to be tackled in future studies. First, the generality of the hypotheses presented here needs to be investigated. My analysis is restricted to fish and more analyses are required to test the applicability of these patterns to other taxa. Given that brain architecture largely differs between animal groups and that some properties are correlated with brain size only in limited groups of animal taxa [e.g. population establishment is correlated with brain size in birds (Sol, Timmermans & Lefebvre 2002; Sol *et al.* 2005), but not in fish (Drake 2007)], it is quite likely that what is represented by brain size differs between animal groups. Second, studies based on a comparative approach, including my analysis represented here, cannot reveal anything about the causes of the observed patterns. In fact, the causality between diet and brain size is a central topic of debate in the evolutionary study of the human brain. While ecological hypotheses have proposed that a larger brain has evolved to cope with environmental factors such as resource quality and availability, the expensive tissue hypothesis suggests that improvement in dietary quality allows for a smaller gut, another metabolically expensive organ, thus allowing the reallocation of energy to a larger brain (Aiello & Wheeler 1995). A promising method to investigate causality would be to conduct controlled experiments (Mery & Kawecki 2002). Third, the aspect such as association between food web structure and brain size in organizations with higher biological levels requires more investigation. That a pattern is found at a level of a part of the community (e.g. prey–predator pair) does not necessarily mean that there is a general pattern at the community level. For example, with respect to the relative brain sizes of prey and predators, are there any patterns in how brain size increases with increasing trophic level? As the brain is metabolically extremely expensive (Aiello & Wheeler 1995), brain size constraints may potentially limit the food chain length. We need information on both trophic level and brain size of species from the same food web to test this. Present data, which consist of prey–predator pairs from a number of different ecosystems, do not fit for this

purpose. In addition, questions as to differences across specific communities also remain open for the same reason.

Brain size is correlated with behavioural flexibility (Sol *et al.* 2005) and switching behaviours (represented as changes in  $g_i$  in Eqn 1; Ersbak & Hasse 1983). This indicates that the role of food web flexibility in food web maintenance (Kondoh 2005) may be investigated by analysing food webs described using brain size information. An interesting mechanism through which prey–predator interaction is modified by learning is prey or predator choice. A predator chooses prey species to use and a prey species chooses predator species to defend against. The theory suggests that not only absolute interaction strength, which was related to the body size in a recent study (Yodzis & Innes 1992; Otto, Rall & Brose 2007), but also flexibility in interaction strength arising from switching behaviours have a powerful impact on population dynamics (Tansky 1978; Teramoto, Kawasaki & Shigesada 1979; Abrams & Matsuda 1996; Kondoh 2003, 2007). Predator switching turns negative indirect effects between prey species that share a predator into positive ones (Tansky 1978; Teramoto, Kawasaki & Shigesada 1979), prey defence switches reverse the negative indirect effects between predators into positive ones (Abrams & Matsuda 1996) and predator–prey switching can create a positive relationship between food web complexity and community persistence (Kondoh 2003, 2007). A brain-based analysis of complex food webs may provide an interesting opportunity to test these untested hypotheses.

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## Supporting information

Additional supporting information may be found in the online version of this article:

**Table S1.** Fish species analysed.

**Table S2.** Prey–predator pairs analysed.

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