

# Predator–prey body size relationships when predators can consume prey larger than themselves

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## Community ecology

# Predator–prey body size relationships when predators can consume prey larger than themselves

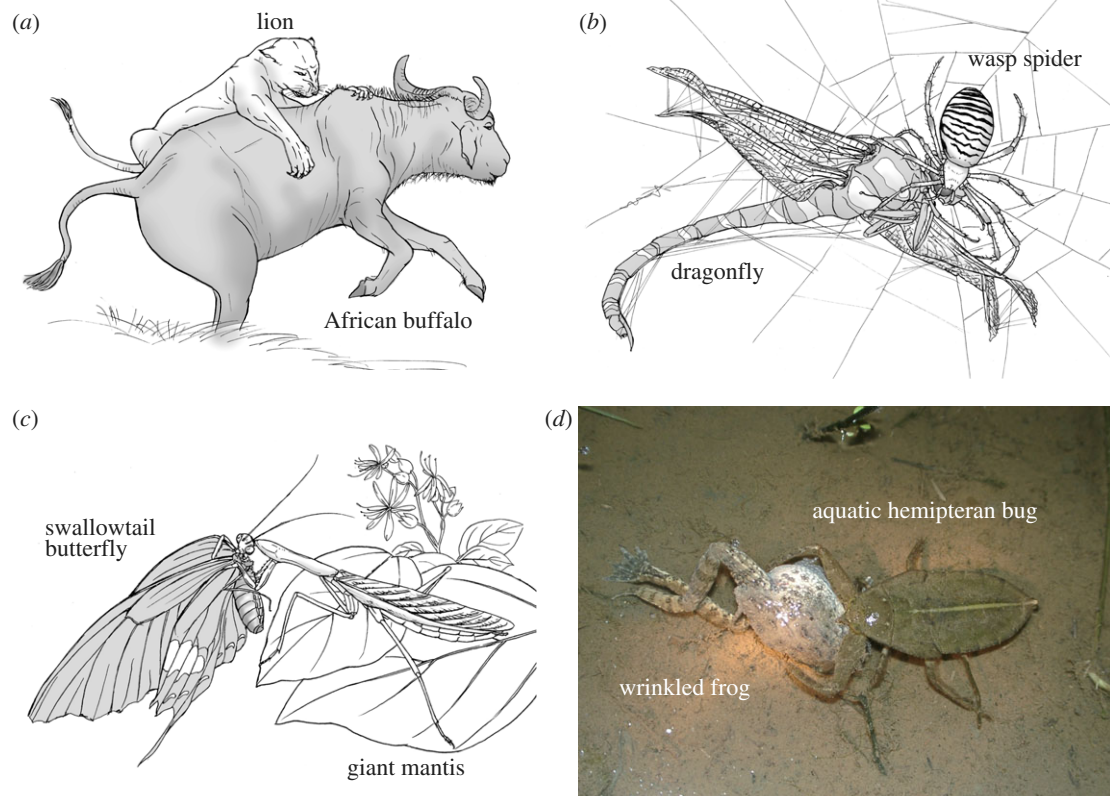
Takefumi Nakazawa<sup>1,2,†</sup>, Shin-ya Ohba<sup>1,3,†</sup> and Masayuki Ushio<sup>1</sup><sup>1</sup>Center for Ecological Research, Kyoto University, Kyoto, Japan<sup>2</sup>Institute of Oceanography, National Taiwan University, Taipei, Taiwan, Republic of China<sup>3</sup>Faculty of Education, Nagasaki University, Nagasaki, Japan

As predator–prey interactions are inherently size-dependent, predator and prey body sizes are key to understanding their feeding relationships. To describe predator–prey size relationships (PPSRs) when predators can consume prey larger than themselves, we conducted field observations targeting three aquatic hemipteran bugs, and assessed their body masses and those of their prey for each hunting event. The data revealed that their PPSR varied with predator size and species identity, although the use of the averaged sizes masked these effects. Specifically, two predators had slightly decreased predator–prey mass ratios (PPMRs) during growth, whereas the other predator specialized on particular sizes of prey, thereby showing a clear positive size–PPMR relationship. We discussed how these patterns could be different from fish predators swallowing smaller prey whole.

## 1. Introduction

As predator–prey interactions are inherently size-dependent, measurements of body sizes of interacting predators and prey are key to understanding their feeding relationships and are increasingly important for food-web studies [1–3]. A previous analysis of global datasets on species body sizes suggested that predator–prey size relationships (PPSRs) may systematically differ among habitat types (e.g. terrestrial versus aquatic) [4]. In general, pelagic consumers (e.g. fish) swallow smaller prey whole, whereas terrestrial or benthic carnivores often capture relatively large prey using hunting tools (e.g. fangs and claws; figure 1). These differences in feeding modes support the traditional view that size constraints on feeding ultimately determine the fundamental nature of food-web structure and dynamics [5]. Furthermore, more recent analyses identified body size and taxonomic identity of predators as additional determinants of PPSR [6–9]. Taken together, it is hypothesized that PPSR qualitatively differ depending on the feeding modes of predators, the understanding of which is essential to establish size-based approaches applicable to a wide range of food webs.

At present, however, data on PPSRs are lacking when predators have a comparable or even smaller body size than their prey (as exemplified in figure 1), except for host–parasitoid interactions [10]. This is because conventional stomach content analysis cannot explicitly assess prey sizes in such situations, the difficulty of measuring body sizes at each hunting event. A common alternative is to use species-averaged body sizes [4,11–13], yet the validity of this remains controversial because feeding relationships are interpreted differently when evaluated at the scale of individual predation events and predator–prey species pairs [7,10,14,15]. In this study, we aim to provide a dataset of PPSR for the understudied type of interaction. We conduct field observations targeting three aquatic hemipteran bugs as easy-to-track model



**Figure 1.** Examples of interactions in which predators attack relatively large prey. (Online version in colour.)

organisms (figure 1d; [16]), and assess their body masses and those of their prey for each hunting event. Furthermore, we identify possible determinants of their PPSR. Specifically, we focus on predator size and species identity for a comparative discussion with gape-limited fish predators [6,7].

## 2. Material and methods

We monitored hunting events of three aquatic hemipteran bugs (*Appasus japonicus*, *Kirkaldyia deyrolli*, and *Laccotrephes japonensis*) in rice fields of central Japan over 1–3 day intervals from May to August in 2005 (see [16] for detailed methodology). They ambush prey at the water surface, capture passing targets by surprise, and insert their proboscis into the victim's body. We searched for hunting events during the night using a flashlight to minimize behavioural interference. For each hunting event, we identified the predator and prey species, measured their body lengths or the lengths of other body parts with callipers, and released them. The length data were converted to weight, based on independent assessments of their allometric relationships:  $(\text{weight}) = \alpha(\text{length})^\beta$  (see the electronic supplementary material, S1). This procedure was to estimate pre-hunting weight without significant over- or underestimation. We recorded a total of 436 hunting events involving 21 prey types. The estimated predator size ranges were 10.51–276.7 mg, 51.92–7144 mg and 6.38–1345 mg for *A. japonicus*, *K. deyrolli* and *L. japonensis*, respectively (see the electronic supplementary material, S2).

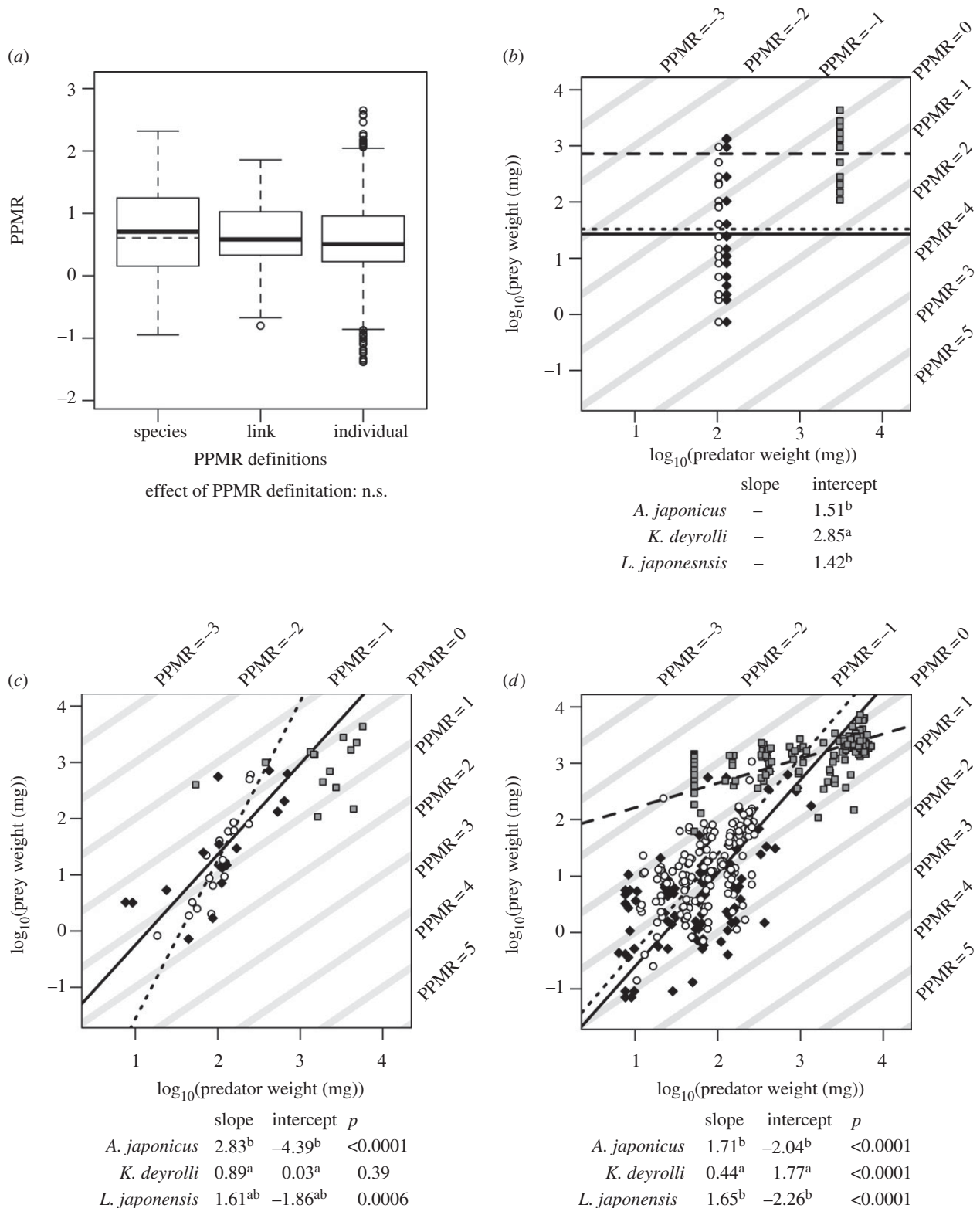
Importantly, PPSR can be defined in various ways depending on the definition of size [7,10,14,15]. Here, we considered three definitions following [7,10,14]: (i) 'species-averaged PPSR' which uses mean body weights (BW) of predator and prey species, (ii) 'link-averaged PPSR' which uses mean BW of predators and prey individuals that actually consume or are consumed by interacting species, and (iii) 'individual-link PPSR' which uses predator and prey individual BW for each hunting event. Note that the last represents the real feeding relationships. We compared prey BW among predators by using a standardized major axis

(SMA) technique to simultaneously consider variations in the two axes [17]. For species-averaged PPSR, we simply used one-way ANOVA because SMA was not applicable. It would be useful to include individual identity of predators as a random factor to avoid a potential pseudo-replication issue [7], yet this was not feasible because the predators we examined moult and shed paint marks for individual identification; however, this would not affect our major conclusions. We also evaluated predator–prey mass ratios (PPMRs) in size-based food-web studies, for the three definitions (see the electronic supplementary material, S3).

To explore possible determinants of PPSR, we tested four statistical models following [7]: (i) a null model, where prey BW is common among all predators (i.e.  $\log_{10}(\text{prey BW}) = \alpha$ ), (ii) a taxonomic model, where prey BW is species-specific (i.e.  $\log_{10}(\text{prey BW}) = \alpha + \beta \times (\text{predator species identity})$ ), (iii) an allometric model, where prey BW is size-dependent (i.e.  $\log_{10}(\text{prey BW}) = \alpha + \beta \times \log_{10}(\text{predator BW})$ ), and (iv) a combined model (i.e.  $\log_{10}(\text{prey BW}) = \alpha + \beta_1 \times (\text{predator species identity}) + \beta_2 \times \log_{10}(\text{predator BW}) + \beta_3 \times (\text{predator species identity}) \times \log_{10}(\text{predator BW})$ ). Here, BW represented individual weights for individual-link PPSR, whereas the mean measurements were used for the other definitions. Calculating the Akaike information criterion (AIC) by ordinary least-squares regression, we determined the best statistical model for each definition. All analyses (including calculations of parameters  $\alpha$  and  $\beta$ ) were conducted using the software R [18].

## 3. Results

For all the definitions, PPMR generally ranged between 0 and 1 on a log scale, i.e. the predators and prey had similar body sizes of the same order of magnitude (figure 2a). For species-averaged definition, *K. deyrolli* had larger prey BW than the other species ( $p < 0.05$ , figure 2b). For link-averaged definition, *A. japonicus* and *L. japonensis* increased their prey size as they grew, whereas *K. deyrolli* did not (figure 2c).



**Figure 2.** Predator–prey size relationships (PPSR) of aquatic hemipteran bug predators. (a) The three definitions of PPMR are shown in box plots. The thick and dashed lines represent the median and mean values, respectively. (b) Species-averaged prey body weight (BW), (c) link-averaged prey BW, and (d) individual-link prey BW are plotted against predator BW on a log–log scale. The open circles with dotted regression, grey squares with dashed regression and black diamonds with solid regression represent *A. japonicus*, *K. deyrolli* and *L. japonensis*, respectively. The grey lines represent contours of PPMR on a log scale. Only significant regressions were shown in (c) and (d). Different superscripts indicate significant differences in regression slope or intercept between species ( $p < 0.05$ ), and '*p*' columns indicate the significance of the regressions.

For individual-link definition, all species showed increases in prey BW during growth, but the regression slope of *K. deyrolli* was significantly lower than the other species (figure 2d). These results indicate that the effects of predator size and species identity were scale-dependent. We plotted contour lines of PPMR (grey lines) in each panel of figure 2b–d. By

comparing these contours with the regressions of predator versus prey BW, we can infer how PPMR during growth (also see the electronic supplementary material, S4 for direct comparison of PPMR versus predator size). We found that *K. deyrolli* clearly increased individual-link PPMR as it grew (i.e. the regression slope was significantly



**Table 1.** AIC values of the four statistical models for the three PPSR definitions.

	null	taxonomic	allometric	combined
species-averaged	146.6	128.2	126.6 <sup>a</sup>	128.2
link-averaged	147.9	119.1	93.90	80.00 <sup>a</sup>
individual-link	1440	832.2	1001	648.1 <sup>a</sup>

<sup>a</sup>The best model with the lowest AIC.

less than 1), whereas the other two predators had slightly decreased individual-link PPMR during growth (i.e. the regression slope is greater than 1) (figure 2*d*). The AIC values showed that species-averaged prey BW was best explained by the allometric model, whereas link-averaged and individual-link prey BWs were best explained by the combined model (table 1; see the electronic supplementary material, S5 for model selection to explain PPMR).

## 4. Discussion

To our knowledge, this is the first published attempt to formally characterize PPSR when predators can consume prey larger than themselves. The data revealed that PPSR varied with predator size and species identity, although the use of the averaged sizes confused these effects (figure 2*b–d* and table 1). This scale dependence is generally consistent with that in fish stomach content datasets [7]. Notably, however, our results showed that species averaging generates a misleading picture of real feeding relationships even though it does not affect PPMR (figure 2*a*), whereas previous studies addressed this problem based on the definition dependence of PPMR [7,14,15]. Therefore, it is important to investigate variability and the determinants of PPSR at the individual level.

The observed PPSR may be qualitatively different from those in gape-limited interactions. In general, fish predators show positive relationships between body size and PPMR [6,7]. This may be explained by ontogenetic niche expansion (i.e. large fish can consume both small and large prey; [19]). In contrast, we observed that PPMR of two predators slightly decreased with increasing body size (figure 2*d*; but also see

the electronic supplementary material, figure S2C in the electronic supplementary material S4). The other predator exceptionally showed a positive size-PPMR relationship similarly to fish predators (figure 2*d*; electronic supplementary material, figure S2C in the electronic supplementary material S4), but this resulted from specialized feeding on particular sizes of prey (anuran amphibians) during growth (i.e. no major ontogenetic diet shift; electronic supplementary material, S2). Although the available data are still limited, predators may exhibit distinct patterns of ontogenetic change in relative prey size depending on their feeding modes. We infer that these differences are related to the fact that terrestrial predators use a smaller subset of species compared with their aquatic counterparts, probably because more specialized morphological and behavioural adaptations are required to effectively handle large-sized prey [5].

In conclusion, body size exerts a critical influence on feeding regardless of whether predators are larger or smaller than their prey, but PPSR seems to be qualitatively different depending on the feeding modes of predators (i.e. whether they swallow smaller prey whole or capture relatively large prey). It is important to be aware of this difference in order to develop size-based approaches to terrestrial or benthic food webs, where predators are often smaller than their prey. Size-associated individual feeding data are laborious to collect, yet quite important for fully understanding trophic relationships. Further research is encouraged to confirm our results.

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## References

1. Brose U. 2010 Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Funct. Ecol.* **24**, 28–34. (doi:10.1111/j.1365-2435.2009.01618.x)
2. Blanchard JL. 2011 Body size and ecosystem dynamics: an introduction. *Oikos* **120**, 481–482. (doi:10.1111/j.1600-0706.2010.19564.x)
3. Yvon-Durocher G, Ress J, Blanchard J, Ebenman B, Perkins DM, Reuman DC, Thierry A, Woodward G, Petchey OL. 2011 Across ecosystem comparisons of size structure: methods, approaches and prospects. *Oikos* **120**, 550–563. (doi:10.1111/j.1600-0706.2010.18863.x)
4. Brose U *et al.* 2006 Consumer-resource body-size relationships in natural food webs. *Ecology* **87**, 2411–2417. (doi:10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2)
5. Shurin JB, Gruner DS, Hillebrand H. 2006 All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc. R. Soc. B* **273**, 1–9. (doi:10.1098/rspb.2005.3377)
6. Barnes C, Maxwell D, Reuman DC, Jennings S. 2010 Global patterns in predator–prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology* **91**, 222–232. (doi:10.1890/08-2061.1)
7. Nakazawa T, Ushio M, Kondoh M. 2011 Scale dependence of predator–prey mass ratio: determinants and applications. *Adv. Ecol. Res.* **45**, 269–302. (doi:10.1016/B978-0-12-386475-8.00007-1)
8. Naisbit RE, Kehrli P, Rohr RP, Bersier LF. 2011 Phylogenetic signal in predator–prey body-size relationships. *Ecology* **92**, 2183–2189. (doi:10.1890/10-2234.1)
9. Riede JO, Brose U, Ebenman B, Jacob U, Thompson R, Townsend CR, Jonsson T. 2011 Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecol. Lett.* **14**, 169–178. (doi:10.1111/j.1461-0248.2010.01568.x)
10. Cohen JE, Jonsson T, Müller CB, Godfray HC, Savage VM. 2005 Body sizes of hosts and parasitoids in individual feeding relationships. *Proc. Natl Acad. Sci. USA* **102**, 684–689. (doi:10.1073/pnas.0408780102)

11. Cohen JE, Pimm SL, Yodzis P, Saldaña J. 1993 Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.* **62**, 67–78. (doi:10.307/5483)
12. Owen-Smith N, Mills MGL. 2008 Predator–prey size relationships in an African large-mammal food web. *J. Anim. Ecol.* **77**, 173–183. (doi:10.1111/j.1365-2656.2007.01314.x)
13. de Visser SN, Freymann BP, Olff H. 2011 The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *J. Anim. Ecol.* **80**, 484–494. (doi:10.1111/j.1365-2656.2010.01787.x)
14. Woodward G, Warren PH. 2007 Body size and predatory interaction in freshwaters: scaling from individuals to communities. In *Body size: the structure and function of aquatic ecosystems* (eds AG Hildrew, D Raffaelli, R Edmonds-Brown), pp. 97–117. Cambridge, UK: Cambridge University Press.
15. Woodward G, Blanchard J, Lauridsen RB, Edwards FK, Jones IJ, Figueroa D, Warren PH, Petchey OL. 2010 Individual-based food webs: species identity, body size and sampling effects. *Adv. Ecol. Res.* **43**, 211–266. (doi:10.1016/B978-0-12-385005-8.00006-X)
16. Ohba S, Tatsuta H, Nakasuji F. 2008 Variation in the geometry of foreleg claws in sympatric giant water bug species: an adaptive trait for catching prey? *Entomol. Exp. Appl.* **129**, 223–227. (doi:10.1111/j.1570-7458.2008.00772.x)
17. Warton DI, Duursma RA, Falster DS, Taskinen S. 2012 smatr 3: an R package for estimation and inference about allometric lines. *Method Ecol. Evol.* **3**, 257–259. (doi:10.1111/j.2041-210X.2011.00153.x)
18. R Development Core Team. 2011 *R: a language and environment for statistical computing*. Vienna, Austria : R Foundation for Statistical Computing.
19. Ward AJW, Webster MM, Hart PJB. 2006 Intraspecific food competition in fishes. *Fish. Fish.* **7**, 231–261. (doi:10.1111/j.1467-2979.2006.00224.x)