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INSIGHT

Trophic allometry in a predator that carries corpses of its prey

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Abstract

Ant-snatching assassin bugs carry a 'backpack' of ant corpses as an antipredator strategy. From photographs, we quantified the relative size and number of ants in these backpacks. We found a trade-off between size and number of carried ants, suggesting that trophic allometry has implications beyond energy acquisition, potentially affecting camouflage.

Abstract in Portuguese is available with online material

KEYWORDS
Allometric scaling, assassin bugs, body size, camouflage, decorating, masking, predation, Reduviidae

1 | INTRODUTION

Understanding the factors that govern trophic relationships is an enduring challenge for ecologists (Paine, 1966). Documenting the myriad of trophic links found in food webs is rarely a trivial task, but the use of allometric scaling approaches has greatly improved our ability to predict these interactions (Garlaschelli et al., 2003). As trophic interactions are influenced by biomechanical mechanisms (Emerson et al., 1994), the relative body size of predators and their prey (i.e., trophic allometry) is an important determinant of trophic links (Brose et al., 2019; Kalinkat et al., 2013). For instance, a predator's body size is often related to its metabolic rate, strength, and speed, which are traits that determine its efficiency in searching, subjugating, and consuming prey (Wootton et al., 2021). In turn, a prey's body size is associated with its energy content and diverse antipredator strategies (Portalier et al., 2019). Therefore, ecological theory predicts that there should be an optimal predator–prey size ratio (PPSR) that maximizes the predator's energy gain (Griffiths, 1980). However, many examples in nature show that predators choose their prey not only seeking to optimize energy intake (Pyke, 1984).

The nymphs of ant-snatching assassin bugs of genera *Acanthaspis* Amyot and Serville 1843 and *Inara* Stål 1859 (Hemiptera: Reduviidae) use their prey not only to obtain energy and nutrients but also for camouflage (Jackson & Pollard, 2007; Odhiambo, 1958). These small voracious predators cover themselves with the remains of their prey, creating a 'backpack' (or a 'mask') made of ant carcasses (Figure 1). This strategy of covering the body with foreign material is known as masking (or decorating) (Castanho & Oliveira, 1997;

Ruxton et al., 2019; Ruxton & Stevens, 2015). First, ant-snatching assassin bugs capture their prey, inject digestive enzymes inside their exoskeleton, suck up their digested tissues, and finally place the carcasses on their back dorsum, which has adhesive threads secreted from the abdomen (Jackson & Pollard, 2007). This backpack of corpses increases assassin bug's survival chances against visually oriented predators by avoiding their recognition as prey (Brandt & Mahsberg, 2002; Jackson & Pollard, 2007). This peculiar behavior of ant-snatching assassin bugs makes them an interesting model to understand the allometry of trophic interactions because they (i) carry a 'history' of several past foraging events on their backpack (which allows us to quantify prey traits) and (ii) might capture their prey not only taking into account the maximization of energy gain, but also the increase in camouflage efficiency.

Here, we used photographs of *Acanthaspis* spp. and *Inara* spp. nymphs to study the still poorly explored trophic ecology of ant-snatching assassin bugs. First, we used photographs of these predators to describe (i) the relative size of predators and prey (predator–prey size ratios, PPSR) and (ii) the number of prey carcasses carried by each predator. We then tested whether there is a trade-off between PPSR and the number of ant carcasses present in an individual's backpack. We predicted that the larger the size of the prey relative to the predator (i.e., lower PPSR) the smaller the number of ants present in the assassin bug's backpack. We expected this pattern because small assassin bugs should not be able to capture and carry relatively large ants, while large predators would have increased costs associated with searching and capturing numerous small prey.

We searched for photographs of *Acanthaspis* and *Inara* individuals in online public image repositories (*Deviant Art*, *Flickr*, *iNaturalist*; search term: "assassin bug"; Table S1) and selected those (i) in high resolution (i.e., enough to precisely visualize the extremities of the bug and ants) and (ii) that showed the assassin bugs in a side view (lateral photograph). These criteria were important to allow for accurate measures of our variables of interest. The morphological distinction between the two genera we studied can only be made in the adult stage, which was impossible since we were using photographs. In each selected photograph, we quantified our two operational variables: PPSR and the number of prey. As PPSR is dimensionless, we measured the size of the predator and the prey in pixels using the ImageJ software since in the photographs there was no scale to know their real size. The predator size was measured by its body length (from the tip of the rostrum to the tip of the abdomen). Even though it was not possible to identify the species of ants, carcasses present on the backpack of each assassin bug have very similar sizes and shapes (Figure 1 and Table S1). Therefore, we assumed that all ants on a given backpack have the same body size. Considering how the ants are aggregated (Figure 1), it is not feasible to accurately measure their body length in the photographs. Thus, we used the head length (from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin) as a proxy for prey size because this dimension is isometric with body length (Tschinkel, 2013). In all selected photographs, at least one head was in a front view and, if there was more than one ant in this position, we calculated the mean head length.

FIGURE 1 Two individuals of ant-snatching assassin bugs carrying a backpack made of carcasses of their favorite prey (ants). This photograph was not used to collect data for this study because assassin bugs are not in a lateral view. Photographer: Melvyn Yeo.

We used a mathematical approximation to estimate the number of ants present in the predator's backpack as it was not possible to count them precisely from the photographs. First, we calculated the volume of a single ant based on Tschinkel (2013), which indicates that the gaster volume of *Solenopsis* represents approximately 57% of its total body volume. We used this proportion for all ants because this fine allometric characterization has rarely been estimated for other genera. Then, considering the ant's gaster as a spheroid (i.e., an ellipsoid with two equal semi-diameters) (Tschinkel, 2013), we measured its length (GL) and width (GW), and used the formula $V = \frac{4}{3}\pi\frac{GL}{2}\left(\frac{GW}{2}\right)^2$ to quantify its volume. In all photographs, at least one abdomen was measurable and, if there was more than one, we calculated the mean volume. Second, given the way carcasses of ants are arranged (Figure 1), we also considered the predator's backpack as a spheroid. To calculate the total volume of the backpack, we measured its length (BL) and height (BH), and used the formula $V = \frac{4}{3}\pi\frac{BL}{2}\left(\frac{BH}{2}\right)^2$. After calculating the two volumes (of the backpack and of an ant), we used the maximally random jammed (MRJ) parameter of $\varphi = 0.637$ (Donev et al., 2004) to estimate the percentage of the backpack volume occupied by ants. This empirical parameter represents the relative volume of amorphous objects packed randomly (Donev et al., 2004). Then, we divided the resulting occupied volume by the volume of an individual ant to estimate the total number of ants.

To test the relationship between the number of carried ant carcasses and the relative size of predators and their prey, we fitted a Generalized Linear Model with Poisson error distribution. PPSR was included as the predictor variable and the number of ants in the backpack (rounded to next integer) as the response variable. Statistical analyses were performed in the R environment (R Core Team, 2021).

We selected 43 photographs of *Acanthaspis* and *Inara* nymphs (Table S1), taken in different places in tropical Southeast Asia (20 from Singapore, 10 from Malaysia, 2 from China, 1 from India and 10 unidentified). As it was not possible to measure all the variables in a few of these photographs, we used 40 photographs to calculate the number of ants present in the backpack and all the 43 to calculate the predator–prey size ratio (PPSR).

The number of carcasses carried by ant-snatching assassin bugs varied widely, while one individual carried only three ants, another carried approximately 102 ants (average = 47.633, SD = 29.002) (Figure 2a). The relative size of predator nymphs and their prey also showed substantial variation. While some predators were about three times longer than the head of their prey, other predators were 10 times longer (PPSR range: 3.60 and 10.37, average = 7.237, SD = 1.723) (Figure 2b). Predators that consumed relatively large ants (i.e., low PPSR) carried fewer prey in their backpack ($\beta = 0.26 \pm 0.01$, df = 39, $p < .0001$) (Figure 2c).

Our results confirm the enduring principle that body size is a key trait shaping trophic interactions (Petchey et al., 2008). Our study brings a new perspective to this tenet by (i) quantifying trophic allometry in gape-unconstrained predators that carry carcasses of their prey as an antipredator strategy and (ii) using photographs available on the internet to quantify the traits of predators and their prey across a wide geographic distribution.

Classical studies on trophic allometry suggested that there should be an optimal and universal theoretical value of PPSR, at which the energy return is maximized (Emerson et al., 1994; West et al., 1997). However, recent studies question this hypothesis, as PPSRs in natural systems are flexible and context-dependent (Brose et al., 2006; Brose et al., 2019; Costa-Pereira et al., 2018; Kuile et al., 2022). Our results corroborate this later idea as we observed a large intraspecific variation in PPSR across predators. Although we have not tested the sources of this variation, studies suggest that the environmental context (e.g., local availability of prey) and interspecific interactions play important roles (Costa-Pereira et al., 2018; Henriques et al., 2021; Tsai et al., 2016). Moreover, because assassin bugs suck the body fluids from their prey, ant body size should not impose biomechanical limitations for consumption, although subduing and capturing relatively large prey should still be challenging for reduviid predators (Ambrose & Kumar, 2016). Other traits, such as defensive traits and cuticle thickness and hardness, may also play a role in these consumption patterns. This highlights the importance of considering aspects of the predator's foraging behavior, such as strategies to capture and consume prey, to understand how allometric relationships emerge in natural systems.

We also found that the larger the relative size of the ant, the smaller the number of prey in the backpack. The antipredator behavior of carrying prey carcasses incurs in additional energetic costs for assassin bugs (Ruxton & Stevens, 2015). Therefore, biomechanical limitations should determine not only PPSRs per se but also the number of ants carried in the backpack (Charnov, 1976). For instance, even if highly effective for camouflage purposes (i.e., avoiding predators by breaking up their shape and no longer being recognized as prey), a pack consisting of numerous large prey (i.e., low PPSR) would be highly costly because bigger ants take more energy to carry than smaller ones. Moreover, the volume of the backpack may also be a relevant limiting factor, as there is a finite availability of space (determined by the size of the predator's back) that can be occupied by ant carcasses. Thus, our results support the hypothesis that there is a trade-off between PPSR and the

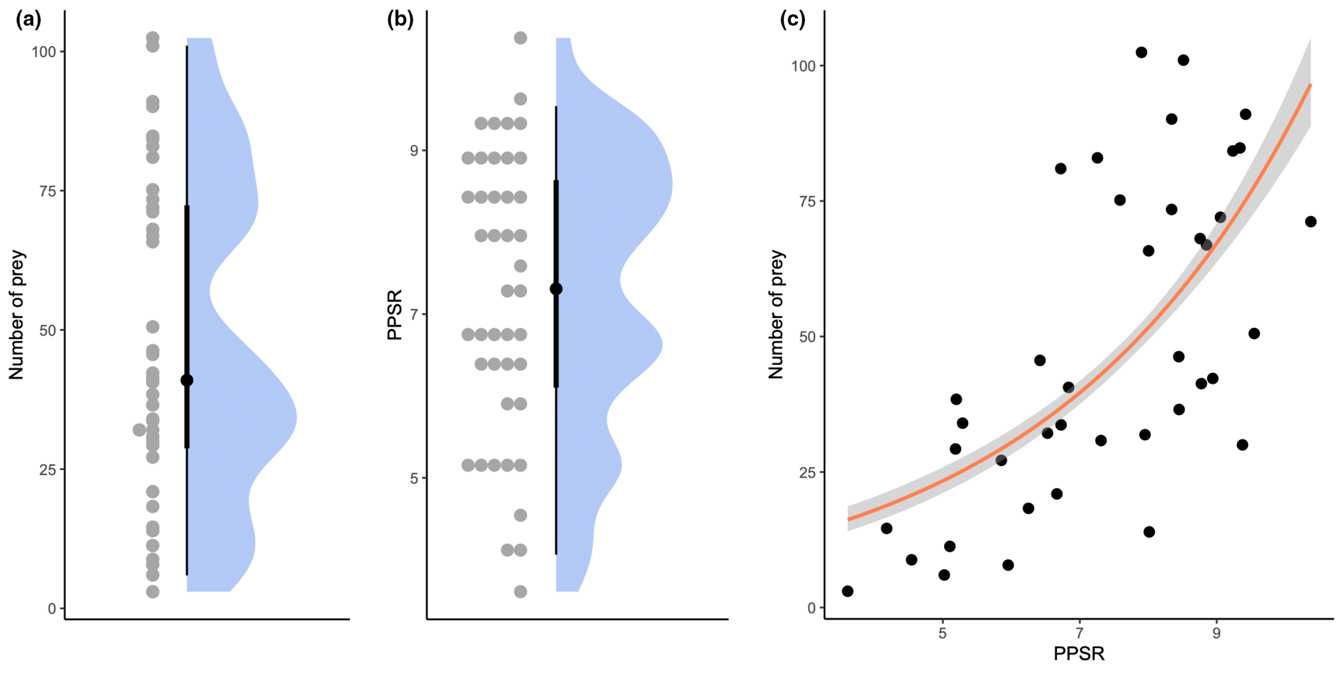

FIGURE 2 Raincloud plots showing density distributions, data points, and summary statistics (median and interquartile range) for (a) the number of prey carcasses carried and (b) predator–prey size ratio (PPSR) in 43 ant-snatching assassin bugs nymphs. (c) Relationship between the number of ants in the backpack and the relative size of the predator and its prey (i.e., large PPSR values correspond to predators that carry relatively small prey). The line in (c) is the fitted Generalized Linear Model with Poisson error distribution and the shaded area is 95% confidence interval.

number of prey used to avoid predators via masking, which has implications not only for the foraging of assassin bugs but also for their defense from predators.

Although our results reveal novel aspects of the trophic ecology of assassin bugs, there are still gaps about how predator and prey allometry influences the camouflage efficiency in this system. Previous studies with ant-snatching assassin bugs have only assessed whether the presence of the backpack acts as a defense mechanism against recognition by predators (Brandt & Mahsberg, 2002; Jackson & Pollard, 2007). However, how the number and relative size of ant carcasses determine the effectiveness of camouflage (i.e., preventing their enemies from recognizing them as prey), and how detection and recognition may be affected by natural backgrounds, remain unknown. It is possible that the greater the number of ants in the backpack, the greater the effectiveness of the camouflage against visually oriented predators. It is also possible that the relative size of the ant influences the efficiency of the masking effect. Thus, future empirical studies should elucidate how these PPSR and number of ants combine to drive camouflage efficiency in this system.

In conclusion, our findings emphasize the importance of studying allometry scaling using unconventional systems and methods (i.e., photographs of interactions) (Bauer, 2021; Nyffeler & Gibbons, 2021; Valenzuela-Rojas et al., 2020). Importantly, studies so far have investigated the allometry between predators and their prey from a trophic (or energetic) perspective (Griffiths, 1980; Nakazawa, 2017). By studying a predator that uses prey not only to obtain energy but also to defend against other predators, our results shed new light on the integration of trophic and predator defense perspectives in a unified framework.

AUTHOR CONTRIBUTION

Conceptualization: RC-P & NRV; Data collection and curation: NRV; Data Analysis: RC-P; Writing: NRV & RC-P.

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CONFLICT OF INTEREST

N.A.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.kprr4xh7d (Victor & Costa-Pereira, 2022).

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SUPPORTING INFORMATION

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