

Specialized morphology corresponds to a generalist diet: linking form and function in smashing mantis shrimp crustaceans

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Abstract Many animals are considered to be specialists because they have feeding structures that are fine-tuned for consuming specific prey. For example, “smasher” mantis shrimp have highly specialized predatory appendages that generate forceful strikes to break apart hard-shelled prey. Anecdotal observations suggest, however, that the diet of smashers may include soft-bodied prey as well. Our goal was to examine the diet breadth of the smasher mantis shrimp, *Neogonodactylus bredini*, to determine whether it has a narrow diet of hard-shelled prey. We combined studies of prey abundance, feeding behavior, and stable isotope analyses of diet in both seagrass and coral rubble to determine if *N. bredini*'s diet was consistent across different habitat types. The abundances of hard-shelled and soft-bodied prey varied between habitats. In feeding experiments, *N. bredini* consumed both prey types. *N. bredini* consumed a range of different prey in the field as well and, unexpectedly, the stable

isotope analysis demonstrated that soft-bodied prey comprised a large proportion (29–53 %) of the diet in both habitats. Using a Bayesian mixing model framework (MixSIAR), we found that this result held even when we used uninformative, or generalist, priors and informative priors reflecting a specialist diet on hard-shelled prey and prey abundances in the field. Thus, contrary to expectation, the specialized feeding morphology of *N. bredini* corresponds to a broad diet of both hard-shelled and soft-bodied prey. Using multiple lines of study to describe the natural diets of other presumed specialists may demonstrate that specialized morphology often broadens rather than narrows diet breadth.

Keywords Stomatopoda · Stable isotopes · Bayesian mixing model · Raptorial appendage · Feeding ecology

Introduction

A pervasive observation in nature is that species with specialized feeding structures consume specific types of prey. The curved beak of the Galapagos cactus finch used to consume the flowers and fruit of prickly pears (Lack 1988), the nectar-sucking proboscis of the hawkmoth, the length of which is specific to the nectar spur of the plants it pollinates (Darwin 1862), and the jaw of the egg-eating snake that engulfs bird eggs by expanding its gape to twice the width of its head (Gartner and Greene 2008) all provide classic examples of the relationship between feeding morphology and diet. Such feeding adaptations are seen in a wide diversity of vertebrates (fishes: Motta 1988; Hegrenes 2001; Hulsey and De León 2005; Mehta 2009; Montaña and Winemiller 2013; lizards: Dearing 1993; Meyers et al. 2006; Stayton 2006; bats: Dumont 1999; Saldaña-Vázquez et al. 2015; pinnipeds: Kienle and Berta 2015) as well as

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invertebrates (crustaceans: Lee 1995; Yamada and Boulding 1998; Warner and Jones 1976; insects: Rezac et al. 2008; Konuma et al. 2011; Gordon and Weirauch 2015; Huang et al. 2015; gastropods: Rudman 1981; Eilertsen and Malaquias 2013). Understanding the relationship between feeding morphology and diet has provided insights into the ecological and evolutionary processes that underlie community structure and that produce the vast morphological diversity seen across organisms (Van Valen 1965; Futuyma and Moreno 1988).

The mechanisms yielding a narrow diet bring into play a variety of biomechanical and ecological factors. Specialized feeding morphology may make otherwise inaccessible foods available, while also compromising access to other prey (Schluter 2000; Ferry-Graham et al. 2002; Mcgee et al. 2015). It may also open access to a kind of prey for which there are few competitors, thereby leading to diet specialization (Futuyma and Moreno 1988; Ferry-Graham et al. 2002). Animals with both specialized morphology and diet sometimes do consume other prey items that are made available by changes in prey abundance (Ferry-Graham et al. 2002). For example, the variety of beak forms in Galapagos finches is a direct result of competition for food (Grant and Grant 1993), and when a preferred food becomes scarce, some species with specialized beaks include a greater range of prey in their diets, while others maintain their specialist diets (Grant 1986).

Mantis shrimp crustaceans are often touted as having highly specialized feeding morphology (Dingle and Caldwell 1978; Patek et al. 2004; Ahyong and Jarman 2009). Smashing mantis shrimp, hereafter ‘*smashers*,’ have modified maxillipeds (mouthparts) called raptorial appendages that produce among the fastest and most powerful strikes in the animal kingdom, allowing them to break apart hard-shelled prey with

hammer-like clubs at the base of these appendages (Caldwell and Dingle 1975; Patek et al. 2004; Weaver et al. 2012) (Fig. 1). Smashers achieve fast strikes using a system in the raptorial appendage that amplifies power. Extensor muscles modified for force production contract to compress elastic elements with high spring constants that store energy in the raptorial appendage’s exoskeleton (Patek et al. 2013; Blanco and Patek 2014). Flexor muscles simultaneously contract to engage latches that prevent appendage rotation. When the latches are released, the appendage rotates forward at speeds reaching 14–23 m s⁻¹ and accelerations that generate forces thousands of times the body weight of the animal (Burrows 1969; Patek et al. 2004, 2007; Zack et al. 2009) (Fig. 1). In contrast, ‘*spearer*’ mantis shrimp strike much more slowly using elongate, streamlined appendages to ambush soft-bodied, evasive prey (deVries et al. 2012). The elastic elements in the exoskeleton of spearing appendages have lower spring constants, and the appendage muscles, which are modified for speed, cannot compress elastic elements as effectively as those of the smasher appendages (Patek et al. 2013; Blanco and Patek 2014).

Both feeding and fighting probably contribute to the evolution of the impressive smashing strike (Dingle and Caldwell 1978). A single blow that is delivered to an opponent when mantis shrimp compete for territory and mates can be lethal (Caldwell and Dingle 1975). Yet, the consequences of this multifunctional strike on diet breadth are of particular interest. The ability of smashers to produce high-impact strikes has been hypothesized to correspond to a specialized diet of hard-shelled mollusks, hermit crabs, and crabs (Caldwell and Dingle 1976; Dingle and Caldwell 1978; Caldwell et al. 1989). Some smasher species, however, have been observed capturing evasive, soft-bodied prey such as shrimps and worms (Dominguez and Reaka 1988; Caldwell et al. 1989). Although the diet breadth of smashers still remains largely unknown, these observations suggest that smashers have a more diverse diet than previously thought and that the morphological specializations for producing high-impact strikes do not necessarily result in a diet limited to hard-shelled prey.

Investigating correlations between diet breadth and feeding morphology requires accurate reconstructions of diet across a range of spatial and temporal scales and a measure of diet specialization that is comparable across taxa (Futuyma and Moreno 1988; Ferry-Graham et al. 2002). Methods such as gut content analysis have been the historic focus of these studies, even though they document only a predator’s most recent meal (Bearhop et al. 2004; Newsome et al. 2007). Mantis shrimp, in particular, digest their prey very quickly, rendering gut content analysis impractical to perform (Dingle and Caldwell 1978). Studies of prey preferences can suggest important dietary components, but laboratory conditions can never accurately replicate spatial and temporal variation in prey availability in the wild (Blackwell et al. 1998).



Fig. 1 The smashing mantis shrimp, *Neogonodactylus bredini*, in lateral view with the *left raptorial appendage* outlined shows the visible spring-like structures that are specialized for producing fast, powerful strikes and the hammer-like heel at the base of the dactyl segment of the appendage modified to withstand high-impact strikes (Burrows 1969; Patek et al. 2004, 2007; Zack et al. 2009; Weaver et al. 2012). Lines from labels point to the spring-like structures (*s*) and the dactyl heel (*h*). Scale bar 5 mm. Image courtesy of R. L. Caldwell

Stable isotope analysis, specifically of carbon and nitrogen isotope ratios (i.e., $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$, respectively), permits in situ comparisons of intra- and interspecific diet specialization (Sabat et al. 2006; Newsome et al. 2007; Araújo et al. 2011). The isotopic composition of a predator's tissues is a mixture of the isotopic compositions of the different prey consumed by the predator (reviewed in Fry 2006). Thus, stable isotope analysis can be used to examine spatial (Fry and Arnold 1982) and temporal (Dalerum and Angerbjörn 2005) shifts in diet within individuals, which helps to provide a more comprehensive description of diet. These features can be used to describe the degree to which individuals, populations, or species may be specialized. For example, quantifying individual variation in stable isotope values allows for determining whether generalist populations are composed of individuals that specialize on different subsets of resources (individual specialists) or whether all individuals are generalists (Semmens et al. 2009; Araújo et al. 2011).

Establishing degree of diet specialization from stable isotopes is often accomplished using mixing models to estimate the proportion of different prey in the diet (Phillips and Gregg 2003) and then calculating diversity metrics from these estimated diet proportions (Newsome et al. 2007). Bayesian mixing models estimate diet proportions using a likelihood framework, which allows for the incorporation of variability in consumer and prey isotope values and covariate information (Moore and Semmens 2008; Parnell et al. 2013). Mixing models require a priori identification of prey types because all prey included in the model are assumed to contribute to the diet (Parnell et al. 2013). These models are, therefore, best used in conjunction with other methods of diet analysis that help to ensure that all possible prey items are included in the models (Franco-Trecu et al. 2013; Phillips et al. 2014).

Our objective was to examine the diet breadth of the smasher, *Neogonodactylus bredini* (Stomatopoda: Crustacea: Gonodactylidea; Manning 1969). We hypothesized that, in line with the tight relationship between morphology and diet observed in many taxa, *N. bredini* would consume primarily hard-shelled prey. To test this hypothesis, we estimated *N. bredini*'s diet with the Bayesian mixing model approach. Given that our previous knowledge of *N. bredini*'s diet was based primarily on anecdotal observations in the literature, we combined prey abundance surveys and feeding behavior experiments to inform the types of prey to include in the mixing model. We further examined whether diet specialization was consistent across two habitat types where prey availability may be expected to differ. To examine the sensitivity of our results to the choice of the prior probability distribution, we used an uninformative “generalist prior,” which is typically used in Bayesian mixing models even though it corresponds

to the generalist hypothesis (Parnell et al. 2010; Newsome et al. 2012). We compared these results to those from two informative priors: a “specialist prior” reflecting the hypothesis that *N. bredini* consumes primarily hard-shelled prey and an “abundance prior” based on the prey abundance data in each habitat. While many studies advocate using multiple lines of evidence to inform stable isotope mixing models, few have constructed informative priors using alternative datasets as we did here (Moore and Semmens 2008; Yeakel et al. 2011; Franco-Trecu et al. 2013; Chiaradia et al. 2014; Phillips et al. 2014). With the mixing model diet estimates, we then calculated a specialization index (ε), which provided a measure of diet specialization that is comparable between populations and species (Newsome et al. 2012).

Materials and methods

Study site and sampling

This study was conducted on the reef flat at the Galeta Point Marine Laboratory (GPML) of the Smithsonian Tropical Research Institute, Colón, Panama (9°24'18"N, 79°51'48.5"W). The intertidal back reef consists of shallow flats that stretch from the shore to the reef crest and are dominated by either coral rubble or seagrass beds. *N. bredini* are found in high densities in coralline algae nodules and coral rubble crevices in both habitats (Caldwell and Steger 1987). Individuals show high fidelity to habitat type, as they usually do not travel more than a few meters from their home cavities (Caldwell et al. 1989). High winds and extreme diurnal low tides in the dry season (December–May) can leave the reef flat exposed causing differential mortality among taxa that are potential prey of mantis shrimp (Cubit et al. 1986). During the wet season (June–November), the extreme low tides are nocturnal, lessening diurnal stresses and mortality, but fresh water input from rainfall increases (reviewed in Caldwell and Steger 1987). Initial collections for stable isotope analysis occurred in the dry season in April, 2008 and included a subset of available prey types. Because the diversity of potential prey on a coral reef flat is quite high, we returned the GPML in the wet season in October, 2008 to collect additional prey types, to quantify prey abundances in both habitats, and to perform a feeding experiment to determine which potential prey *N. bredini* would consume.

Percent cover and relative abundance

To explore which prey were available to *N. bredini*, abundance surveys of potential prey (all animals <120 mm in length) were conducted in both the coral rubble and

seagrass habitats. The size criterion for the prey assumed that *N. bredini* would not capture organisms that were twice its known maximum body length of 65 mm (Caldwell and Steger 1987). Animal counts were performed in two 200 m² plots that were placed 600 m apart in neighboring seagrass and coral rubble habitats. Potential invertebrate prey items were counted in 30 randomly-selected 0.25 m² quadrats within each plot. Coral rubble and rocks in the quadrats were broken with a rock hammer to ensure that crevice-dwelling organisms were counted. The percent cover of seagrass, sand, coral rubble, and rocks was visually assessed on snorkel in each of the 30 quadrats per habitat as well [electronic supplementary material (ESM) Table 1]. Mobile fish prey were counted by swimming along three 10 m transects placed in each of the 200 m² plots. Each of the three transects within each habitat was swum 10 times, resulting in 30 swims per habitat at varying times during daylight hours to account for changes in fish abundance throughout the day. Fish that were within 1 m of the transect lines were counted. Mean [\pm standard deviation (SD)] relative abundances were calculated for all animals in each habitat and Welch two-sample *t* tests were used to compare habitat features and organism abundances between the seagrass and coral rubble using R Statistical Software v.3.1.2 (R Development Core Team 2014).

Feeding experiment

A feeding behavior experiment was performed to determine which of the available types of prey *N. bredini* would consume, regardless of habitat and natural diets. Potential prey items were selected based on previous reports of *N. bredini* diet (Caldwell et al. 1989) and the abundance counts described above. Animals that were abundant and <120 mm in length were included (again assuming that *N. bredini* would not eat prey that were twice as large as its known maximum size of 65 mm). Eight types of animal prey were identified: crabs (Xanthidae), apheid shrimp (*Alpheus spp.*), brittle stars (*Ophiothrix angulata*; Say, 1825), clams (*Arcopsis adamsi*, Dall 1886), snails (*Cerithium atratum*, Born 1778), fish (*Harengula spp.*), hermit crabs (*Clibanarius tricolor*, Bouvier, 1918), and worms (*Pontodrilus littoralis*, Perrier, 1874). Seagrass (*Thalassia testudinum*, Koenig, 1805; 50 mm² pieces) was also included as a potential prey item in case *N. bredini* consumes plant material (total prey types = 9). All prey types chosen were present diurnally, as *N. bredini* is known to be a diurnal predator that remains inside its cavity at night and blocks the cavity entrance with a rock (Caldwell et al. 1989). For these experiments, *N. bredini* individuals were collected opportunistically from a habitat with both seagrass and coral rubble. *N. bredini* body sizes, measured from rostrum to telson, ranged from 31 to

55 mm (mean \pm SD: 41 \pm 4 mm). Prey item body sizes ranged from a 6 mm clam to a 112 mm worm.

The experiment was conducted at the GPML in an aquarium system with 16 1.5 L aquaria and filtered seawater. A 7.4 cc artificial cement cavity with one entrance hole, constructed based on Caldwell et al. (1989), was placed in each aquarium so that individuals could hunt from a place of hiding. A layer of beach sand soaked in freshwater and dried in the sun for 24 h was also placed in each aquarium. One mantis shrimp was released in each aquarium and given 24 h to acclimate. Each aquarium was then stocked with one of the potential types of prey. Ten feeding trials for each of the nine different prey types were conducted with a different mantis shrimp individual and a different prey item for each trial (total trials = 90). A prey item was scored as “consumed” if *N. bredini* was observed eating it or if the item was found dead with missing tissue and marks where *N. bredini* had hammered the prey or torn at soft tissue. We were able to determine if all prey items were still alive or had been consumed because we examined each prey item before and after it was placed in an aquarium, and prey items remained visible for the duration of the trials. Trials were terminated after 4 days if the prey item had not yet been consumed. If a mantis shrimp molted, laid eggs, or died during a trial, then the trial was discarded and conducted anew with a different shrimp. Aquaria were cleaned between trials.

We also made visual observations of when and how prey were captured and consumed. We made approximate estimates of search and handling times by observing each trial for 1 min every 30 min from 06:00 to 18:00, when *N. bredini* are active, for the duration of the experiment. Search time began when the prey item was placed in the aquarium and ended when the mantis shrimp captured the prey. Handling time was the time it took for the mantis shrimp to consume the prey once captured. Captures were often visible, but handling and consumption of prey usually occurred in cavities, especially for less mobile prey, such as hermit crabs and snails. For these prey types, the end of handling time was determined when *N. bredini* individuals deposited shell remains outside of the cavities. Given that the aquaria were monitored every half-hour, we estimated search and handling times to the nearest 30 min.

Animal collection and sample preparation for stable isotope analysis

Ten *N. bredini* individuals from coral rubble and 11 individuals from seagrass were collected during the dry season (April 2008). Three *N. bredini* individuals from coral rubble and five individuals from seagrass were collected during the wet season (October 2008), which was thought to be sufficient for capturing variability in stable isotopes within each reef flat habitat (Wyatt et al. 2010). *N. bredini* body sizes

ranged from 30 to 46 mm (mean \pm SD = 37 ± 4 mm). We collected alpheid shrimp, brittle stars, clams, crabs, fish, hermit crabs, snails, and worms from both habitats and during both seasons (3–23 individuals per prey type; Table 2). However, we did not recognize certain animals as possible prey until after the abundance study and feeding experiment were carried out later in the wet season. We, therefore, have instances of missing prey types from certain habitats and seasons (Table 2). The body sizes of prey items ranged from a 5 mm snail to a 40 mm worm.

Upon collection, all animals were frozen and stored at -20 °C until they were dissected and prepared for stable isotope analysis. Hemolymph and muscle tissues were dissected following deVries et al. (2015). In short, hemolymph was removed from *N. bredini* that were collected in the wet season but not in the dry season due to insufficient preservation of hemolymph from this season. Muscle was also dissected from abdominal somites 2–6 from *N. bredini* individuals collected in both seasons (deVries et al. 2015). For prey items, muscle was dissected and separated from the gut to prevent contamination from stomach contents. All samples were freeze-dried for 48 h and homogenized before analysis.

Samples for stable isotope analysis were placed in tin capsules and weighed (Costech Analytical Technologies, Valencia, CA, USA; mean \pm SD: 180 ± 50 μ g for all muscle tissue and 220 ± 50 μ g for *N. bredini* hemolymph). Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios and the elemental concentrations of C and N were analyzed with continuous-flow isotope ratio mass spectrometry at the University of California Berkeley Center for Stable Isotope Biogeochemistry using a CHNOS Elemental Analyzer (vario ISOTOPE cube, Elementar, Hanau, Germany) coupled with an IsoPrime100 Isotope Ratio Mass Spectrometer (IsoPrime, Cheadle, UK). Isotope ratios are expressed in parts per thousand (per mil, ‰) using delta-notation as:

$$\delta^h X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where h is the high mass number, X is the element, R is the high mass-to-low mass isotope ratio, and R_{standard} is Vienna Pee Dee belemnite (VPDB) for carbon and air for nitrogen. Peach leaves (Standard Reference Material [SRM] No. 1547, $n = 60$, SD of $\delta^{13}\text{C} = 0.1$ ‰ and $\delta^{15}\text{N} = 0.2$ ‰) and bovine liver (SRM No. 1577, $n = 7$, SD of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was $= 0.1$ ‰) were used as references and standards and to correct for instrument drift and linearity. Samples were analyzed in bulk form without extraction of lipids or other compounds (Mateo et al. 2008; deVries et al. 2015).

Statistical analysis of stable isotope data

All stable isotope data were tested for normality using the Shapiro–Wilk test before further analysis. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between *N. bredini*'s muscle and

hemolymph tissues that were collected from the wet season were evaluated using Welch's two-sample t test. We also examined whether $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in *N. bredini* were affected by habitat, seasonality, and their interaction using a two-way ANOVA. The two-way ANOVA was repeated for the prey collected over both seasons. Significance for all ANOVA tests was evaluated using a Bonferroni correction ($\alpha = 0.003$). While some of the prey did exhibit significant differences between seasons (Table 2), their position in the food web relative to the mantis shrimp did not shift substantially. For the mixing model analysis, we therefore combined stable isotope values across seasons. This approach assumes that the prey collected in only one season (Table 2) also do not shift substantially in their relative positions in the food web. We think that this is a valid assumption, given that seasonal changes should primarily affect differential mortality, as mentioned previously. Analyses were performed using R v. 3.1.2 software (R Development Core Team 2014).

To determine *N. bredini*'s relative consumption of hard-shelled and soft-bodied prey within each habitat, we used MixSIAR, a Bayesian framework for constructing stable isotope mixing models (Stock and Semmens 2013). MixSIAR estimates the proportion of each source (prey) in a mixture (predator diet), while accounting for uncertainty in trophic discrimination factors (Δ , the difference between the predator and prey stable isotope ratios), concentration dependence (concentrations of carbon and nitrogen, as in Phillips and Koch 2002), and the variability in predator stable isotope values that results from predators finitely "sampling" from prey isotope distributions many times (Moore and Semmens 2008; Parnell et al. 2010). However, unlike previous approaches, MixSIAR estimates prey means and variances within the model (Ward et al. 2010) and allows for variability in predator diet using random, fixed, and continuous effects (Semmens et al. 2009; Francis et al. 2011; Parnell et al. 2013). MixSIAR constructs and fits mixing models using R v.3.1.3 and JAGS software (Plummer 2003; R Development Core Team 2014). The modified MixSIAR script and data files are available at: https://github.com/brianstock/mantis_shrimp_diet.

We used experimentally-determined trophic discrimination factors for *N. bredini* muscle in the mixing model ($\Delta^{15}\text{N} = 0.9 \pm 0.3$ ‰, $\Delta^{13}\text{C} = 3.0 \pm 0.6$ ‰; after deVries et al. 2015). Concentrations of carbon and nitrogen in each prey source were also included (concentration dependence). To reduce the number of sources in the model, we combined prey types whose stable isotope values did not differ statistically (reviewed in Phillips et al. 2014) and that were consumed in a similar manner; alpheid shrimp and worms were combined (both prey are generally captured with the maxillipeds and then subdued with raptorial strikes; ESM Table 3), as were hermit crabs and crabs (both

Table 1 Mean and range relative abundance (%) per m² of each potential type of prey in the seagrass and coral rubble habitats

Prey type	Seagrass		Coral rubble		Significance	
	Mean ± SD	Range (min, max)	Mean ± SD	Range (min, max)	$t_{(df)}$	P
<i>Soft-bodied prey</i>	<i>0.58 ± 0.74</i>		<i>11.7 ± 11.60</i>			
Alpheid shrimp	0.0 ± 0.0	0, 0	14.97 ± 35.33	0, 41	3.75 ₍₂₇₎	<0.006*
Brittle star	1.67 ± 5.44	0, 90	0.0 ± 0.0	0, 0	−1.67 ₍₂₉₎	0.11
Fish	0.29 ± 1.44	0, 2.1	4.22 ± 3.12	0, 5.2	4.76 _(86.96)	<0.006*
Worm	0.37 ± 1.21	0, 5.0	25.88 ± 34.75	0, 71	6.11 _(29.07)	<0.006*
<i>Hard-shelled prey</i>	<i>29.63 ± 26.95</i>		<i>13.74 ± 6.22</i>			
Clam	0.46 ± 2.5	0, 0.55	16.20 ± 29.88	0, 71	3.51 _(41.37)	<0.006*
Crab	0.28 ± 0.85	0, 8.0	4.92 ± 8.06	0, 33	2.92 _(29.39)	0.007
Hermit crab	53.51 ± 57.42	0, 98	14.45 ± 43.44	0, 94	−4.64 _(51.38)	<0.006*
Snail	43.40 ± 71.30	0, 100	19.37 ± 69.23	0, 84	−3.07 _(52.81)	<0.006*

Prey are aggregated into two categories: soft-bodied and hard-shelled prey (italics). Note that alpheid shrimp and brittle stars are categorized as “soft-bodied” because they are handled similarly to fish and worms and their exoskeletons are much softer than those of the hard-shelled prey

* Significant differences in mean relative abundance of prey types between the two habitats (Bonferroni corrected significance value of $p < 0.006$, eight comparisons). $n = 30$ quadrats per habitat

prey are carried to cavities and broken apart with raptorial strikes in the cavities; ESM Table 3).

Bayesian mixing models require prior distributions to be specified for estimated parameters (i.e., the diet proportions of each prey type). A Bayesian prior reflects knowledge of a system before (prior to) an experiment and is then updated by data to arrive at the result, which is the posterior distribution. We compared the results from models run with uninformative Dirichlet priors (predator consumes all n prey in equal proportions, $1/n$, $\alpha = 1,1,1,1,1,1$) that weight the posteriors toward a generalist diet, to those from models run with informative Dirichlet priors constructed from the prey abundance data (α for each prey type are in Table 1 scaled so that $\Sigma\alpha = 6$, the number of sources) to examine the influence of prey abundance on model results. We then constructed a second informative prior that gave hard-shelled prey (clams, crabs, and snails) four times the weight of soft-bodied prey (alpheid shrimp/worms, brittle stars, and fish), i.e., $\alpha_{\text{soft}} = 1$ for soft-bodied and $\alpha_{\text{hard}} = 4$ for hard-shelled prey based on dietary observations of *N. bredini* (Caldwell et al. 1989). This approach resulted in a more conservative test of the hypothesis that *N. bredini* specializes on hard-shelled prey. For all three analyses, we aggregated the six sources into hard-shelled prey (clams, crabs, and snails) and soft-bodied prey (alpheid shrimp/worms, brittle stars, fish) categories a posteriori (Phillips et al. 2014). The categories were determined based on observations of prey handling during the feeding experiment. Hard-shelled prey were struck repeatedly, while soft-bodied prey were struck only to subdue the prey that were then handled with the maxillipeds. While alpheid shrimp and brittle stars have exoskeletons, they

were considered soft-bodied because their exoskeletons are much softer than those of the hard-shelled prey, and *N. bredini* handled them a similar manner as fish and worms.

We used three Markov chain Monte Carlo (MCMC) chains to fit the mixing model and assessed convergence using the Gelman–Rubin diagnostic (Gelman et al. 2003). Our best fit model, as determined by deviance information criterion (DIC), included habitat (coral rubble, seagrass) as a fixed effect, prey data by habitat, concentration dependence, and the MixSIR error term (ESM Table 2).

To quantify diet specialization at the population level for each habitat, we calculated the specialization index, ε (Eq. 5 in Newsome et al. 2012), from the mixing model estimates of dietary proportions. The specialization index can range from 0 (ultra-generalist) to 1 (ultra-specialist). Mixing model and specialization index results are presented as medians (95 % credible interval, CI).

Results

Relative prey abundance

Hermit crabs and snails were the main types of prey in the seagrass habitat (Table 1). In the coral rubble, alpheid shrimp, worms, and hard-shelled prey (clams, crabs, and hermit crabs) were present in similar abundances (Table 1). Very few clams and no alpheid shrimp were found in seagrass, likely because we encountered only a few rubble pieces in which these animals are found. Brittle stars were not found in coral rubble because the habitat was

dominated by hard rocks that lack crevices for brittle star dwellings. Regardless, these prey types were included in the subsequent feeding experiment and stable isotope analyses because of their abundances in the other habitats.

Feeding experiment

Neogonodactylus bredini consumed all prey offered to them except for seagrass. Thus, only data from the animal prey are presented. The order, from the most to the fewest number of trials in which prey were consumed, was: alpheid shrimp = worms > clams > fish > crabs = hermit crabs > brittle stars = snails (ESM Table 3). Search times ranged from 0 to 40 h. Handling times ranged from 0 to 6 h, but only brittle stars were handled for more than 1 h (ESM Table 3). *N. bredini* used their predatory appendages to hammer every prey item, except for brittle stars. While it is possible that brittle stars were hammered, we did not directly observe this behavior or see evidence of tissue damage due to hammering on brittle star bodies. All prey items were consumed inside the mantis shrimps' cavities,

except for crabs, which were consumed outside of the cavities in two trials, and fish, which were consumed outside of the cavities in eight trials.

Statistical and mixing model analyses of stable isotope data

As expected, *N. bredini*'s $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were enriched relative to the prey (Table 2). The stable isotope values of all animals shifted at least 1 ‰ between habitats, seasons, or both, and these shifts were significant in *N. bredini*, snails, alpheid shrimp, fish, and worms (Table 2). Despite these differences, the positions of the prey relative to mantis shrimp in dual isotope space (i.e., a $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ plot; Fig. 2) did not shift substantially between seasons (Table 2), which is why we focused on diet differences between habitats in the mixing model analysis of *N. bredini* diet. Given that the stable isotope values of *N. bredini*'s hemolymph and muscle tissue did not differ significantly in the wet season (Table 2), we only used muscle tissue values in the mixing model analyses.

Table 2 Mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *N. bredini* and its prey from both habitats and seasons

Animal	Seagrass			Coral rubble		
	<i>n</i>	$\delta^{13}\text{C} \pm \text{SD} (\text{‰})$	$\delta^{15}\text{N} \pm \text{SD} (\text{‰})$	<i>n</i>	$\delta^{13}\text{C} \pm \text{SD} (\text{‰})$	$\delta^{15}\text{N} \pm \text{SD} (\text{‰})$
Dry season						
<i>N. bredini</i> muscle	11	-10.0 ± 0.7	7.3 ± 0.4	10	$-12.0 \pm 0.9^{h,s,i}$	8.0 ± 0.5^s
Alpheid shrimp	NA	NA	NA	5	-13.0 ± 0.3^s	6.3 ± 0.5
Clam	5	-12.4 ± 0.6	5.2 ± 0.4	5	-14.4 ± 2.2	5.4 ± 0.3
Crab	4	-12.5 ± 1.4	3.2 ± 0.9	4	-14.0 ± 1.2	5.0 ± 1.9
Fish	5	-9.0 ± 1.2^s	7.6 ± 0.9	8	-13.7 ± 0.8	8.6 ± 1.0
Hermit crab	4	-10.3 ± 0.8	3.4 ± 0.2	4	-11.2 ± 1.1	3.5 ± 1.0
Snail	4	-7.9 ± 0.7	3.6 ± 2.0	5	-9.9 ± 1.4^h	5.8 ± 0.2^i
Worm	NA	NA	NA	5	-12.5 ± 0.9^s	6.8 ± 1.0
Wet season						
<i>N. bredini</i> muscle	5	-9.3 ± 0.6	6.9 ± 0.4	3	-8.5 ± 1.1	6.7 ± 1.1
<i>N. bredini</i> hemolymph	5	-9.7 ± 0.6	6.3 ± 0.5	2	-8.6 ± 1.6	6.4 ± 0.6
Alpheid shrimp	8	-11.0 ± 1.4	6.4 ± 0.2	10	-10.2 ± 0.6	6.0 ± 0.2
Brittle star	8	-4.1 ± 1.1	5.3 ± 0.4	8	-5.6 ± 2.8	7.0 ± 1.3
Clam	3	-13.3 ± 0.6	5.6 ± 0.2	3	-9.6 ± 1.1	5.1 ± 0.2
Crab	NA	NA	NA	15	-11.1 ± 2.8	3.9 ± 0.8
Fish	7	-16.3 ± 0.3	8.3 ± 0.4	NA	NA	NA
Hermit crab	23	-11.8 ± 1.2	3.8 ± 0.5	9	-11.0 ± 2.1	3.5 ± 0.5
Snail	22	-8.7 ± 0.9	4.5 ± 0.4	27	-11.4 ± 3.3	4.2 ± 0.7
Worm	3	-10.8 ± 0.1	5.1 ± 0.1	10	-9.9 ± 0.9	6.6 ± 1.3

Prey values are uncorrected for isotopic discrimination. Significant differences in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Bonferroni corrected significance value of $p < 0.003$, 18 comparisons) are indicated by superscripts: *h* = differences between habitats, *s* = differences between seasons, *i* = interaction term of habitat \times season. *h* and *i* are indicated in the coral rubble columns but the seasonal difference in the $\delta^{13}\text{C}$ of fish is noted in the seagrass column (because no fish were collected in coral rubble in the wet season). *n* = number of individuals analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. NA signifies missing data

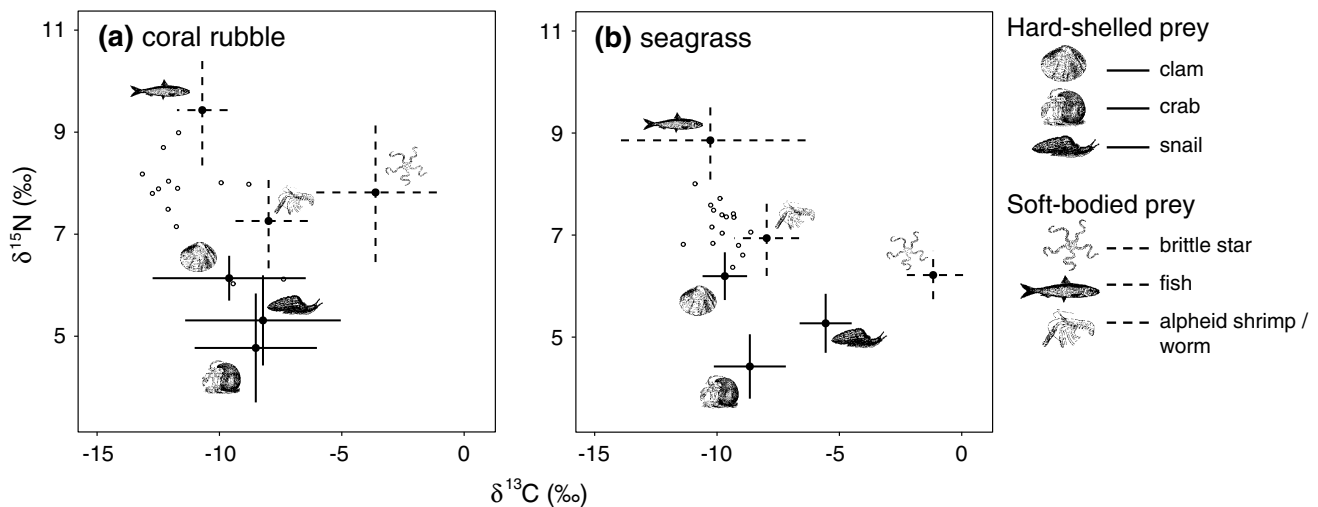


Fig. 2 Position of *N. bredini* (open circles) in dual isotope space relative to its potential prey items (closed circles). Specifically, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *N. bredini* corrected for trophic discrimination factors and overall mean ($\pm\text{SD}$) values of potential prey collected from **a** coral rubble and **b** seagrass are shown. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are

combined across the wet and dry seasons. Prey types are depicted by line drawings and divided into hard-shelled ($\pm\text{SD}$ = solid lines) and soft-bodied ($\pm\text{SD}$ = dashed lines) categories. For sample sizes of *N. bredini* and prey sources, see Table 2

Table 3 Bayesian mixing model median estimates (95 % CI) of the proportional contributions of each prey type to *N. bredini*'s diet in seagrass and coral rubble habitats

Prey type	Uninformative prior		Specialist prior		Abundance prior	
	Seagrass (%)	Coral rubble (%)	Seagrass (%)	Coral rubble (%)	Seagrass (%)	Coral rubble (%)
<i>Soft-bodied</i>	48.2 (35.3, 63.4)	31.6 (19.3, 55.6)	43.8 (31.9, 59.0)	29.1 (18.1, 48.9)	41.0 (33.6, 54.0)	52.5 (39.3, 69.8)
Alpheid/worm	3.8 (0.2, 17.9)	2.8 (0.1, 30.2)	0.9 (0.0, 10.7)	0.6 (0.0, 19.7)	0.0 (0.0, 16.2)	10.7 (1.9, 27.2)
Brittle star	2.1 (0.1, 14.0)	1.3 (0, 10.2)	0.5 (0.0, 7.4)	0.3 (0.0, 7.1)	0.0 (0.0, 10.6)	0.0 (0.0, 0.0)
Fish	39.6 (26.9, 54.7)	24.2 (15.3, 35.4)	40.3 (28.7, 55.1)	25.7 (16.4, 37.3)	39.2 (31.3, 47.0)	42.3 (28.6, 59.3)
<i>Hard-shelled</i>	51.8 (36.6, 64.7)	68.4 (44.4, 80.7)	56.2 (41.0, 68.1)	70.9 (51.1, 81.9)	59.0 (46.0, 66.4)	47.5 (30.2, 60.7)
Clam	42.3 (24.5, 58.6)	62.8 (28.5, 78.5)	41.3 (22.9, 58.3)	63.0 (28.7, 78.6)	0.0 (0.0, 15.4)	30.4 (0.8, 51.6)
Crab	3.4 (0.01, 17.3)	1.8 (0, 19.6)	5.9 (0.5, 21.8)	2.9 (0.2, 21.7)	38.5 (17.5, 55.3)	6.2 (0.02, 22.9)
Snail	3.1 (0.1, 16.4)	1.6 (0, 14.5)	5.9 (0.6, 24.2)	2.9 (0.2, 17.7)	18.5 (4.8, 38.4)	10.3 (0.3, 42.2)

Results are given for models run with an “uninformative prior” constructed from the Dirichlet Bayesian prior, and two different informative priors: a “specialist prior” constructed from giving hard-shelled prey four times the weight of soft-bodied prey, and an “abundance prior” constructed from the prey abundance data in Table 1. Prey are aggregated a posteriori into two categories: soft-bodied and hard-shelled prey (italics). All mixing models run with the different priors and habitats indicate that a substantial fraction of *N. bredini*'s diet is soft-bodied prey (29–53 %), particularly fish

The mixing model estimates using the uninformative prior as well as both informative priors indicated that the diet of mantis shrimp in both habitats was dominated by a combination of clams and fish (>70 %; Table 3), even though relative abundances of these prey were low (in the seagrass and coral rubble, respectively, fish were 0.3 and 4 % and clams were 0.5 and 16 %; see Table 1). The one exception was the estimates from the informative prior based on seagrass prey abundance, because the main prey items in the diet were estimated to be fish, crabs, and snails, as opposed to fish and

clams (Table 3; Fig. 3). When aggregated into hard-shelled and soft-bodied categories, soft-bodied prey comprised 29–53 % of the diet and hard-shelled prey was 48–71 % regardless of which prior was used in the mixing model analysis (Table 3). Given that the uninformative prior results (ESM Fig. 1, ESM Fig. 2) were similar to the results from both informative priors (Table 3), we chose to focus on the results from the informative priors (Figs. 3, 4, ESM Fig. 3).

Even when using an informative prior for a specialist on hard-shelled prey (specialization index calculated from the

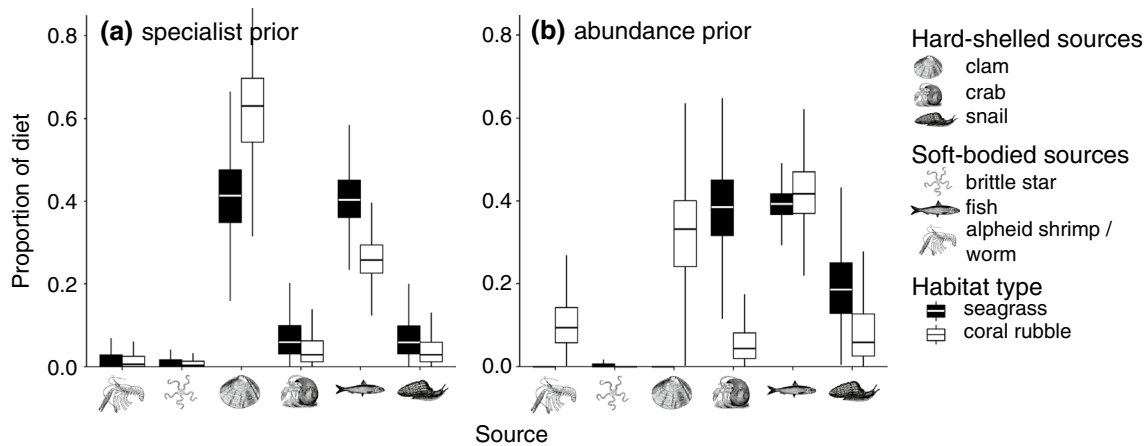


Fig. 3 Median (lines in center of boxes = median, box boundaries = 50 % CI, error bars = 95 % CI) proportional contributions of each prey item to *N. bredini*'s diet calculated with two informative priors: **a** the “specialist prior” constructed by giving hard-shelled prey four times the weight of soft-bodied prey and **b** the “abundance

prior” constructed from the abundance data of the prey collected from both the seagrass (black boxes) and coral rubble (white boxes) habitats. Prey types are depicted by line drawings and divided into hard-shelled and soft-bodied categories. For median (95 % CI) values, see Table 3. For sample sizes of *N. bredini* and prey sources, see Table 2

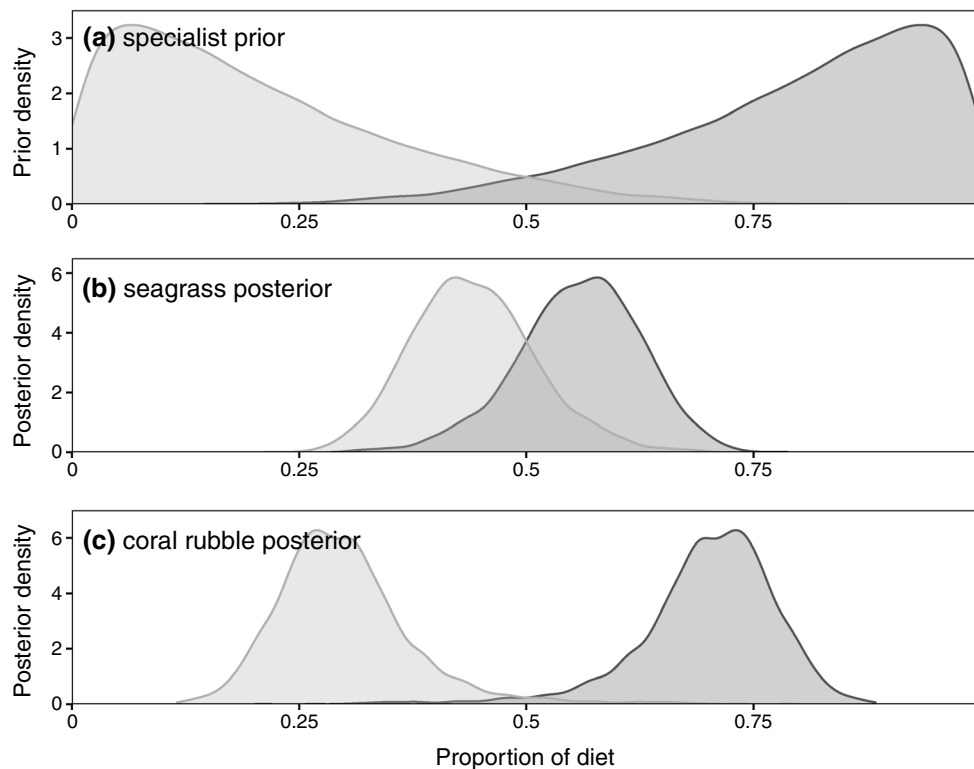


Fig. 4 Prior and posterior density plots from the best fit Bayesian mixing model based on the “specialist prior” show the proportional contributions of hard-shelled prey (dark gray) and soft-bodied prey (light gray) in *N. bredini*'s diet. Prey are aggregated into categories of hard-shelled prey (clams, crabs, and snails; $n = 65$), and soft-bodied

prey (alpheid shrimp/worms, brittle stars, and fish; $n = 31$). Despite the **a** “specialist” informative prior giving hard-shelled prey four times the weight of soft-bodied prey, posterior densities from both the **b** seagrass and **c** coral rubble mixing model results show that soft-bodied prey comprise 29–53 % of diet

prior $\epsilon = 0.67$), mantis shrimp were on the generalist end of the continuum in both the seagrass ($\epsilon = 0.14$ [0.01–0.37]), and coral rubble ($\epsilon = 0.42$ [0.09–0.64]) (Fig. 4) habitats.

Models using priors based on the abundance data even more strongly estimated a generalist diet; there were stark increases in soft-bodied prey in the posterior distributions

compared to the prior distributions in both habitats (ESM Fig. 3), and specialization indices were well below 0.5 (seagrass $\varepsilon = 0.18$ [0.02–0.33], coral rubble $\varepsilon = 0.11$ [0.01–0.40]).

Discussion

Despite the long-standing belief that *N. bredini* specializes on hard-shelled prey, our stable isotope mixing model calculations revealed that this species has a more general diet, consuming a substantial amount of soft-bodied prey, particularly fish, irrespective of the habitat and season. Here, we examine the proportional contributions of the different prey to the diet as they relate to the behavior of the mixing model. We then examine these results in the context of the functional ecology of the raptorial appendage strike and the potential role of *N. bredini* as an opportunistic, generalist predator in intertidal coral reef food webs.

N. bredini as a generalist predator

The complementary approaches we used to describe mantis shrimp feeding ecology demonstrate that soft-bodied prey are prevalent in the diet, regardless of their low abundances in both seagrass and coral rubble. Focusing on the stable isotope data, the results from the models run with the specialist prior demonstrate that even when *N. bredini* is categorized as a specialist on hard-shelled prey, soft-bodied prey are still estimated to be a relatively large portion of the diet (Fig. 4). The results were similar when the abundance priors were used (ESM Fig. 3), which suggests that *N. bredini*'s consumption of particular prey items is not driven by the relative abundances of prey in each habitat. Beyond general prey categories, fish and clams consistently emerged as primary contributors to the diet. Fish comprised 25–42 % of the diet in both habitats across all models, while clams were 33–63 % of the diet in almost all models except for in the seagrass habitat when the prey abundance prior was used (Table 3; Fig. 3).

These results for the seagrass habitat using the prey abundance prior (Table 3; Fig. 3b) bear further explanation. The discrepancy is due to high correlations among diet proportions in this model. One criterion for valid mixing model analyses is that the source stable isotope ratios must be sufficiently separated so that the model can differentiate among them (Phillips et al. 2014). Indistinct values of isotope ratios for different prey result in correlated estimates of diet proportions. These correlations are aggravated by a constraint of the mixing model that proportions of different prey in the diet must sum to one (increasing any one proportion necessitates reducing another, resulting in negative correlations). The diagnostic matrix plots for the seagrass

habitat reveal *positive* correlations between the fish, crab, and snail proportions (ESM Fig. 4). When the proportion of clams in the diet is estimated to be 0 % (because clam abundance in the prior is 0 %), the model compensates by markedly increasing the proportions of crabs and snails. This results in the model estimating a diet of fish, crabs, and snails, as opposed to a diet of fish and clams (Fig. 3b). It is, therefore, possible that crabs and snails contribute more to *N. bredini*'s diet than our mixing model analyses show. When compared to the feeding experiment, however, it seems more plausible that clams do in fact comprise a larger component of the diet than snails and crabs because clams were consumed in more feeding trials than were the other two prey items (ESM Table 3). Moreover, in the abundance counts, we found very few coral rubble pieces on which clams live, suggesting that clams could simply have been undercounted in seagrass.

As this example demonstrates, mixing models cannot provide definitive proportions of each prey type in the diet. Additionally, we do not have abundance data or large sample sizes of *N. bredini* individuals during the dry season, meaning that we were unable to accurately determine how *N. bredini*'s diet may change seasonally due to changes in prey availability. Regardless, our results were relatively consistent between the three different priors used in the mixing models and between the two habitats. Using the dietary proportion estimates to calculate the specialization index substantiated the finding that *N. bredini* consistently includes both hard-shelled and soft-bodied prey in its diet. Except for in coral rubble using the hard-shelled specialist prior ($\varepsilon = 0.42$), the specialization index was <0.2 for all priors and habitats, placing *N. bredini* well into the generalist category (Newsome et al. 2012). In addition, *N. bredini* individuals consumed fish in eight out of the ten feeding trials in which fish were presented to them (ESM Table 3), further illustrating that even though fish are not very abundant in either habitat, *N. bredini* will readily consume them when they are present.

Given these results, how do *N. bredini* capture and consume clams and fish? Clams are often found in large aggregations (~50 individuals) on the same coral rubble pieces in which *N. bredini* live (Caldwell and Steger 1987). *N. bredini* may consume clams in higher proportions simply because clams are easily accessible from coral rubble cavities where, as the feeding trials suggest, individuals prefer to crack open and consume prey (ESM Table 3). *N. bredini* have never been seen to scavenge dead fish in the wild. Smashing strikes are fast enough to capture evasive fish (deVries et al. 2012). *N. bredini* may, therefore, include fish in the diet by striking opportunistically at fish that pass close to its home cavity.

For 2–3 weeks after mantis shrimp molt and shed their old exoskeleton, the new exoskeleton has not fully hardened

(Reaka 1975) and mantis shrimp are unable to strike forcefully. When strike force is reduced, *N. bredini* may be limited to a diet of soft-bodied prey that require high speeds to capture but not high forces to break apart (deVries et al. 2012). We were unable to detect differences in diet between fully hardened and recently molted individuals in our stable isotope data because the time between molting and being fully hardened is short relative to the 3-month period over which diet assimilates into muscle tissue (deVries et al. 2015). Stable isotope analysis of hemolymph could allow for differentiating between the diets of individuals that had and had not recently molted because this tissue assimilates diet over three days to one month depending on which stable isotope is analyzed (deVries et al. 2015). In this study, however, hemolymph stable isotope values were not significantly different from those of muscle meaning that hemolymph provides the same diet information as muscle at least during the wet season. Thus, it is unlikely that *N. bredini* consumes soft-bodied prey only for a short period after molting.

An alternative possibility is that *N. bredini* does specialize on hard-shelled prey but is also significantly cannibalistic (Caldwell et al. 1989). Our stable isotope data, however, do not support this explanation. If we had included *N. bredini* as a prey source, they would have been higher in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compared to the *N. bredini* consumers when the trophic discrimination factors were added to *N. bredini* as prey (in Fig. 2, *N. bredini* as a prey source would be shifted up on the y axis +0.9 for $\delta^{15}\text{N}$ and right on the x axis +3.0 for $\delta^{13}\text{C}$). Thus, *N. bredini* consumers would remain isotopically more similar to clams and fish, as opposed to *N. bredini* as a prey source, and the model would still estimate a diet dominated by clams and fish.

Given that *N. bredini* are generalist predators at the population level, could they individually be specialists (Bolnick et al. 2003)? While stable isotope analysis is particularly useful for determining the degree of individual specialization in a population (Bolnick et al. 2002; Semmens et al. 2009), most of the *N. bredini* individuals in this study had similar stable isotope values to fish, clams, and alpheid shrimp/worms (Fig. 2). Therefore, the main finding that *N. bredini* eats soft-bodied prey in some proportion would hold across the individuals studied here. Individuals may vary considerably in their prey preferences, however, as is indicated by the range of estimates of prey contributions to the diet (Table 3). Future studies using stable isotopes to determine individual prey preferences in the wild would give great insight into specific feeding patterns of *N. bredini*. Nevertheless, all individuals are equipped with raptorial appendages to break apart and consume hard-shelled

prey, which does not limit their diets either as a group or as individuals.

The functional ecology of *N. bredini*'s raptorial strike

Many feeding specializations are thought to have performance trade-offs, whereby gaining access to a new dietary niche consequentially limits accessibility to other niches (Schluter 2000; Mcgee et al. 2015), but this does not seem to be the case for *N. bredini*. The high speeds and accelerations generated by the raptorial appendage allow *N. bredini* to both break apart hard-shelled prey with high-impact strikes and to capture fast-moving, soft-bodied prey. Similarly, ecological factors, such as competition for prey, also do not seem to limit the diet of *N. bredini* to only hard-shelled prey, as their field diet is composed of a considerable portion of soft-bodied prey. Thus, while initial selection pressure from competition for food resources may have contributed to the evolution of the ability to break apart hard-shelled prey (Caldwell and Dingle 1976), individuals with this ability remained strong competitors for soft-bodied prey.

Being an opportunistic, generalist predator that can eat prey that are challenging for other animals to consume presents distinct advantages for *N. bredini*. Mantis shrimp are known to fight frequently with conspecifics to maintain control over limited cavity space. Having the ability to rapidly apprehend soft-bodied prey or to gather and then crush hard-shelled prey that are close to the cavities in which individuals live allows *N. bredini* to forage successfully at a relatively low risk of exposure to predators outside its cavity or losing its cavity to a competitor. For example, *N. bredini* selects small- and medium-sized snails when given snails of varying sizes because these snails are easier to carry back to cavities where they are processed with multiple strikes (Caldwell and Childress 1989; Full et al. 1989).

Aggressive interactions between conspecifics are also thought to contribute to the evolution of the raptorial appendage (Caldwell and Dingle 1975). It is, therefore, possible that the ability to break apart hard-shelled prey is, in part, a pleiotrophic effect of selection to produce forceful strikes to win fights. Yet, the evolution of the smashing appendage is thought to coincide with a movement into coral rubble habitats (Ahyong 1997; Ahyong and Harling 2000) where being able to break hard-shelled prey and compete for cavity space would both be advantageous. Separating the effects of social competition for cavities from the effects of competition for hard-shelled prey on the production of forceful strikes is challenging because both modes of selection are likely to be aligned and acting in concert.

Conclusions

Recent advances in stable isotope mixing model analyses have provided unique opportunities to quantify dietary niche width (Semmens et al. 2009; Martínez del Río et al. 2009; Newsome et al. 2012). Our analyses provide the foundation for comparing the degree of diet specialization across mantis shrimp. We can postulate, for example, that smashers likely have a much wider diet breadth compared to spearers, which do not produce high-impact strikes for breaking apart hard-shelled prey (deVries et al. 2012; Patek et al. 2013). The morphological diversity of raptorial appendages, however, is impressive (Ahyong 2001), and many species do not fall into strict categories of spearers or smashers. Thus, an exciting avenue of research is to consider correlations between diet and morphology across the mantis shrimp phylogeny using the techniques in stable isotope analysis developed here to help determine the role of feeding behavior in the evolution of this impressive feeding structure.

Overall, our findings provide novel insights into the discordant relationship between specialized morphology and a generalized diet. Although the association between morphology and diet is a common pattern in nature, over the past two decades, observations of animals with specialized feeding morphology consistently consuming a diversity of prey that do not necessarily require specialized mechanics have become more prevalent. Most of these observations have been documented in fishes (butterflyfish: Motta et al. 1995; cardinalfish: Barnett et al. 2006; surgeonfish: Brandl et al. 2015; wrasse and parrotfish: Sanderson 1990; Bellwood et al. 2006). African cichlids present one of the more extreme and well-documented examples; one species in particular has mouthparts that are either twisted to the left or right to more easily consume the scales from the side of another fish (Hori 1993). Yet, most of the time, this species feeds on algae and zooplankton (Liem 1980; Binning et al. 2009). Fossil records of ungulates moving into grasslands also show that the evolution of specialized dentition for consuming grass did not prevent ungulates from eating other plants (Feranec 2007). Green crabs have large claws with high mechanical advantages used to crush hard-shelled prey, but their diets in soft sediments include a considerable portion soft-bodied polychaetes and arthropods (Wilcox and Rochette 2015). The painted ghost crab, *Ocypode gaudichaudii*, has claws modified to shovel sediments and forage for diatoms, but they regularly consume animal prey as well (Lim et al. 2016). These examples, coupled with our discovery in mantis shrimp, suggest that highly specialized morphology may more often correspond to a generalist diet than is currently recognized. This general finding would yield a fundamental shift in our understanding of form-function relationships and pose new questions about the ecological role of animals with specialized morphology.

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Author contribution statement MSdV formulated the original idea. MSdV and JHC conceived and designed experiments. MSdV performed experiments. MSdV and TED performed stable isotope analyses. BCS analyzed the stable isotope data and MSdV analyzed the other datasets. GRG provided significant input on data analysis and interpretation. MSdV wrote the manuscript but BCS wrote the stable isotope statistical analysis methods and results. All authors contributed substantially to the interpretation of results and by giving critical conceptual and editorial advice.

Compliance with ethical standards

All applicable institutional and/or national guidelines for the care and use of invertebrates were followed.

Conflict of interest The authors declare that they have no conflict of interest.

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