Arthropod Predation of Vertebrates Structures Trophic Dynamics in Island Ecosystems

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abstract: On isolated islands, large arthropods can play an important functional role in ecosystem dynamics. On the Norfolk Islands group, South Pacific, we monitored the diet and foraging activity of an endemic chilopod, the Phillip Island centipede (*Cormocephalus coynei*), and used a stable isotope mixing model to estimate dietary proportions. Phillip Island centipede diet is represented by vertebrate animals (48%) and invertebrates (52%), with 30.5% consisting of squamates, including the Lord Howe Island skink (*Oligosoma lichenigera*) and Günther's island gecko (*Christinus guentheri*); 7.9% consisting of black-winged petrel (*Pterodroma nigripennis*) nestlings; and 9.6% consisting of marine fishes scavenged from regurgitated seabird meals. Centipede predation was the principal source of petrel nestling mortality, with annual rates of predation varying between 11.1% and 19.6% of nestlings. This means that 2,109–3,724 black-winged petrel nestlings may be predated by centipedes annually. Petrels produce a single offspring per year; therefore, predation of nestlings by centipedes represents total breeding failure for a pair in a given year. Our work demonstrates that arthropods can play a leading role in influencing vertebrate reproductive output and modifying trophic structures and nutrient flow in island ecosystems.

Keywords: seabirds, reptiles, centipedes, insects, trophic estimation, stable isotopes.

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Introduction

Predator-prey interactions are important processes that regulate the structure of ecological communities, population dynamics, and nutrient transfer in food webs (Paine 1966; Sih et al. 1985; Krebs 2011; Ripple and Beschta 2012). These processes are central to many ecological studies and provide a foundation to better understand how ecosystems function, including how natural systems can maintain critical function in the face of anthropogenic disturbance and environmental change (Yodzis 1988; Johnson et al. 1996). Interactions between vertebrate predators and their prey have been described in a great diversity of phyla (McLaren and Peterson 2008; Krebs 2011). Whereas invertebrates have been relatively well documented as important predators of vertebrate animals in marine (Terlau et al. 1996; Brodeur et al. 2008; Wangvoralak et al. 2011) and freshwater (Brodie and Formanowicz 1983; Mori 2004; Van Buskirk et al. 2004; Ohba et al. 2008) systems, examples of terrestrial invertebrate-vertebrate predation are comparatively scarce (Toledo 2005; Nyffeler and Knörnschild 2013; Nyffeler et al. 2017; Nordberg et al. 2018*a*; Emery et al. 2020).

Among invertebrates, arthropods are especially well suited to vertebrate predation because they are often larger than many potential vertebrate prey and have evolutionary adaptations that increase their predatory efficiency, such as venoms and toxins to incapacitate prey (Undheim et al. 2015; Luo et al. 2018). Systematic reviews have revealed widespread reports of arthropod-vertebrate predation, with arthropods in six classes and 83 families observed to prey on vertebrates in five classes and 162 families (McCormick and Polis 1982;

Valdez 2020). However, these reports generally result from opportunistic observations (McCormick and Polis 1982; Valdez 2020), and few arthropod-vertebrate predation systems have been the focus of in situ study (e.g., Kopp et al. 2006; Nordberg et al. 2018*a*), with most conducted in laboratory settings (e.g., Pearman 1995; Wizen and Gasith 2011).

Few studies (e.g., Emery et al. 2020) have established or quantified arthropod prey choice because it is challenging to study in a natural context. While it may be relatively easy to observe, identify, and quantify foraging in large mammals, birds, and reptiles that kill large prey, it can be more difficult to observe invertebrates foraging in situ because their behavior tends to be cryptic, nocturnal, and concealed in leaf litter or subterranean (Symondson 2002; Nordberg et al. 2018*a*). Classifying and quantifying invertebrate diet are also acutely challenging because most invertebrates are fluid feeders such that ingested prey cannot easily be identified using traditional methods, such as gastric dissection (Shine 1977), gastric lavage (Antonelis et al. 1987) or pellet/fecal sampling (Southern 1954; Nordberg et al. 2018*b*). Moreover, laboratory simulations are unlikely to replicate conditions that produce natural behavior in both predator and prey (Symondson 2002). Many of these challenges can be resolved with relatively new technologies and forensic methods, such as stable isotope analysis (Fry 2006; Layman et al. 2012) and molecular screening, including the use of polymerase chain reaction–based methods for detecting prey DNA (Symondson 2002).

Here, we use a stable isotope approach paired with systematic in situ observations of foraging in a population of a large, endemic arthropod to explore the hypotheses that (*a*) vertebrates can form significant proportions of arthropod diet and (*b*) arthropod-vertebrate predation is capable of reducing reproductive output in a vertebrate population. Using a subtropical island system as an exemplar, we show that vertebrates, including reptiles, fish, and seabirds, form an important dietary component for a large, endemic chilopod, the ground-dwelling Phillip Island centipede (*Cormocephalus coynei*; fig. 1). Our results illustrate that arthropods play a major role in structuring trophic dynamics and nutrient flow in an island ecosystem.

Methods

Study Area

Phillip Island (29°07′S, 167°57′E; fig. 2) is a small (207 ha), uninhabited subtropical island located approximately 6 km south of Norfolk Island in the South Pacific. Phillip Island supports breeding populations of 13 seabird species, the most abundant being the black-winged petrel (*Pterodroma nigripennis*; 15,000–19,000 pairs; Priddel et al. 2010; N. Carlile, unpublished data). The island also supports native reptiles and invertebrates, including Lord Howe Island skinks (*Oligosoma lichenigera*), Günther's island geckos (*Christinus guentheri*), endemic Phillip Island centipedes (*Cormocephalus coynei*), endemic Phillip Island crickets (*Nesitathra phillipensis*), and native flightless crickets, including *Dictyonemobius pacificus* and *Dictyonemobius lateralis* (Koch 1984; Otte and Rentz 1985; Rentz 1988). In addition to these native species, introduced populations of rabbits, pigs, and goats occurred on the island until the 1980s, causing widespread degradation and vegetation denudation. Following the successful eradication of these introduced species, the island's vegetation has steadily been recovering (Coyne 2010; fig. 2).

Systematic Observation of Predation Events

To identify and document the range of centipede prey, we searched for foraging centipedes nocturnally in six 100-m² survey plots in four habitat types known to be used by Phillip Island centipedes and in five transects approximately 300 m long interconnected between each survey plot. Three survey plots were in woodland dominated by white oak (*Lagunaria patersonia*), and one each was in red-leg grass (*Bothriochloa macra*) grassland, Norfolk pine (*Araucaria heterophylla*) forest, and exposed soil habitat (fig. 2). Each of the six plots was surveyed in randomized order for 30 min per night over 17 nights (total 51 h) between February 27 and March 29, 2019. A further 81 h was spent opportunistically searching for foraging centipedes on transects between plots. During each survey, we searched for centipedes on the forest floor and on or around any habitat features, such as rocks, logs, and small trees, using a 400-lm white LED light. We did not disturb ground features, such as rocks and logs, because of the high density of active seabird burrows and risk of crushing them. Upon detection of a centipede, the light source was switched to a red LED to minimize disturbance. We recorded the body length of each individual centipede and the species of prey if the individual was actively hunting (striking at prey) or feeding.

Predation of Seabird Nestlings

We monitored black-winged petrel (2018, $n = 56$; 2019, $n = 45$) and white-necked petrel (*Pterodroma cervicalis*; 2018, $n = 22$; 2019, $n = 19$) nestlings over two breeding seasons and recorded nestling body weight at ~3-day intervals from near hatch date to ~45 days. Where direct predation of nestlings by centipedes was not witnessed, it was inferred from a consistent pattern of predation pathology that was directly observed in instances of centipedes consuming nestlings. In these cases, centipedes had specifically targeted the hind neck, rasping away flesh from this region,

Figure 1: Phillip Island centipede (*Cormocephalus coynei*; *foreground*) with an adult black-winged petrel (*Pterodroma nigripennis*; *background*). Some foreshortening effect exists in this image, with the largest Phillip Island centipede measured at 23.5 cm (this study) and the combined head and body length of an adult black-winged petrel estimated at 28–30 cm (Marchant and Higgins 1990). Image by L. Halpin, 2018.

the head, and soft tissue at the lower mandible (fig. 3). This pattern of predation is consistent with anecdotal reports of scolopendrid centipede predation (Cloudsley-Thompson 1968; Molinari et al. 2005).

Tissue Sampling

Tissue samples from centipedes and their prey were collected from February to April in 2018 and 2019 and January to February in 2020 (table S1, available online). We sampled down feathers from black-winged petrel nestlings in the first week after hatching. The black-winged petrel was chosen because it is the only seabird species on the island that met the following criteria, which we believe contributes to its importance in the diet of centipedes: (1) has a breeding population of >1,000 pairs, (2) nests in burrows, (3) is small bodied (adults <250 g), and (4) nests in the summer, when centipedes are likely to be most active. Samples of freshly deceased centipedes, geckos, skinks, *Dictyonemobius* sp. crickets, and fish spilled from regurgitated meals of tree-nesting black

noddies (*Anous minutus*) were collected opportunistically from within the seabird colony.

Sample Processing and Analysis

Stable isotope analysis was conducted on an ANCA GSL2 elemental analyzer interfaced to a Hydra 20-22 continuous-flow isotope ratio mass spectrometer (Sercon, Cheshire, United Kingdom). We used multiple internal standards calibrated against internationally recognized reference materials for quality control (for detailed methods, see the supplemental PDF, available online).

Proportion of Prey Items in Centipede Diet

We used a Bayesian dietary source mixing model with the package simmr (Parnell and Inger 2020) in R (R Development Core Team 2020). We applied a simmr model with diet-to-tissue trophic enrichment factors (TEFs). Published TEFs from laboratory feeding experiments for centipedes are unavailable, so we used TEFs ($\delta^{13}C = -0.4‰ \pm 0.1‰$ SD;
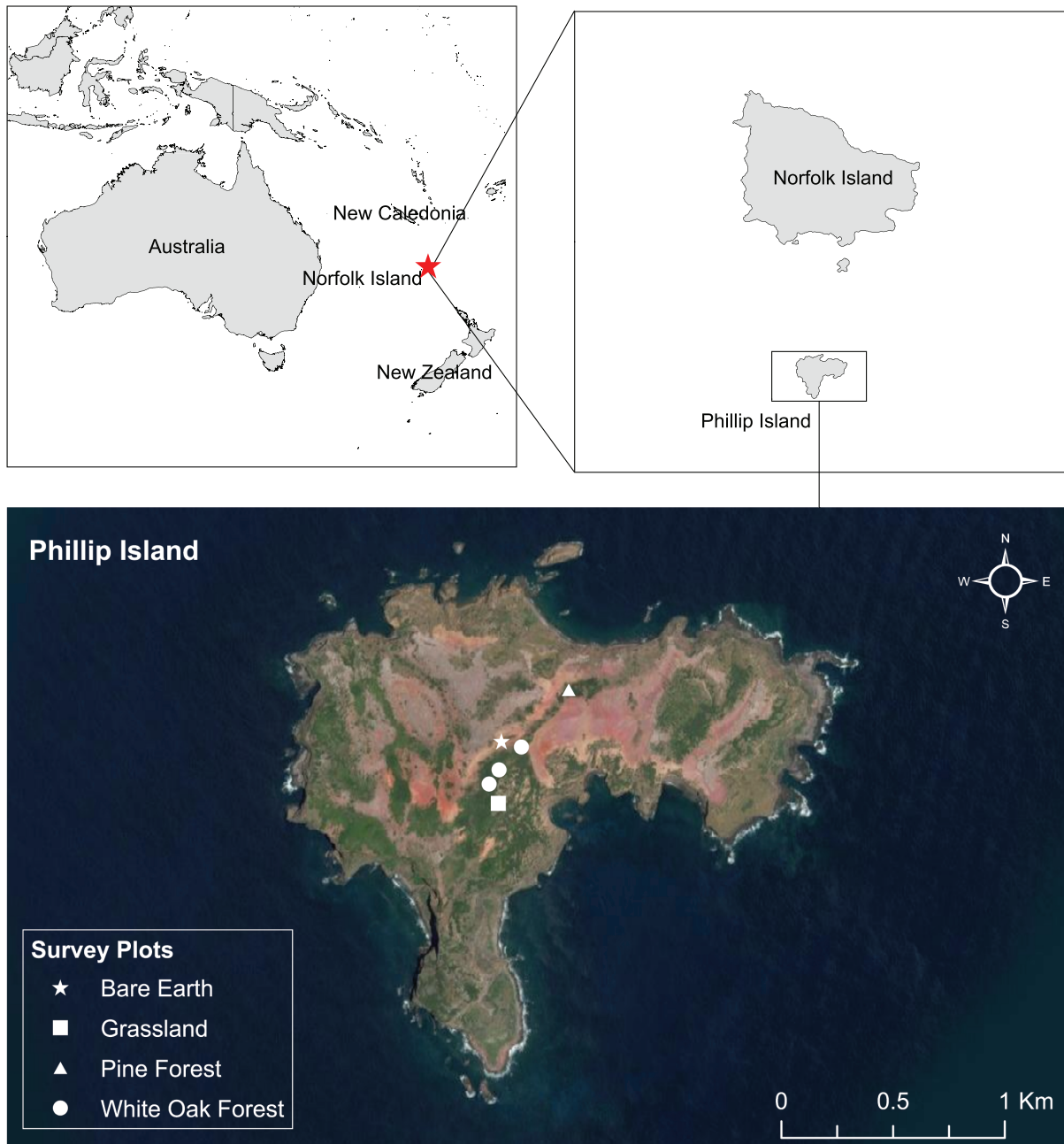
Figure 2: Phillip Island (*bottom*) and its location within the Australasian region (*top left*) and the Norfolk Island group (*top right*), where Phillip Island centipede (*Cormocephalus coynei*) foraging behavior was studied. Points represent survey plot locations.

δ^{15}N = 2.1‰ ± 0.4‰ SD) from an ex situ feeding experiment of a generalist invertebrate predator, lycosid spiders that were fed a carnivorous diet (Oelbermann and Scheu 2002). To test the suitability of selected TEFs, we used a mixing polygon simulation following Smith et al. (2013) to ensure that the consumer isotopic signatures could be explained by our proposed model (fig. S1; figs. S1–S3 are available online). Data and code underlying the Bayesian dietary source mixing

model have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.9kd51c5g2; Halpin et al. 2021).

Results

Centipede Foraging

During 132 h of in situ foraging surveys, we observed Phillip Island centipedes hunting or consuming a range of

Figure 3: Black-winged petrel (*Pterodroma nigripennis*) nestlings that have been preyed on by Phillip Island centipedes (*Cormocephalus coynei*). Images by L. Halpin, 2018, 2019.

invertebrate, reptile, fish, and bird prey from 32 observed strikes and 21 observed feeding events (table 1). Phillip Island centipedes are large scolopendrids (median body length: 19 cm; range: 1–23.5 cm; $n = 440$). In 2018 and 2019, respectively, 19.6% (11 of 56 nests) and 11.1% (5 of 45 nests) of regularly monitored black-winged petrel nestlings were preyed on by centipedes. During the same periods, none of the monitored white-necked petrel nestlings were preyed on by centipedes. Before predation, black-winged petrel nestlings appeared healthy and were being provisioned by parents as indicated by an average mass gain (±SD) of 23.5 ± 14.7 g in the approximate 3-day interval immediately before predation (fig. S2). The mean body mass (±SD) of nestlings at the last measurement before their predation was 87.7 ± 33 g (range: 44–147 g; fig. S2). In 2018 and 2019, respectively, there were only one and two nestling mortalities that did not exhibit signs of centipede predation and were attributed to other causes. We observed one instance of envenomation of

a black-winged petrel nestling by a centipede (video S1; videos S1, S2 are available online) in an exposed burrow that ultimately resulted in nestling death, where the centipede did not consume the nestling at the time of observation. We also observed a centipede consuming a nestling (video S2) from the group of study nests that, earlier on the same day, was observed alive and well and was regularly being fed by its parents.

Crickets were the most frequently targeted and consumed prey item. Hunting strike success rates were low for frequently targeted species, including observations of five strikes at Günther's island geckos where all focal individuals evaded capture. All six observations of vertebrates being consumed on the forest floor were presumably the result of scavenging. These included four instances of fish consumption, one black noddy nestling presumed to have fallen from an arboreal nest, and one Günther's island gecko in a state of advanced decomposition (fig. S3).

Table 1: Proportion of prey strikes, successful strikes, and feeding events by Phillip Island centipedes

Prey class, species	Strikes (%)	Successful strikes (%)	Feeding (%)
Insecta:			
Ant sp.	6.3	100	9.5
Crickets (*Dictyonemobius pacificus, Dictyonemobius lateralis, Nesitathra phillipensis*)	65.6	19	28.6
Beetle sp.	0	0	4.8
Moth sp.	0	0	4.8
Arachnida:			
Spider sp.	0	0	4.8
Diplopoda:			
Oxidus gracilis	3.1	100	9.5
Chilopoda:			
Cormocephalus coynei	3.1	0	4.8
Osteichthyes:			
Engraulis australis, fish sp.	0	0	19
Reptilia:			
Christinus guentheri	15.6	0	4.8
Aves:			
Anous minutus	0	0	4.8
Pterodroma nigripennis	6.3	50	0

Note: Strikes are defined as the percentage of the total number ($n = 32$) of strikes accounted for by strikes at that prey taxon. Successful strikes are the percentage of those strikes that resulted in successful capture. Feeding is the percentage of the total number of feeding observations ($n = 21$) where a centipede was observed consuming a given prey taxon. Fish are deceased and discarded from tree-nesting seabirds.

Bayesian Dietary Source Model Results

The Bayesian dietary source mixing model (fig. 4) estimated that vertebrates form a large proportion (48%) of centipede diet, with 38.4% of the diet consisting of terrestrial vertebrates: geckos (17.7%; 95% credibility interval [CI]: 2.8–38.6), skinks (12.8%; 95% CI: 1.8–31.2), and seabird nestlings (7.9%; 95% CI: 1.6–16.9). Fish scavenged from regurgitated meals of seabirds formed 9.6% (95% CI: 1.6–22.5) of centipede diet. The remainder of the Phillip Island centipede diet (52.1%; 95% CI: 33.2–69.2) consisted of invertebrates (crickets). While skinks were not directly observed being hunted or consumed by Phillip Island centipedes, similarly sized giant centipedes are known to prey on skinks in other systems (e.g., Emery et al. 2020, 2021). It is likely that Phillip Island centipedes prey on skinks belowground or under loose leaf litter; thus, skinks were included in the dietary mixing model.

Our results demonstrate a system in which the exchange of nutrients is largely driven by arthropod predation. A schematic diagram (fig. 5) depicts the direction and strength of the trophic linkages predicted by the model, hypothesized linkages, and the general flow of nutrients. Marine fish enter this terrestrial food web as discards from seabirds.

Discussion

Our results demonstrate that through high rates of predation on vertebrates, arthropods can play an important role in structuring ecosystem nutrient cycling in island ecosystems. On Phillip Island, centipedes that prey on seabirds increase enrichment of the nutrient pool with marine-derived nutrients by consuming seabird nestlings that are nourished by their parents exclusively with pelagic fish and squid. Predation by centipedes likely produces a more homogenous nutrient landscape. Nutrient deposition in seabird colonies is typically patchy and localized, with nutrients accumulating around nest sites via spilled food, dead nestlings and adults, abandoned eggs, and deposition of guano (Gillham 1956; Heatwole 1971; Anderson and Polis 1999; Sánchez-Piñero and Polis 2000; Harding et al. 2004). Predation of nestlings by centipedes means that centipedes are likely to actively translocate nutrients around the island (Schmitz et al. 2010). On an island depauperate of vertebrate predators, this is a potentially important process that could expand the regeneration of the island's vegetation into degraded areas (e.g., if centipedes roam into degraded environments that are unsuitable for burrow-nesting petrels).

Our observations revealed that centipedes targeted seabird nestlings with small body sizes reflective of a young and relatively defenseless age class. By extrapolating the observed rates of centipede predation on monitored petrel nestlings, which differed between years (19.6% in 2018 and 11.1% in 2019), to the upper bound of the most recent black-winged petrel population estimate (19,000 breeding pairs in 2017; N. Carlile, unpublished data), we estimate that Phillip Island centipedes consume between 2,109 and 3,724 seabird nestlings annually. Black-winged petrels are long-lived (>30 years) seabirds that produce a single offspring per year (Hutton and Priddel 2002). This means that each centipede predation of a seabird nestling represents total reproductive failure for a breeding pair in a given year. Arthropods are therefore able to reduce the lifetime reproductive output of long-lived, K-selected vertebrates. Our results not only suggest that predatory arthropods are important trophic engineers that structure nutrient flow on islands but also verify that they are important predators of terrestrial vertebrates in some ecosystems (Nordberg et al. 2018a; Valdez 2020).

Our results are consistent with reports of scolopendrid centipedes preying on vertebrates, including amphibians (Forti et al. 2007), bats (Molinari et al. 2005; Noronha et al. 2015; Lindley et al. 2017), lizards (Nordberg et al.
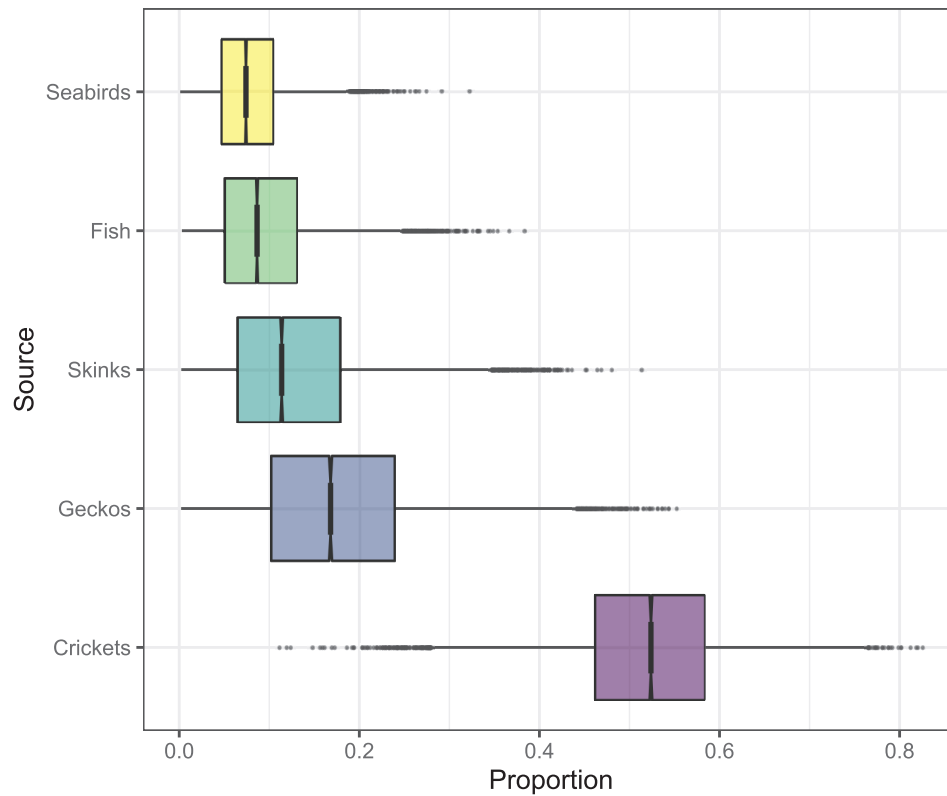
Figure 4: Estimated contribution of prey items in the diet of Phillip Island centipedes. Results present the relative proportions of dietary source contributions to centipede tissue predicted by the Bayesian dietary source mixing model (median, interquartile range, and maximum/minimum values of the posterior probability distribution).

2018*a*; Emery et al. 2020), and snakes (Smart et al. 2010; Arsovski et al. 2014). Remarkably, however, seabirds have not previously been reported as centipede prey despite centipedes and seabirds co-occurring on many islands. Our study appears to be a rare documented example in which seabirds have been identified as direct prey of an arthropod, thereby demonstrating a novel pathway for transfer of nutrients from the marine to terrestrial environment.

The dietary source mixing model we used cannot differentiate between prey that is captured and killed and prey that is scavenged. However, results of our in situ observations demonstrate that the Phillip Island centipede is both an active predator that was the principal driver of seabird nestling mortality and an opportunistic scavenger of other species, including reptiles and black noddy nestlings that fall from tree nests. Our foraging surveys were limited in scope (conducted on only the surface of the forest floor) and were therefore unlikely to have detected centipedes foraging under deep leaf litter or in subterranean cavities. Therefore, prey items captured and consumed underground (e.g., predation of burrow-nesting black-winged petrels) are likely to be underrepresented by our monitoring. Results of

the dietary mixing model indicate a larger squamate contribution to centipede diet than we observed in foraging surveys, which suggests that centipedes may be more successful at preying on geckos and skinks underground.

Further supporting the conclusion that black-winged petrel nestlings were actively preyed on rather than scavenged is our observation that no white-necked petrel nestlings were consumed by Phillip Island centipedes during nest monitoring. White-necked petrel body mass is almost three times larger (Marchant and Higgins 1990), with their nestlings reaching a larger body mass more quickly than black-winged petrel nestlings, and presumably, nestlings are able to defend themselves from centipedes at a younger age. This accords with our observation that Phillip Island centipedes preyed predominantly on smaller-sized black-winged petrel nestlings. Vulnerability to predation by rats (*Rattus* spp.) shows a similar age-dependent pattern in gray-faced petrels (*Pterodroma gouldi*), with predation risk declining to very low levels at ~3 weeks after hatching (Imber et al. 2000). Nevertheless, centipedes are generalists and will likely consume any deceased vertebrates encountered during foraging.
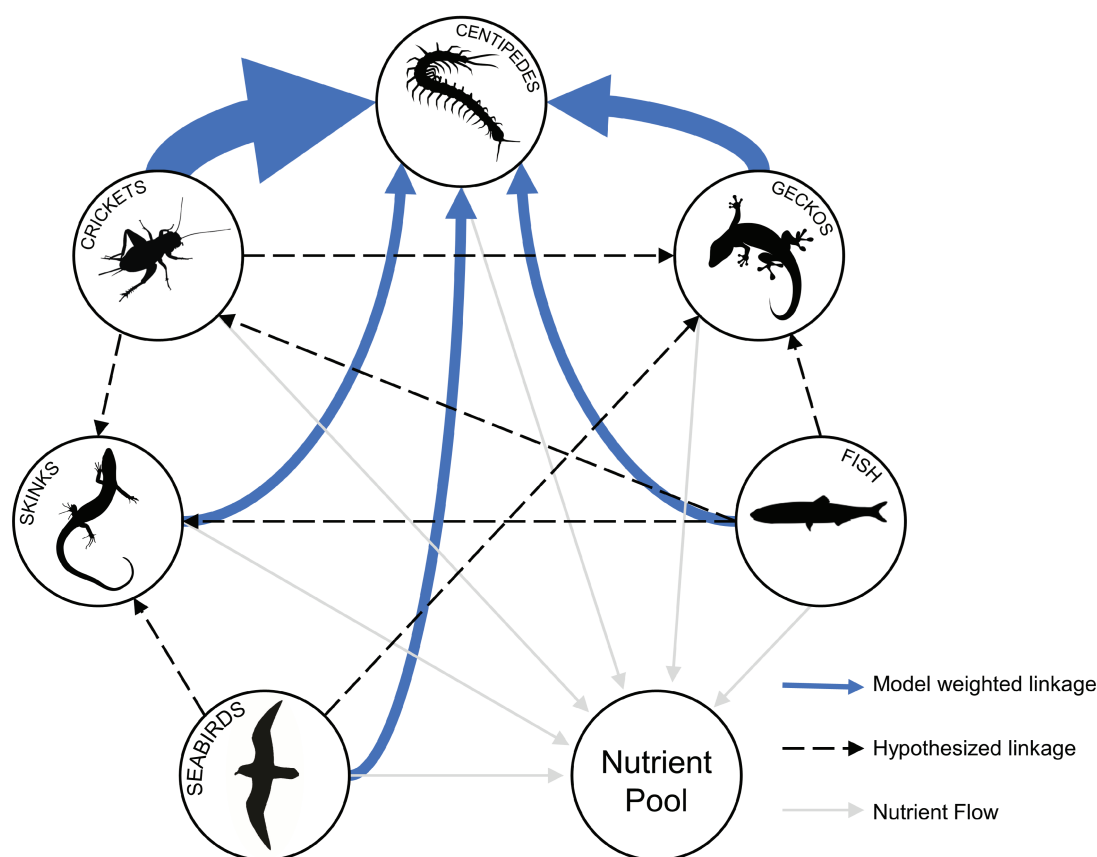
Figure 5: Schematic diagram of the general Phillip Island food web with the thickness of dietary linkages to centipedes weighted according to proportional contributions of centipede prey taxa to centipede tissue isotopic values.

Although nestlings of other seabird species may also have contributed to the isotopic signature of Phillip Island centipedes, we believe that black-winged petrel chicks are the major seabird diet constituent on the basis of our foraging observations and aspects of the ecology of the breeding seabird community. For example, black-winged petrels are the only small-bodied, burrow-nesting seabird that breeds in summer (coincident with the timing of stable isotope tissue sampling) on Phillip Island. They are also the most abundant breeding seabird on the island, with an abundance one to two orders of magnitude greater than nine of the 12 other breeding seabird species.

We observed a single cannibalism event among Phillip Island centipedes, which is otherwise common in many food webs (Ings et al. 2009). We did not attempt to quantify the dietary contribution of cannibalism in the dietary mixing model given the challenges of distinguishing cannibalism from other forms of intraguild predation (Greenwood et al. 2010; Traugott et al. 2013).

Large scolopendrid centipedes have been introduced to many islands, especially in tropical and subtropical regions (Shelley 2004; Shelley et al. 2014; Waldock and Lewis 2014) and have recently been implicated in the extinction of an endemic island vertebrate (Emery et al. 2020). Systems slated for conservation efforts (e.g., reintroductions of extirpated species) where large introduced centipedes or other predatory arthropods are present will likely require innovative solutions or centipede control to minimize impacts to recovering or colonizing species targeted for conservation (e.g., Emery et al. 2020). By contrast, innovative approaches may be necessary in disturbed systems given the potential interactions between native predatory arthropods and potential prey of conservation importance (e.g., Feher 2019; Valdez 2019).

We provide a novel understanding of the role of predatory arthropods in structuring trophic dynamics on islands. We demonstrated that arthropods can increase the flow of marine nutrients in an island ecosystem by preying on

the offspring of vertebrates that forage exclusively in pelagic environments. We demonstrate how predatory arthropods can exert top-down pressure on vertebrate populations through predation-mediated reductions in reproductive output. This could have important consequences for understanding trophic structures on islands and how vertebrate communities are shaped, perhaps especially so on islands, where arthropod gigantism is common and evolutionary processes have allowed invertebrates to occupy novel niches.

Acknowledgments

Statement of Authorship

L.R.H. conceived the study, acquired funding and scientific permits, collected field data, performed lab analyses, analyzed the data, and led the writing of the manuscript. D.I.T. collected field data and assisted with data analysis. H.P.J. and R.M. contributed to research development and assisted with data analysis. D.C.D. collected field data. W.W.W. conducted stable isotope lab analyses. R.H.C. and N.C. contributed to project development, acquisition of scientific permits, funding, and fieldwork. All authors contributed substantially to the manuscript and gave final approval for publication.

Data and Code Availability

All data and code have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.9kd51c5g2; Halpin et al. 2021).

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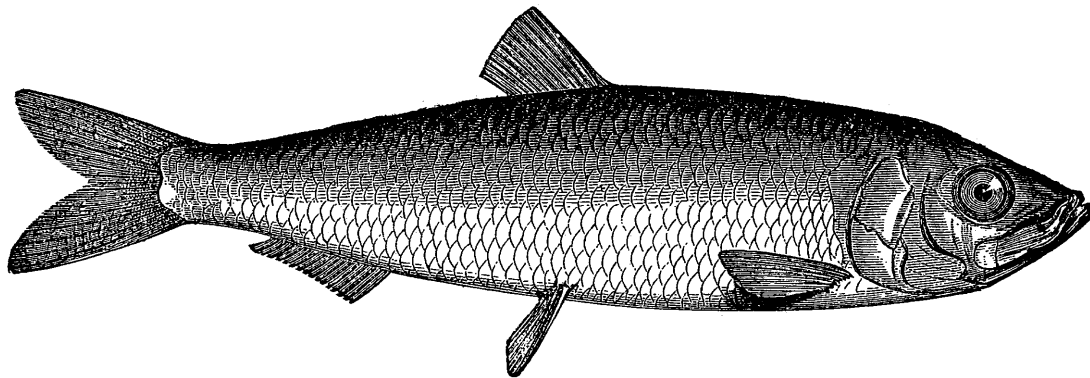
"In respect to our smaller fishes, the Herring (*Clupea elongata*), etc., we observe a considerable decrease in the numbers which now annually visit our shores, as compared with their former numbers." From "The Habits and Migrations of Some of the Marine Fishes of Massachusetts" by James H. Blake (*The American Naturalist*, 1870, 4:513–521).