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Size matters: trap size primarily determines prey spectra differences among sympatric species of carnivorous sundews

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Abstract. Even though carnivorous plants (CPs) are a popular focus of ecological research, surprisingly few studies have investigated their prey spectra (the number and composition of captured prey). This knowledge gap has important implications for our understanding of sympatric speciation processes in CPs and may potentially hinder effective conservation and ecological restoration efforts. We applied a novel photography-based analysis method to characterize the in situ prey spectra of eight species from *Drosera* sect. *Arachnopus*, including five species that were studied across multiple populations in northern Australia. The prey spectra of all studied species predominantly comprised of flying insects, with small Nematocera (Diptera) being the most common prey group across all species. While the prey spectra of most species varied significantly among locations, differences in prey spectra among sympatric species were most strongly determined by trap size. The number of prey captured per plant and per centimeter of trapping leaf was strongly associated with increasing leaf length, and species with larger trapping leaves also captured comparatively greater numbers of large prey items than species producing smaller trapping leaves. Although niche segregation in prey spectra was not observed at any of the study sites, at one location *D. fragrans* (a species producing a strong, honey-like scent from trapping leaves) was found to capture significantly more winged Hymenoptera than the unscented sympatric *D. aquatica*, potentially indicating selective prey attraction in *D. fragrans*. Small species (such as *D. nana*) captured a disproportionally low amount of prey, despite being relatively widespread over large areas of northern Australia. Results indicate that carnivory may not have been a primary driver of diversification in *D.* sect. *Arachnopus*.

Key words: carnivorous plant; *Drosera*; *Drosera* sect. *Arachnopus*; niche segregation; plant–animal interactions; prey analysis; prey spectra; sympatry; trap size.

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INTRODUCTION

Prey selectivity among sympatric predatory organisms is thought to be an important ecological driver of sympatric speciation (Doebeli and Dieckmann 2000, Bürger et al. 2006). Research in this area has generally focused on the detection of competition-driven prey selectivity in the animal kingdom and even uncovered several cases of likely sympatric speciation events (Knudsen et al. 2010). However, few studies have examined the potential for prey selectivity to act as an evolutionary driver in carnivorous plants (CPs), species notorious for trapping, killing, and deriving nutritional benefit from animal prey (Juniper et al. 1989, Ellison and Adamec 2018), despite evidence that CPs represent true passive predators (Cross and Bateman 2018). Despite the

ecological novelty of CPs, there have been surprisingly few published studies documenting their prey spectra, particularly in terms of prey quantity and quality (i.e., the number and composition of captured prey; Darnowski et al. 2018). This research gap is especially poignant for Australian species, given that Australia, and Western Australia in particular, is recognized as both a global center of CP biodiversity and a region harboring significant CP morphological, functional, and ecological diversity (Lowrie 2014, Clarke et al. 2018, Cross 2019). To date, the prey spectra of only eight out of ~250 Australian CP taxa have been studied: seven species of *Drosera* L. (four in *D*. sect. *Ergaleium* (DC.) Planch., two in *D*. sect. *Bryastrum* Planch., and one in *D*. sect. *Coelophylla* Planch.; Verbeek and Boasson 1993) and of one species of bladderwort (*Utricularia volubilis* R.Br.; Płachno et al. 2014). This essential lack of knowledge regarding prey selectivity in CPs limits our understanding of their ecological requirements (Cross et al. 2018), which is important for detecting sympatric speciation processes and may potentially hinder effective conservation and ecological restoration efforts (Clarke et al. 2018).

Previous studies comparing the prey spectra of sympatric CP species (i.e., species that are exposed to the same prey availability in their shared habitat) have attributed statistically significant differences in number and composition of captured prey to contrasting morphology, for example, trap shape (in *Nepenthes* L.; Gaume et al. 2016), color and ultraviolet patterns (several genera; Joel et al. 1985, Juniper et al. 1989, Moran et al. 1999), or growth habit (*Drosera*; Verbeek and Boasson 1993). Achterberg (1973) and Thum (1986) interpreted observed differences in prey spectra between the sympatric European species *Drosera intermedia* Hayne and *Drosera rotundifolia* L. to be caused by their contrasting growth habit (but not by differences in leaf shape or size), as significantly more flying insects (mainly Diptera) were captured by the erect leaves of *D. intermedia* (Thum 1986), while the decumbent leaves of *D. rotundifolia* primarily captured ground-inhabiting prey (Achterberg 1973, Thum 1986). This apparent importance of leaf morphology on prey spectra was also observed by Verbeek and Boasson (1993), who conducted the only published prey spectra comparison of sympatric *Drosera* species from Australia. They found the prey spectrum of the flat-rosetted *Drosera erythrorhiza* Lindl. to contain only around 10% of flying insects, in contrast to that of the tall, upright-growing *Drosera menziesii* R.Br. ex DC., which consisted exclusively of flying insects. More recently, however, Volkova et al. (2010) found no significant differences in the prey spectra of *Drosera anglica* Huds. (erect leaves), *D. rotundifolia* (decumbent leaves), and their natural hybrid *Drosera* × *obovata* Mert. and W.D.J. Koch (erect leaves) from Russia. Clearly, additional research is necessary to better understand the role of differential leaf morphology in prey spectra of sympatric CP species, especially within the morphologically diverse Australian *Drosera*.

Despite observed differences in prey spectra among some sympatric *Drosera*, no evidence has been presented for niche segregation as a result of interspecific competition for prey in this genus. In a meta-analysis of the data from 30 studies on the prey spectra of CPs (including those on sympatric *Drosera*, i.e., Achterberg 1973, Thum 1986, Verbeek and Boasson 1993), Ellison and Gotelli (2009) found no statistical evidence for niche segregation in any of the studied genera. They found the niche overlap observed in the three studies on sympatric *Drosera* species to be greater than the expected niche overlap, which directly contrasts the idea of niche segregation. Similarly, greater-than-expected niche overlap was presented for the prey spectra of *D. anglica*, *D. rotundifolia,* and *D.* × *obovata* by Volkova et al. (2010). However, niche segregation has been demonstrated for tropical pitcher plants (*Nepenthes*), after identifying the prey of sympatric species to subordinal taxonomic ranks and thoroughly investigating general prey availability in the habitat using artificial traps (Chin et al. 2014).

The monophyletic *D*. sect. *Arachnopus* Planch. (also known as the *Drosera indica* L. complex) consists of eleven described species of predominantly northern Australian distribution that are characterized by an annual life cycle and a relatively large, erect growth habit. These species produce narrowly linear–lanceolate (thread-like) leaves covered with stalked glands for prey capture (Lowrie et al. 2017). Although all species of *D*. sect. *Arachnopus* share similar morphology and growth habit, they exhibit species-specific morphological differences that may contribute to

prey spectra dissimilarity. Leaf size, for example, varies consistently among species in *D*. sect. *Arachnopus*, with *Drosera cucullata* Lowrie, *Drosera fragrans* Lowrie, and *Drosera serpens* Planch. producing leaves ~10–20 cm long while the smallest species (*Drosera nana* Lowrie) typically produces leaves only 1.5–2.0 cm in length (Lowrie 2014; T. Krueger, *personal observation*). Leaf length is likely to affect the total number of prey captured by an individual, as has been previously demonstrated for *Drosophyllum lusitanicum* L. (Bertol et al. 2015), and may also affect prey spectra composition given that CPs with larger leaves more frequently capture larger prey items (Gibson 1991). While most species of *D*. sect. *Arachnopus* produce odorless leaves, the leaves of *D. fragrans* and *Drosera finlaysoniana* Wall. ex Arn. produce a strong, honey-like scent; Fleischmann (2016) hypothesized that scent may contribute to prey attraction as greater numbers of captured butterflies and moths were observed on the scented *D. fragrans* than on the non-scented, sympatric *Drosera aquatica* Lowrie. Additionally, many species from *D*. sect. *Arachnopus* produce characteristic and species-specific eglandular structures on leaves, stems, and inflorescences, and it has been hypothesized that these structures are involved in prey attraction (Hartmeyer and Hartmeyer 2006, Lowrie et al. 2017). For example, the yellow blackberry-shaped emergences of *Drosera hartmeyerorum* Schlauer have been interpreted by Hartmeyer and Hartmeyer (2006) as optical lenses to focus light, creating visual effects which the authors hypothesized to be particularly attractive to grasshoppers.

This study aimed to provide an overview and comparison of the prey spectra of eight closely related species from *D*. sect. *Arachnopus*, with the primary goal of detecting differential prey selectivity and niche segregation due to interspecific competition for prey—as these would be potential indications of past sympatric speciation events in this group. Plants were studied through in situ examination of the prey captured by each species at different locations across northern Australia (to account for among-site variability in available prey). We hypothesized that sympatric species from *D*. sect. *Arachnopus* would exhibit differences in prey spectra, primarily due to morphological differences among species such as differences in leaf size, eglandular appendages, and scents. Additionally, we expected that these differences would yield evidence of niche segregation among sympatric species. Specifically, we hypothesized that species with larger leaves would capture more prey items, particularly more large prey items, than small-leaved species. Species producing very characteristic eglandular appendages or scents (e.g., *D. hartmeyerorum* or *D. fragrans*) were predicted to catch either more prey items or a more distinctive composition of prey items than sympatric species lacking such features.

Methods

Study area

The prey spectra of seven species from *D*. sect. *Arachnopus* were studied at 10 locations in the Top End (Northern Territory) and Kimberley region (Western Australia) of northern Australia in April 2017 and April 2019 (Table 1). Additionally, a population of *D. indica* was sampled on an inselberg in central Madagascar during March 2017 for comparison (Table 1).

Data collection

At each site, all prey captured was qualitatively studied and quantified on at least three randomly selected plants of each species by taking photographs of all captured prey from multiple angles. All active, mucilage-secreting leaves of each plant were systematically photographed from multiple angles in order to maximize the amount of discernible morphological features for each prey item. Inactive older leaves (i.e., those that had ceased production of mucilage) were excluded from analysis, as prey items on such leaves were excessively digested or degraded and impossible to assign to prey groups by morphology, even in high-resolution images. As number of leaves varied strongly among both individuals and species, prey count values were analyzed on a per-leaf basis rather than per-individual. All prey items were photographed using high-resolution macro images, regardless of size or state (e.g., even heavily digested and unidentifiable crumbs were included). Photographs were captured using a Nikon D5100 DSLR (Nikon, Tokyo, Japan) and Panasonic Lumix G81 (Panasonic, Osaka, Japan), both with standard lenses and Raynox DCR-150 or DCR-250 macro adapters (Raynox,

Table 1. Summary of the eleven study sites in northern Australia and Madagascar where the prey spectra of species from *D.* sect. *Arachnopus* were studied.

Site	Location	Study date	No. prey pictures	Species studied	No. studied plants	No. studied leaves
Site 1	Acacia Hills, Darwin, Northern Territory	21 April 2017	2873	*D. aquatica*	5	57
				D. serpens	5	6
Site 2	Argyle Road, Kununurra, Western Australia	06 April 2017	1703	*D. aquatica*	3	26
				D. hartmeyerorum	3	20
				D. serpens	3	13
Site 3	Katherine, Northern Territory	11 April 2017	1966	*D. aquatica*	3	12
				D. cucullata	6	21
				D. serpens	4	16
Site 4	Mount Bundey, Northern Territory	29 March 2017	674	*D. aquatica*	3	20
				D. fragrans	3	10
Site 5	Rum Jungle, Northern Territory	15 April 2017	891	*D. aquatica*	3	25
				D. serpens	3	17
Site 6	Theda Station, Western Australia	19 April 2019	3328	*D. barrettiorum*	3	30
				D. cucullata	3	11
Site 7	Girraween Road, Darwin, Northern Territory	18 April 2017	596	*D. fragrans*	3	13
				D. nana	4	24
Site 8	Jenkins Road, Darwin, Northern Territory	17 April 2017	1750	*D. fragrans*	6	45
				D. nana	3	21
Site 9	Acacia Hills, Darwin, Northern Territory	21 April 2017	1221	*D. fragrans*	5	24
Site 10	Ihosy, Madagascar	14 March 2017	198	*D. indica*	3	14
Site 11	Katherine, Northern Territory	11 April 2017	493	*D. fragrans*	3	13

Tokyo, Japan). All high-resolution macro pictures were taken in situ on plants in vivo. The number of leaves studied, number of prey items per leaf, and the file names of the relevant photographs were recorded for each location and for each species. Total sample size (number of studied leaves) was $n = 458$, and a total of 15,693 prey photographs were analyzed.

This study is the first to employ a photographic methodology for prey spectra analysis in CPs. Previous studies examining prey spectra in species with adhesive traps (e.g., *Drosera*, *Drosophyllum* L., and *Pinguicula* L.) placed the leaves in vials or removed prey items from the leaves using forceps and preserved them in alcohol for subsequent morphological analysis using a binocular microscope (Zamora 1990, Verbeek and Boasson 1993, Bertol et al. 2015). This technique is time-consuming and destructive to in vivo plants and may alter prey composition by disregarding cumulative effects of prey attraction (Fleischmann 2016). In contrast, photographic analysis is similarly accurate, is nondestructive, and allows for the direct in situ collection of data using minimal equipment and time. These outcomes are highly desirable when conducting field research in remote areas where access can be extremely challenging, such as the Top End and North Kimberley (Buters et al. 2019). However, due to the remoteness of these study sites, no multiday observations were made, and the analyzed prey spectra can thus only be regarded as a snapshot of the potential prey spectra.

Data analysis

Where possible, all prey items were identified by the authors to the lowest possible taxonomic rank and at least to arthropod order, on the basis of morphological features. Data were then compiled into a per-leaf prey composition matrix, with leaf variables including species, location, leaf length, and leaf age, and prey variables including the total number of captured prey items as well as the number of captured prey items identified to each prey group (Appendix S3). Leaf length was derived from the literature (mean values from Lowrie 2014, Robinson et al. 2017) except for *D. cucullata* at Site 3 (where unusually large

plants were encountered, producing leaves 10–15 cm in length as opposed to the 5–9 cm values presented by Lowrie 2014) and for *D. indica* at Site 10 which consisted of small plants unanimously at the lower end of the 1–10 cm range Robinson et al. (2017) provide for the leaf length of this species. Leaves were counted starting with the youngest fully developed leaf, and these numbers thus represented an approximation for leaf age in this study.

To compare the total number of captured prey items per leaf among sympatric species at each study site, Kruskal–Wallis tests with Dunn–Bonferroni post hoc pairwise comparisons were employed in SPSS (SPSS Statistics 23; IBM, Armonk, New York, USA). Compositional differences among prey spectra of sympatric species were analyzed for each study site using analysis of similarity (ANOSIM) in PRIMER 7 (Clarke and Gorley 2015), following the methods of Cross et al. (2016). Leaf replicates without captured prey and prey groups with no observed items were omitted, and Bray–Curtis resemblance matrices based on $\log_{(X+1)}$-transformed prey count data were created before conducting ANOSIM. Prey spectra dissimilarity was quantified using the ANOSIM R statistic, ranging from 0 (no dissimilarity) to 1 (maximum dissimilarity; Clarke and Gorley 2015). Individual prey groups contributing most to prey spectra dissimilarity were assessed using similarity percentages (SIMPER) in PRIMER 7 (Clarke and Gorley 2015). Prey groups contributing more than 15% to prey spectra dissimilarity were further compared among sympatric *Drosera* species using Kruskal–Wallis tests with Dunn–Bonferroni post hoc pairwise comparisons in SPSS. Kruskal–Wallis tests and ANOSIM were also conducted to compare prey spectra of each species among different sites.

Multiple linear regression models using backward stepwise variable selection were constructed in SPSS to determine the influence of independent variables (species, location, leaf length, and leaf age) on the abundance of total prey items per leaf and total prey items per centimeter of leaf length, as well as their influence on the frequencies of the most common prey groups (those contributing ≥5% of the identifiable prey). Additional linear regression models were created to assess the relationship between abiotic factors (annual mean temperature and annual precipitation, data provided by WorldClim 2; Fick and Hijmans 2017) on prey abundances. Each predictor was assessed for collinearity, with variables featuring a variance inflation factor (VIF) >10 removed. These regression models allow for the identification of all independent variables significantly predicting total prey capture and capture of individual prey groups.

Niche segregation among sympatric *Drosera* species (in terms of prey spectra) was quantified with a null model analysis using Pianka's (1973) index of overlap in resource use. During this analysis, the observed overlap in prey spectra was compared to an artificially created expected overlap (which is based on the null hypothesis that random interactions, and not competition, would be the cause of any observed prey spectra overlap; Ellison and Gotelli 2009). Null model analysis was conducted in EcoSimR (V 1.00; Gotelli and Ellison 2013) using the RA-3 algorithm which is frequently used in the literature due to its good statistical properties (Ellison and Gotelli 2009).

Results

Captured prey in D. *sect.* Arachnopus

In total, 7063 prey items were counted from the 458 leaves examined in this study, of which 1407 (20%) were identifiable (Table 2). The remaining 80% of prey items were heavily digested, degraded, or otherwise unidentifiable and thus could not be assigned to specific prey groups. Unidentifiable prey items were excluded from further analysis of prey spectra compositions.

The identifiable prey spectra of *D*. sect. *Arachnopus* represented taxa from 10 arthropod orders, predominantly comprising flying insects (Fig. 1). Three prey orders (Diptera, Hemiptera, and Hymenoptera) could be further divided into different subordinal ranks based on clearly identifiable morphological features of the captured prey. The six largest prey groups, each comprising at least five percent of the total identifiable prey, were Small Nematocera (Fig. 1E; 34%), Brachycera (Fig. 1C; 15%), Winged Hymenoptera (Fig. 1J; 15%), Cicadoidea (Fig. 1F; 14%), Thysanoptera (Fig. 1O; 6%), and Coleoptera (Fig. 1B; 5%; Table 2).

Small Nematocera were the most common prey group in all eight studied *Drosera* species,

Table 2. Arthropods captured by the eight studied *Drosera* species.

Prey group	All species	*D. a.*	*D. b.*	*D. c.*	*D. f.*	*D. h.*	*D. n.*	*D. s.*	*D. i.*†
Araneae	5 (0.4)	0 (0.0)	1 (1.7)	1 (0.5)	2 (0.4)	0 (0.0)	0 (0.0)	1 (0.3)	0 (0.0)
Coleoptera	74 (5.3)	8 (3.4)	11 (18.3)	11 (5.4)	31 (6.5)	0 (0.0)	0 (0.0)	13 (3.5)	0 (0.0)
Diptera									
Brachycera	206 (14.6)	32 (16.3)	8 (13.3)	31 (15.2)	69 (14.4)	5 (15.2)	1 (14.3)	56 (15.2)	4 (19.1)
Large Nematocera	35 (2.5)	9 (3.8)	3 (5.0)	5 (2.5)	7 (1.5)	0 (0.0)	0 (0.0)	11 (3.0)	0 (0.0)
Small Nematocera	483 34.3)	106 (45.1)	15 (25.0)	60 (29.4)	133 (27.8)	22 (66.7)	4 (57.1)	128 (34.8)	15 (71.4)
Hemiptera									
Cicadoidea	200 14.2)	43 (18.3)	8 (13.3)	50 (24.5)	49 (10.2)	5 (15.2)	0 (0.0)	43 (11.7)	2 (9.5)
Setocoris	9 (0.6)	1 (0.4)	0 (0.0)	0 (0.0)	5 (1.0)	0 (0.0)	0 (0.0)	3 (0.8)	0 (0.0)
Other	31 (2.2)	6 (2.6)	0 (0.0)	4 (2.0)	14 (2.9)	0 (0.0)	0 (0.0)	7 (1.9)	0 (0.0)
Hymenoptera									
Formicidae	4 (0.3)	1 (0.4)	1 (1.7)	1 (0.5)	1 (0.2)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Winged Hymenoptera	204 (14.5)	10 (4.3)	5 (8.3)	20 (9.8)	105 (21.9)	1 (3.0)	1 (14.3)	62 (16.9)	0 (0.0)
Lepidoptera	52 (3.7)	2 (0.9)	0 (0.0)	18 (8.8)	16 (3.3)	0 (0.0)	0 (0.0)	16 (4.4)	0 (0.0)
Odonata	3 (0.2)	1 (0.4)	0 (0.0)	0 (0.0)	1 (0.2)	0 (0.0)	0 (0.0)	1 (0.3)	0 (0.0)
Orthoptera	11 (0.8)	1 (0.4)	2 (3.3)	3 (1.5)	3 (0.6)	0 (0.0)	0 (0.0)	2 (0.5)	0 (0.0)
Psocoptera	2 (0.1)	0 (0.0)	2 (3.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Thysanoptera	88 (6.3)	15 (6.4)	4 (6.7)	0 (0.0)	43 (9.0)	0 (0.0)	1 (14.3)	25 (6.8)	0 (0.0)
Total identifiable	1407 (19.9)	235 (27.2)	60 (12.3)	204 (21.4)	479 (16.7)	33 (21.7)	7 (30.4)	368 (22.1)	21 (47.7)
Total prey items	7063	865	486	954	2873	152	23	1666	44
Sample size (leaves, *n*)	458	140	30	32	105	20	45	72	14

Notes: D. a., D. aquatica; *D. b., D. barrettiorum*; *D. c., D. cucullata*; *D. f., D. fragrans*; *D. h., D. hartmeyerorum; D. n., D. nana*; *D. s., D. serpens*; *D. i., D. indica*. Absolute numbers of prey observed for each species are given, with percentages of each prey group on the total amount of identifiable prey in parentheses.

† The non-Australian *Drosera indica* is additionally listed here for comparison as it was studied in Madagascar where it is exposed to potentially different available prey spectra.

comprising between 25% (*D. barrettiorum*) and 71% (*D. indica*) of all identifiable prey, and Brachycera and Cicadoidea were also relatively ubiquitous prey (Table 2). The physically largest observed prey items (those belonging to Coleoptera, Large Nematocera, Lepidoptera, Odonata, and Orthoptera) were generally absent in *D. hartmeyerorum* and *D. nana*. The contribution of other prey groups to total prey capture varied considerably among *Drosera* species (Table 2).

Prey spectra comparison of sympatric species in D. *sect.* Arachnopus

Significant differences in the prey spectra of sympatric *Drosera* species were found at most study sites, in terms of both the total quantity and composition of prey captured. The total number of captured prey per leaf differed significantly among species at seven of the eight study sites where the studied *Drosera* occurred sympatrically (Fig. 2), with only the number of prey captured by *D. barrettiorum* and *D. cucullata* at Site 6 exhibiting no statistically significant difference (Mann–Whitney U test, $U = 110.50$, $P = 0.110$). However, only one of the three pairwise comparisons at Site 2 (*D. hartmeyerorum–D. serpens*) and two of the three pairwise comparisons at Site 3 (*D. aquatica–D. cucullata* and *D. aquatica–D. serpens*) were significantly different (Fig. 2).

Analysis of similarity indicated significant compositional dissimilarity in the prey spectra among sympatric species at all study sites except for Site 2 (which, however, still contained the significant species pair *D. hartmeyerorum–D. serpens*; Fig. 3). At Site 3, only the species pair *D. aquatica–D. serpens* exhibited no significantly different prey spectra composition (Fig. 3).

SIMPER analysis indicated the common prey group Small Nematocera to be the strongest contributor to prey spectra dissimilarity in all but one of the pairwise comparisons (Fig. 3). The contribution of Small Nematocera ranged from 19% (between *D. barrettiorum* and *D. cucullata* at Site 6) to 42% (between *D. aquatica* and *D. hartmeyerorum* at Site 2; Fig. 3). Brachycera contributed

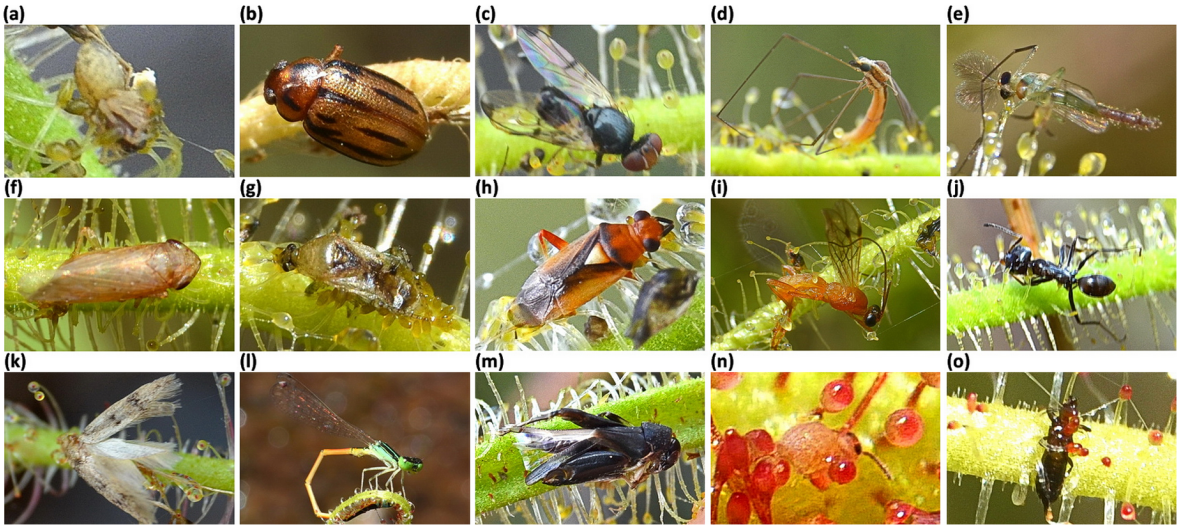

Fig. 1. Examples of photograph-documented arthropod prey captured by the eight studied species of *D.* sect. *Arachnopus*. (a) Araneae; (b) Coleoptera; (c) Diptera: Brachycera; (d) Diptera: Large Nematocera; (e) Diptera: Small Nematocera; (f) Hemiptera: Cicadoidea; (g) Hemiptera: *Setocoris*; (h) Other Hemiptera; (i) Winged Hymenoptera; (j) Hymenoptera: Formicidae; (k) Lepidoptera; (l) Odonata; (m) Orthoptera; (n) Psocoptera; (o) Thysanoptera. All photographs by T. Krueger.

greater than 15% to prey spectra dissimilarity for eight of the 12 pairwise comparisons, and Cicadoidea contributed greater than 15% for six pairwise comparisons (Fig. 3). Winged Hymenoptera was the strongest contributor to prey spectra dissimilarity between *D. aquatica* and *D. fragrans* at Site 4 (37%; Fig. 3), being captured in significantly greater numbers by *D. fragrans* (Mann–Whitney *U* test, $U = 153.00$, $P < 0.001$), representing the most striking example of two sympatric species having captured significantly different quantities of one prey taxon.

The effect of location on prey spectrum

Among the five species that could be studied at multiple locations (Table 1), significant among-location differences in the total amount of captured prey per leaf were found for *D. aquatica* (five sites compared; Kruskal–Wallis test, $H_4 = 43.12$, $P < 0.001$), *D. cucullata* (two sites; Mann–Whitney *U* test, $U = 5.50$, $P < 0.001$), and *D. serpens* (four sites; Kruskal–Wallis test, $H_3 = 12.14$, $P = 0.007$). However, prey amount did not differ significantly among locations for *D. fragrans* (five sites studied; Kruskal–Wallis test, $H_4 = 7.85$, $P = 0.097$) or *D. nana* (two sites; Mann–Whitney *U* test, $U = 178.50$, $P = 0.055$). Dunn–Bonferroni post hoc pairwise comparisons indicated that two of the six location pairs for *D. serpens* and six of the 10 location pairs for *D. aquatica* differed significantly in the amount of captured prey per leaf (Appendix S2).

Significant differences in prey composition among locations were found for four of the five species studied at multiple sites (Table 3). It was not possible to perform ANOSIM for *D. nana* due to the very low number of identifiable prey items at both studied sites of this species.

Predictors of prey spectra in D. *sect.* Arachnopus

Total prey per leaf was best predicted by a regression model incorporating leaf length (beta = 0.722, $P < 0.001$) and leaf age (beta = 0.226, $P < 0.001$; Table 4). The variable species was excluded by the backward selection approach, while location was a nonsignificant predictor (Table 4). Similarly, total prey per centimeter of leaf length was significantly predicted by leaf length, leaf age, and species with location as nonsignificant predictor (Table 4).

Leaf length significantly predicted the abundance of each of the six most common prey groups (contributing ≥5% of the identifiable prey), with beta values ranging from 0.227

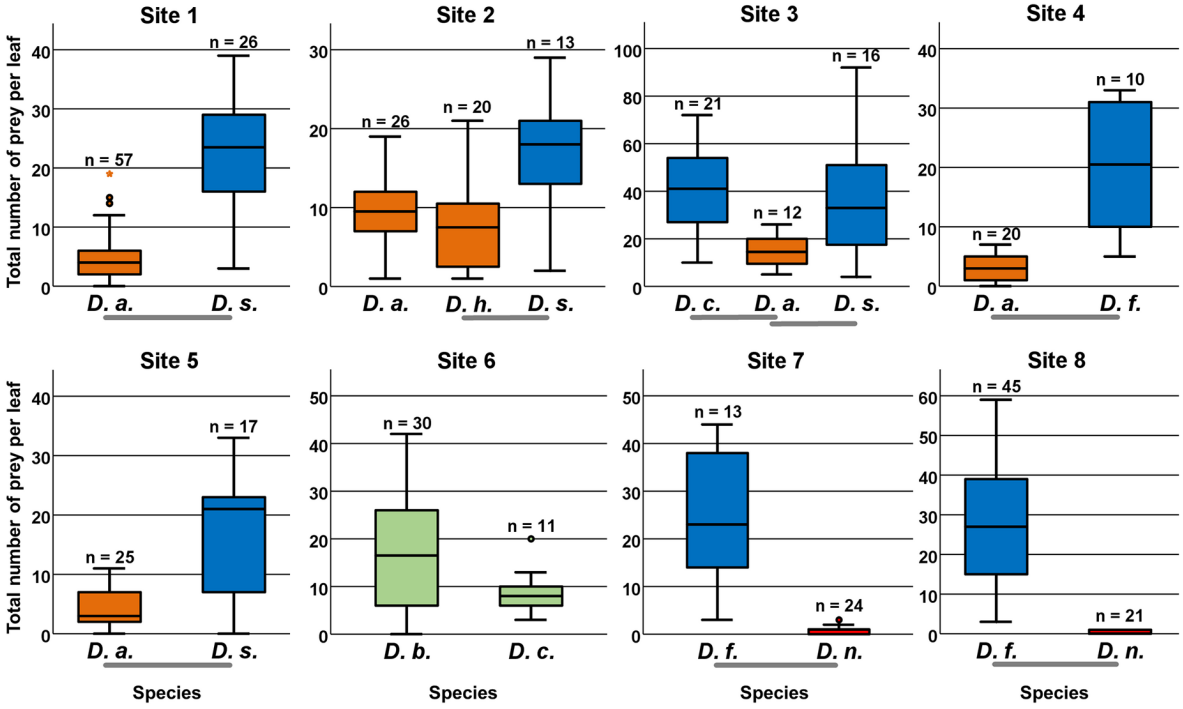

Fig. 2. Comparison of prey quantity (number of captured prey per leaf) among sympatric species of *Drosera* at eight sites in northern Australia. Colors indicate category of leaf size: red = 1.5–2.0 cm, orange = 4–6 cm, green = 5–9 cm, and blue = 10–20 cm. Gray horizontal bars indicate statistically significant differences in prey amount in pairwise comparisons. Abbreviations are *D. a.*, *D. aquatica*; *D. b.*, *D. barrettiorum*; *D. c.*, *D. cucullata*; *D. f.*, *D. fragrans*; *D. h.*, *D. hartmeyerorum; D. n.*, *D. nana*; and *D. s.*, *D. serpens*.

(Thysanoptera) to 0.423 (Winged Hymenoptera; Table 4). Location was a significant predictor for Brachycera, Small Nematocera, Coleoptera, and Thysanoptera, while leaf age significantly predicted the abundance of Cicadoidea and Coleoptera. None of the six most common prey groups were significantly predicted by species.

Annual precipitation predicted the abundance of total prey, Small Nematocera, Cicadoidea, Coleoptera, and Winged Hymenoptera, with beta values ranging from −0.156 to 0.101 (Appendix S4). The second evaluated bioclimatic variable annual mean temperature did only predict the abundance of total prey (beta: 0.117; Appendix S4).

Niche segregation in D. *sect.* Arachnopus

No evidence could be found for niche segregation regarding prey capture among sympatric species from *D.* sect. *Arachnopus* at any of the study sites. At four of the six locations, significantly greater prey overlap among species was observed than could be expected by random capture (Table 5). Greatest overlap was found at the two sites with three sympatric *Drosera* species (Sites 2 and 3), while the lowest overlap was found between *D. aquatica* and *D. fragrans* at Site 4 (Table 5).

Discussion

Captured prey in D. *sect.* Arachnopus

The prey spectrum from *D.* sect. *Arachnopus* consisted almost exclusively of flying insects (>99% of all identifiable captured prey), with the only ground-inhabiting prey groups being Araneae (spiders, 0.36%) and Formicidae (ants, 0.28%; Table 2). This observed dominance of flying insects in the prey spectrum is in line with previous studies investigating the prey spectra of

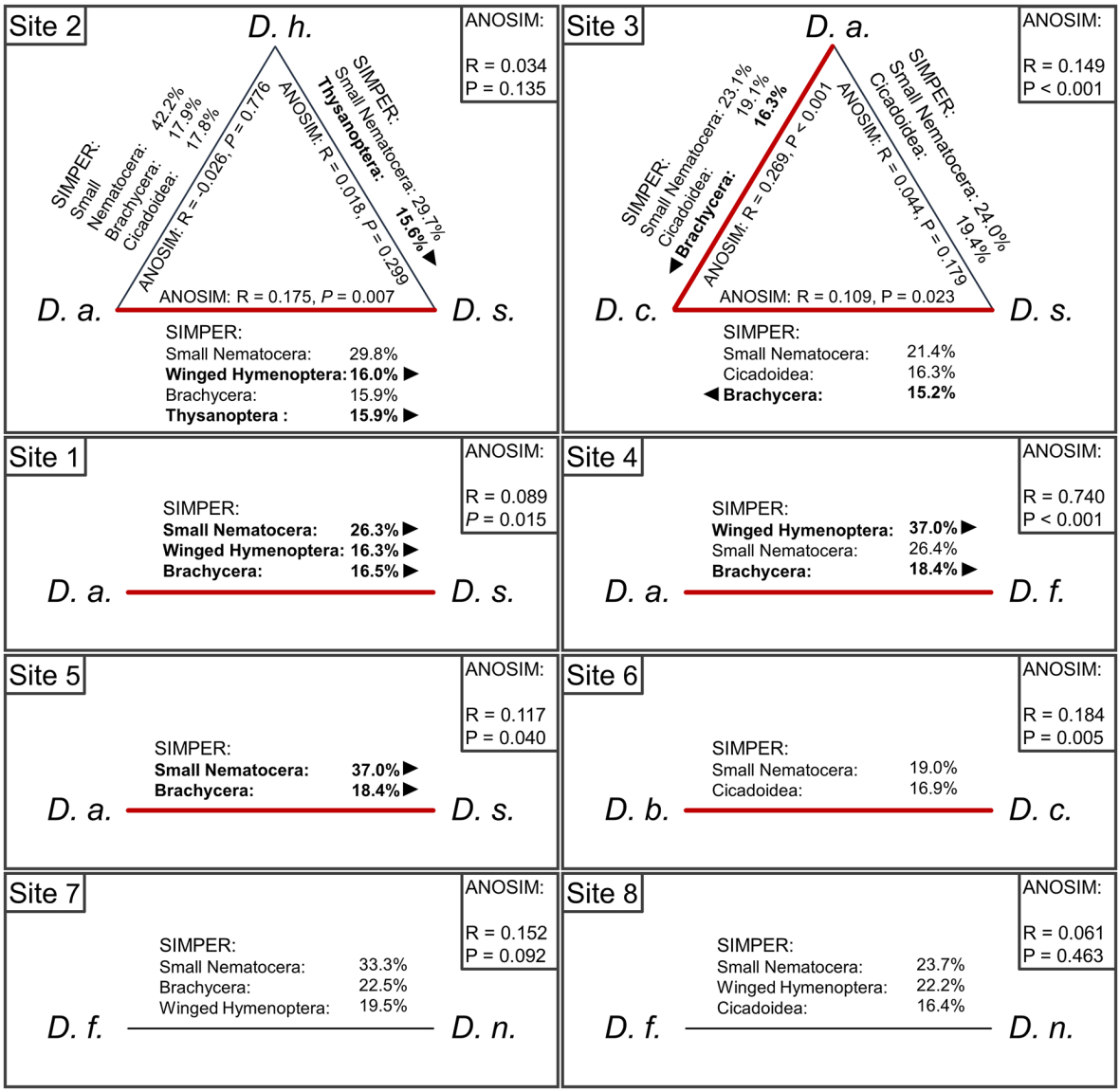

Fig. 3. Differences in prey spectra composition among sympatric species of *Drosera* at eight sites in northern Australia, with prey groups contributing more than 15 to dissimilarity listed. Red lines indicate statistically significant differences between prey spectra of *Drosera* species. Boldened prey groups are those that contributed statistically significantly to dissimilarity, with black triangles indicating the *Drosera* species having captured more of each significant prey group. Abbreviations are *D. a.*, *D. aquatica*; *D. b.*, *D. barrettiorum*; *D. c.*, *D. cucullata*; *D. f.*, *D. fragrans*; *D. h.*, *D. hartmeyerorum*; *D. n.*, *D. nana*; and *D. s.*, *D. serpens*.

Drosera species producing erect leaves (Achterberg 1973, Thum 1986, Verbeek and Boasson 1993, Costa et al. 2014). Furthermore, Diptera (especially Small Nematocera) comprised the highest percentage of identifiable captured prey in all eight studied *Drosera* species (Table 2), again similar to the results of these previous studies. However, the percentage of Cicadoidea (cicadas, 14%) in the prey spectrum from *D.* sect. *Arachnopus* was much higher than that

Table 3. ANOSIM values for among-location differences in prey composition of four *Drosera* species in northern Australia.

Species	Location	ANOSIM *R* statistic	*P*
D. aquatica	1-2-3-4-5	0.077	0.023
D. cucullata	3-6	0.555	<0.001
D. fragrans	4-7-8-9-11	0.070	0.027
D. serpens	1-2-3-5	0.146	<0.001

Note: *Drosera nana* is not listed due to insufficient numbers of identifiable prey items.

in above-mentioned studies on other *Drosera* species (Table 2). This may be explained by the comparative ubiquity and abundance of this prey group throughout tropical northern Australia, similar to other tropical regions, where the greatest diversity of Cicadoidea is found (Moulds 1990). Unexpectedly, single dead individuals of *Setocoris* (Hemiptera: Miridae) were occasionally found adhering to the leaves of *Drosera*, their host plants (Lowrie et al. 2017). However, the circumstances under which these mutualistic arthropods were captured remain unclear, whether they were trapped as regular prey and whether it was aged, dying individuals, or leftovers of intra- or interspecific fights.

Although no direct measurements of prey size were taken in this study, the physically largest prey items generally belonged to prey groups Coleoptera, Large Nematocera, Lepidoptera, Odonata, and Orthoptera (Fig. 1). These largest prey groups were conspicuously absent from the two smallest species, *D. hartmeyerorum* and *D. nana* (and from the Madagascan population of *D. indica*), potentially due to large prey being able to escape from the smaller traps of these species (a process described as "differential escape"; Gibson 1991). A similarly increased likelihood of larger prey escaping *Drosera* traps, often facilitated by limb autotomy, was observed by Cross and Bateman (2018).

A large number (80%; Table 2) of prey items could not be identified by photographic methods. Due to their heavily digested state, many prey items lacked the morphological features required to assign them to specific prey groups. However, detailed examination suggested that most nonidentifiable prey likely belonged to prey group Small Nematocera, and these represented the most common prey group in *D.* sect. *Arachnopus* (34%; Table 2). These soft-bodied insects are quickly digested by *Drosera*

Table 4. Predictors of prey spectrum in *D.* sect. *Arachnopus:* summary of the best regression model statistics and significant environmental predictors for total captured prey, total prey per centimeter of leaf length, and the most common prey groups (those comprising ≥5% of the identifiable prey).

Prey group	Total abundance	*n* (leaves)	Regression model summary			Significant predictors	Beta	*P*
			R^2	*F*	*P*			
Total prey	7063	458	0.498	150.262	<0.001	Leaf length	0.725	<0.001
						Leaf age	0.227	<0.001
Total prey per cm of leaf length	7063	458	0.315	69.464	<0.001	Leaf length	0.518	<0.001
						Leaf age	0.378	<0.001
						Species	−0.125	0.004
Brachycera	205	458	0.160	43.347	<0.001	Leaf length	0.379	<0.001
						Location	−0.135	0.001
Small Nematocera	483	458	0.142	37.522	<0.001	Leaf length	0.350	<0.001
						Location	−0.144	0.001
Cicadoidea	200	458	0.098	24.644	<0.001	Leaf length	0.310	<0.001
						Leaf age	0.165	<0.001
Coleoptera	74	458	0.082	13.570	<0.001	Leaf length	0.260	<0.001
						Leaf age	0.140	0.003
						Location	0.116	0.010
Winged Hymenoptera	204	458	0.179	99.517	<0.001	Leaf length	0.423	<0.001
Thysanoptera	88	458	0.073	17.981	<0.001	Leaf length	0.227	<0.001
						Location	−0.152	0.001

Table 5. Niche segregation in *D.* sect. *Arachnopus*: null model analysis of niche overlap in prey utilization of sympatric species from the *D. indica* complex at six different locations in northern Australia.

Site	Species	Niche overlap		*P*
		Observed	Expected	
Site 1	2	0.847	0.390	
Site 2	3	0.937	0.302	0.999
Site 3	3	0.933	0.379	0.999
Site 4	2	0.422	0.137	0.893
Site 5	2	0.880	0.545	0.992
Site 6	2	0.676	0.500	0.854

Notes: The observed and expected average pairwise niche overlap values and the *P* values are given. Sites 7 and 8 are not listed due to insufficient numbers of identifiable prey items for *D. nana*.

mucilage (see also Costa et al. 2014), and most of the Small Nematocera that could be identified in this study had clearly been freshly captured (indeed, some were still alive at the time of examination). Given that Small Nematocera were the most abundant prey group and the strongest contributor to dissimilarity among most sympatric species (Fig. 3), classification of unidentifiable prey items may further strengthen our findings. Even though the collection of prey items for laboratory analysis (e.g., by DNA metabarcoding; Morinière et al. 2016) may have enabled a more precise identification of some prey items, the large number of samples and remoteness of our study site made such an approach logistically challenging, and DNA barcoding methods may not yet possess the DNA libraries required to reliably compare prey quantities (A. Hausmann, *personal communication*). However, we believe that photographic observation and DNA barcoding could be used in conjunction to accurately analyze both quantitative and qualitative aspects of CP prey spectra.

Prey spectra comparison of sympatric species in D. *sect.* Arachnopus

Our data supported the hypothesis that sympatric *Drosera* would exhibit among-species differences in number and composition of captured prey. However, it was notable that most differences occurred between medium-sized *Drosera* (4–6 cm leaf length), such as *D. aquatica* and *D. hartmeyerorum*, and larger species (10–20 cm leaf length) including *D. cucullata* and *D. serpens* (Fig. 2; Lowrie 2014). In terms of total captured prey per leaf, the strongest differences among sympatric species were found between the large *D. fragrans* (10–15 cm leaf length) and the very small *D. nana* (1.5–2.0 cm leaf length), further highlighting this obvious and apparent importance of leaf size in prey capture (Fig. 2; Lowrie 2014).

While ANOSIM found significant differences in the prey spectra of sympatric species at most study sites, the fact that Small Nematocera (the overall most common prey group; Table 2) contributed most to prey spectra dissimilarity in all but one pairwise comparison suggests that the studied *Drosera* species exhibit little specialization on captured prey (Fig. 3). The only exception was Site 4, where Winged Hymenoptera were captured significantly more frequently by *D. fragrans* compared to the sympatric *D. aquatica* (Fig. 3). Winged Hymenoptera were also found to contribute more than 15% to prey spectra dissimilarity at Sites 7 and 8, where *D. fragrans* and *D. nana* occurred sympatrically (Fig. 3). Most Hymenoptera are nectar feeders frequently guided by nectar/flower scent clues—not only pollinators but also herbivores and parasites (Dudareva and Pichersky 2006; Kehl et al. 2010). Therefore, it can be hypothesized that the scented leaves of *D. fragrans* might play a role in the larger amount of captured Winged Hymenoptera observed for this species. To further investigate the potential role of leaf scent in prey capture by *Drosera*, future studies should focus on comparing the prey spectra of *D. fragrans* at multiple study sites with similar-sized sympatric species producing non-scented leaves.

Additional research is required to determine potential functions of the eglandular emergences found in *D.* sect. *Arachnopus*. Differences in prey spectra composition between *D. hartmeyerorum* (a species with very characteristic yellow, blackberry-shaped eglandular emergences) and *D. serpens* (a species lacking these emergences) at Site 2 (Figs. 2, 3) likely resulted from size differences among these two species (i.e., *D. serpens* producing much larger leaves). In addition, no significant differences were found between the similar leaf-sized *D. aquatica* and *D. hartmeyerorum* or between *D. barrettiorum* (which also produces large yellow eglandular appendages; Lowrie 2014) and *D. cucullata* (Figs. 2, 3). We therefore

found no evidence supporting a direct role for the yellow eglandular appendages of *D. barrettiorum* and *D. hartmeyerorum* in prey attraction. Similarly, our data did not support the hypothesis of Hartmeyer and Hartmeyer (2006) that these eglandular appendages on *D. hartmeyerorum* attracted grasshoppers, as no Orthoptera were observed on any studied *D. hartmeyerorum* leaves (Table 2). Future research on the eglandular appendages in *D*. sect. *Arachnopus* should consider a wider range of possible functions, including prey attraction and herbivore defense (i.e., insect egg mimicry).

The effect of location on prey spectrum

Location significantly affected prey spectra in studied *Drosera*, likely due to differential prey abundance and composition among different habitats. The fact that no significant differences in total prey capture were observed between the two sites of *D. nana* (Appendix S2) can be attributed to the generally extremely small number of captured prey from this species (which also precluded ANOSIM). The regression model (Table 4) further supported our observation that location has a significant effect on prey spectra composition (four of the six most common prey groups were significantly predicted by location; Table 4). However, the effect of location clearly appears to be smaller than the effect of leaf size on prey spectra (lower beta values in Table 4). Our regression analysis of bioclimatic variables did not find a strong relationship between annual precipitation or annual mean temperature and prey abundances as *R* square and beta values were generally small (Appendix S4). Insect abundance in the habitat depends on many more factors such as microhabitats and landscape relief, but also biotic factors such as the presence or absence of food or host plants, predator density, and especially interspecific population dynamics.

Predictors of prey spectra in D. *sect.* Arachnopus

Regression analysis indicated that species was not a significant predictor of any prey variables, further supporting the null hypothesis that studied species from *D*. sect. *Arachnopus* did not selectively attract prey (with the possible exception of *D. fragrans* for Winged Hymenoptera as mentioned previously). A similar lack of selective prey attraction has been observed for *Drosera brevifolia* (*D*. sect. *Drosera* L.) by Potts and Krupa (2016). Our results suggest that carnivory may not have been a primary driver of diversification in *D*. sect. *Arachnopus* and is unlikely to have played an overt role in speciation within this section. For example, *D. nana* is common and relatively widespread throughout northern Australia, despite its small leaf size and comparatively low prey capture rate. This follows a general pattern observed when reconstructing the evolution of CP lineages, where the evolution of the carnivorous syndrome itself does not explain extant species richness in most species-rich lineages (e.g., *Nepenthes*, *Drosera*, and *Utricularia* L.); hence, carnivory was not a driver but prerequisite for subsequent geographic, geological, or sympatric radiation in suitable habitats (Fleischmann et al. 2018).

Our regression models further indicated that leaf length most strongly predicted prey spectra in *D*. sect. *Arachnopus*. Plants producing larger leaves generally captured more total prey per leaf, as well as more of each of the six most common prey groups (Table 4). However, leaf length was also the strongest predictor of total prey per cm of leaf length, indicating that larger *Drosera* species captured disproportionally greater amounts of prey compared with smaller species. Indeed, the smallest species, *D. nana*, captured an average of only ~0.5 prey items per leaf, markedly lower even than the closely related yet twofold larger *D. aquatica* which captured an average of ~6.2 prey items per leaf (Appendix S1). One possible contributor to the very low numbers of captured prey observed on *D. nana* may be its very short stem, resulting in its leaves being held much closer to the ground than in other species and therefore attracting fewer flying prey (comparable to how taller flower stalks frequently attract more pollinators; Anderson 2010).

Older leaves generally harbored greater numbers of total prey items (as indicated by leaf age being a significant predictor for total prey and total prey per cm of leaf length; Table 4) probably due to the longer period of time these traps had been active. Of the six most common prey groups, however, only Cicadoidea and Coleoptera were significantly predicted by leaf age (Table 4). This likely represents a sampling

artifact, as beetles and cicadas have hard-bodied carapaces that degrade slowly or are not degraded by *Drosera* mucilage and likely remain visible and identifiable until the leaves senesce (A. Fleischmann, *personal observation*).

Niche segregation in prey spectra in D. *sect.* Arachnopus

Prey niche segregation was not observed at any of the study sites, which is in line with previous studies analyzing niche segregation among the prey spectra of sympatric *Drosera* (Ellison and Gotelli 2009, Volkova et al. 2010). Although this result would further support our null hypothesis of no (or very limited) prey specialization in *D*. sect. *Arachnopus*, it is important to note that general prey availability in the habitat was not recorded (it also could not be estimated based on known arthropod numbers for the range, as these are unknown or poorly studied for northern Australia for most taxa) and that taxonomic identification to family rank or below was not possible for most prey groups. These two methodological limitations have been identified by Ellison and Gotelli (2009) as possible reasons for the apparent absence of niche segregation in previous studies on the prey spectra of sympatric *Drosera*. However, although no niche segregation was detected in the present study, ANOSIM showed significant compositional differences in the prey spectra between sympatric species at five of the six study sites (Fig. 3), possibly indicating that the null model analysis used to detect niche segregation may be overly conservative. Future research should include a detailed study of prey availability in the habitat, finer scale taxonomic identification of prey, which, however, may be very difficult to impossible by name-based morphology alone. This task might be solved when relying on DNA barcoding of captured prey by next-generation sequencing, comparable to prey analysis of long-time insect survey traps (Morinière et al. 2016). Although most prey might not be able to be identified to any species name by this method (due to a lack of reference DNA barcode libraries for most northern Australian insects), differences in prey composition could nevertheless be readily detected with this method by simply comparing different operational taxonomic units (OTUs). Thus, this method may help to discover possible prey niche segregation among sympatric *Drosera* species.

Conclusion

Our data contribute to the understanding of prey spectra, prey attraction, and prey specialization in CPs. Although the composition of prey spectra in the eight studied *Drosera* species was generally consistent with previous studies on species from this genus producing erect leaves (i.e., flying insects, primarily Nematocera), significant differences not only in prey composition but also in total prey capture were found among sympatric species. These differences, however, were mostly confined to species producing different sized trapping leaves, indicating a strong effect of trap area (leaf size) on prey spectra. A particularly notable result was a significantly increased capture of Winged Hymenoptera by the scented *D. fragrans* compared with the sympatric but non-scented *D. aquatica*. Future studies should thoroughly investigate this relationship by comparing scented species like *D. fragrans* with sympatric, similar-sized, and non-scented species across multiple locations. Niche segregation as a result of competition for prey was not observed between any of the sympatric species. As leaf length was a significant predictor for the number of prey items per cm of leaf length, and some of the smaller, but widely distributed species (particularly *D. nana*) captured disproportionally few prey items, we hypothesize that carnivory may not have been a primary driver in the speciation of *D*. sect. *Arachnopus*.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3179/full