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Investment in visual system predicted by floral associations in sap beetles (Coleoptera: Nitidulidae)

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Abstract

Patterns in morphological variation are a central theme of evolution. Uncovering links between morphological character evolution and natural history, specifically feeding behaviour, is important to understanding biological diversity. Species within the sap beetles (Nitidulidae) exhibit a tremendous diversity of feeding behaviours. This immense diversity of feeding can be seen both between major lineages and very closely related taxa. Feeding behaviour diversity may drive morphological variation in several character systems (e.g., eyes). For example, in a shift from feeding on rotting fruit to flower-visiting (anthophily), selective pressures on the visual system may vary and ultimately lead to differences in eye morphology. We tested for potential morphological shifts in relative eye size among adult beetles. We specifically tested for significant relationships between relative eye size and the following factors flower-visiting and sex. We also tested for the influence of phylogeny on the evolution of relative eye size, implementing tests of trait correlation across a topology. We found greater relative eye size in taxa exhibiting anthophilous behaviour, regardless of phylogenetic relatedness or feeding behaviour of sister taxa. We were unable to recover a relationship between relative eye size and sex. Thus, feeding behaviour is currently the strongest predictor of eye size in sap beetles.

KEYWORDS
anthophily, character evolution, Coleoptera, feeding shifts, foraging ecology

INTRODUCTION

Behaviour driving morphological adaptations is a central focus of evolutionary research (Mayr, 1959; Plotkin, 1988). Morphological shifts in response to behaviour have been demonstrated in multiple systems (Dayan & Simberloff, 2005; Sih et al., 2004). Some classical examples of behaviour shaping morphology include beak shape and size of Darwin finches shifting according to seed feeding (Grant & Grant, 2002), jaw morphology in Malawi fishes associated with a variety of feeding behaviours (Fryer & Iles, 1972) and increased size and structural variation of male scarab beetle horns driven by male–male competition (McCullough et al., 2014). More recent investigations continue to yield compelling examples of morphological convergence tied to behaviour; mantid ecomorphs and sexual dimorphism are predicted by habitat and behaviour (Svenson et al., 2015; Svenson et al., 2016) and cross-continental convergence in body and wing shape among two lineages of damselflies that are specialist predators of orb-weaver spiders (Toussaint et al., 2019). Some of these morphological shifts can also be seen among sensory structures; examples include seminal work focused on investment in extended ambulatory and sensory appendages in cave-dwelling crayfish (Cooper, 1969) and an expanded antenna associated with mate finding in many insect groups (e.g., Schneider, 1964).

Eye morphology, specifically eye size, can evolve in response to biological and environmental factors (Potier et al., 2017; Thomas et al., 2006; Veilleux & Kirk, 2014) even resulting in the loss of eyes (Cooper, 1969; Krishnan & Rohner, 2017). Bauer and Kredler (1993) found a significant relationship between relative eye size (an increase in eye width) and day–night foraging among carabid beetles, with species active in low-light conditions demonstrating increased investment in eyes over those species active in full daylight. Stanger-Hall et al. (2018) found a similar phenomenon tied to sexual selection and demonstrated that both modes of signalling and mate searching behaviour, pheromone and flashing, explained much of the variation observed in relative eye size among fireflies.

During both museum research and fieldwork, we observed that sap beetles (Coleoptera: Nitidulidae) can display large amounts of variation in relative eye size, even between closely related species. Potential factors influencing eye size across animals are often not well-understood. Thus, a close examination of relative eye size variation in sap beetles may provide deeper insight into eye size variation in animals, at least among arthropods. One potential predictor of variable investment in eye size could be selective pressures placed on the eye due to feeding behaviour (Potier et al., 2017; Thomas et al., 2006; Veilleux & Kirk, 2014). Nitidulid beetles exhibit tremendous variation in feeding behaviours including anthophily, frugivory, fungivory, necrophagy, predation and saprophagy (Audisio, 1993; Kirejtshuk, 1997; Parsons, 1943). Nitidulidae is comprised of more than 4500 species and several hundred genera (Kirejtshuk, 2008). The family is geographically ubiquitous, morphologically variable and ecologically diverse. Yet little focus has been placed on their evolution, either in terms of morphology or ecology. We set out to test the relationship between relative eye size and feeding behaviour in sap beetles. Specifically, we asked the question ‘Does flower-visiting (anthophily) predict larger eye size?’

MATERIALS AND METHODS

Taxon sampling

Representative specimens for 140 species from all 10 subfamilies and 58 of 236 genera of Nitidulidae, and outgroup families Kateretidae and Smicripidae (Table 1) were examined. Primary type specimens were used in all cases to eliminate potential issues with species-level identification, the vast majority of these specimens are male. We also investigate sexual dimorphism among a subset of taxa where large, authoritatively determined series were available. Specimens examined are deposited in the following institutions Australian National Insect Collection, Canberra, ACT, Australia (ANIC); California State Collection of Arthropods, Sacramento, CA, USA (CSCA); Museum of Comparative Zoology, Cambridge, MA, USA (MCZ); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museum für Naturkunde, Berlin, Germany (MNHUB); Natural History Museum, London, United Kingdom (NHM) and Národní Muzeum, Prague, Czech Republic (NMPC).

Measurements

Specimens were imaged using either scanning electron microscopy with a JEOL JSM-5510 LV scanning electron microscope, or high-resolution stacked images from a Vision Digital Passport Imaging System. The resulting scanning electron micrographs (for 16 species) or high-resolution stacked images (for 140 species) were automatically size calibrated and imported into Adobe Photoshop v.19.1.6 for morphological measurements. The head of each specimen was measured at the widest point (i.e., the widest point from the lateral edge of one eye to the other), then from the narrowest point between the two eyes (Figure 1). Using these measurements, a percentage of lateral head space dedicated to eye tissue (i.e., relative eye size) was generated for the dorsal perspective with the following formula adapted from methods used by Bauer and Kredler (1993) and Stanger-Hall et al. (2018).

$$(\text{total head width} - \text{interocular distance})/\text{total head width} \times 100.$$

Relative eye size is used as a proxy for investment in visual systems. For the subset of taxa with scanning electron micrographs, individual

TABLE 1 Sampling for morphological measurements by subfamily or family group names, with total number of included species, presence of anthophilous behaviour in each of those clades, and corresponding means for relative eye size grouped by the presence/absence of anthophilous behaviour

Taxon	# of included species	Presence of anthophily (Y/N)	Mean for non-anthophilous	Mean for anthophilous
Amphicrossinae	4	N	29.67	–
Calonecrinae	2	N	31.25	–
Carpophilinae	33	Y	24.65	37.92
Cillaeinae	19	Y	20.01	37.56
Cryptarchinae	10	N	20.79	–
Epuraeinae	8	Y	28.07	41.02
Kateretidae	3	Y	–	33.22
Maynipeplinae	1	N	37.31	–
Meligethinae	22	Y	–	36.21
Nitidulinae	34	Y	26.12	40.07
Prometopinae	3	N	25.75	–
Smicripidae	1	N	19.35	–
Total	140		26.29	37.67

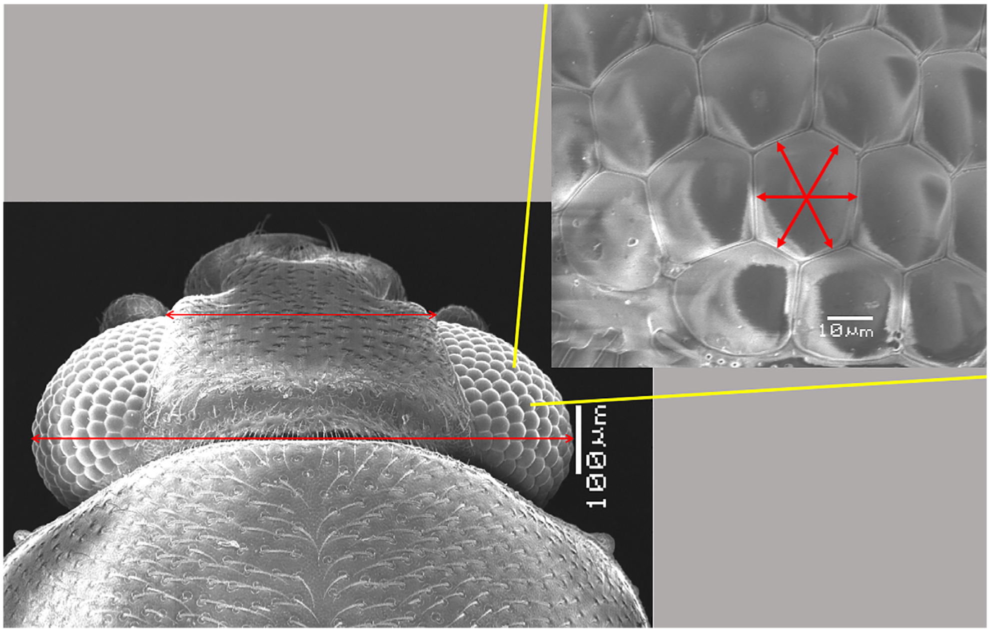

FIGURE 1 Example of scanning electron micrograph used for eye measurements

facet width was also measured from opposing edges of the hexagonal structure in all three directions and averaged.

Intraspecies variation

To capture the potential intraspecific variation of eye size we measured 8–12 specimens for 20 species of Carpophilinae. We did this to make sure that intraspecific variation was not a significant contributor to relative eye size, allowing us to infer eye sizes from smaller sample sizes for all 140 species included herein (e.g., a single primary type specimen).

Sexual dimorphism

Sexual dimorphism is unusual across Nitidulidae, notable exceptions do exist: antennal length in Mystropini (Gillogly, 1955) and tibial armature in Meligethinae (Audisio, 1993); however, no sexual dimorphism in eye size is currently reported. Despite this, and even though the vast majority of primary type specimens are male, we wanted to ensure potential sexual dimorphism was tested for. Therefore, where possible we measured for potential differences in eye size between males and females to empirically test for sexual dimorphism. As a result, ten male and ten female conspecifics were measured for ten representative species from across the four most diverse subfamilies (Table S1), allowing us to utilize single representative specimens for each species.

Day/night activity

We monitored the arrival of nitidulid beetles to fermenting bait traps in Gabon (February), Vanuatu (May/June) and the USA (July/August), at dawn and dusk over several days. From this monitoring, we were able to code beetles as active during either the low-light night conditions or full daylight. Other collecting methods including actively checking environmental food resources (e.g., fungi, fruit, flowers, etc.) throughout the day and night allowed additional species to be coded for a specific activity period. The majority of taxa examined did not exhibit specific activity periods.

Feeding behaviours

We compiled feeding behaviours for each of the 140 species. Each species had published hosts, was personally observed in the field or had specific associations recorded from museum label data for multiple collecting events to allow the species to be reliably coded as ‘anthophilous’.

Statistics

To test for correlation between eye size and anthophily as well as the other potential factors listed above (e.g., sex) Mann–Whitney *U* tests were used to assess the significance of each variable listed above. Statistical analyses were performed in SPSS v.25.

Phylogenetics

A phylogenetic estimate was generated by compiling molecular data (two to five loci) from previous studies (Audisio et al., 2008, Cline et al., 2014, Powell et al., 2020) as well as several newly sequenced representatives to better sample ecological diversity within the group. A total of 60 taxa were included, representing eight of ten subfamilies and three genera of Kateretidae as outgroups (Table S4). Alignment was performed using MAFFT (Katoh & Standley, 2013) implemented in Geneious (Geneious Prime https://www.geneious.com) and then exported for maximum likelihood (ML) analysis using IQ-Tree (Nguyen et al., 2015). The ancestral states of both relative eye size and anthophily were reconstructed using Mesquite (Maddison & Maddison, 2019) as continuous and binary categorical variables respectively and utilizing branch lengths for the given topology. The correlation between relative eye size and flower feeding was tested using an independent contrast correlation model implemented in BayesTraits (Pagel & Meade, 2007). A log marginal likelihood is generated for each and a log Bayes factor is calculated to assess the correlation between the two using: $\mathrm{logBF} = 2(-\mathrm{logML1} - -\mathrm{logML2})$.

RESULTS

Anthophilous beetles have significantly larger eyes than non-anthophilus beetles ($p < 0.001$) (Figures 2 and 3). Among members of the same species, relative eye size varied only 1%–2% between individuals (Table S1), with no observed variation between the sexes (i.e., no sexual dimorphism) (Table S2).

The vast majority of taxa were collected across the day–night cycle and were not able to be grouped by any consistent time of day or light condition. For example, from collecting efforts in both Vanuatu and the USA only a single species exhibited a single activity period (i.e., were solely day active or night active) out of the more than 65 collected. Shorter-term collecting efforts in Gabon resulted in about half of the ~90 species collected is limited to a single activity period. Of these, most were represented by a single collecting event or even a single specimen and thus could be due to rarity and not specificity in activity period for the species. Since nearly all included nitidulid species were found to have broad day–night activity and the anecdotal nature of the few that were recorded as specific (Table S3), we were not able to test this as a predictor of relative eye size variation.

Phylogenetic analyses recover five independent origins of anthophily within the Nitidulidae, with a sixth in the Kateretidae (Figure 5). Each of these six instances of anthophily corresponds to a significant increase in relative eye size. Ancestral state reconstruction recovers relative eye size to be lower along the backbone of the nitidulid phylogeny (i.e., ancestral eyes are smaller), with specific increases in each of the anthophilous clades as well as some species of Cyllodini. In at least two cases (i.e., *Meligethes* Stephens vs. *Lobiopa* Erichson and *Conotelus* Erichson vs. *Cillaeus* Laporte de Castelnau), the smallest observed relative eye sizes were recovered in the sister genera to flower-visiting taxa with large eyes. To phylogenetically test if flower-visiting behaviour and relative eye size are related, we employed an independent contrast correlation model. This model compares the null hypothesis, in this case, the two traits would not correlate, with the alternate, they would be phylogenetically correlated. Results from the independent contrast correlation model strongly support a significant correlation between relative eye size and anthophily (logBF = 0.0057) across the nitidulid tree.

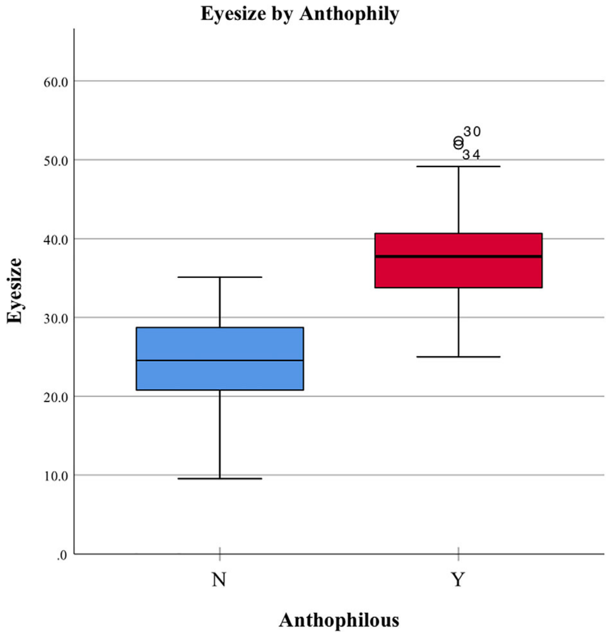

FIGURE 2 Boxplot depicting anthophily versus eye size

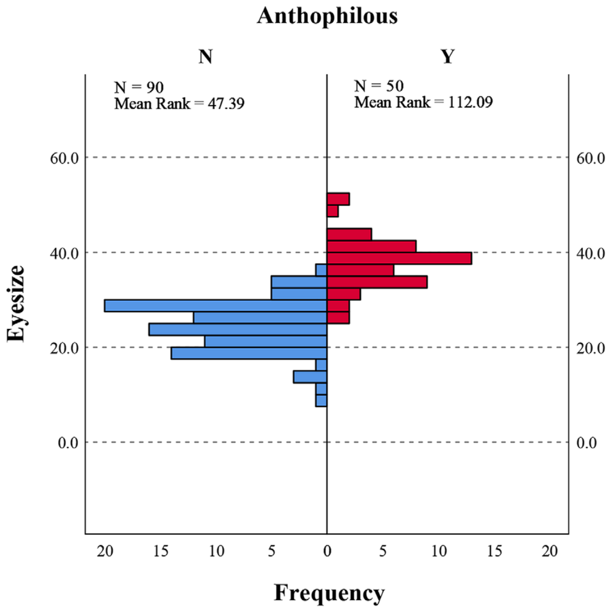

FIGURE 3 Mann–Whitney *U* test for anthophily versus eye size

DISCUSSION

We found strong evidence that flower-visiting species of nitidulid beetles have increased visual system investment ($p < 0.001$). This

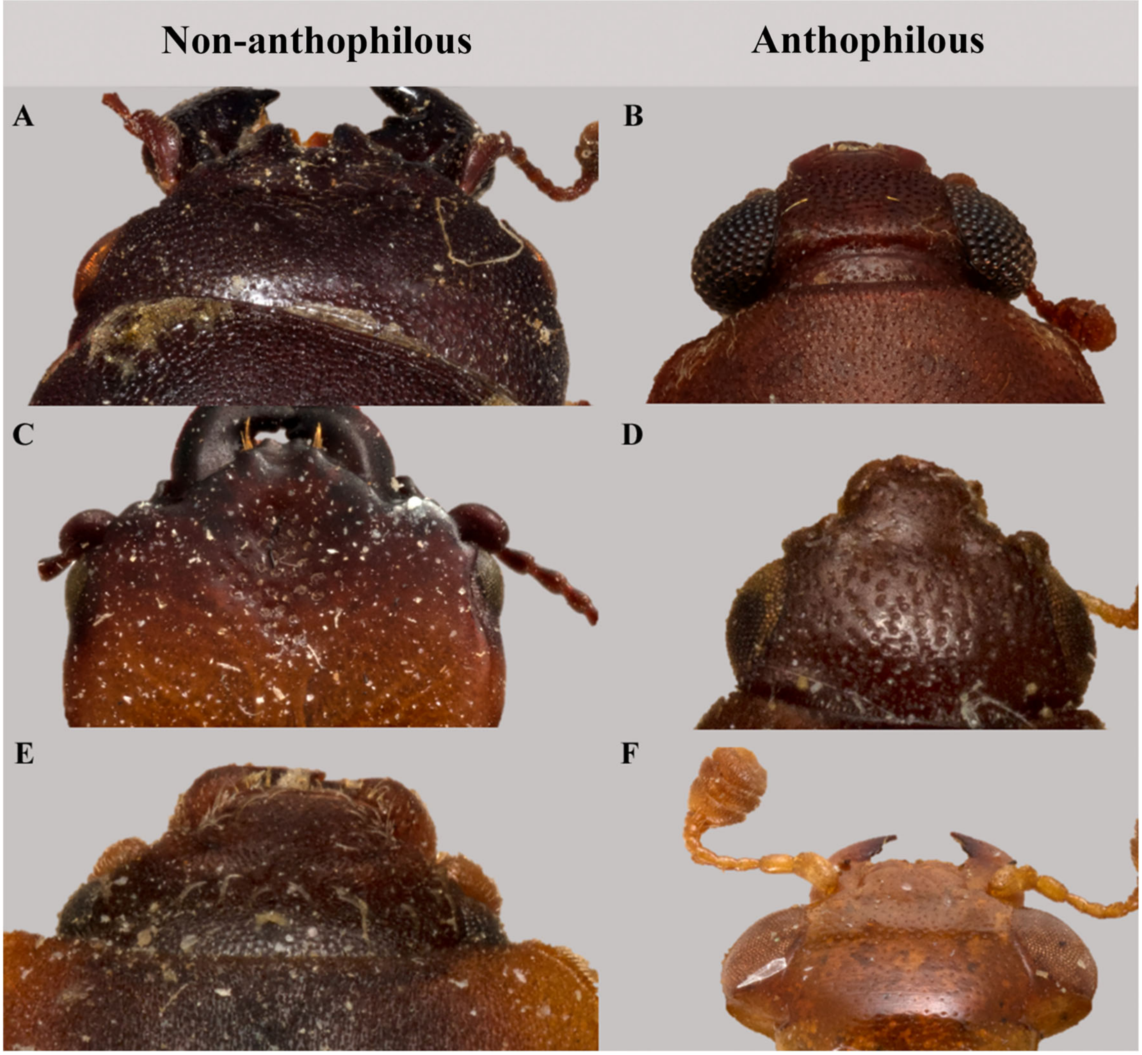

FIGURE 4 Range of eye size (given as a percentage of total head width) across members of the same subfamily differing in feeding behaviour; (a and b) Carpophilinae, (c and d) Cillaeinae, (e and f) Nitidulinae. (a) *Ctilodes palawanensis* Hisamatsu (19.84%), (b) *Nitops megalops* Dobson (52.38%), (c) *Ithypenes gestroi* Reitter (9.52%), (d) *Conotelus fuscipennis* Erichson (42.85%), (e) *Nitidula flavomaculata* Rossi (19.27%), (f) *Camptodes exoletus* Erichson (44.66%)

result was present across each of the five most diverse subfamilies of sap beetles and in the sister group to the Nitidulidae, Kateretidae. These six groups include >90% of the described species diversity in the lineage and all of the known instances of flower-visiting. The correlation between investment in the visual system and anthophilous behaviour was observable between higher-level taxonomic entities (e.g., tribes/subfamilies) that exhibit differing feeding behaviours (logBF = 0.0057). For example, the difference between the average relative eye size across the primarily saprophagous Cryptarchinae (19.73%, $n = 10$) and the anthophilous Meligethinae (40.21%, $n = 21$) is more than double. The same pattern of increased visual investment correlated with feeding behaviour is also recovered between closely related taxa, such as between species hypothesized to be within the same genus (e.g., *Carpophilus* Stephens, *Epuraea* Erichson). Thus, eye size evolution as it relates to flower-visiting is a highly malleable and perhaps a relatively fast evolutionary process that may even be observed in very recent evolutionary splits.

It seems as though increased investment in eyes has been accomplished in several ways in nitidulids: the number of facets has increased, the facets themselves have gotten larger, or even some combination of both. Species of the genus *Nitops* Murray (Carpophilinae) are perhaps the best example of the facets themselves getting larger (Figure 4b). Many Meligethinae or the genus *Camptodes* Erichson (Nitidulinae) seem to have facets of comparable size to their non-anthophilous counterparts but have a large increase in the actual number of facets (Figure 4f). It appears some taxa, for example, the genus *Conotelus* (Cillaeinae), have increased both the number of facets and size of each facet (Figure 4d).

There are alternative hypotheses that could potentially explain the variation in eye size observed across nitidulids (e.g., sexual selection, phylogenetic relatedness). We discuss each below.

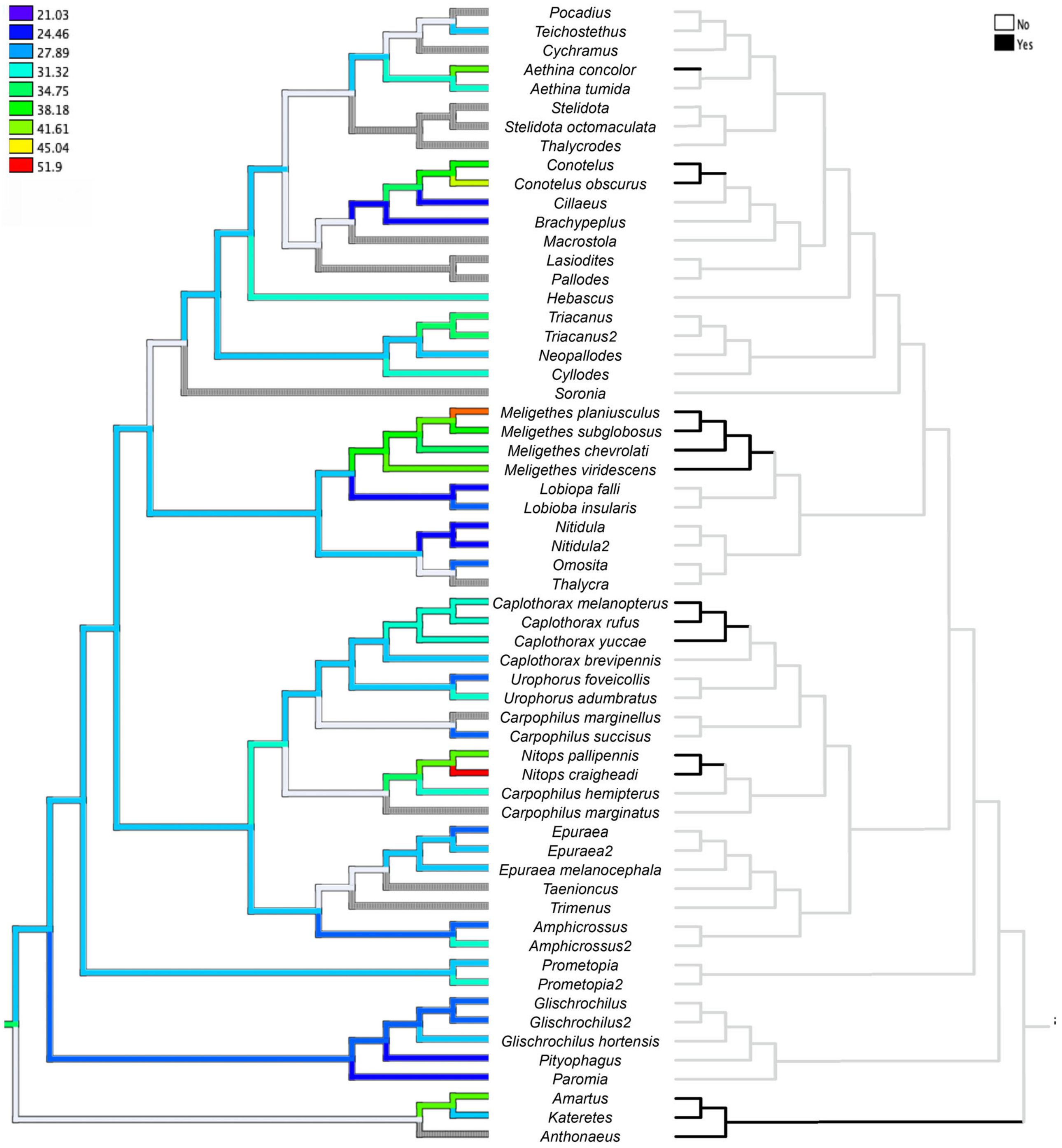

FIGURE 5 Patterns of eye size and anthophilous behaviour for 57 species of Nitidulidae and related groups. Results are based on maximum likelihood (ML) estimates from the combination of previously published and newly generated molecular data for the group (Table S4). The left cladogram depicts a likehood-based ancestral state reconstruction for relative eye size. The right cladogram shows the known origins of anthophilous behaviour

Large beetles equal large eyes

The methods used to generate the final value for relative eye size (percentage of the head dedicated to compound eyes), were chosen in an attempt to account for the potentially confounding factor that larger beetles will simply have larger eyes. With several genera of nitidulid (e.g., *Prometopia* Erichson, *Colopterus* Erichson, *Brachypeplus* Erichson) being heavily dorso-ventrally flattened, the head may be laterally expanded also expanded the eyes; conversely, it is possible this expansion only increases the area between the eyes. The general body form is often very variable in sap beetles and interestingly even between taxa that might operate in similar niches. For example, anthophilous taxa can be either extremely convex (i.e., *Camptodes*) or quite dorso-ventrally flattened (i.e., *Carpophilus* [*Ecnomorphus*] Motshulsky), so it is unlikely body convexity explains the observed variation. While nitidulid body length (mandible to pygidium) is highly variable among species ranging widely from <1 to >18 mm, head size is more consistent.

Sexual selection

Another alternative hypothesis for the variation in relative eye size in sap beetles could be mate recognition. Two factors could support this argument but were not found sexual dimorphism in relative eye size or sexual dimorphism in colour or patterning of the individuals. In cases of sexual selection, one would expect to see larger eyes in the sex that searches for a mate (e.g., Stanger-Hall et al., 2018). Our study found no sexual dimorphism in eye size among the species we examined, with some species having slightly larger eyes in the females and others slightly larger in the males. Alternatively, species using vision to find mates would be predicted to be more colourful and/or more patterned (Lelito et al., 2007) than those using chemical cues. We did not observe and there is no reported instance of colour or patterning dimorphism in the group, countering an argument for mating displays or recognition. We acknowledge the possibility that colour could play a role in relative eye size and that it is difficult to determine with basic observational data based on the human visual system. However, as both flower and non-flower-visiting sap beetles exhibit the same array of colours (largely black and brown) and patterns (usually very little) we did not investigate colouration as a predictor of relative eye size.

Phylogeny

Phylogenetic relatedness could also have been a simple explanation of eye size variation. For example, relatively larger eyes could have one or a few origins across the nitidulid tree of life and persisted within those lineages. Under this model, we would expect to find one or a few taxonomic groups with large eyes independent of ecological trait-like feeding behaviour. We examined the possibility of phylogenetic relatedness as an explanation of eye size using a novel phylogenetic estimate based on 57 taxa, which represent all major lineages (Figure 5). This topology and current nitidulid classification do not support such a scenario, eye size was not observed to be phylogenetically informative. All higher-level taxonomic groups sampled include species with both larger and smaller eyes, variation in eye size is large even among relatively closely related species (i.e., within the same genus) (Figure 5). Eye size is shown to increase in at least seven lineages, all of which exhibit anthophilous behaviour.

Anthophily

Our dataset suggests a compelling relationship between investment in larger eyes and anthophilous behaviour and allows for a much broader discussion across this diverse group. There are ~4500 described species of nitidulid beetles currently; however, the feeding habits for the vast majority of these taxa remain unknown. It would be nearly impossible to gather field observations for each of the thousands of described species, let alone the many undescribed that are constantly being discovered. Even capturing natural history data from the hundreds of thousands of museum specimens spread across the world would be lifetimes of work and is riddled with problems of incomplete data, misleading notes, or locality labels devoid of behavioural data. Our findings here allow us to measure the eyes of a museum specimen of any age, origin or condition, providing the head is still present and predict an association with flowers. While there is some overlap in the distributions of eye size between the species with a known association with flowers and those without, however, there are levels where an association with flowers is highly supported or refuted (i.e., >35% and <27.5%, respectively). The broad phylogenetic sampling across Nitidulidae presented here and the consistency of the correlation between the trait and the behaviour demonstrated by our data allows us to make predictions across Nitidulidae and likely closely related families. The predictive power of these data permits us to ask broader questions about feeding behaviour evolution and morphological change than would be possible with the current knowledge and resources for the group.

Possible predictors of morphological variation are a central theme in evolutionary biology. What circumstances led to the tremendous diversity in form, function and behaviour? Here, we have compelling evidence for feeding behaviour predicting an increase in eye size investment in a group of animals. Not only do species of sap beetle that have associations with flowers seem to have an overall larger relative eyes size, but these eyes also make up a significantly larger proportion of the lateral headspace of those individuals ($p < 0.001$). Although not investigated here, it is logical to assume that more of the overall head being dedicated to vision could result in trade-offs in other regions (i.e., a reduction in antennae or mouthparts) (Emlen, 2001; Simmons & Emlen, 2006; Stanger-Hall et al., 2018), further supporting the importance of the visual system to these organisms. Previous studies were able to find a close association between eye size and foraging time, beetles searching for the same resources were able to overcome the limitations of lower light conditions by increasing the surface area of their compound eyes (Bauer & Kredler, 1993). Our study provides additional insight into the evolution of increased investment in visual/sensory systems due to differences in target resource (anthophily), independent of light conditions. Relationships between eye size and feeding, or foraging behaviour, have been investigated in avian systems (Fernández-Juricic et al., 2004; Garamszegi et al., 2002); however, these studies are focused on more efficient prey capture and light conditions, not a total shift in feeding guild. The incredible feeding diversity of sap beetles allows for an exploration of the possible morphological shifts associated with major changes in natural history. Sap beetles are associated with many different feeding strategies, but our data specifically support shifts to flowers as the best predictor of larger eyes for this group of animals. This pattern was consistent across every lineage where anthophily was present, showing that the relationship between eye size and flower-loving transcends phylogenetic placement, lineage age and species diversity.

The predictive power of our results makes it possible to tackle further evolutionary scenarios across a broader range of specimens within a phylogenetic context in the future. Such data are already being generated. Nitidulids offer an interesting and tractable system to study the evolution of the visual system in relation to feeding behaviour as a potential driver of increased relative eye size (e.g., increased facet number and/or facet size). Exploring eye size evolution at the facet level in generalist versus specialist flower feeders is a focus of future research. The diversity in feeding behaviours in this group makes this discovery important in assessing the evolution of these traits across such an overlooked but ubiquitous group of animals. These data serve as an initial foray into the study of morphological evolution of sensory structures in relation to feeding behaviour in animals, specifically arthropods.

CONCLUSION

This study shows a compelling and highly significant relationship between feeding behaviour, specifically flower-visiting and an increase in relative eye size in animals. Increases in eye size have been demonstrated in invertebrates to be associated with sexual selection (Stanger-Hall et al., 2018) and activity period (Bauer & Kredler, 1993). To our knowledge, this is the first case where an increase in relative eye size is correlated with a specific feeding behaviour like anthophily. When considering the diversity of beetles, and invertebrates in general, the opportunities to gain insight into the evolution of morphological traits are untapped. This study system provides unique insight into the morphological evolution of sensory systems in invertebrates and complements the more historically well-studied vertebrate systems.

AUTHOR CONTRIBUTIONS

Seth Bybee: Conceptualization (supporting); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (lead); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

All data used in this study will be made available as Supporting Information Materials and is included in the submission for the review process.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

TABLE S1 Eye measurements for all included taxa. Anthophilous coding for each species as well as listed references for presence of that behaviour. Raw measurements for total head width as well as interocular distance is provided. These values were then used to calculate the proportion of lateral head space dedicated to eye tissue used for further analyses.

TABLE S2 Mean eye size between sexes of 10 representative species of sap beetle (10 males and 10 females for each).

TABLE S3 Nitidulidae day-night activity periods.

TABLE S4 Taxon and gene sampling for phylogenetic analyses with Genbank accession numbers.

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