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Research

Evolution

Vision-Linked Traits Associated With Antenna Size and Foraging Ecology Across Ants

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Abstract

Visual systems in animals often conspicuously reflect the demands of their ecological interactions. Ants occupy a wide range of terrestrial microhabitats and ecological roles. Additionally, ant eye morphology is highly variable; species range from eyeless subterranean-dwellers to highly visual predators or desert navigators. Through a comparative approach spanning 64 species, we evaluated the relationship between ecology and eye morphology on a wide taxonomic scale. Using worker caste specimens, we developed two- and three-dimensional measurements to quantify eye morphology and position, as well as antennal scape length. Surprisingly, we find limited associations between ecology and most eye traits, however, we recover significant relationships between antennal scape length and some vision-linked attributes. While accounting for shared ancestry, we find that two- and three-dimensional eye area is correlated with foraging niche and ommatidia density is significantly associated with trophic level in our sample of ant taxa. Perhaps signifying a resource investment tradeoff between visual and olfactory or tactile acuity, we find that ommatidia density is negatively correlated with antennal scape length. Additionally, we find that eye position is significantly related to antennal scape length and also report a positive correlation between scape length and eye height, which may be related to the shared developmental origin of these structures. Along with previously known relationships between two-dimensional eye size and ant ecology, our results join reports from other organismal lineages suggesting that morphological traits with intuitive links to ecology may also be shaped by developmental restrictions and energetic trade-offs.

Key words: comparative morphology, visual system, antenna, Formicidae, ecology

Sensory systems are vital to survival as they determine how an individual receives and responds to stimuli within their environment. Because vision-related tissues are energetically costly, their retention and development may be especially sensitive to selective pressures (Niven and Laughlin 2008, Moran et al. 2015). Such a pattern may be best exemplified among conspecific cavefish populations that have undergone recent repeated independent evolution of eye degeneration (Herman et al. 2018). Links between ecology and vision are also apparent across deep evolutionary timescales, for example, eye size significantly differs between nocturnal and diurnal gecko species, as well as ground-dwelling and climbing species (Werner 1969). Selection pressures may also lead to differing vision-related traits beyond eye size itself; forward-facing eyes are found in many predatory species of mammals and birds relative to herbivorous species (Land and Nilsson 2012). Among insects, some dipteran species exhibit a trade-off between visual resolution and sensitivity that is directly linked to predation strategy, where species that are diurnal aerial predators have significantly higher visual acuity than those that are slow-moving and crepuscular (Gonzalez-Bellido et al. 2011). Honeybees also exhibit distinct, intraspecific investment in eye size and ommatidia number across castes within the same colony; these differences are linked to differing needs of visual resolution that are related to each morphological caste's role within the colony (Streinzer et al. 2013).

Ants (Hymenoptera: Formicidae) are diverse in morphology and ecology. This diversity is also reflected in vision-related morphology.

For example, arboreal species within the pseudomyrmecine genus *Tetraponera* possess relatively large eyes that occupy ~15% of their head capsule while the genus *Pseudomyrmex*'s Lund, 1831 eyes comprise as much as 23% of the head (Ward 1990). On the other hand, the army ant genus *Dorylus* Fabricius, 1793 includes species that forage underground and entirely lack eyes in the worker caste (Wheeler 1916, Bolton 1995, Schoning et al. 2005). Ants occupy, forage, and nest within a variety of microhabitats which may be categorized as hypogaeic, or subterranean, and epigaeic, or above-ground (Schmidt and Solar 2010). Epigaeic occupations may be further subdivided into general epigaeic, leaf litter, and arboreal (Longino and Nadkarni 1990). Species may also forage in a microhabitat that is distinct from their nesting location.

Microhabitat and trophic position are correlated with morphological variation in ants (Kaspari 1993, Kaspari and Weiser 1999, Gibb et al. 2015, Sosiak and Barden 2021). Across species, eye size and position have been found to be associated with trophic level, foraging niche, and habitat complexity (Weiser and Kaspari 2006, Gibb et al. 2015, Gibb and Parr 2013, Guilherme et al. 2019). Arboreal ants in particular are well known to exhibit larger eyes, while eye size may be smaller among predatory ants or species that occupy more complex environments (Weiser and Kaspari 2006, Guilherme et al. 2019). Furthermore, Divieso et al. (2020) investigated how eye length varies among reproductive castes in 678 ant species of ants and found that eye length is greater in males than queens across ant lineages. Even as described associations between ecology and eye morphology have revealed important links between form and function, a number of vision-based traits have not yet been evaluated in a phylogenetic context across distantly related ant lineages. Here, using a new suite of morphological metrics we ask: Does ecology play a significant role in the diversity of sensory systems across ant lineages?

Intuitively, a larger eye may indicate a greater reliance on eyesight; vision is central to orientation, navigation, and foraging for many ant species (Hölldobler 1980, Gronenberg and Hölldobler 1999, Knaden and Graham 2016). However, additional features of eye morphology beyond size may convey information related to visual acuity and investment. Apposition compound eyes are composed of ommatidia which appear on the surface of the eye as a facet (Cronin et al. 2014, Land and Nilsson 2012). Each ommatidium is composed of a corneal lens and crystalline cone that focus light onto the rhabdom, a receptive rod that detects the amount of light present (Land and Nilsson 2012, Schoenemann et al. 2017). The ommatidia together create a mosaic of an effectively pixelated image (Land and Nilsson 2012, Schoenemann et al. 2017). Increased ommatidia number broadly indicates greater visual acuity (Streinzer et al. 2013, Gonzalez-Bellido 2011, Land and Nilsson 2012, Schoenemann et al. 2017). Furthermore, larger rhabdoms indicate a greater amount of light captured by the eye and a greater acceptance angle of the rhabdoms is also indicative of a higher resolution of vision (Cronin et al. 2014, Narendra et al. 2011, Nilsson and Odselius 1981). Ommatidia number is strongly associated with eye size, however, ommatidia density may also vary across taxa. Intraspecific variation in fine-scale eye morphology has been linked to caste ecology in *Myrmecia* ants (Narendra et al. 2011), however, comparative interspecific assessments of vision and ecology have been limited to gross morphology (e.g., eye length, lateral position). Moreover, eyes are three-dimensional and variation in height or anatomical topography may correspond with visual acuity—this aspect may not be captured with traditional two-dimensional measurements. In the case of intraspecific variation in *Myrmecia* Fabricius, 1804, activity schedules of both alates and workers are correlated with surface area of the eye, ommatidia number, and ommatidia size (Narendra et al. 2011). Ecology can affect ommatidia composition and three-dimensional size within a single species, but does this hold true across distantly related lineages?

In addition to ecology, vision-linked diversity may be shaped by energetic trade-offs associated with development. Under the assumption that sensory systems are under ecological selective pressures but are also energetically costly, we may predict that a greater investment in one sensory trait may result in a reduced investment in another due to finite energetic resources (e.g., Emlen 2001, Keesey et al. 2019). In holometabolous insect larvae, imaginal discs contain cells with defined developmental fates—Drosophila larvae possess nine paired discs that ultimately form external elements of the head, thorax, and legs (de Celis and García-Bellido 2013). As the name suggests, cells within the eye-antennal imaginal disc not only give rise to the compound eye, but also the head cuticle and antennae (Haynie and Bryant 1986). A recent survey of 62 Drosophila species suggests that the imaginal disc may be a constraint on sensory diversity: there is an inverse relationship between visual and olfactory investment that is directly linked to the shared developmental origin of the eye and antenna in flies (Keesey et al. 2019). Because these morphological traits are developmentally linked and, because ants rely heavily on tactile and chemosensory input from antennae, we incorporated measurements of antennae to ask: Is there a tradeoff between eye and antennal morphology across ant taxa?

There are several possible explanations for the diversity of vision-linked morphological variation across ant lineages. Based on previous reports, we devised two main predictions for the outcomes of this study: (1) Some niches (e.g., predatory taxa that forage arboreally) will possess larger, more elevated eyes with a greater number of ommatidia and ommatidial density associated with ecology. (2) There is a negative relationship between eye size and antennal scape length, suggesting a potential trade-off between investment in energetically costly tactile/olfactory and visual sensory tissues. These hypotheses are not mutually exclusive and are interconnected, however, evaluating each may provide a more complete understanding of the factors that influence the evolution of sensory systems in worker caste ants.

Methods

Sampling

To assess the relationship between ecology and eye morphology, we constructed a dataset of niche occupation and morphometric measurements for 64 species spanning nine subfamilies and 64 genera (Supp Table 1 [online only]). We gathered foraging microhabitat and trophic occupation data for all species from a literature survey and the data repository AntWiki (2020). We have included all citations for ecological binnings in the Supp Data [online only] (See "Ecological Citations" in Supp Data 1 [online only]). Some of our sampled species do not have known ecologies, these were coded as "Uk" in the appropriate category and excluded from relevant analyses. With respect to foraging habitat, we subdivided occupations into four binnings, concordant with previous work (Longino and Nadkarni 1990, Schmidt and Solar 2010, Weiser and Kaspari 2006): the dataset included 11 arboreal, 21 epigaeic, five hypogaeic, and 19 leaf litter species. Our trophic occupation scheme comprised two binnings: 31 omnivores, and 28 predators (with fungivores, granivores, and herbivores scored as omnivores). For genera with a wide range of known ecological habits, occupations corresponded with the ecology of the species that was sampled for morphological measurements. For the purpose of this study we only included unspecialized (non-major) worker caste specimens as this is the caste that most frequently forages.

Measurements were obtained from pinned specimens at the BAL collection at the New Jersey Institute of Technology (NJIT). Specimens originate from Australia, Belize, Canada, Ghana, Grand Cayman, Guyana, Malaysia, Mozambique, and the United States. The specimens are from a large range of biomes including temperate forests, tropical rainforest, and savanna. A total of 19 measurements were taken from each specimen using a Nikon SMZ25 stereoscope with extended focus automontage on a fine-scale stepper-motor (Table 1) using the software NIS Elements. We measured a single specimen for each species. While sampling multiple individuals for each species may be preferable (e.g., when attempting to accurately obtain species mean values), intraspecific variation accounts for as little as 1–4% of morphological measurement variation within members of the same minor caste when comparing across taxa (Gaudard et al. 2019).

Our morphometric sampling includes typical metrics of ant morphology, such as eye length and two-dimensional eye area, along with newly developed measurements (Table 1). Three-dimensional eye area was calculated using an approximate formula for the surface area of a scalene ellipsoid ($4\pi \cdot \left(\frac{a^p b^p + a^p c^p + b^p c^p}{3}\right)^{1/p}$ where $P = 1.6075$) divided by two. We used eye height, eye length, and eye width as the radii *a*, *b*, and *c*. Because ommatidia size may vary across the eye, we averaged ommatidia size across the lateral-, dorsolateral-, and dorsal-most margins of the eye (see Table 1 for a more detailed description). These three locations were selected after measuring several eyes and determining that these three locations often differ in ommatidia size. Three-dimensional eye area was divided by the average ommatidia area to estimate the total number of ommatidia. We calculated ommatidia heterogeneity as the maximum ommatidia area divided by the minimum for each eye, indicating the percent difference between ommatidia sizes across an individual's eye.

Because the length of the scape—the first antennal segment—provides a limitation on sensory gathering distance and most frequently comprises the largest segment of total antennal size, we measured its length as an indicator of tactile/olfactory sensory investment (Weiser and Kaspari 2006). Although an elongated scape is a synapomorphy of crown ants, there is considerable diversity among extant genera.

Ommatidia number and eye size increase with body size across ants (Menzel and Wehner 1970, Bernstein and Finn 1971, Klotz et al. 1992, Baker and Ma 2006). Therefore, we normalized

Table 1. Brief summary of measured traits and rationales

Measurement	Description	Relevance
Head Length	From vertex of head to anterior margin of clypeus in frontal view, at midline.	Used to estimate head area and normalize measurements to body size.
Head Width	Maximum width of head capsule excluding eyes from the frontal view.	
Eye Height	Distance between maximum and minimum eye elevation taken in profile/lateral view; minimum elevation corresponds with eye margin, where the marginal ommatidia abut the head capsule cuticle—measured from position of maximal eye width, using the stacking tool with a minimum step size of 8µm.	Potential indicator of peripheral vision; used to calculate three-dimensional area.
2D Area	Two-dimensional area of eye by perimeter, measured from position of maximal eye width taken in profile/lateral view.	Expansion of traditional two-dimensional eye length and width metric.
Eye Length	Maximal length of longest eye axis taken in profile/lateral view.	Traditional eye size metrics (Weiser and Kaspari 2006).
Eye Width	Maximal width of the eye taken perpendicular to the eye length axis in profile/lateral view.	
3D Eye Area	Using formula for the surface area of an ellipsoid, divided by two.	Comprehensive metric of total visual area; used to estimate ommatidia number.
Average Ommatidial Area	Two-dimensional ommatidial area taken by perimeter in profile/lateral view. Average value from three measurements of compound eye: lateral/proximal- (ommatidium positioned nearest head capsule cuticle), dorsolateral/medial- (approximate midpoint of eye radius), and dorsal-most/distal (center of eye at maximal elevation).	Used to calculate an estimate of ommatidia number; may impact visual acuity. Similar to 'facet diameter' of Narendra et al. (2011).
Ommatidia Number	Three-dimensional eye area divided by average ommatidial area.	Estimate of approximate visual resolution and acuity (Narendra et al. 2011).
Anteroposterior position of eye	Distance from center of eye to anterior margin of clypeus divided by head length in profile/lateral view.	Metrics describing position of the eye in profile view. Similar to, and expanded from metrics of Gibb and Parr (2013) and Silva and Brandão (2014)
Dorsoventral position of eye	Distance from center of eye to dorsal margin of the head capsule divided by maximal head height in profile/lateral view.	
Scape Length	Length of the antennal scape (antennal segment I).	Metric used to describe relative tactile/olfactory investment, provides limitation on sensory input distance (Weiser and Kaspari 2006).
Ommatidia Density	Ommatidia number as described above scaled to 1mm^2.	Indicative of potential visual resolution of the eye, normalized to remove impact of body size.
Ommatidia Heterogeneity	Maximum ommatidium area divided by minimum ommatidium area (used in ommatidia area metric).	Percent difference between the size of ommatidia in the eye. Indicative of the variability of the ommatidial area across the eye.

our measurements to estimated head area (maximum head length × maximum head width in frontal view) to account for variation in body size. To evaluate alternate normalizing methods, we also scaled measurements by lateral head area, head surface area, and head width. Head surface area was calculated in the same manner as three-dimensional eye area, except the final number was not divided by two. Lateral head area was obtained by multiplying the maximum head length by the maximum head depth in profile view. Three-dimensional eye area, two-dimensional eye area, ommatidia number, eye length, eye height, and scape length were scaled by body size using all scaling methods (we only report those scaled by frontal head area here, other values reported in Supp Data 1 [online only]). Dorsoventral eye position and anteroposterior eye position are already scaled by body size (Table 1). Ommatidia heterogeneity was not scaled by body size.

Analyses

Because species are not statistically independent (Felsenstein 1985), we assessed relationships among measurements and between measurements and niche occupation through phylogenetic independent contrasts (PIC) and phylogenetic least squares (PLS) (Garland et al. 1992). We generated PIC scores and PLS from our continuous data based on the most recent genus-level phylogeny of Blanchard and Moreau (2017). We pruned the Blanchard and Moreau (2017) phylogeny to genus-level tips for which we had congeneric specimen data using the *drop.tip* command in the R package ape v5.4 (Paradis and Schliep 2018) and visually mapped key traits onto the tree using the package phytools v0.6-99 (Revell 2012). To assess the relationship between scape length and eye measurements, we used phylogenetic generalized least squares (PGLS) (Martins and Hansen 1997) in the R package caper v1.0.1 (Orme et al. 2012) under both Brownian Motion (BM) and estimated lambda models using the same phylogeny. We compared models using Akaike information criterion (AIC) scores and selected the model that was the best fit for each trait and ran regression analyses using the gls command in the R package nlme (Pinheiro et al. 2020) to export fit lines, which we overlaid onto a plot of raw trait data. Additionally, PIC scores were generated with the *pic* function in ape under a Brownian Motion model. We performed linear regressions on resulting PIC scores to compare scape length to eye measurements. To determine whether or not eye morphology was distinct among foraging and trophic niches, we also performed analyses of variance (ANOVAs) using PGLS (under both Brownian Motion and estimated lamba models, which were assessed with AIC scores) using the *pgls* command in the R package *caper*. Because there were only five hypogaeic species within the data set, which may drive sample-size biased results, this category was combined with leaf litter species, as both of these reflect low light microhabitats.

Results

Dataset

We recover considerable diversity among specimens measured (Figs. 1 and 2). The largest estimated head area recorded was over 293 times greater than the smallest head area (*Paltothyreus* is the largest genus measured and *Leptanilla* the smallest). Eye size is also highly variable with estimated ommatidia number ranging from over 800 to 1 (excluding eyeless genera). Body size normalized eye height and scape length varied across 43x, and 25x, respectively (excluding eyeless genera). Ommatidia heterogeneity ranges from a value of 1, indicating identical size across the eye in taxa such as *Monomorium* and *Pseudomyrmex*, to 2, indicating a 100% size variance between the largest and smallest ommatidia in genera such as *Oecophylla* and *Iridomyrmex* sampled here. Variation among traits is not restricted to any monophyletic group within our sampled lineages, although some closely related species are similar in eye morphology (Fig. 1). We also recover significant diversity in both anteroposterior and dorsoventral eye positions (Fig. 3).

Phylogenetic Generalized Least Squares

We find that ommatidia number, scape length, as well as two- and three-dimensional eye area are significantly correlated with foraging niche, while the only trait significantly correlated with trophic level is ommatidia density. For the remaining measurements tested (y, ommatidia heterogeneity, eye length, eye height, dorsoventral eye position, and anteroposterior eye position,) no significant relationships were found with respect to either trophic occupation or foraging niche (Table 2; Fig. 2). In addition, we find that ommatidia density, ommatidia number, anteroposterior eye position, dorsoventral eye position, and eye height are significantly correlated with scape length (Fig. 4).

Phylogenetic Independent Contrasts

We find that scape length has a significant positive correlation with eye height. We also find that scape length has a significant negative correlation with anteroposterior eye position, dorsoventral eye position, and ommatidia density. We do not recover significant relationships with any other vision-related metrics and scape length. These results can be found in the Supp Data [online only].

Discussion

We investigated links between vision-associated morphology and ecology across ant lineages using a suite of two- and three-dimensional metrics. We also explored possible energetic trade-offs between visual and olfactory or tactile traits. Based on our sampling, we find limited associations between ecology and most eye traits, however, we recover multiple significant relationships between antennal scape length and some eye attributes, including position.

Our results suggest that ommatidia number, as well as two and three-dimensional eye area, are significantly related to foraging niche, while trophic level is significantly correlated only with ommatidia density. Other traits such as eye position, eye height, and facet heterogeneity were not significantly related to ecological occupations assessed here.This may be in part due to our conservative ecological binning scheme, in which hypogaeic(n = 5) and leaf litter taxa (n = 19) were grouped, and all non-predatory ants were coded as omnivorous. This binning may have eroded some previously identified trends linking eye morphology to ecology; there is no question that hypogaeic and arboreal ants possess distinct eye morphologies, for example. Furthermore, the current ecological binnings widely used in myrmecology are broad and at times do not have well defined boundaries. In addition, trait variation may be related to other factors such as predation risk, social behaviors, and habitat complexity (Fichaux et al. 2019). Although limited, our ecology-based results further illustrate the impact that microhabitat has on the morphological diversity of ants, which has been shown previously (Kaspari 1993, Kaspari and Weiser 1999, Weiser and Kaspari 2006, Silva and Brandào 2014).

We predicted that arboreal and predatory taxa would have the greatest investment in visual acuity, however, results based on our

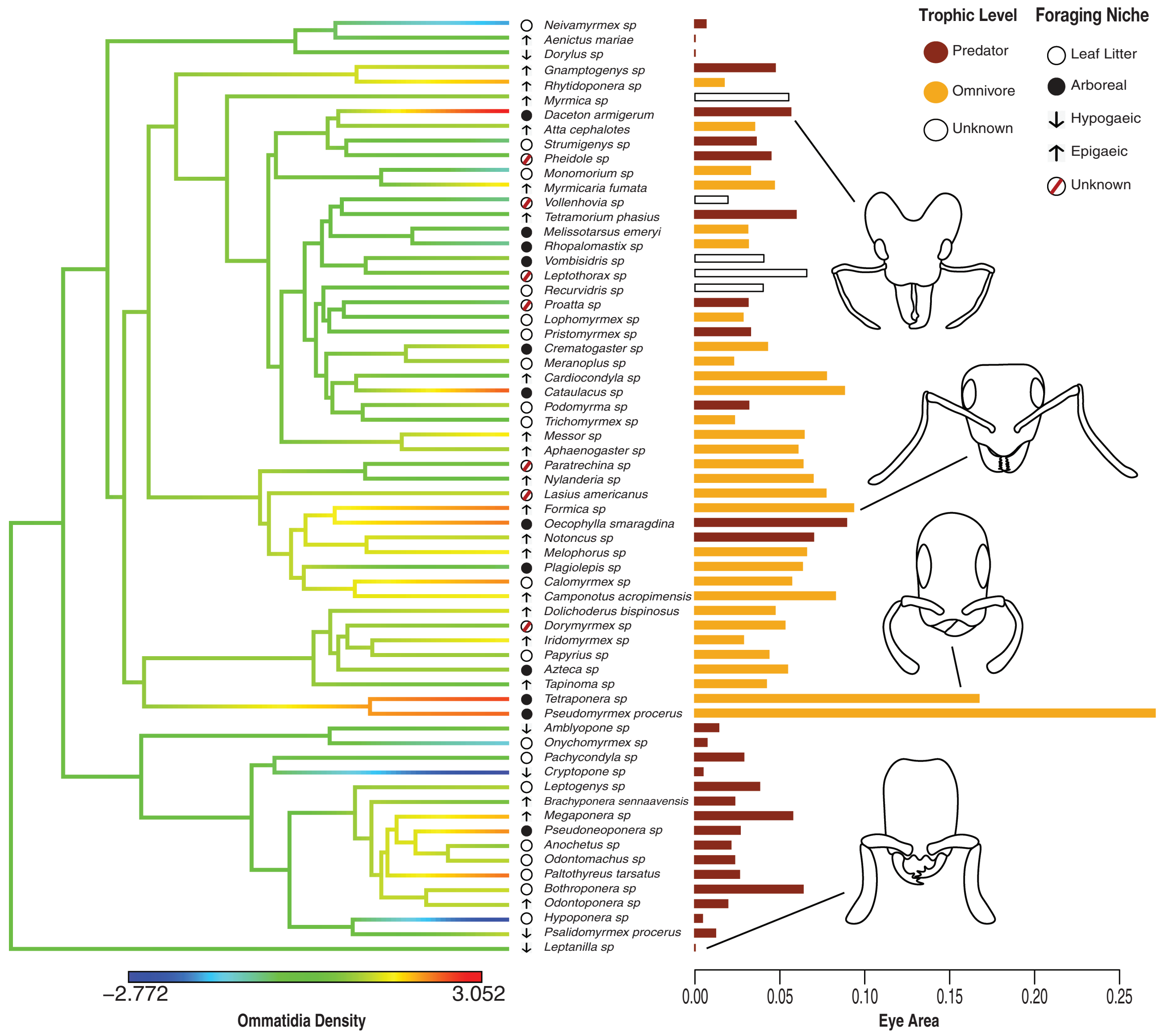

Fig. 1. Variation among vision-based traits across sampled taxa. Pruned phylogenetic tree from Blanchard and Moreau (2017) with log adjusted ommatidia density mapped along branches. The raw units for ommatidia density are ommatidia per 1mm². Ecological niche occupation indicated with icons and bar graph colors, includes foraging niche and trophic level. (Right) Eye area normalized by frontal head area across sampled species. Corresponding PGLS results in Fig. 2, Table 2.

sampling indicate that mean eye area is greatest in epigaeic and omnivorous taxa. Although epigaeic taxa have the greatest mean three-dimensional eye area, arboreal taxa have a greater range of eye areas recorded, while means and extremes are both greater in our sample of omnivorous ants. Extremes were primarily driven by pseudomyrmecine species such as the arboreal omnivorous genus *Pseudomyrmex* (Figs. 1 and 2). Intuitively, subterranean species possess the smallest eyes within our data set. For example, workers belonging to the predacious genus *Leptanilla* Emery, 1870 are eyeless, along with several other hypogaeic or subterranean genera (Masuko 1990). Lower light levels are a likely driving factor in the reduction of the eye as this trend is seen within other arthropod lineages (Barr 1986, Trajano and Bichuette 2010, Peck 1990, Leys et al. 2005).

Eye area and ommatidia number exhibit a positive linear relationship across measured taxa, however, there is a wide range of eye:ommatidia ratios (Fig. 5). Variance indicates diversity in ommatidia density, which is also apparent at the phylogenetic level (Fig. 1). Extremes in density include arboreal taxa such as *Pseudomyrmex*, *Tetraponera* Smith, 1852, and *Daceton* Perty, 1833, although several arboreal species possess density values near our formicidae-wide average.

While we predicted that predators would exhibit a greater investment in visual acuity, we recover no significant relationships between trophic level and the great majority of our sampled measurements (Table 2). Only ommatidia density was found to be correlated with trophic level, with higher density in omnivores. We also recorded greater mean values for three-dimensional eye area, eye height, and ommatidia density for omnivorous taxa (Fig. 2), however, these differences were slight. On the other hand, it is notable that all of the eyeless taxa in our dataset are predatory.

We recover wide diversity in eye position, although there are limitations on where eyes are found on the head (Fig. 3). The position of the eye, on both anteroposterior and dorsoventral axes, is not correlated with ecology in our sampling regime. Our results are

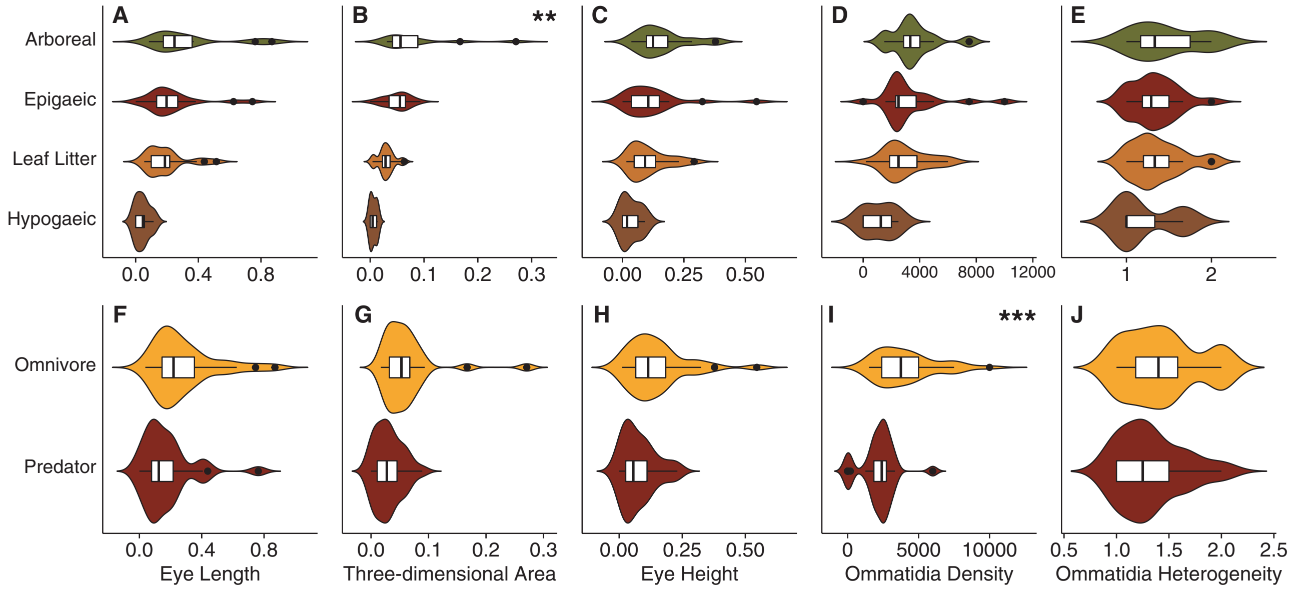

Fig. 2. Comparison of eye morphology across foraging niche and trophic occupation. (Top; A–E) Two-dimensional eye length, three-dimensional eye area, eye height, ommatidia density, and ommatidia heterogeneity across foraging microhabitats. AB, arboreal (*n* = 11); EG, epigeic (*n* = 21); HG, hypogaeic (*n* = 5); LL, leaf litter (*n* = 19). (Bottom; F–J) Eye length, three-dimensional eye area, eye height, ommatidia density, and ommatidia heterogeneity between omnivorous (*n* = 31) and predatory (*n* = 28) ant species. A–C; F–H measurements are scaled by frontal head area. * denotes $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. Significance values from PGLS results detailed in Table 2, hypogaeic and leaf litter categories were combined for statistical analyses.

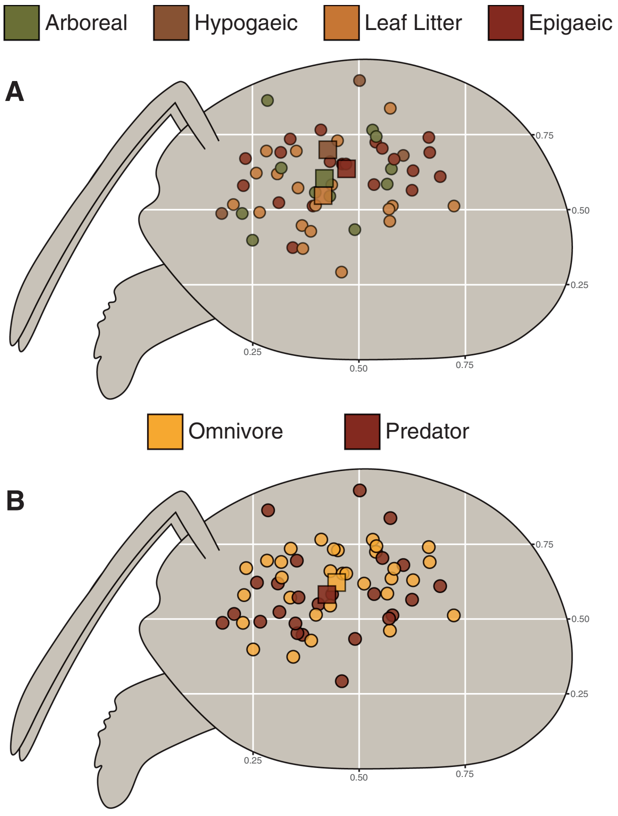

Fig. 3. Mapped lateral eye positions according to ecology. Species indicated by circles, squares represent mean values for ecological binnings. (A) Eye position, both dorsoventral and anteroposterior, mapped on a theoretical ant head. Colors are indicative of foraging niche. (B) Eye position measurements with colors indicating trophic level. Illustrated head proportions based on ratio of mean head length and depth in lateral view across taxa sampled; head length is approximately 40% greater than head depth in profile view on average.

in contrast to previous work identifying a relationship between eye position and habitat (Silva and Brandào 2014; Gibb and Parr 2013), this is most likely due to our taxonomic sampling. Contrasting results could also be a result of explicit incorporation of phylogenetic relationships or alternate approaches in describing eye position. Alternatively, the positioning of the eye could potentially be nonadaptive with respect to the ecological binnings we employed here, suggesting that the positioning of the eye may be more driven by developmental processes than by the sensory demands of the environment (Wheeler 1910). Indeed, we identified previously unreported relationships between antenna size and eye placement as well as eye morphology.

Eye position, both dorsoventral and anteroposterior, is correlated with scape length in our dataset. Larger scape lengths are correlated with eyes that are closer to the clypeus and higher on the head capsule in lateral view. Both eye position and scape length could together define an individual's spacial sensory acquisition, and so these traits may be under the same selective pressures. The length of the scape is indicative of the distance at which an individual can gather tactile/olfactory information and eye position may represent a similar limitation for vision (Weiser and Kaspari 2006). While this is one possible explanation of the result, the eyes and antennae within some holometabolous insects are derived from the same nearby tissue in development (Blair 2009, Held 2002, Koch et al. 2021). This linked development corresponds with our second hypothesis, which examined the energetic trade-offs between visual and tactile/olfactory investment.

Eye height is positively correlated with scape length across ant lineages, however, this trend does not appear to be linked to ecology as assessed here. We find that scape length is significantly different across foraging ecologies but not trophic level. However, we did not recover any significant relationships between eye height and ecology. In addition, ommatidia density is negatively correlated with scape length. Individual ommatidia visual inputs coalesce to create a pixelated image (Lorus and Milne 1948, Borst

Table 2. Summary statistics from ANOVA of Phylogenetic Least Squares (PGLS) under Brownian Motion (BM) and estimated lambda (λ) model using the R package *caper*

	Trophic Level	Foraging Niche
Three-Dimensional Eye Area	P = 0.9739, F = 0.001084 (BM)	**P = 0.004015, F = 6.134 (BM)**
Two-Dimensional Eye Area	P = 0.9861, F = 0.0003065 (BM)	**P = 0.01288, F = 4.73 (BM)**
Scape Length	P = 0.2264, F = 1.495 (λ)	**P = 0.04642, F = 3.255 (λ)**
Eye Height	P = 0.3985, F = 0.7236 (λ)	P = 0.1435, F = 2.014 (λ)
Dorsoventral Eye Position	P = 0.07505, F = 3.288 (λ)	P = 0.3879, F = 0.9641 (λ)
Anteroposterior Eye Position	P = 0.5155, F = 0.4281 (BM)	P = 0.8815, F = 0.1265 (λ)
Ommatidia Number	P = 0.3838, F = 0.7704 (BM)	**P = 0.01475, F = 4.571 (BM)**
Ommatidia Density	**P = 0.0001072, F = 17.34 (λ)**	P = 0.8913, F = 0.11535 (λ)
Ommatidia Heterogeneity	P = 0.3537, F = 0.8742 (λ)	P = 0.2707, F = 1.339 (BM)
Eye Length	P = 0.5228, F = 0.4135 (BM)	P = 0.05629, F = 3.039 (BM)

Significant results are bolded. Results from PGLS using the *nlme* package can be found in Supp Data [online only].

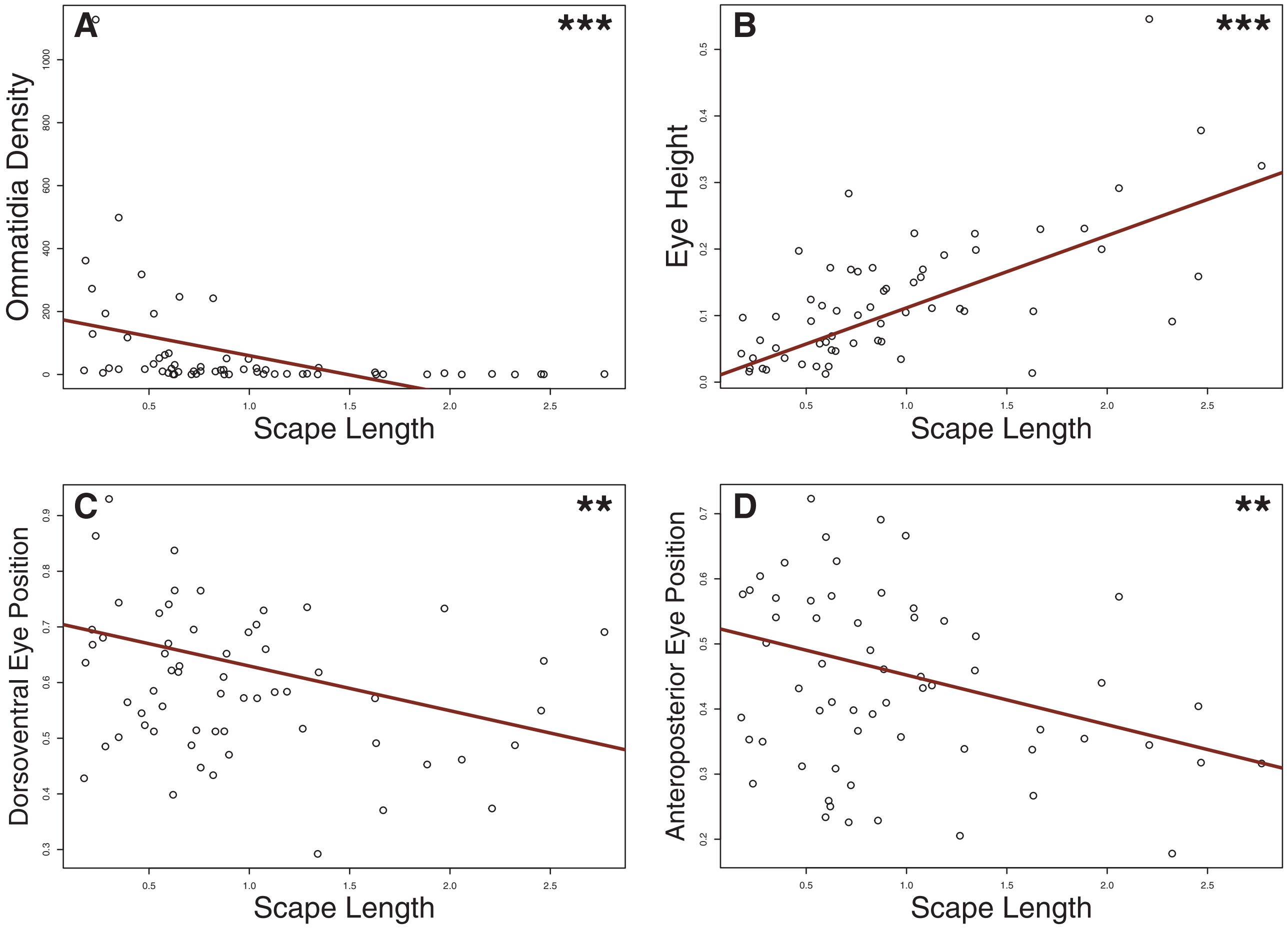

Fig. 4. Phylogenetic Generalized Least Squares regression of scape length and eye traits. Results of linear regressions of visual traits against scape length; (A) ommatidia density R^2 = 0.1754, P = 0.0004615; (B) eye height R^2 = 0.4735, P = 5.40 x 10^{-10}; (C) dorsoventral eye position R = 0.1365, P = 0.001975; (D) anteroposterior eye position R^2 = 0.1286, P = 0.002643. Scape and eye height are scaled by head area. All specimens were included in analyses (n = 64); PGLS relationships from Blanchard and Moreau 2017. ** denotes $P \leq 0.01$; *** $P \leq 0.001$.

2009, Streinzer et al. 2013, Gonzalez-Bellido 2011, Land and Nilsson 2012, Schoenemann et al. 2017). Decreasing ommatidia density relative to scape length increases may indicate a possible trade-off between visual acuity and tactile/olfactory investment. Although, it is important to note that none of the other measurements of visual acuity (e.g., eye size) display a similar relationship with antennal scape length.

Even as some morphological measurements are directly linked to ecology, developmental and energetic trade-offs contribute to observed phenotypic diversity. In holometabolous insects, developmentally linked traits are limited by a finite amount of resources available to proximate tissues during the larval state but are also affected by adult ecological selection pressures. Notable examples include alternate positions of sexually-selected cranial and

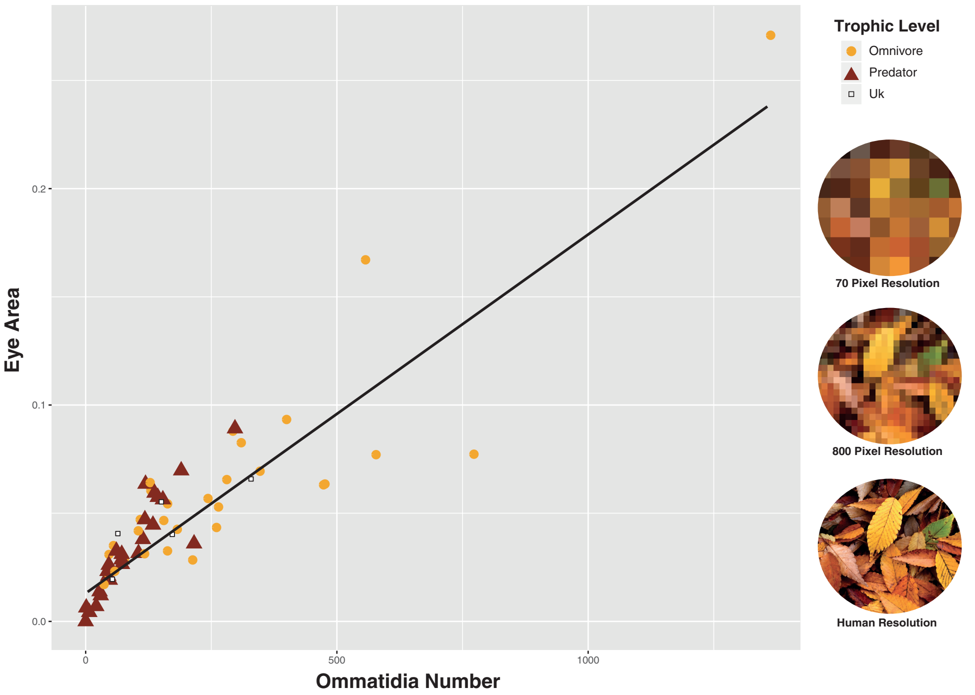

Fig. 5. Visual acuity and trophic level. (Left) Variation between eye area and ommatidia number across sampled ant species. Trophic level information displays omnivorous (n = 31) and predatory (n = 28) ant species. Unknowns are also included (n = 11). Trendline shows linear regression of ommatidia number and eye area ($R^2 = 0.7908$, $P = < 2.2 \times 10^{-16}$). Both measurements are scaled by frontal head area. (Right) Simplified, hypothetical representation of visual acuity based on ommatidia number.

pronotal horns in dynastid beetles that are coupled with apparent trade-offs in proximal non-horn structures such as antennae or wings (Emlen 2001); a diverse assemblage of horns across species is therefore ultimately a result of complex trade-offs among ecologically relevant features (Emlen et al. 2005). Such trade-offs may be especially prevalent in sensory tissues, as these are relatively costly during development (Niven and Laughlin 2008, Keesey et al. 2019). The positive relationship between eye height and scape length may also be linked to close proximity of developmental tissues. If a common developmental factor is responsible for elevation increases in both structures, these elements would be expected to covary—this has been proposed as an explanation for positive covariation between weevil rostrum and antennae, for example (Painting and Holwell 2013). Linked mechanisms may also explain apparent relationships between scape length and eye placement. At the same time, energetic trade-offs between proximate structures in development may inversely link ommatidial and antennal tissue development. Without more intensive sampling and developmental experiments, our explanations remain speculative, however, our results appear to further underscore the complex relationship between developmental constraints and ecological selective pressures.

Because our focus was on interspecific variation at a broad scale, our dataset was limited to only include specimens of the worker caste. It is also important to note that there are intraspecific trends in varying investment in visual systems due to the division of labor within colonies (Arganda et al. 2020). Alates generally exhibit a larger investment in vision due to the demands of navigating their environment while flying (Narendra et al. 2011). It is notable that eyes are retained in queens and males among species with eyeless workers. Additionally, species with worker polymorphism may exhibit distinct trends in sensory investment. With foundational work conducted by Divieso et al. (2020) examining how visual traits differ among castes, incorporating ecological occupation may reveal the processes governing variation in eyes and other features.

Although we did not assess the trait here, ommatidial angle could also yield insight into the diversity of eyes. The ommatidial angle limits the amount of light captured and can, therefore, impact the resolution of vision (Narendra et al. 2011, Nilsson and Odselius 1981). Diurnal and nocturnal species of ants as well as bees exhibit differing eye area and ommatidial diameters (Greiner et al. 2007, Narendra et al. 2011, Jander and Jander 2002, Greiner et al. 2004, Somanathan et al. 2009, Yilmaz et al. 2014). Furthermore, colony size, behavior, and nesting niche may also be playing a role in the diversity of the eye across ants. These functional traits are vital to the success of ant lineages and therefore may be informative in driving variation among sensory tissues.

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

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Author Contributions

C.J. and P.B. are credited with conceptualization and methodology; C.J. collected data; C.J. and P.B. analyzed data; visualization was done by C.J. and P.B., and C.J. and P.B. wrote the manuscript.

References Cited

Arganda, S., A. P. Hoadley, E. S. Razdan, I. B. Muratore, and J. F. Traniello. 2020. The neuroplasticity of division of labor: worker polymorphism, compound eye structure and brain organization in the leafcutter ant *Atta cephalotes*. J Comp Physiol A. 206: 2020-03.

Baker, G. T. and P. W. Ma. 2006. Morphology and number of ommatidia in the compound eyes of *Solenopsis invicta*, *Solenopsis richteri*, and their hybrid (Hymenoptera: Formicidae). Zool Anz. 245: 121–125.

Barr, T. C. 1986. An eyeless subterranean beetle (Pseudanophthalmus) from a Kentucky coal mine (Coleoptera: Carabidae: Trechinae). Psyche. 93: 47–50.

Bernstein, S. and C. Finn. 1971. Ant compound eye: size-related ommatidium differences within a single wood ant nest. Experientia. 27: 708–710.

Blair, S. S. 2009. Imaginal discs, pp. 489–492. In V. H. Resh and R. T. Cardé (eds.), Encyclopedia of insects, 2nd ed. Academic Press, Cambridge, USA.

Blanchard, B. D. and C. S. Moreau. 2017. Defensive traits exhibit an evolutionary trade-off and drive diversification in ants. Evolution. 71: 315–328.

Bolton, B. 1995. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, MA.

Borst, A. 2009. Drosophila's view on insect vision. Curr biol. 19: R36–R47.

Cronin, T. W., S. Johnsen, N. J. Marshall, and E. J. Warrant. 2014. Visual ecology. Princeton University Press, Princeton, NJ.

De Celis, J. F. and A. García-Bellido. 2013. Imaginal Disks, pp.19–23. In S. Maloy and K. Hughes (eds.), Brenner's Encyclopedia of Genetics, 2nd ed. Academic Press, Cambridge, USA.

Divieso, R., T. S. Silva, and M. R. Pie. 2020. Morphological evolution in the ant reproductive caste. Biol J Linn Soc. 131: 465–475.

Emlen, D. J. 2001. Costs and the diversification of exaggerated animal structures. Science. 291: 1534–1536.

Emlen, D. J., J. Marangelo, B. Ball, and C. W. Cunningham. 2005. Diversity in the weapons of sexual selection: horn evolution in the beetle genus Onthophagus (Coleoptera: Scarabaeidae). Evolution. 59: 1060–1084.

Felsenstein, J. 1985. Phylogenies and the comparative method. Am Nat. 125: 1–15.

Fichaux, M., B. Béchade, J. Donald, A. Weyna, J. H. C. Delabie, J. Murienne, C. Baraloto, and J. Orivel. 2019. Habitats shape taxonomic and functional composition of Neotropical ant assemblages. Oecologia. 189: 501–513.

Garland, T. Jr, P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst Biol. 41:18–32.

Gaudard, C. A., M. P. Robertson, and T. R. Bishop. 2019. Low levels of intraspecific trait variation in a keystone invertebrate group. Oecologia. 190: 725–735.

Gibb, H. and C. L. Parr. 2013. Does structural complexity determine the morphology of assemblages? An experimental test on three continents. PLoS One. 8: e64005.

Gibb, H., J. Stoklosa, D. I. Warton, A. M. Brown, N. R. Andrew, and S. A. Cunningham. 2015. Does morphology predict trophic position and habitat use of ant species and assemblages? Oecologia. 177: 519–531.

Gonzalez-Bellido, P. T., T. J. Wardill, and M. Juusola. 2011. Compound eyes and retinal information processing in miniature dipteran species match their specific ecological demands. P Natl Acad Sci. 108: 4224–4229.

Greiner, B., W. A. Ribi, and E. J. Warrant. 2004. Retinal and optical adaptations for nocturnal vision in the halictid bee *Megalopta genalis*. Cell. Tissue. Res. 316: 377–390.

Greiner, B., A. Narendra, S. F. Reid, M. Dacke, W. A. Ribi, and J. Zeil. 2007. Eye structure correlates with distinct foraging-bout timing in primitive ants. Curr. Biol. 17: R879–R880.

Gronenberg, W. and B. Hölldobler. 1999. Morphologic representation of visual and antennal information in the ant brain. J. Comp. Neurol. 412: 229–240.

Guilherme, D. R., J. L. P. Souza, E. Franklin, P. A. C. L. Pequeno, A. C. das Chagas, and F. B. Baccaro. 2019. Can environmental complexity predict functional trait composition of ground-dwelling ant assemblages? A test across the Amazon Basin. Acta. Oecol. 99: 103434.

Haynie, J. L., and P. J. Bryant. 1986. Development of the eye-antenna imaginal disc and morphogenesis of the adult head in *Drosophila melanogaster*. J. Exp. Zool. 237: 293–308.

Held, L. I. J. 2002. Imaginal discs: the genetic and cellular logic of pattern formation. Cambridge University Press, Cambridge, UK.

Herman, A., Y. Brandvain, J. Weagley, W. R. Jeffery, A. C. Keene, T. J. Kono, H. Bilandžija, R. Borowsky, L. Espinasa, K. O'Quin, and C. P. Ornelas-García. 2018. The role of gene flow in rapid and repeated evolution of cave-related traits in Mexican tetra, *Astyanax mexicanus*. Mol. Ecol. 27: 4397–4416.

Hölldobler, B. 1980. Canopy orientation: a new kind of orientation in ants. Science. 210: 86–88.

Jander, U. and R. Jander. 2002. Allometry and resolution of bee eyes (Apoidea). Arthropod. Struct. Dev. 30: 179–193.

Kaspari, M. 1993. Body size and microclimate use in Neotropical granivorous ants. Oecologia. 96: 500–507.

Kaspari, M. and M. D. Weiser. 1999. The size–grain hypothesis and interspecific scaling in ants. Funct. Ecol. 13: 530–538.

Keesey, I. W., V. Grabe, L. Gruber, S. Koerte, G. F. Obiero, G. Bolton, M. A. Khallaf, G. Kunert, S. Lavista-Llanos, D. R. Valenzano, and J. Rybak. 2019. Inverse resource allocation between vision and olfaction across the genus Drosophila. Nat. Commun. 10: 1162.

Klotz, J. H., B. L. Reid, and W. C. Gordon. 1992. Variation of ommatidia number as a function of worker size in *Camponotus pennsylvanicus* (DeGeer)(Hymenoptera: Formicidae). Insectes. Soc. 39: 233–236.

Knaden, M. and P. Graham. 2016. The sensory ecology of ant navigation: from natural environments to neural mechanisms. Annul. Rev. Entomol. 61: 63–76.

Koch, S., R. Tahara, A. Vasquez-Correa, and E. Abouheif. 2021. Nano-CT characterization reveals coordinated growth of a rudimentary organ necessary for soldier development in the ant Pheidole hyatti. *bioRxiv*.

Land, M. F., and D. E. Nilsson. 2012. Animal eyes. Oxford University Press, Oxford, UK.

Leys, R., S. J. Cooper, U. Strecker, and H. Wilkens. 2005. Regressive evolution of an eye pigment gene in independently evolved eyeless subterranean diving beetles. Biol. Letters. 1: 496–499.

Longino, J. T. and N. M. Nadkarni. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. Psyche. 97: 81–93.

Lorus, J. and M. J. Milne. 1948. Insect vision. Sci. Am. 179: 42–45.

Martins, E. P. and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am. Nat. 149: 646–667.

Masuko, K., 1990. Behavior and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani (Hymenoptera: Formicidae: Leptanillinae). Insectes. Soc. 37: 31–57.

Menzel, R. and R. Wehner. 1970. Eye structures in workers of different sizes from *Cataglyphis bicolor* make (Formicidae, Hymenoptera). J. Comp. Physiol. 68: 446–449.

Moran, D., R. Softley, and E. J. Warrant. 2015. The energetic cost of vision and the evolution of eyeless Mexican cavefish. Sci. Adv. 1: p.e1500363.

Narendra, A., S. F. Reid, B. Greiner, R. A. Peters, J. M. Hemmi, W. A. Ribi, and J. Zeil. 2011. Caste-specific visual adaptations to distinct daily activity schedules in Australian Myrmecia ants. Proc. Biol. Sci. 278: 1141–1149.

Nilsson, D. E., and R. Odselius. 1981. A new mechanism for light-dark adaptation in the Artemia compound eye (Anostraca, Crustacea). J. Comp. Physiol. 143: 389–399.

Niven, J. E. and S. B. Laughlin. 2008. Energy limitation as a selective pressure on the evolution of sensory systems. J. Exp. Biol. 211: 1792–1804.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, N. Isaac, and W. Pearse. 2012. Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5. https://cran.r-project.org/web/packages/caper/caper.pdf. Accessed 1 July 2021.

Painting, C. J. and G. I. Holwell. 2013. Exaggerated trait allometry, compensation and trade-offs in the New Zealand giraffe weevil (*Lasiorhynchus barbicornis*). PloS One. 8: p.e82467.

Paradis, E. and K. Schliep, 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics. 25: 526–528.

Peck, S. B. 1990. Eyeless arthropods of the Galapagos Islands, Ecuador: composition and origin of the cryptozoic fauna of a young, tropical, oceanic archipelago. Biotropica. 22: 366–381.

Pinheiro J., D. Bates, S. DebRoy, D. Sarkar, R Core Team. **2020**. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-148. https://cran.r-project.org/web/packages/nlme/index.html. Accessed 1 July 2021.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods. Ecol. Evol. 3: 217–223.

Schmidt, F. A. and R. R. C. Solar. 2010. Hypogaeic pitfall traps: methodological advances and remarks to improve the sampling of a hidden ant fauna. Insectes. Soc. 57: 261–266.

Schoenemann, B., H. Pärnaste, and E. N. Clarkson. 2017. Structure and function of a compound eye, more than half a billion years old. Proc. Natl. Acad. Sci. U. S. A. 114: 13489–13494.

Schöning, C., W. Kinuthia, and N. R. Franks. 2005. Evolution of allometries in the worker caste of Dorylus army ants. Oikos. 110: 231–240.

Silva, R. R., and C. R. F. Brandão. 2014. Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. PLoS One. 9: 93049.

Somanathan, H., A. Kelber, R. M. Borges, R. Wallén, and E. J. Warrant. 2009. Visual ecology of Indian carpenter bees II: adaptations of eyes and ocelli to nocturnal and diurnal lifestyles. J. Comp. Physiol. A. 195: 571–583.

Sosiak, C. E., and P. Barden. 2021. Multidimensional trait morphology predicts ecology across ant lineages. Funct. Ecol. 35: 139–152.

Streinzer, M., A. Brockmann, N. Nagaraja, and J. Spaethe. 2013. Sex and caste-specific variation in compound eye morphology of five honeybee species. PLoS One. 8: e57702.

Trajano, E. and M. E. Bichuette. 2010. Diversity of Brazilian subterranean invertebrates, with a list of troglomorphic taxa. Subterr Biol. 7: 1–16.

Ward, P. S. 1990. The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): generic revision and relationship to other formicids. Syst. Ent. 15: 449–489.

Weiser, M. D. and M. Kaspari. 2006. Ecological morphospace of New World ants. Ecol. Entomol. 31: 131–142.

Werner, Y. L. 1969. Eye size in geckos of various ecological types (Reptilia: Gekkonidae and Sphaerodactylidae). Isr. J. Ecol. Evol. 18: 291–316.

Wheeler, W. M. 1910. Ants: their structure, development and behavior (Vol. 9). Columbia University Press, New York City, USA.

Wheeler, W. M. 1916. An anomalous blind worker ant. Psyche. 23: 143–145.

Yilmaz, A., V. Aksoy, Y. Camlitepe, and M. Giurfa. 2014. Eye structure, activity rhythms, and visually-driven behavior are tuned to visual niche in ants. Front. Behav. Neurosci. 8: 1–9.