

1 Comparative prey transport behaviour, demographics, and diet of two sympatric driver ant species in a
2 central African rainforest

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21

22 **Author Contribution**

23 MPTGT conceived and designed the study and led the field sampling. SH conducted the
24 laboratory analyses, curated and analysed the data, and led the statistical analysis and
25 visualization. SH and MPTGT jointly developed the analytical approach and interpreted the
26 results. SH wrote the original manuscript. MPTGT and LLP contributed to manuscript
27 development and revision and supervised the study. LLP provided senior academic guidance
28 and contributed to the interpretation and revision of the manuscript. All authors reviewed and
29 approved the final manuscript.
30

31 **Data and code availability**

32 All data and R code were documented in a Git repository
33 (https://github.com/huberseb/dorylus_preay).
34
35

36 **Conflict of interest**

37 The authors declare no conflict of interest.
38

Abstract

Driver ants (*Dorylus*) are considered to be the predominant invertebrate predators in Afrotropical ecosystems, conducting vast predatory raids across the forest floor. Although these raids are fundamental to driver ant ecology, quantitative data on the diet and prey transport behaviour across the worker demographic spectrum remain limited. We describe prey transport biomechanics and diet composition of *Dorylus wilverthi* and *D. sjostedti* from primary and secondary rainforest in mainland Equatorial Guinea, using 2,933 prey samples from 25 raids across 16 colonies (4,610 measured workers). Both species exhibit continuous worker polymorphism but differ in demographic structure. Contrary to earlier studies, *D. wilverthi* shows three distinct worker size modes, including a large worker mode absent from *D. sjostedti* (two modes). Worker allometries and size range did not differ between species. Prey mass increased with worker mass ($\beta = 1.37$), whereas relative load per worker declined with worker mass ($\beta = -0.63$), indicating a size-dependent division of labour consistent with classical strength-scaling laws. Ants engaged in cooperative transport carried heavier absolute loads than solitary carriers even when accommodating that loads are shared. Cooperative transport was therefore primarily associated with larger prey items and did not function mainly to reduce individual loading, instead extending the upper limit of transportable prey. Driver ant diet was highly generalist with 25 prey orders identified; *D. wilverthi* and *D. sjostedti* exhibited near-complete order-level diet overlap (Pianka = 0.956). Our multifaceted approach provides a detailed description of prey transport ecology in driver ants, connecting worker morphology to prey characteristics, and reveals the shared biomechanical constraints of two ecologically similar driver ant species.

Key Words: morphometrics, diet analysis, army ants, biomechanics, collective behaviour, individual loading.

Introduction

Army ants are characterized by a distinct set of behavioural and reproductive traits, referred to as the ‘army ant syndrome’ (Kronauer 2009). This includes obligate collective foraging on animal prey, colony nomadism and specialised permanently wingless queens whose abdomens are capable of substantial expansion during the reproductive phase (Brady 2003). Unlike most ant species, they do not rely on individual scouts to locate food. Instead, army ants deploy large groups of foragers that move as a coordinated mass to detect and overwhelm prey (**Figure 1 A, B, D**; Kronauer 2009). The genus *Dorylus* represents a major group within the Afrotropical Dorylinae, a subfamily consisting entirely of army ants. While most *Dorylus* species forage underground (hypogaeic), members of the *Dorylus nigricans* species group, commonly referred to as driver ants (Schöning *et al.* 2026), forage on the leaf litter and climb high into the vegetation (Gotwald 1995). These ants conduct massive surface raids that can span 25 m wide

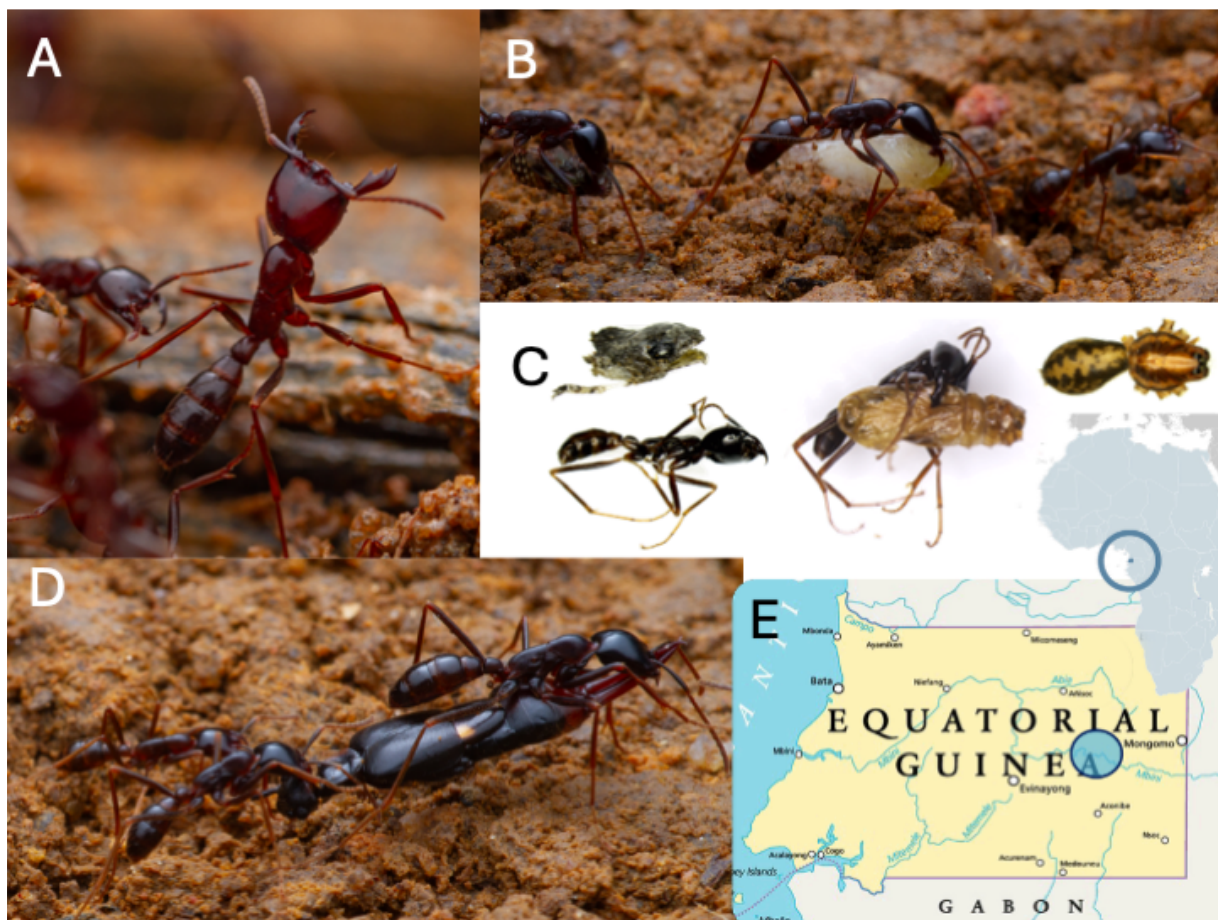


FIGURE 1, A: Driver ant (*Dorylus* sp.) worker in a defensive position. **B:** Column of *D. sjostedti* workers carrying prey to the nest. **C:** Examples of measured prey items with the corresponding *D. sjostedti* workers. **D:** *Dorylus sjostedti* cooperating to transport a large prey item. **E:** Location of the study site within Equatorial Guinea, near the capital Ciudad de la Paz. Photo credits: A, B and D by Norina Vicente, C by SH, E by MPTGT.

and 150 m long (Raignier and van Boven 1955, Leroux 1977), performed by several million workers searching the ground and vegetation for prey (Gotwald 1995; Schöning *et al.* 2008). Given the scale and presumed ecological impact of their raids, driver ants are thought to be the predominant invertebrate predators in tropical ecosystems across Africa (Gotwald 1995). Driver ant raids may influence the population dynamics of animals on or near the forest floor of Afrotropical rainforest and savannah ecosystems (Kronauer 2009). Moreover, colonies of driver ants attract a huge diversity of associates that live within the nest, follow raids, or emigrate with the colony. Associations may be obligate or facultative, parasitic or commensal, and can be seen in birds, mammals, reptiles, arachnids, worms and many orders of insect represented by over 500 described species (Kistner 1979; Kronauer 2020). A particularly well documented example of such associations are the ant-following birds. Several bird species track army ant raids in order to prey on arthropods flushed by the ants, a behaviour that has been documented in both the Afro- and Neotropics (Willis & Oniki 1978; Willson 2004; Peters *et al.* 2008; Kronauer 2009; Craig 2022; Rodrigues 2024).

In contrast to the Afrotropical genus *Dorylus*, Neotropical *Eciton* army ants have enjoyed substantial ecological study. A storied history of behavioural and ecological research suggests that *Eciton burchellii* is the predominant Neotropical invertebrate predator and hosts the largest associate assemblage yet known to science (Boswell *et al.* 1998; Rettenmeyer *et al.* 2011). Notably, the associates of *E. burchellii* have been comparatively very well studied compared to the driver ant system in the Afrotropics, showing that the assemblage of ant-following birds are (klepto-) parasitic, as the birds significantly reduce the ants' foraging success (Wrege *et al.* 2005). Moreover, certain butterfly species have evolved to exploit this interaction by feeding on the faecal remains left behind by the birds near the active raids (Ray & Andrews 1980). These examples highlight the complex direct and indirect relationships driven by the foraging behaviour of army ants, emphasizing their ecological significance and underscoring the need to investigate whether *Dorylus* species play a similarly integral role in their ecosystems. Understanding the dietary habits and biomechanical foraging boundaries of such dominant predators is crucial to comprehend their ecological roles, particularly in complex ecosystems such as central African rainforests. Moreover, the prey transport behaviour of driver ants is fundamental to their biology, and their ability to convey large quantities of prey biomass back to the nest fuels colony growth and activity. While past studies into *Dorylus* foraging ecology and diet have mainly relied on empirical observations, a quantitative analysis is missing, especially in West Africa (Schöning *et al.* 2008).

To this end, we combined quantitative diet analysis with biometric measurements to explore the predatory ecology of the two driver ant species *D. wilverthi* Emery, 1899 and *D. sjostedti* (formerly *D. nigricans sjostedti* Emery, 1899). We collected prey samples from these two driver ant species from raids occurring in rainforests in Equatorial Guinea, utilizing quantitative methodologies to overcome the limitations of previous qualitative studies, as well as closing the research gap for West Africa (Schöning 2004; Schöning *et al.* 2008).

Specifically, our goals were to (1) reveal the prey transport biomechanics and demographics of *D. wilverthi* and *D. sjostedti*, noting any similarities and differences, and (2) understand the broad diet composition of *D. wilverthi* and *D. sjostedti* given their sympatry. To achieve this, we morphologically identified prey items to order- or family-level that were collected in the field in Equatorial Guinea. Further, we measured the size and weight of prey items and the ants that were carrying them to gain insight into driver ant worker demographics, the intra and interspecies allometric relationships regarding their biomechanical constraints, and division of prey transport labour among workers. We then compared the diet of the two driver ant species to identify potential differences, which could indicate niche separation or specialisation regarding prey preferences. Since the samples have been collected in both primary and secondary forest plots, we further examined whether diet composition and biometrics varied with forest type.

Methods

Study location

Our study took place in a lowland rainforest adjacent to the city of Ciudad de la Paz in mainland Equatorial Guinea (**Figure 1E**). Our sites consist of two ca. 70 ha plots in tall, closed canopy forest as part of a much wider continuous forest broken only by a handful of lightly travelled roads. One plot (1°36'57.5"N 10°52'37.5"E) is characterized as primary forest and has not been significantly logged; the other plot (1°36'57.8"N 10°51'49.1"E) is characterized as secondary forest, remains closed-canopy, but has been regularly selectively logged for decades, with the last harvest in the mid-to-late 2010s.

Collection of prey items and their carriers

To collect prey samples, we located driver ant foraging columns along a network of small trails cut through the forest. Upon finding a column, we searched for a safe space near the column to

collect prey items travelling back to the nest. Using forceps and/or aspirators, we collected individual prey items and all the ants carrying them in separate 2 mL collection tubes filled with 95% ethanol; ants reacting aggressively towards us were not included in the sample – only the ants originally carrying the prey item. We collected a total of 4278 prey item (Figure 1C) samples from 25 raids across 16 different driver ant colonies between two field seasons spanning from 13th July to 22nd August 2024 and from 23rd January to 11th February 2025. We collected samples from 17 raids in the primary forest and 8 in the secondary forest.

Specimen identification and measurements

In the laboratory we identified prey items morphologically to order- or family-level, where possible. Prey items that were ants were often also identified to genus level (Fisher & Bolton 2016). We documented the number of ants carrying each prey item. For the prey items we further recorded its life stage, whether it has been dismantled by the ants for transportation, and whether it was a holometabolous species or not. When an item was unidentifiable, it was marked as such. Samples with two prey items and samples with multiple prey items and multiple ants were not considered. In total we removed 1,345 prey samples because they either contained multiple prey items in a single tube, making it impossible to assign the prey item to an individual ant, no prey item was present in the tube, or contained a prey item that had disintegrated and could not be reliably measured or identified.

After excluding such samples, a total of 2933 prey item samples were taken forward for analysis. Across these samples, 68 % were collected from *D. sjostedti* (n = 2010) in 15 observed raids from 11 different colonies and 32 % were of *D. wilverthi* (n = 923) in 10 raids from 6 different colonies. Further, 62 % of all *D. sjostedti* samples were collected in primary forest and 67 % were single carrying ants, while 38 % of all *D. wilverthi* samples were collected in primary forest and 59 % were single carrying ants. Samples contained a total of 4610 ants with *D. sjostedti* contributing 65 % (n = 3015) and *D. wilverthi* 35 % (n = 1595).

We measured prey items and driver ant specimens in length and width using digital callipers (Preciva LF41, ± 0.01 mm). For prey items, we took the maximum possible length and width. For *Dorylus*, we measured width by taking the maximal head width and length by measuring from the end of the clypeus to the end of the gaster with the ant body pulled lengthways to its maximal size. For weight we measured wet weight on a high precision scale (Ohaus Analytical Plus AP210, ± 0.1 mg). Before measuring, we surface dried each specimen on a clean sheet of

standard laboratory tissue for 10 seconds to remove any droplets of ethanol. Prey shape was calculated by dividing the length by the width, generating a ratio of the two dimensions.

Statistical analyses

We $\log_{10}$ transformed all measured biometric traits for ants and prey items to better meet the assumptions of parametric analyses and linearize the relationships between variables. After transformation, the Shapiro-Wilk tests showed significance (all $p < 0.0001$), which was expected given the large sample size ($n = 2933$). However, high W-values ($W = 0.956 - 0.988$) suggested an acceptable approximation to normality. We analysed mean differences in biometric traits of workers between species on log-transformed data using Welch's t-tests.

To analyse the demographic differences of worker size and weight between the two *Dorylus* species, we tested distributional differences on the non-log-transformed data. Overall differences in the distributions were first tested using a two-sample Kolmogorov-Smirnov test and a more tail sensitive two-sample Anderson-Darling test from the R package "kSamples" (Scholz & Zhu 2025). To further characterize the demographic structure of worker biometrics within each species, unimodality and minimum number of modes were assessed. Multimodality was tested with Hartigan's dip test from the R package "dipTest" (Maechler 2025). The number of at least k modes was evaluated using Silverman's critical bandwidth test from the R package "multimode", testing for $k = 1$, $k = 2$ and $k = 3$ (Ameijeiras-Alonso *et al.* 2025).

We fitted linear regression models on $\log_{10}$ -transformed continuous data to analyse the relationships between biometric traits of ants and prey items. We constructed a base model for ant body allometry (AA; $\log_{10}(\text{ant head width}) \sim \log_{10}(\text{ant body length})$), ant-prey weight allometry (AP; $\log_{10}(\text{prey weight}) \sim \log_{10}(\text{ant weight})$), relative loading (RL; $\log_{10}(\text{relative loading}) \sim \log_{10}(\text{ant weight})$, with relative loading defined as $\text{prey weight} / \text{ant weight}^2$) and absolute loading (AL; $\log_{10}(\text{load per ant}) \sim \log_{10}(\text{ant weight})$), with load per ant defined as $\text{ant loading} / \text{total number of carrying ants}$). We used data from all measured ants to fit the models for ant allometry (AA) and absolute loading (AL). The ant-prey weight allometry model (AP) as well as the relative loading model (RL) was fitted based on data from only single carrying ants.

Subsequently, we created a series of models with various covariates as main effects or interactions to the base models. Covariates included ant species (*D. wilverthi* and *D. sjostedti*),

forest type (primary and secondary forest), prey shape (prey length per prey width) and carrier type (single and multiple carriers). Interaction terms were used to test for species-specific differences in allometric scaling, whereas additive terms tested for shifts in intercepts. Heteroscedasticity was tested using Breusch-Pagan tests from the R package “lmtest” (Zeileis & Hothorn 2002). The residual patterns and the conducted Breusch-Pagan tests (all $p < 0.0001$) showed clear signs of heteroscedasticity in all models (Supplementary Information S1). Therefore, all statistical results for all linear models were adjusted to heteroscedasticity-consistent (HC3) robust standard errors from the R package “sandwich” (Zeileis 2004; Zeileis *et al.* 2020). A more detailed description of model performance and model selection can be found in the supplementary information (S2).

For simplification in visualization of the fitted models we used the base model without interacting factors and main effects, whereas we choose the corresponding models of best fit for ecological interpretation. Equations of the base models are stated within the figure descriptions. All plots were created with the R package “ggplot2” (Wickham 2016). All statistical analyses were conducted in R (R Core Team 2024).

We fitted multivariate generalized linear models to analyse dietary differences between the two *Dorylus* species with forest type added as an interaction term (MGLMs; multivariate prey abundance ~ ant species $\times$ forest type) in the R package “mvabund” (Wang *et al.* 2012). MGLMs were based on raid-level pooled prey counts and implemented with the “manyglm” function on a negative binomial error distribution. We evaluated model significances using likelihood ratio tests with Monte Carlo resampling (999 iterations) via the “anova.manyglm” function, with adjusted univariate p-values. Furthermore, we tested the observed dietary niche overlap between the two *Dorylus* species against a null model of resource use. Niche overlap was quantified using Pianka’s niche overlap index (Pianka 1973) from the R package “EcoSimR” (Gotelli *et al.* 2015), with null distributions generated by the “ra3” randomization algorithm over 10,000 replications from the “niche_null_model” function.

Results

Ant Biometrics

We first compared the measured biometric traits, shown in **Table 1**, to determine basic morphological size differences between the two species. The mean biometric traits between species only differed significantly in ant body length (Welch’s t-test on $\log_{10}$ transformed data:

$t = -3.526$, $p = 0.0004$). Workers of *D. wilverthi* were 5.7 % longer (mean = 7.32 mm) than workers of *D. sjostedti* (mean = 7.02 mm). The mean head width was 1.62 mm for *D. sjostedti* and 1.66 mm for *D. wilverthi* with no significance between log transformed data (Welch's t-test, $t = -0.517$, $p = 0.6053$). The mean body weight was 6.7 mg for *D. sjostedti* and 7.7 mg for *D. wilverthi* with no significant difference between log transformed data (Welch's t-test, $t = -1.789$, $p = 0.0737$).

TABLE 1 Ant and prey biometric data with differences ($\Delta\%$) between *D. sjostedti* (DS) and *D. wilverthi* (DW). Statistical differences were evaluated with Welch's t-tests on $\log_{10}$ transformed data.

Metric	mean DS ($\pm$ 95% CL)	mean DW ($\pm$ 95% CL)	$\Delta\%$	t	p	Sig
Ant body length [mm]	7.02 (6.94 – 7.09)	7.32 (7.20 – 7.43)	4.1	-3.53	0.0004	**
Ant head width [mm]	1.62 (1.60 – 1.64)	1.66 (1.62 – 1.69)	2.4	-0.52	0.6053	n.s.
Ant weight [mg]	6.7 (6.52 – 6.93)	7.7 (7.33 – 8.05)	12.5	-1.79	0.0737	n.s.
Prey length [mm]	6.23 (6.10 – 6.35)	6.91 (6.69 – 7.13)	9.8	-5.42	< 0.0001	***
Prey width [mm]	2.55 (2.50 – 2.61)	2.95 (2.86 – 3.04)	13.6	-7.56	< 0.0001	***
Prey weight [mg]	14.3 (13.61 – 14.90)	18.2 (17.10 – 19.36)	21.8	-6.25	< 0.0001	***
Prey shape	2.79 (2.71 – 2.87)	2.74 (2.61 – 2.87)	1.8	2.27	0.0237	*
Prey area [mm ²]	17.15 (16.60 – 17.70)	21.61 (20.55 – 22.67)	20.60	-7.70	< 0.0001	***

DS = *D. sjostedti*, DW = *D. wilverthi*, 95% CL = 95% Confidence Level, t = t-value, p = p-value with * $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$ and n.s. = not statistically significant.

Furthermore, the distributional differences in biometrics were assessed to investigate demographical differences. The two-sample Kolmogorov-Smirnov test suggested significant distributional differences between the two species in length ($D = 0.0908$, $p < 0.0001$), width ($D = 0.0673$, $p < 0.0001$) and weight ($D = 0.0788$, $p < 0.0001$). Furthermore, the more tail sensitive two-sample Anderson-Darling test revealed significant (all $p < 0.0001$) deviations in overall distributional shape for all ant biometrics (length AD = 17.05; width AD = 7.23; weight AD = 9.12). This indicates that the biometrics of the two ant species differ particularly in their tail regions of the distributions.

Demographic structures in worker biometrics were further analysed with a Hartigan's Dip test, which showed significant deviation from unimodality in all biometric traits ($p < 0.026$) in both species. Further, the Silverman's critical bandwidth test (SM) for *D. wilverthi* indicates a minimum of three distinct modes, with no indication of four modes, for body length (SM $k = 2$, $p = 0.0060$; SM $k = 3$, $p = 0.8869$) and head width (SM $k = 2$, $p = 0.0250$; SM $k = 3$, $p = 0.9349$). In contrast, the Silverman's test for *D. sjostedti* indicates a minimum of two modes, with no indication of a third mode for both body length (SM $k = 1$, $p = 0.0010$; SM $k = 2$, $p =$

0.2863) and head width (SM $k = 1$, $p < 0.0001$; SM $k = 2$, $p = 0.5495$). For ant weight, Silverman's test showed no significant evidence for multimodality, suggesting the absence of a clearly separated additional mode. The histograms in **Figure 2** also showed that *D. wilverthi* had a clear third mode in body length and head width distribution, whilst *D. sjostedti* only showed two. This indicates three distinguishable main worker size groups within *D. wilverthi* and two within *D. sjostedti* along an overall continuous polymorphic distribution.

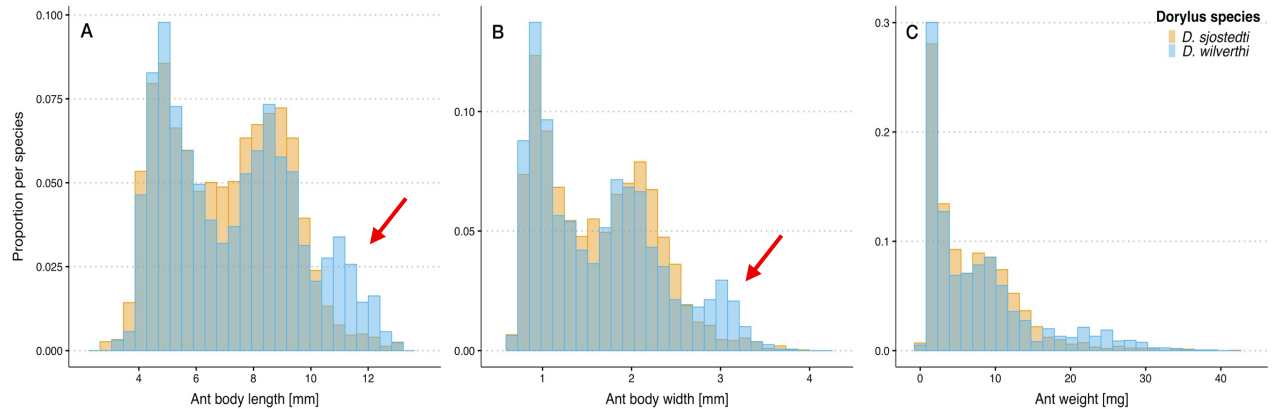


FIGURE 2 Overview of ant biometrics. Histograms showing the proportional distribution of ant body length (A), ant head width (B) and ant weight (C) for *D. sjostedti* (orange) and *D. wilverthi* (blue). The red arrow indicates the third size category of larger workers only occurring in *D. wilverthi*.

We fitted a linear model to investigate the allometric scaling between ant body length and head width (AA; head width $\sim$ body length $\times$ ant species + forest type). The model revealed a strong positive allometric relationship between ant body length and head width ($\beta = 1.285$, $p < 0.0001$; **Table 2**). The model explained 96.8 % ($R^2 = 0.968$) of the variation in head width, with body length being the dominant predictor (**S2**). Workers of *D. wilverthi* had significantly narrower head than *D. sjostedti* at a given body length, but the effect size was low ($\beta = -0.028$, $p < 0.0001$). Workers from secondary forests had slightly wider heads than those from primary forests at comparable body length, with a similarly low effect size ($\beta = 0.0069$, $p < 0.0001$). The interaction between body length and ant species was not significant ($\beta = 0.0158$, $p = 0.0540$), indicating no statistically significant species-specific differences in the allometric relationship. Therefore, both *Dorylus* species follow the same allometric scaling pattern, as illustrated in **Figure 3**. The linear model AA explaining the allometric relationship between ant body length and head width is described as Head Width = $10^{(0.8887 - 0.0285 \times \text{Species} + 0.0069 \times \text{Forest}) \times \text{Body Length}^{(1.288 + 0.0158 \times \text{Species})}$ (model default is *D. sjostedti* in primary forest).

TABLE 2 Estimates (HC3 corrected) of linear regression models describing the allometric scaling for ant allometry (AA), ant-prey relationship (AP), relative loading (RL) and absolute loading (AL).

Predictor	Est.	SE	t	p	Sig.
Ant Allometry – AA					
Intercept	-0.8887	0.0047	-190.39	< 0.0001	***
log10(Ant Length)	1.2855	0.0054	238.70	< 0.0001	***
Ant Species	-0.0285	0.0072	-3.95	< 0.0001	***
Forest Type	0.0069	0.0010	6.84	< 0.0001	***
log10(Ant Length) × Ant Species	0.0158	0.0082	1.93	0.0540	n.s.
Ant Prey Relationship – AP					
Intercept	-0.2861	0.0389	-7.36	< 0.0001	***
log10(Ant Weight)	1.3654	0.0329	41.47	< 0.0001	***
Ant Species	-0.0194	0.0604	-0.32	0.7488	n.s.
Forest Type	-0.0018	0.0161	-0.11	0.9102	n.s.
Prey Shape	-0.0018	0.0065	-0.28	0.7820	n.s.
log10(Ant Weight) × Ant Species	0.0226	0.0612	0.37	0.7125	n.s.
Relative Loading – RL					
Intercept	-0.2861	0.0389	-7.36	< 0.0001	***
log10(Ant Weight)	-0.6345	0.0329	-19.27	< 0.0001	***
Ant Species	-0.0194	0.0604	-0.32	0.7488	n.s.
Forest Type	-0.0018	0.0161	-0.11	0.9102	n.s.
Prey Shape	-0.0018	0.0065	-0.28	0.7820	n.s.
log10(Ant Weight) × Ant Species	0.0226	0.0612	0.37	0.7125	n.s.
Absolute Loading – AL					
Intercept	0.4594	0.0183	25.12	< 0.0001	***
log10(Ant Weight)	-0.4579	0.0166	-27.64	< 0.0001	***
Carrier Type	-0.0601	0.0158	-3.81	0.0001	***
Ant Species	0.0306	0.0155	1.97	0.0485	*
Forest Type	0.0317	0.0125	2.53	0.0112	*
Prey Shape	-0.0178	0.0031	-5.68	< 0.0001	***
Carrier Type × Ant Species	0.0476	0.0264	1.8	0.0720	n.s.

Est. = Estimates, SE = Standard Error, t = t-value, p = p-value with * p<0.05, ** p<0.001, *** p<0.0001 and n.s = not statistically significant

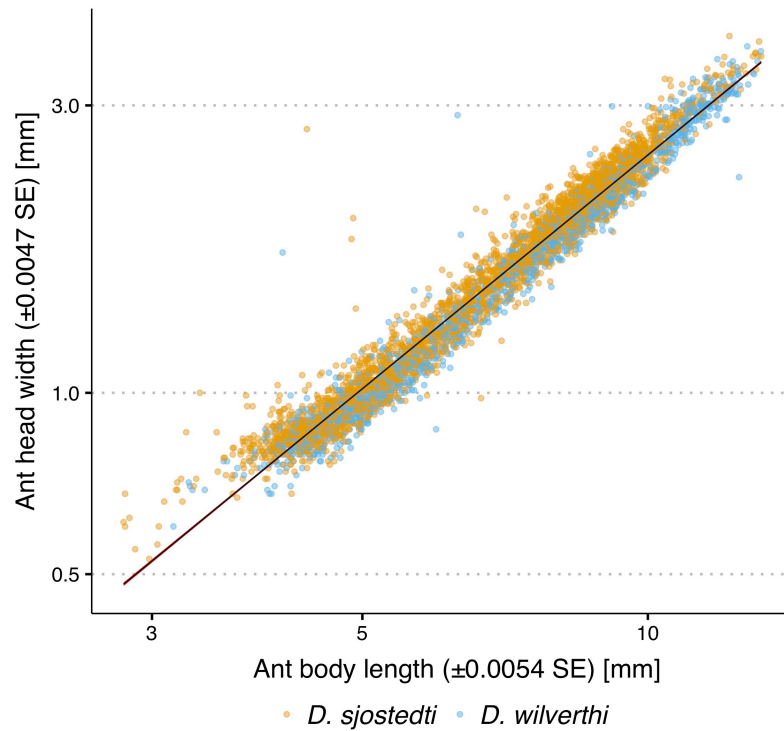


FIGURE 3. LRM for the allometric relationship between ant head width and ant body length for both species. Regression line shows fit from a reduced base model without interacting term and main effects. The standard error of the regression line is displayed, but not clearly visible due to small values. The relationship shown here is described by: $Head\ Width = 0.1277 \times Body\ Length^{1.289}$

Prey biometrics

We assessed whether prey biometrics varied between the two *Dorylus* species and across forest types (**Figure 4**). All size related prey item metrics had a highly significant difference between the two ant species (Welch's t-test on $\log_{10}$ transformed data, all p-values < 0.0001; **Table 1**). Prey shape (length ÷ width) ($p = 0.0237$) and prey size (length x width) ($p < 0.0001$) also displayed significant differences between the two *Dorylus* species. *Dorylus sjostedti* carried items with a mean length of 6.23 mm, width of 2.55 mm and weight of 14.3 mg, whereas *D. wilverthi* carried items with a mean length of 6.91 mm, width of 2.95 mm and weight of 18.2 mg. Prey items carried by *D. wilverthi* were 9.8% longer, 13.6 % wider and 21.8 % heavier than prey items carried by *D. sjostedti*. On average, *D. sjostedti* carried 1.8% more elongate prey items, but 20.6 % smaller by area than *D. wilverthi* (mean prey size: DS = 17.15 mm², DW = 21.61 mm²).

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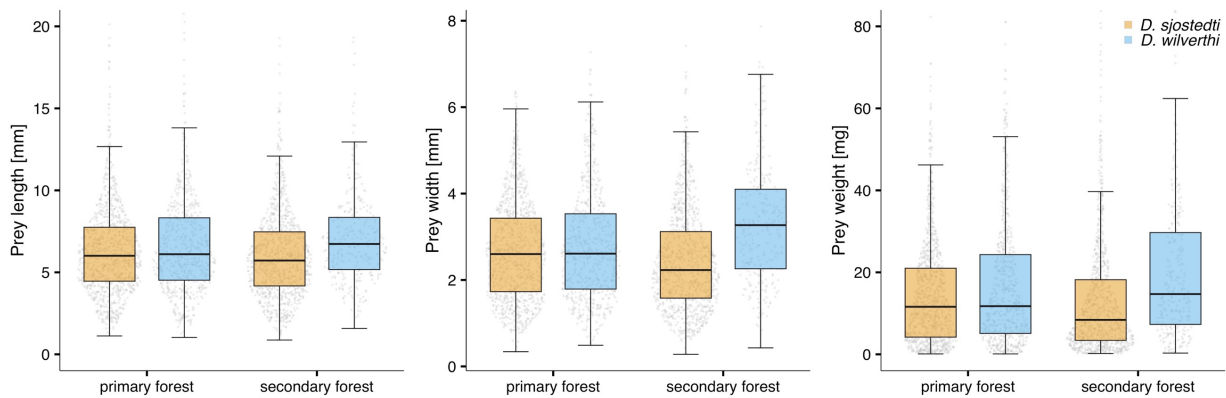


FIGURE 4 Boxplots showing prey metrics length (mm), width (mm) and weight (mg) for *Dorylus wilverthi* (blue) and *D. sjostedti* (orange) separated for primary and secondary forest. Individual prey items are shown using jittered points along the boxplot y axis.

283 Allometric relationships between ant and prey

284 We fitted a linear model to examine the allometric relationship between prey weight and ant
 285 weight (AP; prey weight $\sim$ ant weight $\times$ ant species + forest type + prey shape). For visualization
 286 of the overall scaling pattern **Figure 5** shows the corresponding reduced base model without
 287 interacting term or main effects. Statistical inference and interpretation were based on the linear
 288 model AP, describing the allometric relationship between prey weight and ant weight expressed
 289 as Prey Weight = $10^{(-0.2861 - 0.0194 \times \text{Species} - 0.0018 \times \text{Forest} - 0.0018 \times \text{Prey Shape})} \times \text{Ant Weight}^{(1.3654 + 0.0226 \times \text{Species})}$ (model default is *D. sjostedti* in primary forest).

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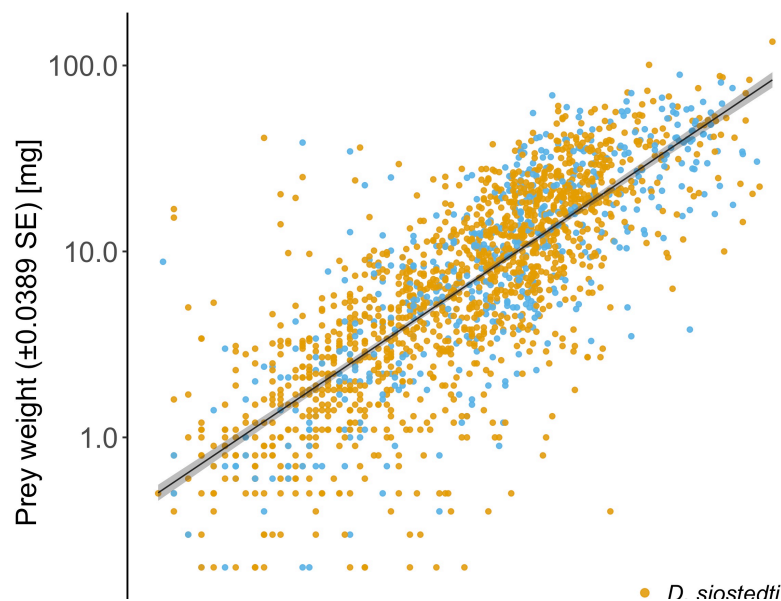


Figure 5. The allometric relationship between individual ants and their prey items for *D. wilverthi* (blue) and *D. sjostedti* (orange). Regression line represents reduced linear model without interaction terms and main effects, fitted for visualization only; statistical inference and interpretation are based on the AP M3 model. Base model is expressed by Prey Weight = $0.5304 \times \text{Ant Weight}^{1.3732}$

The AP model revealed a strong positive allometric relationship between single carrying worker weight and prey weight ($\beta = 1.365$, $p < 0.0001$; **Table 2**). Prey weight increased substantially with ant weight, demonstrating that heavier workers carried heavier prey items in absolute terms. The model explained 61.2 % (adjusted R^2) of the variation in prey weight, with ant weight being the dominant predictor. In contrast, the two ant species did not differ in the weight of the prey they carried at a given ant weight ($\beta = -0.0194$, $p = 0.7488$). Forest type ($\beta = -0.0018$, $p = 0.9102$) and prey shape ($\beta = -0.0018$, $p = 0.7820$) did not explain additional variation in prey weight. The interaction between ant weight and ant species was not significant ($\beta = 0.0226$, $p = 0.7125$), indicating no statistical evidence for species-specific differences in the relationship between ant weight and prey weight.

To test whether smaller workers carry proportionally heavier loads than larger workers, we analysed the allometric scaling of relative load with ant body weight, which is expressed by the linear model RL (RL; ant weight $\sim$ relative load $\times$ ant species + forest type + prey shape). For visualization of the overall scaling pattern **Figure 6** shows the corresponding reduced base model without interacting term or main effects. Statistical inference and interpretation were based on the linear model RL, describing the allometric relationship between load carries and ant weight in single carriers as $\text{Relative Load} = 10^{(-0.2861 - 0.0194 \times \text{Species} - 0.0018 \times \text{Forest} - 0.0018 \times \text{Prey Shape})} \times \text{Ant Weight}^{(-0.6345 + 0.0226 \times \text{Species})}$ (model default is *D. sjostedti* in primary forest).

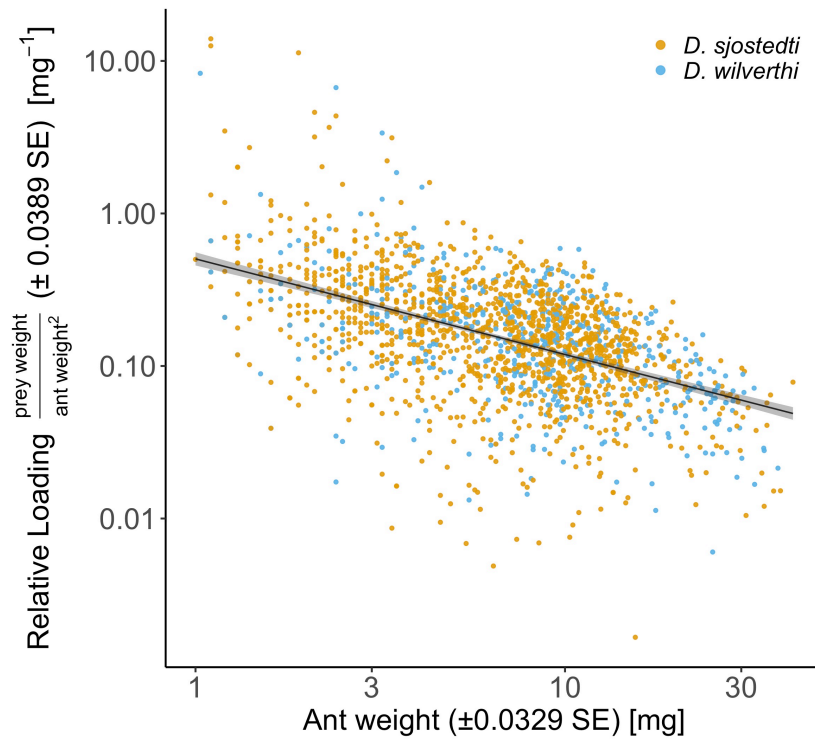
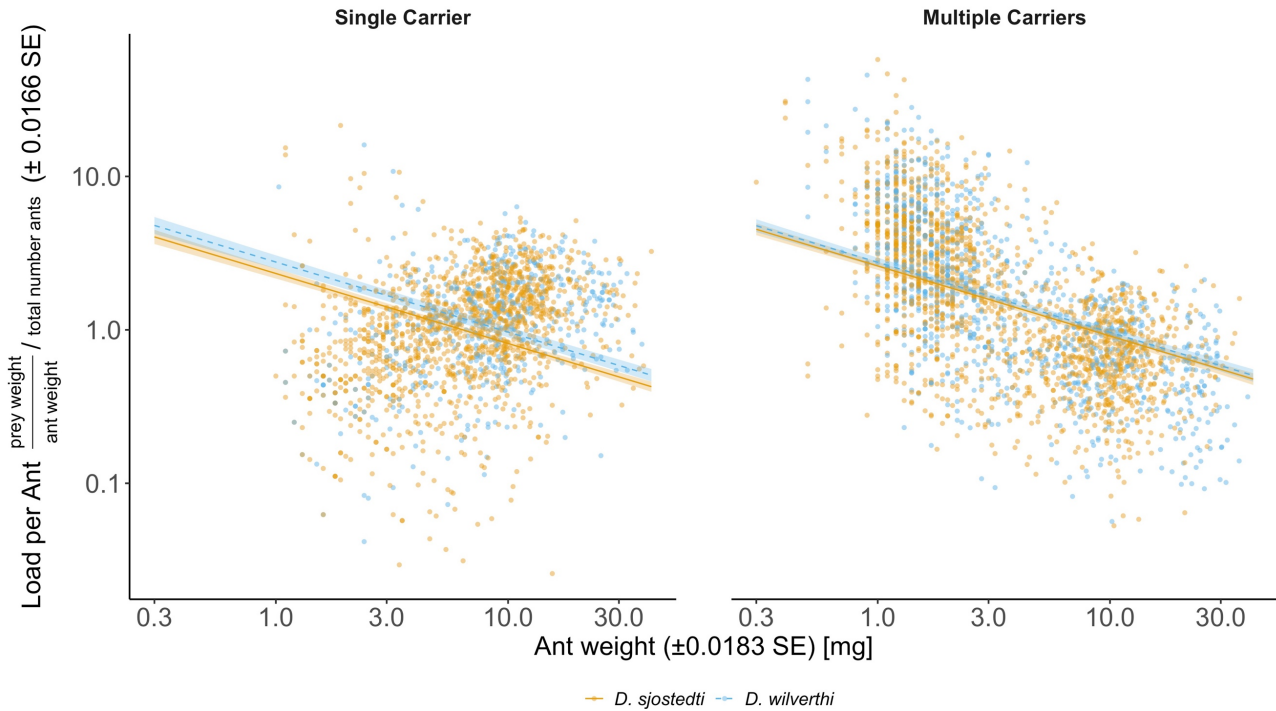


Figure 6. The relative load carried by single workers of *D. wilverthi* (blue) and *D. sjostedti* (orange), where relative load = prey weight ÷ ant weight². The regression line represents a reduced linear model without interaction terms and main effects, fitted for visualization only; statistical inference and interpretation are based on the RL M3 model. Base model is expressed by Relative Loading = $0.5304 \times \text{Ant Weight}^{-0.6268}$

The RL model revealed a strong negative allometric relationship between worker weight and their loads relative to their body mass ($\beta = -0.6345$, $p < 0.0001$; **Table 2**). Relative load decreased substantially with ant weight, demonstrating that heavier workers are less loaded than lighter ones relative to their own body mass. The model explained 61.2 % of the variation within relative loading (adjusted $R^2 = 0.612$), with ant weight being the dominant predictor (**Table 2**). The two driver ant species did not differ in the relative load carried at a given ant weight (Ant Species: $\beta = -0.0194$, $p = 0.7488$). Forest type ($\beta = -0.0018$, $p = 0.9102$) and prey shape ($\beta = -0.0018$, $p = 0.7820$) did not explain additional variation in relative load. The interaction between relative load and ant species was not significant ($\beta = 0.0226$, $p = 0.7125$), indicating no evidence for species-specific differences in the relationship between ant weight and relative load.

To investigate how individual workers contribute to prey transport depending on their body weight in single and multiple carriers we analysed the allometric relationship between ant body weight and the absolute load carried per worker (AL; ant weight ~ load per ant + carrier typ × ant species + forest type + prey shape). For visualization of the overall scaling pattern **Figure 7** shows a predicted model without main effects. Statistical inference and interpretation were

336 based on the linear model AL, describing allometric relationship between the absolute load per
 337 ant and ant weight as $\text{Absolute Load} = \text{Ant weight}^{(-0.4579)} \times 10^{(0.4594+0.0306 \times \text{Species} + 0.0317 \times \text{Forest} - 0.0178$
 338 $\times \text{Prey shape}) \times 10^{(-0.0601 \times \text{Carrier} + 0.0476(\text{Carrier} \times \text{Species}))}$ (model default is *D. sjostedti* in primary forest).
 339



340 **Figure 7.** Absolute load per ant (prey weight ÷ number of ants) in relation to ant weight for single carriers
 341 (left) and multiple carriers (right) as well as *D. sjostedti* (orange; full line) and *D. wilverthi* (blue; dotted line).
 342 Regression lines represent reduced and linear models without forest type and prey shape included. Regression
 343 lines are expressed as Load per Ant (*D. sjostedti*; multiple) = $2.6110 \times \text{Ant Weight}^{-0.4562}$; Load per Ant (*D.*
 344 *sjostedti*; single) = $2.3300 \times \text{Ant Weight}^{-0.4562}$; Load per Ant (*D. wilverthi*; multiple) = $2.7560 \times \text{Ant Weight}^{-0.4562}$
 345 and Load per Ant (*D. wilverthi*; single) = $2.7670 \times \text{Ant Weight}^{-0.4562}$.

346
 347 The AL model showed a strong negative allometric relationship between ant body weight and
 348 the absolute load carried per worker ($\beta = -0.4579$, $p < 0.0001$; **Table 2**). Single carriers
 349 transported slightly less load than individuals in multiple carrier teams at the same body weight
 350 ($\beta = -0.0601$, $p < 0.0001$), but the effect size was small. Workers of *D. wilverthi* carried slightly
 351 more absolute load per ant than *D. sjostedti* workers, although the effect size was small
 352 ($\beta = 0.0306$, $p = 0.00485$). Forest type had a similar small but significant effect, with workers
 353 in secondary forest carrying slightly heavier loads ($\beta = 0.0317$, $p = 0.0112$) than those in
 354 primary forest at a given body weight. Prey shape had a negative effect on absolute load per ant
 355 ($\beta = -0.0178$, $p < 0.0001$), indicating that elongated prey items decreased the load of individual
 356 workers. The carrier type–species interaction was not statistically significant ($\beta = 0.0476$,
 357 $p = 0.0720$).
 358

Diet composition

We identified a total of 2557 prey items from 25 different animal orders. For *D. wilverthi* we identified a total of 818 prey samples, 68% from primary and 32% from secondary forests, and for *D. sjostedti* a total of 1739 prey samples, 52% from primary and 48% from secondary forests. The diet of *D. wilverthi* consisted mainly of Lepidoptera (22.4%), Blattodea (16.9%), Araneae (16.5%), Hymenoptera (13.2%) and Orthoptera (9.3%; **Figure 8**). The diet of *D. sjostedti* consisted mainly of Lepidoptera (25.9%), Blattodea (20.6%), Hymenoptera (17.7%), Orthoptera 10.3%) and Araneae (7.5%; **Figure 8**). Formicidae accounted for 85.2% and 79.5% of all hymenopteran prey items in *D. wilverthi* and *D. sjostedti*, respectively.

We tested differences in prey composition between species and forest types by using multivariate generalized models (MGLM). The models revealed no significant differences between the prey composition of the two *Dorylus* species (Dev = 29.83, $p = 0.215$). In contrast the MGLMs showed a significant difference between the forest types (Dev = 49.10, $p = 0.002$), and a significant effect of ant species-forest interaction (Dev = 58.37, $p = 0.001$). This indicates that *D. wilverthi* and *D. sjostedti* do not differ in their prey spectra fundamentally (when measured at the taxonomic resolution of this study) and compositional differences between them only emerged in relation to forest type. The plot showing the NMDS can be found in the supplemental information (**S4**).

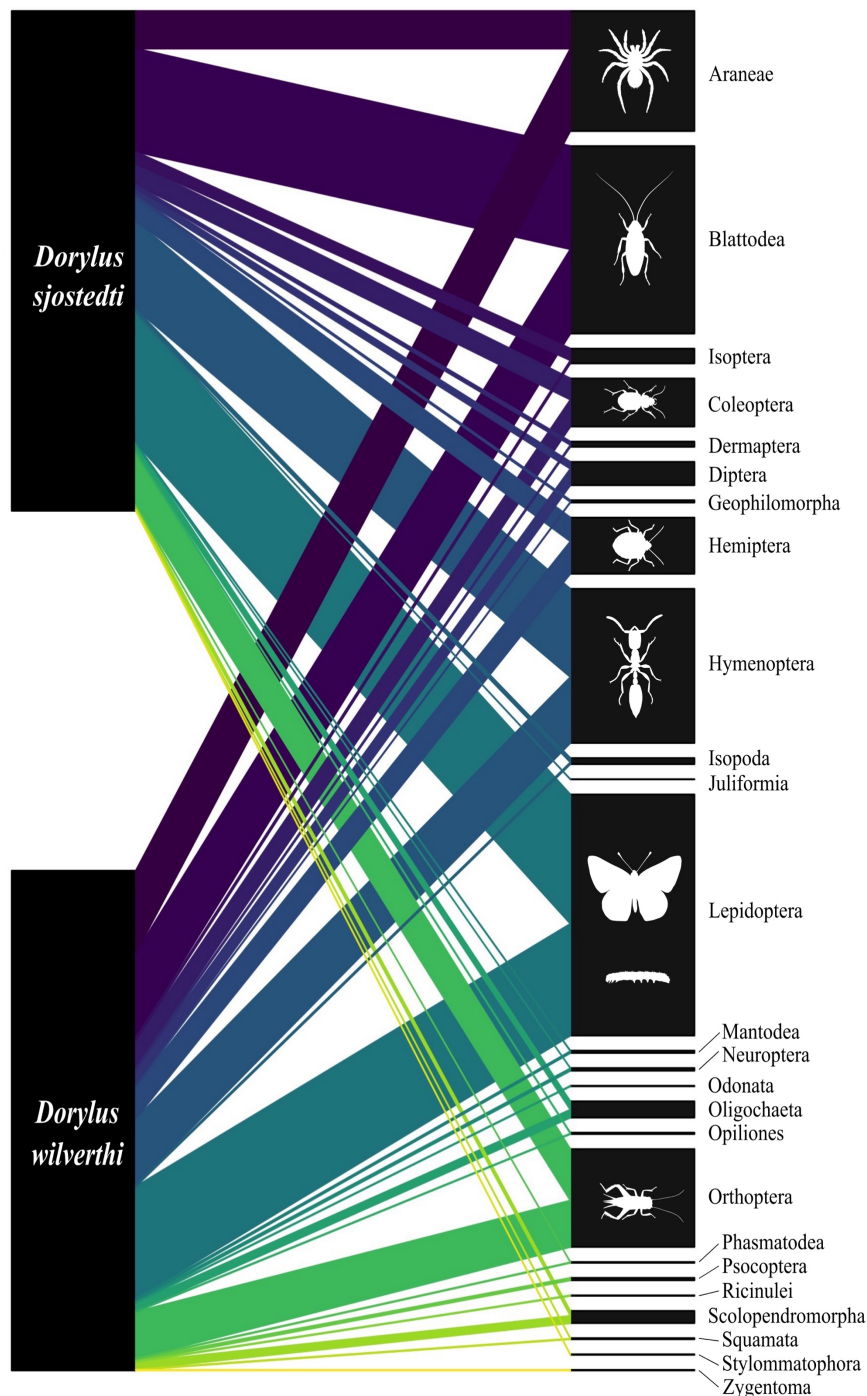


FIGURE 8. Proportional prey use illustrating the broad overlap in diet composition between the two driver ant species. For both species, Lepidoptera, Blattodea, Araneae, Orthoptera and Hymenoptera accounted for the majority of prey items, while numerous other arthropod and invertebrate groups were preyed on only rarely. Detailed image licensing can be found in Supplements S5.

We tested for differences in the contribution of individual prey taxa with univariate tests. They showed a significance response for the species-forest interaction within Coleoptera (Dev = 10.70, $p = 0.011$). Indicating a difference in how the two driver ant species prey upon Coleoptera in the different forest types, with *D. sjostedti* preying more on Coleoptera in secondary forest than *D. wilverthi*. There were no differences in other taxa.

We calculated niche overlap using Pianka's index to further assess if the two *Dorylus* species occupy different trophic niches. The observed niche overlap was extremely high (Pianka index = 0.9563), denoting that both species feed almost identical prey at the order-level. Under the null model, expected overlap was much lower (mean simulated index = 0.26348 ± 0.0221) and the observed value exceeded all 10,000 simulated values (SES = 4.65, lower-tail $p > 0.9999$, upper-tail $p < 0.0001$).

Where possible, we further classified the life stage of insect prey items to assess differences in the predation of larvae/nymphs and adults between *D. sjostedti* and *D. wilverthi*. We noted life stage information for 2348 prey items. Prey collected by *D. wilverthi* were 26% adult, 29% larva, 25% nymphs, 19% pupa and 1% eggs, with a nearly identical distribution of life stages across prey taken by *D. sjostedti* (27% adult, 29% larva, 25% nymphs, 19% pupa and 1% eggs). The MGLM comparing the distributions of prey life stages between the two species and forest types showed no significant differences between the prey composition of the two *Dorylus* species (Dev = 4.389, $p = 0.487$) but did detect a significant difference between forest types (Dev = 18.657, $p = 0.003$) as well as a significant effect of ant species-forest interaction (Dev = 12.423, $p = 0.019$). This indicates that *D. wilverthi* and *D. sjostedti* prey upon insects at approximately the same distribution across life stages, but differences do arise in relation to forest type and how the two driver ant species react to those differences. Univariate tests showed significant differences for the species-forest interaction only for larvae (Dev = 7.43, $p = 0.028$), where *D. wilverthi* retrieved more larvae (32.4% of all prey) in primary forest than *D. sjostedti* (25% of all prey), whereas in secondary forest the pattern reversed (*D. wilverthi*: 19.1%; *D. sjostedti*: 33.1%).

Discussion

Our study reveals that both *D. wilverthi* and *D. sjostedti* are highly generalist predators on the forest floor, consuming a vast array of different invertebrate groups across 25 orders. Whilst less common, we also observe consumption of vertebrate prey. Both driver ant species show very similar diets, with nearly complete overlap in diet composition and trophic niche occupation; observed dietary differences occurred only at the habitat scale between primary and secondary forests, indicating that the local availability of prey may be an important proximal determinant of diet rather than strong prey preferences *per se*. Moreover, biometric analyses show for the first time that there are substantial differences in worker demographics between *D. wilverthi* and *D. sjostedti*. While *D. sjostedti* exhibited two distinct worker size modes, *D. wilverthi* showed three, including an additional category of supermajor workers. Furthermore, our prey transport analyses show that both species conformed to expected allometric scaling laws, with heavier workers carrying heavier prey in absolute terms but lower loads relative to their own weight. When multiple ants cooperated in prey retrieval individual workers as part of the carrying party bear heavier loads than single individuals of the same weight. Cooperative transport therefore did not reduce loading but instead enables the ants to carry overall heavier prey items.

Biometrics of D. wilverthi and D. sjostedti

This study shows that the two *Dorylus* species do not differ substantially in worker biometrics. Instead, the main differences between species appears to lie in the demographic structure of their worker populations, with *D. wilverthi* exhibiting an additional worker size category. The demographic differences likely account for the observed differences in mean body length, while the shared allometric pattern indicates similar functional constraints in both species.

Average worker biometrics of *Dorylus wilverthi* and *Dorylus sjostedti* differed only marginally. Mean body length was the only biometric trait showing a statistically significant difference between species, with workers of *D. wilverthi* (mean length 7.32 mm) being on average 6% longer than *D. sjostedti* workers (mean length 7.02 mm). The biological relevance of the difference in mean body length should be interpreted with caution since it is only marginal, but it is reasonable to assume it arises due to the differences in demographic structure of the two species. While both species showed continuous worker polymorphism, *D. wilverthi* exhibited three distinguishable size modes in distribution of body length and head width, whereas *D. sjostedti* showed only two. For body mass, no clear multimodality was detected in either species. The additional size category in *D. wilverthi* likely shifted the overall mean body length

upwards and provides a plausible explanation for the observed differences in mean size, without implying fundamental differences in worker biometrics.

Although there are no quantitative studies on the biometrics or demographics of *D. sjostedti* (formerly *Dorylus nigricans sjostedti*) there are studies done on *D. nigricans* with no further specification of subspecies (Hollingworth 1960). Hollingworth (1960) observed a bimodality in *D. nigricans*, which would be consistent with the results shown here. In contrast there are such studies for *D. wilverthi*. Raignier and Van Boven (1955) described worker size variation in *Dorylus wilverthi* as a continuous and unimodal polymorphism, based on a large sample of workers collected from a single colony. They therefore rejected the biological relevance of discrete size classes such as minor, media and major. This conclusion was based on a large sample size ($n = 854$) from a single colony. Our analysis, based on a larger dataset spanning multiple colonies, instead revealed multimodal worker size distributions, supporting three discrete size categories across a continuous polymorphic worker population. This discrepancy most likely reflects differences in sampling scale rather than a fundamental contradiction between studies. Sampling ants from a single colony in a short space of time may show a unimodal size distribution, but the broader sampling across colonies and at different times employed here captures additional demographic and ecological variability.

Importantly, the observed multimodality does not contradict continuous allometric scaling, as the data still show the presence of all intermediate forms. This is further supported by the allometric scaling of head width and body length. Head width scaled positively with body length ($\alpha = 1.28$) in both species, with no significant interaction between body length and species. This indicates that both species follow the same allometric scaling relationship and are consistent with the findings of earlier studies (Raignier & Van Boven 1955; Hollingsworth 1960).

Prey size

Prey items carried by *Dorylus wilverthi* and *Dorylus sjostedti* differed significantly in all measured size related metrics. Consequently, mean prey items were 20.6 % larger (prey area) and 21.8 % heavier for *D. wilverthi* than for *D. sjostedti*. In contrast, prey items carried by *D. sjostedti* were slightly more elongate (1.8%), as indicated by a small but significant difference in prey shape.

Forest type also influenced prey item biometrics. On average, prey items collected in primary forest were wider, heavier, and larger by area than those collected in the secondary forest, whereas prey length and prey shape did not differ significantly between forest types. This indicates that part of the variation in prey metrics reflects differences in prey availability related to forest structure rather than species-specific prey selection alone. Differences in arthropod community composition between forest types have been reported for lowland African rainforest, particularly in relation to forest management history and differences in successional stages (Nummelin & Zilihona 2004). Structural changes following (selective) logging, such as in the secondary forest of the study site, can shift arthropod community by altering canopy coverage and changes in understory structure, further influencing arthropod availability and size distribution (Aggarwal *et al.* 2023). These potential differences in arthropod communities may result in different prey availability and concomitant composition that explains the observed variation in prey metrics between primary and secondary forest.

The ant-prey weight relationship provides further insight into how these differences in prey metrics arise. The linear model revealed a strong positive allometric relationship between worker body mass and prey mass, indicating that heavier workers consistently carried heavier prey items. Importantly, this relationship did not differ significantly between the two species, demonstrating that both species follow the same biomechanical scaling laws during prey transport. At the level of individual workers, prey weight is largely determined by ant body mass rather than by species identity. This pattern is consistent with a previous comparative study on worker-prey allometry in *Eciton* and *Dorylus* highlighting the consistency of biometric scaling within surface-swarmer army ants (Franks *et al.* 1999).

Taken together, the observed differences in mean prey metrics between species can be interpreted as the combined effect of environmental and demographic factors. Differences in prey size availability between forest types may set the overall range of prey size, while the demographic structure of the worker populations determines how this range is expressed on a species level. The presence of an additional larger worker size category in *D. wilverthi* increased the likelihood that heavier workers participate in prey transport, which, given the positive ant-prey allometry, shifts mean prey size and weight upwards. Given this, we suggest that the differences in prey biometrics between *D. wilverthi* and *D. sjostedti* do not reflect fundamental differences in prey handling capacity or foraging strategy. Instead, variation in prey size is probably primarily driven by habitat related differences in prey availability, while

species-specific worker demography shifts the resulting mean values through shared allometric constraints.

Prey transport by individuals and groups

The relative loading model revealed a negative relationship between ant body mass and relative load in single carriers. Smaller workers carried prey items that were heavier relative to their body mass compared to larger workers. This relationship was consistent across both *D. wilverthi* and *D. sjostedti* and did not differ between forest types, suggesting that relative loading is mainly determined by worker size rather than by species identity or habitat. Such a decline in relative load with increasing body mass is consistent with basic biomechanical expectations, because force generation scales with muscle cross sectional area rather than body mass (Klowden 2013). However, higher relative loading in smaller workers does not necessarily imply higher transport efficiency in an energetic sense, instead it rather indicates that small workers can sustain and operated under higher load ratios than larger ones.

Ecologically, this size dependence can be interpreted in the context of polymorphism and task trade offs within army ant worker populations. In *Dorylus (Anomma)*, size related division of labour has been documented, where minor workers are often involved in carrying liquid prey and in digging activities, whereas larger workers tend to carry prey pieces and are more strongly associated with defence or hunting related functions (Gotwald 1978). Morphologically, head and mandible traits in *Dorylus* scale with worker sizes towards an adaptation for higher defence and biting capability, whereas smaller workers are more adapted for digging and carrying (Gotwald 1978). At the same time, longer legs in bigger workers, increase the locomotive performance and the ability to straddle bulky prey carried beneath the body (Schöning *et al.* 2005). Taken together, these relationships support a functional division in which very large workers are not optimized for transport in a single dimension, but are shaped by multiple demands (e.g., defence and prey processing), while smaller workers remain capable of carrying high relative loads to support major workers in transport (Franks *et al.* 2001).

Consistent with the relative loading results, absolute load per ant decreased with worker body weight, indicating that larger workers were relatively less loaded than smaller workers. Absolute load per ant differed between single and multiple carriers, with individuals involved in cooperative transport carrying slightly higher absolute loads per worker than solitary carriers.

Overall, species-specific differences in absolute loading were small. Although workers of *D. wilverthi* carried marginally heavier absolute loads per worker than *D. sjostedti*, the effect size was small, indicating broadly similar biomechanical constraint on prey transport in both species. The higher absolute load in multiple carrying ants suggest, that cooperative transport functions mainly as a mechanism that enables the movement of large prey items, rather than as a strategy to reduce individual workload or increase efficiency. This interpretation is consistent with previous studies showing that team transport is primarily associated with the retrieval of larger prey items that may be difficult or impossible to move by single workers alone (Franks *et al.* 1999).

Together, the relative and absolute load models indicate that prey transport follows shared worker size dependencies in both species. Cooperative transport increases the upper limit of transportable prey size, while smaller workers contribute disproportionately in terms of higher relative and absolute load ratios. These findings are consistent with previous studies on prey transport in *D. wilverthi* which also demonstrated a strong positive relationship between prey mass and worker or team mass, showing that cooperative transport is mostly associated with large prey items (Franks *et al.* 1999). Importantly, the results of Franks *et al.* also suggest that cooperation extends the range of prey sizes that can be retrieved, rather than reducing the absolute load carried by individual workers. Further support of our interpretation comes from another analysis by Franks *et al.* (2001) on division of labour within *D. wilverthi* worker teams. They showed that prey retrieval groups have a non-random size composition, typically consisting of an unusually large front runner and one or more much smaller followers, as shown in **Figure 1D**. The authors suggested that the front runner bears most of the load, whereas smaller workers mainly contribute to stabilization and movement efficiency rather than to load sharing. Such a mechanism in cooperation is consistent with the observed higher absolute loads in multiple carriers.

Diet of D. wilverthi and D. sjostedti

The dietary composition of *D. wilverthi* and *D. sjostedti* was very similar at the order level. Across both species and forest types, a total of 25 prey orders were recorded. In both species, the diet primarily consisted of Lepidoptera, Blattodea, Hymenoptera, Araneae and Orthoptera, with only minor differences in their relative contribution.

MGLMs showed no significant overall differences in prey composition between the two *Dorylus* species. In contrast, prey composition differed significantly between forest types and a significant species-forest interaction was detected. This indicates that forest type influences prey composition. Although the species-forest interaction was statistically significant, its ecological interpretation is uncertain and should be interpreted cautiously, it may partly reflect sampling structure rather than consistent species-specific prey choice. Univariate analyses of individual prey taxa only showed a significant difference in the forest–species interaction within Coleoptera, where *D. sjostedti* preyed more on Coleoptera in secondary forests than *D. wilverthi*. No further species-specific differences were detected.

Earlier studies on *Dorylus* biology mainly provided qualitative descriptions of foraging behaviour and only rarely distinguish prey consumption at the species level (Raignier & Van Boven 1955; Gotwald 1974, 1978, 1995; Schöning 2004; Schöning *et al.* 2008). Whilst quantitative dietary studies have never been undertaken and published for *D. sjostedti*, Schöning *et al.* (2008) reported a comprehensive analysis of the prey spectrum of *D. wilverthi* in Uganda. In their study, prey composition was reported based on the proportion of dried prey biomass per order, which limits direct quantitative comparison with the present results that are based on prey counts on raid level. Nevertheless, the overall patterns are comparable. Schöning *et al.* reported a diet primarily consisting of Lepidoptera and Coleoptera, while Arachnida and Hymenoptera occurred in small proportions. This study also shows that Lepidoptera and Blattodea greatly contribute to the diet of *D. wilverthi*, but with a much higher intake of Hymenopterans and Arachnids than reported by Schöning *et al.* (2008). Nonetheless, they further report an extensive variation even within study sites, season and species leading to the suggestion that prey availability is the most important factor driving prey consumption in *D. wilverthi* (Schöning *et al.* 2008).

The relative proportions of prey life stages were nearly identical between the two *Dorylus* species. Multivariate analyses showed no significant differences in foraged prey life stages between the species, but forest type did show a significant effect. This suggests that prey life stage composition varies primarily between primary and secondary forest. Although the species-forest interaction was statistically significant, the biological meaning of this interaction is not clear and should be interpreted cautiously as it may partly reflect sampling structure. Univariate tests indicated that this interaction was statistically detectable only for larval prey, with larvae consumed more in primary forests by *D. wilverthi*, whereas in secondary forests *D. sjostedti* consumed more. There were no consistent differences observed for other life stages.

Both species primarily foraged on early life stages like larvae and pupa. This pattern is consistent with the literature and can be explained by the lower mobility and limited escape ability of those life stages, which makes them more accessible to swarm raiding ants (Franks *et al.* 1999).

The great similarity in prey spectra of the two species was further supported by the niche overlap analysis. Observed dietary niche overlap between the *D. wilverthi* and *D. sjostedti* was extremely high, with an observed Pianka index indicating a near complete overlap at the order level, exceeding all generated values under the null model. The occupation of a nearly identical trophic niche and the occurrence of differences of prey spectra only between forest types suggests that both species are true opportunistic generalists, which is consistent with the literature (Gotwald 1978, 1995; Schöning 2004; Cumming *et al.* 2008; Schöning *et al.* 2008).

While our findings provide robust quantitative insights into the dietary breadth of *D. wilverthi* and *D. sjostedti*, a methodological limitation regarding prey identification must be considered. Given constraints in time and resources, we relied on morphological identification of prey items to an order level. This approach may result in an underrepresentation of certain prey taxa. The identification of dismembered prey items, solely based on morphological traits is inherently biased towards taxa with hard exoskeletons, as these provide easily recognizable key features even on higher grades of dismemberment. In contrast soft bodied prey taxa such as annelids or chordates are probably under detected in this study since they often lack recognizable morphological features in a dismembered state. Genetic identification approaches, such as DNA barcoding or metabarcoding could overcome this limitation by allowing the identification of otherwise unrecognizable prey and thereby provide a more comprehensive assessment into the dietary niches of the two *Dorylus* species. Additionally, such genetic approaches would allow a higher taxonomic resolution of prey item identification, leading to a more comprehensive answer of prey spectra.

Conclusion

In this study, we demonstrated that *Dorylus wilverthi* and *Dorylus sjostedti* share highly similar biomechanical constraints and occupy a nearly identical trophic niche, functioning as opportunistic generalist predators with almost complete dietary overlap when prey identity is considered at the order level. Both species exhibited conserved allometric scaling in morphology and prey transport. Despite these ecological similarities, they differ significantly in worker demography. *Dorylus wilverthi* exhibits a third, super major size mode that is absent

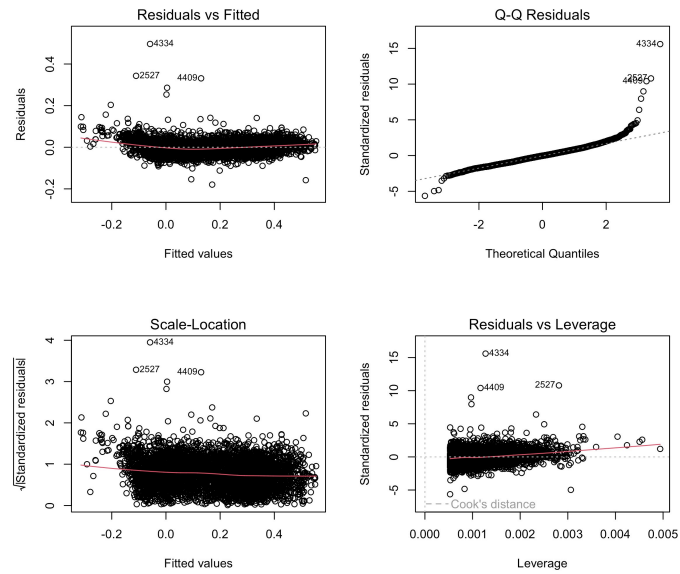
in *D. sjostedti*. Furthermore, minor variations in diet were driven primarily by forest type rather than species-specific prey preferences, reflecting habitat-specific prey availability. This suggests that the coexistence of these sympatric species is not facilitated by trophic niche separation, but rather by subtle demographic differences combined with other ecological factors. Future research should explore additional dimensions of niche separation, including spatio-temporal foraging dynamics, raid depth and habitat use, while also integrating quantitative arthropod community assessments to comprehensively understand prey availability and the species-specific prey usage.

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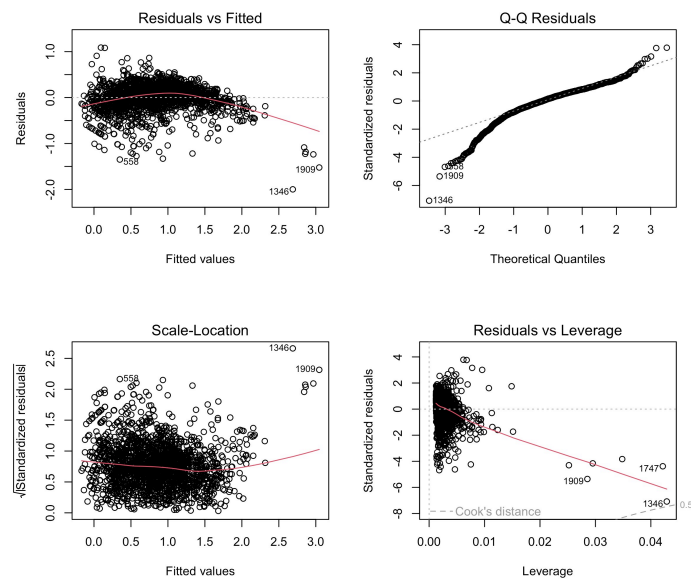
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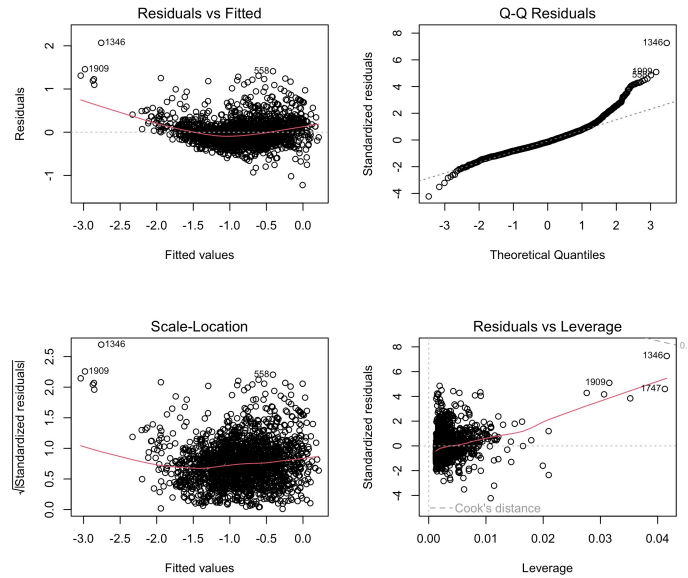
742 **Supplementary Information**
 743 **S1 – Residual Plots for LRM's**



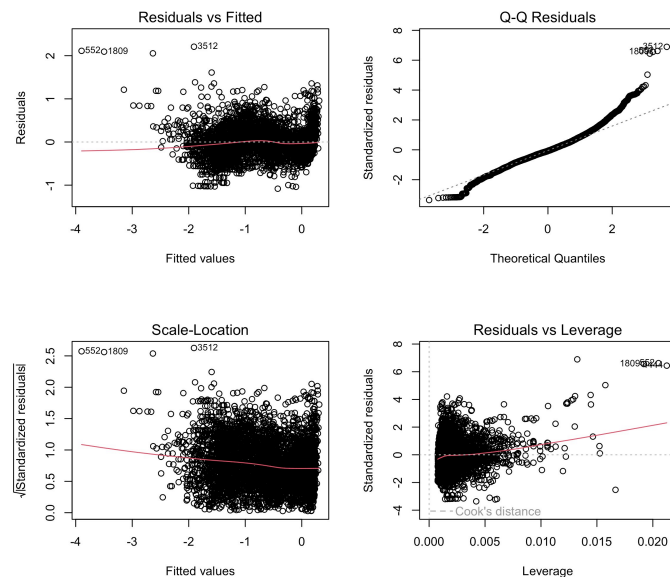
744 **S1. Residual plots for linear model explaining ant body length to head width ratio.**
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748 **S2. Residual plots for ant-prey-weight relations.**
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S3. Residual plots for Linear Model for relative load in single workers against ant length.



S4 Residual plot for Linear model for Load per ant for the two carrier types.

S2 – Model Performance and Selection

Model performance was evaluated using adjusted R^2 values, Akaike Information Criterion (AIC) and ANOVA. Model assumptions were evaluated with standard diagnostic plots (residuals vs. fitted values, Q-Q plot, scale-location, residuals vs. leverage; Supplementary Figures S1-S4). Across all models, linearity and the absence of influential observations were met. Heteroscedasticity was tested using Breusch-Pagan tests. The residual patterns and the conducted Breusch-Pagan tests (all $p < 0.0001$) showed clear signs of heteroscedasticity in all models (SUPPLEMENTAL TABLE 1). Therefore, all statistical results for all linear models were adjusted to heteroscedasticity-consistent (HC3).

SUPPLEMENTAL TABLE 1 Model testing metrics. Model options contained a base model with ant species and carrier type as interacting as well as main effect and additional main effects forest type and prey shape. Tested linear models were ant allometry (AA; head width ~ body length), ant prey weight allometry (AP; prey weight ~ ant weight), relative loading in single carriers (RL; ant weight ~ relative load); and absolute loading (AL; load per ant for both carrier types ~ ant weight).

Model	Adj. R ²	SE (df)	AIC	ΔAIC	BP	ANOVA
Ant Allometry (AA)						
AA (M1): Base model	0.9651	0.0330 (4608)	-18374	27	< 0.0001	–
AA (M2): Base model + ant species + forest type	0.9674	0.0319 (4606)	-18688	3	< 0.0001	< 0.0001
AA (M3): Base model × ant species + forest type	0.9675	0.0318 (4605)	-18691	–	< 0.0001	0.0287
Ant Prey Weight Allometry (AP)						
AP (M1): Base model	0.6130	0.3418 (1915)	1328	–	< 0.0001	–
AP (M2): Base model + ant species + forest type + prey shape	0.6124	0.3420 (1912)	1334	6	< 0.0001	0.9815
AP (M3): Base model × ant species + forest type + prey shape	0.6122	0.3420 (1911)	1336	8	< 0.0001	0.6838
Relative Loading (RL)						
RL (M1): Base model	0.6130	0.3418 (1915)	1328	–	< 0.0001	–
RL (M2): Base model + ant species + forest type + prey shape	0.6124	0.3420 (1912)	1334	6	< 0.0001	0.9815
RL (M3): Base model × ant species + forest type + prey shape	0.6122	0.3421(1911)	1336	8	< 0.0001	0.6838
Absolute Loading (AL)						
AL (M1): Base model + carrier type + ant species	0.5914	0.4658 (4606)	6044	22	< 0.0001	–
AL (M2): Base model + carrier type × ant species	0.5916	0.4656 (4605)	6042	20	< 0.0001	0.0469
AL (M3): Base model + carrier type × ant species + forest type + prey shape	0.5936	0.4645 (4603)	6022	–	< 0.0001	< 0.0001

Adj. R² = adjusted R², SE(df) = standard error and degrees of freedom, AIC = Akaike Information Criterion, ΔAIC = difference of AIC from lowest AIC measured within model set, BP = p – values from Breusch-Pagan-test, ANOVA = p – values from ANOVA,

For each set of models, the final selected model was selected based on a combination of biological interpretability and statistical performance. As shown in SUPPLEMENTAL TABLE 2, model 3 (M3) of ant allometry, with interacting term ant species and main effect forest showed the best overall performance tests (adjusted R² = 0.9675; lowest AIC = -18691; ANOVA p < 0.05) and was therefore selected to represent the ant body allometric relationship.

Metrics for the ant-prey allometry (AP), and relative loading (RL) suggested the base model as the best fit (AP: adj. $R^2 = 0.6122$, lowest measured AIC = 1328; RL: adj. $R^2 = 0.6122$, lowest measured AIC). The M3 models with ant species as interaction term and forest type and prey shapes as main factors showed a higher AIC in both ant-prey allometry ($\Delta AIC = 8$) and relative loading ($\Delta AIC = 8$). Although the base model showed the lowest AIC, we chose the M3 models to express the AP and RL relationship, since these models were more suitable to test the species-specific differences, we were interested in.

Within the model set for absolute load (AL), model M3 with ant species added as an interaction term was the best fit (adjusted $R^2 = 0.5936$; lowest measured AIC = 6022, ANOVA $p < 0.0001$).

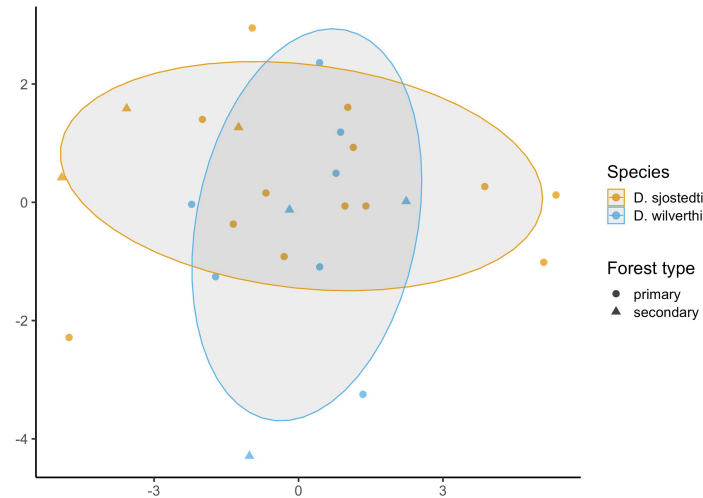
S3 – Results of Demographic Analysis

SUPPLEMENTAL TABLE 2 Test results on multimodality (Hartigan's dip test; Dip D) and maximal number of k modes (Silverman's critical bandwidth test; SM p-values) within the demographic distributions of worker biometrics in *D. wilverthi* (DW) and *D. sjostedti* (DS). Both species showed multimodality in body length and head width, with *D. wilverthi* exhibiting a minimum of 3 distinguishable size modes, whereas *D. sjostedti* has a minimum of two modes.

Metric	Species	Dip D	SM (k=1)	SM (k=2)	SM (k=3)
Ant body length [mm]	DW	0.0253***	0.0020*	0.0060*	0.8869 ^{n.s.}
	DS	0.0243***	0.0010*	0.2863 ^{n.s.}	0.3944 ^{n.s.}
Ant head width [mm]	DW	0.0245***	0.0010*	0.0250*	0.9349 ^{n.s.}
	DS	0.0215***	<0.0001***	0.5495 ^{n.s.}	0.3634 ^{n.s.}
Ant weight [mg]	DW	0.0138*	0.1181 ^{n.s.}	0.2002 ^{n.s.}	0.1451 ^{n.s.}
	DS	0.0131*	0.7047 ^{n.s.}	0.4424 ^{n.s.}	0.0781 ^{n.s.}

p-value with * $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$ and n.s = not statistically significant.

S4 – NMDS for Prey Composition of both Species



S5 Variation in prey composition between *D. sjostedti* (orange) and *D. wilverthi* (blue) among the 25 observed raids in primary (circles) and secondary (triangles) forest. Visualized using NMDS biplot based on binomial dissimilarities of prey composition. The underlying fitted MGLMs showed no statistically significant differences between the diet composition of the two species (Dev = 29.83, $p = 0.215$). In contrast, forest type had a significant effect on prey composition (Dev = 49.10, $p = 0.002$). Stress = 0.159.

S5 – Image attribution for Bipartite Plot

SUPPLEMENTAL TABLE 3. Licenses and image details of arthropod silhouettes used in Bipartite plot (Figure 8)

Graphic	Description	Author	License	Uploaded	Accessed	Source Link
Araneae	Silhouette Image of <i>Liphistius desultor</i>	T. Michael Keesey	CC0 1.0 Universal Public Domain	01.08.13	12.01.26	https://www.phylopic.org/images/882a9d18-5724-44a9-b439-1b2686339a00/liphistius-desultor
Blattodea	Silhouette Image of <i>Blattella germanica</i>	Guillaume Dera	CC0 1.0 Universal Public Domain	17.06.23	12.01.26	https://www.phylopic.org/images/b2e26249-80be-441b-8648-4c0361892ee0/blattella-germanica
Coleoptera	Silhouette Image of <i>Licinus depressus</i>	Pascal Abel	CC0 1.0 Universal Public Domain	07.07.25	12.01.26	https://www.phylopic.org/images/4b15a810-1e3c-47ca-a5ab-f91c6eab2848/licinus-depressus
Hemiptera	Silhouette Image of <i>Nezara viridula</i>	Darrin Schultz	CC0 1.0 Universal Public Domain	01.10.25	12.01.26	https://www.phylopic.org/images/ac91ee0b-7404-4748-b90e-08a0c5481d6b/nezara-viridula
Hymenoptera	Silhouette Image of <i>Leptanilla swani</i>	T. Michael Keesey	CC0 1.0 Universal Public Domain	09.05.18	12.01.26	https://www.phylopic.org/images/45ccedd3-d5cb-42e8-b158-7e027ab1ff22/leptanilla-swani

Lepidoptera a	Silhouette Image of <i>Hamearis lucina</i>	Matt Hayes	CC0 1.0 Universal Public Domain	28.03.20	12.01.26	https://www.phylopic.org/images/ab6182d2-5093-444b-92e5-84468218ebf0/hamearis-lucina
Caterpillar	Silhouette Image of <i>Spodoptera frugiperda</i>	Kai Sonder	Public Domain Mark 1.0	23.04.20	12.01.26	https://www.phylopic.org/images/577f5112-1873-4474-90b2-7fdf2dc2b6a7/spodoptera-frugiperda
Orthoptera	Silhouette Image of <i>Acheta domestica</i>	Guillaume Dera	CC0 1.0 Universal Public Domain	09.01.23	12.01.26	https://www.phylopic.org/images/6e42ac62-37f4-458c-bf44-3f7decblf14e/acheta-domestica