Bee foraging distances dependent on body mass and level of eusociality - a meta-analysis

Kendall, L.K.¹, Bartomeus, I.², Portman, Z.³, Cariveau, D.³ and Mola, J.⁴

26 March, 2021

Affiliations:

- ¹ Centre for Environmental and Climate Science, Lunds Universitet, Lund, Sweden
- ² Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio 26, Isla de la Cartuja, E-41092 Sevilla, Spain
- ³ University of Minnesota
- ⁴ U.S.D.A. Geological Survey? *Correspondence: liam.k.kendall@gmail.com

##THOUGHTS - while writing and reading

Is distance the right word? I cant decide between distance or range, range seems more synonymous with resource use and therefore maybe better i.e. they will forage within this range, rather than less than this distance

I think the physiological ~ functional split in estimates (feeder and homing vs. all others) is very interesting. I am open to ideas regarding the names - maybe behavioural is better than functional?

I didn't find an effect of polylecty for either maximum or typical distances - i thought there was one but there were a few estimates which were incorrectly coded- and after fixing these, we lost the effect. Two options: we focus just on eusociality, as the result is strong, or add the lecty does not have an effect in solitary species? Lecty results are not here at present, but model objects are - have lecty in the name i.e. (max.lecty.phylo.brm.1 etc)

Not enough coverage to use Family as a predictor (see table(forage.traitsFamily, forage.traitsdistance_type2))

Henrik had an interesting idea - use colony size instead of categorical eusociality

##IDEAS Include measure of variance in intraspecific ITD into models as measurement error

Abstract

Introduction

Paragraph One: Ecological significance of foraging in terms of ecosystem function. Effects on foraging - landscape context etc -links to body size

Types of measurements Structure that feeder and homing as physiological measures - others as functional

Why should this be revisited? -Many more studies -new analytical methods -need to incorporate things like phylogeny etc

##Research questions

- 1) How accurate is body size in predicting foraging distance in bees?
- 2) Do bees differ in terms of their physiological and functional constraints in foraging distance/range?

Group	Type	Type2	Definition
Type of distance	Typical		Typical foraging distance was defined as the mean (or media
			mode) foraging distance by a species within a study.
	Maximum		Maximum foraging distance was defined as the maximum dis
			observed within a experiment (if multiple trials were conduct
			study
	Observed		Observed foraging distances were those estaimtes that could
			definied as either typical or maximum distances i.e
Method	Functional	Associative	Associative studies were those that measured foraging distar
			associating known nests / hives and floral resources
		Mark-recapture	Feeder studies involved
		Molecular	Homing studies
		Tracking	Mark-recapture
		Waggle dance	Molecular
	Physiological	Feeder	Tracking
		Homing	Dancing

- 3) i) Does level of eusociality nfluence foraging distance?
- ii) Do the functional and physiological constraints on foraging distance differ between eusocial and solitary bee species?
- 3) Does floral specialisation structure species-level foraging distance in solitary bee species?

Materials and Methods

To identify relevant publications for our meta-analysis, we compiled foraging distance estimates from a previous meta-analysis by Greenleaf et al. 2007 and a litearture review by Zurbuchen et al. 2010. We then undertook a systematic Scopus database search with the following search terms: TITLE-ABS-KEY ((bee OR apoid*) AND (forag* AND distanc*) OR "flight range"). As of 12 March 2021, this returned 643 articles. We then subsetted this database to articles published post-2006 (to coincide with Greenleaf et al. 2007) and screened all articles for foraging distance estimates (n = 180 articles). For each estimate, we delimited estimate by type of distances measured (maximum, typical or observed) and methodology used to measure foraging distance (see Table 1 for definitions), following Greenleaf et al. 2007. We focussed on female bees, excluding all species that focussed on males or specifically dispersal patterns.

```
##
## Attaching package: 'kableExtra'
## The following object is masked from 'package:dplyr':
##
## group_rows
```

Table 1. Types of bee foraging estimates and methodologies...

##Species taxonomy and functional traits

We checked the validity of species' names using X, Y, and Z. We then collected the following traits for each species: female body size (measured as the intertegular distance, Cane et al. 1987), level of eusociality and floral specialisation. We obtained body size from literature sources (i.e. pollimetry, brazilian trait dataset, traitbase) and by directly contacting researchers. Where multiple ITD measurements for a given species were found, we took the mean value. For eusocial species with castes, we obtained ITD measurements for the caste used within the study (i.e. workers or queens).

We delimited species into three levels of sociality: obligate solitary, primitively eusocial or highly eusocial. Obligate solitary species were those bees species that provision their own nest cells. This group includes

species that live communally or in aggregations. Primitively eusocial species were those species that have non-permanent colonies and that are founded by a single female. This group included bumblebees *Bombus* species, as well as socially flexible *Lasioglossum* species, and those with overlapping generations e.g. *Xylocopa* species. Highly eusocial species were those species that had permanent colonies, which reproduce by budding. This group included all honeybees *Apis* species, and the stingless bees (Meliponini).

Lastly, we grouped species, based on their level of floral specialisation, as either *oligolectic* or *polylectic*. Oligolectic speies were defined as those species who consistently collect pollen from a single plant species or group of similar or related plant species, even the presene of other pollen sources. Polylectic species were defined as those that use multiple, unrelated species for pollen.

Nesting? I have not done any analysis on this (yet).

##Statistical analysis

All statistical analyses were undertaken in R (citation).

We used Bayesian generalized linear mixed effect models to analyze the effect of body size, functional traits and study design on bee foraging distances. We modeled typical and maximum foraging distance separately. Observed foraging distances were not analysed. Further, we excluded all estimates within unknown metholodogy. As is typical in allometric studies, we log-transformed foraging distance prior to analyses. However, as intertegular distance is logarithmically related to body size (Cane et al. 1987; Kendall et al. 2019), we compared the predictive accuracy (\mathbb{R}^2) of models with and without log-transformed ITD. We present models with the raw ITD, as these were significantly more predictive than $\mathbb{I}(\mathbb{I}^2)$.

For these purposes we specified the following models: 1) Foraging distance as a function of ITD, 2) foraging distance as a function of ITD * eusociality (categorical, three levels), using the complete dataset, 3) foraging distance as a function of ITD * Lecty in solitary bees species, as oligolecty is only found within solitary species and 4) foraging distance as a function of ITD * Metric type (physiological or functional) * eusociality. Floral specialisation was not tested in conjunction with metric type due to small sample sizes.

For models 1, 2 and 3), the random effect structure consisted of intercepts for publication and bee species, a phylogenetic effect, which consisted of a phylogenetic relatedness correlation matrix between bee genera, and a random intercept and slope for metric. Model (4) had the same random structure but without the metric effect as this was modelled as a fixed effect. For the phylogenetic effect, we constructed a bee phylogeny using an available bee genera tree (Hedtke, Patiny, & Danforth, 2013). We removed non-represented genera and then fitted a chronogram from this phylogeny by penalized likelihood, and a correlated rate model (Paradis et al. 2004). We then converted this to a phylogenetic correlation matrix using ape package.

We assessed the significance of the main- and interactive effects in each models by assessing whether 95% credible intervals bracketed zero. We then removed unsignificant interactions. In model (i), the interaction between ITD and eusociality was non-significant for both typical and maximum foraging distance, so we fitted and present the reduced models.

We parameterised each model with a *Gaussian* distribution, which was run for 2000 iterations, and a burn-in of 1000 iterations. We set weakly informative priors and manipulated DELTA and maximum tree depth to avoid divergent transitions. We visualised posterior predictive checks using bayesplot (v1.6.0, Gabry & Mahr 2017) and assessed chain convergence for each sub-model separately. We considered effects were considered significant when 95% credible intervals did not bracket zero.

Results

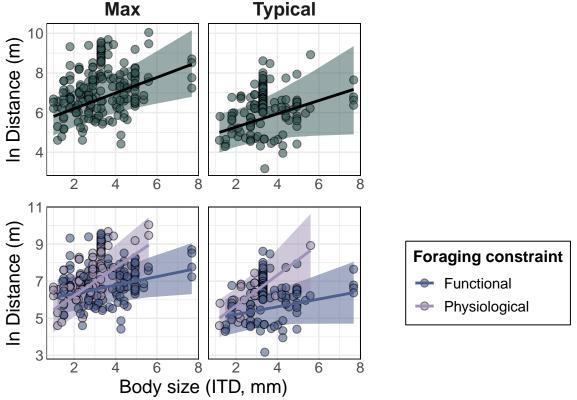
##Summary

In total, we included 352 estimates of foraging distance (typical, n = 159) & maximum, n = 193) in our analyses. These included estimates from 78 species, 29 genera and 6 families. Honeybees Apis spp. (124 estimates) and bumblebees Bombus spp. (98 estimates) were the most commonly studied taxa. Maximum foraging distance estimates ranged from 83 metres ($Andrena\ hattorfiana$) to 23 kilometres ($Eufriesea\ surinamensis$).

Typical foraging distance estimates ranged from 23.8 metres (Bombus flavifrons) to 7.5 kilometres (Xylocopa virginica).

ADD TABLE OF ESTIMATES -species summary

In addition, we compiled 32 'observed' foraging distance estimates that were not analysed.



1: Relationship between maximum (left) and typical (right) bee foraging distance (log-transformed metres) and foraging distances. Top: Overall trend, bottom: type of measurement used to estimate foraging distance: physiological (feeder or homing experiments), functional (other methods, see **Table 1**). Bold lines and ribbons indicate lines of best fit and corresponding 95% credible intervals. Circles denote raw data.

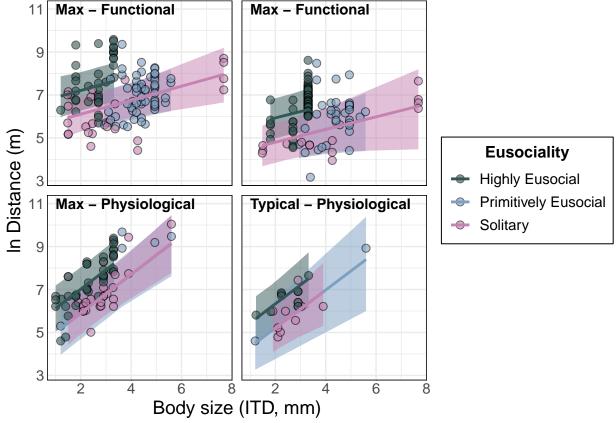


Figure 2: Relationship between eusociality and physiological or functional bee foraging distances (log-transformed metres) and maximum (left) and typical (right) foraging distances. Top: Overall trend, bottom: type of measurement used to estimate foraging distance: physiological (feeder or homing experiments), functional (other methods, see Table 1). Bold lines and ribbons indicate lines of best fit and corresponding 95% credible intervals. Circles denote raw data.

##Q1 Overall trends - predicting maximum and typical foraging distances

Overall, body size was positively related to both maximum (Marginal $R^2 = 0.16$) and typical (Marginal $R^2 = 0.39$) foraging distances (Figure 1). For example, the typical and maximum foraging distances of a middle sized bee (ITD: 4mm) are predicted to be 1082.8706264m and 379.5269265m, which are 589.8500221m and 185.1911578m longer than a small sized bee (ITD: 2mm, Max: 493.0206043m, Typ: 194.3357687).

#Q2 Differences in constraints on foraging distances

We found that physiological and functional constraints/measurements upon foraging distances differ in their relationship (slope) with body size (Model table, Figure 2). Specifically, physiological measurements of foraging distances increased at a greater rate per unit ITD than functional constraints/measurements (significant interaction with ITD, steeper slope). For example, in small bees (e.g. ITD of 2mm), physiological and functional measurements of foraging distance are similar (e.g. Typical: functional 182.3714474,physiological 2;Maximum: functional 564.3035091,physiological 2). However, in larger bees (ITD: 4mm), whereas physiological limits upon forging distance increase considerably, typical - functm, maximum - functm, functional limits do not: typical, 0.4760869m; maximum, 0.4639263m.

##Q2A) Effect of eusociality on physiological and functional bee foraging distances

Eusociality was highly important in structuring species differences in bee foraging distances ($Marginal R^2$: Typical distance: 0.359787145910967, Maximum distance: 0.372438633426443. In particular, highly eusocial bees (Apis species and stingless bees (Tribe: Meliponini)) exhibited significantly higher physiological and functional foraging distances than either primitively eusocial or solitary species (MODEL TABLE of

"max.euc.phylo.reduced.brm"). Primitively eusocial and soitary species exhibited near-identical estimates of foraging distance. For example, a European honeybee *Apis mellifera* (ITD:) is expected to have a physiological foraging distances of between 1778.5161409 and 3604.2148763m. In contrast, a primitively eusocial or solitary bee of the same size, such as *Osmia pedicornis*, is expected to have a physiological foraging distances of between 573.0238225 and 1193.9309174m.

Table SX-XX. Model tables

Group-Level Effects:

```
Family: gaussian
##
     Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | gr(Genus, cov = Bg))
      Data: forage.traits.mean (Number of observations: 159)
  Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
##
##
            total post-warmup samples = 4000
##
## Group-Level Effects:
  ~Authors (Number of levels: 47)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
##
## sd(Intercept)
                     0.53
                                0.11
                                         0.33
                                                  0.77 1.00
                                                                  940
                                                                          2086
##
##
  ~Genus (Number of levels: 17)
##
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                     0.89
                                0.44
                                         0.11
                                                  1.81 1.00
## sd(Intercept)
                                                                 1233
                                                                          1292
##
## ~Metric2 (Number of levels: 6)
                      Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
##
## sd(Intercept)
                           0.42
                                     0.34
                                              0.01
                                                        1.28 1.00
                                                                      2731
                                                                               2391
## sd(ITD)
                           0.28
                                     0.16
                                              0.06
                                                        0.67 1.00
                                                                      1195
                                                                               1417
                                                        0.91 1.00
##
  cor(Intercept,ITD)
                          -0.22
                                     0.57
                                             -0.98
                                                                       971
                                                                               1591
##
  ~spp (Number of levels: 47)
##
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)
                     0.46
                                0.11
                                         0.25
                                                  0.70 1.00
                                                                 1188
                                                                          2051
##
## Population-Level Effects:
             Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
                            0.59
                                     3.44
                                              5.73 1.00
## Intercept
                 4.60
                                                             3019
                                                                      2867
## ITD
                 0.33
                            0.18
                                    -0.02
                                              0.68 1.00
                                                             2007
                                                                      1992
##
## Family Specific Parameters:
         Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
##
             0.45
                       0.03
                                 0.39
                                          0.51 1.00
## sigma
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
    Family: gaussian
     Links: mu = identity; sigma = identity
##
## Formula: log.dist ~ ITD + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | gr(Genus, cov = Ag))
      Data: forage.traits.max (Number of observations: 193)
##
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
##
            total post-warmup samples = 4000
```

```
## ~Authors (Number of levels: 81)
##
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
                                         0.39
## sd(Intercept)
                     0.55
                                0.09
                                                  0.73 1.01
                                                                 1015
##
## ~Genus (Number of levels: 29)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
                                                  1.95 1.00
## sd(Intercept)
                     1.21
                                0.34
                                         0.61
                                                                 1509
##
## ~Metric2 (Number of levels: 7)
##
                      Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)
                           0.70
                                     0.44
                                              0.05
                                                        1.72 1.00
                                                                                717
                           0.21
                                     0.13
                                              0.02
                                                       0.53 1.00
                                                                       627
## sd(ITD)
## cor(Intercept,ITD)
                         -0.27
                                     0.54
                                             -0.94
                                                       0.89 1.00
                                                                      1008
                                                                               1548
##
## ~spp (Number of levels: 78)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                0.08
                                         0.24
                                                  0.56 1.01
## sd(Intercept)
                     0.39
                                                                 1238
                                                                          1814
##
## Population-Level Effects:
             Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
## Intercept
                 5.41
                           0.56
                                     4.33
                                              6.53 1.00
                                                             2277
                                                                      2615
                 0.39
                           0.13
                                     0.12
                                              0.67 1.00
                                                             2226
                                                                      2578
## ITD
##
## Family Specific Parameters:
         Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma
             0.51
                       0.04
                                 0.43
                                          0.59 1.00
                                                         1084
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
   Family: gaussian
    Links: mu = identity; sigma = identity
##
## Formula: log.dist ~ ITD * limits + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | gr(Genus, cov
      Data: forage.traits.mean (Number of observations: 159)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
            total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 47)
##
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
                                0.10
                                         0.34
                                                  0.75 1.00
                                                                          2336
## sd(Intercept)
                     0.53
                                                                 1214
##
## ~Genus (Number of levels: 17)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)
                     0.78
                                0.42
                                         0.06
                                                  1.66 1.00
                                                                 1172
                                                                          1480
## ~Metric2 (Number of levels: 6)
                      Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)
                                     0.30
                                              0.02
                           0.37
                                                        1.15 1.00
                                                                      2251
                                                                                1795
## sd(ITD)
                           0.14
                                     0.11
                                              0.01
                                                       0.43 1.00
                                                                      1332
                                                                               2001
## cor(Intercept,ITD)
                                     0.58
                                             -0.96
                                                       0.93 1.00
                                                                      2152
                                                                               2404
                         -0.14
## ~spp (Number of levels: 47)
```

```
Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
                     0.46
                               0.11
                                        0.25
                                                 0.70 1.00
                                                                1133
## sd(Intercept)
## Population-Level Effects:
                    Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                 0.62
                                           3.55
                                                    5.95 1.00
                                                                   2524
## Intercept
                        4.79
                                  0.14
                                          -0.07
## ITD
                        0.21
                                                    0.50 1.00
                                                                   2213
                                                                            2463
## limitsphysio
                       -0.78
                                  0.67
                                          -2.11
                                                    0.53 1.00
                                                                   2890
                                                                            2837
## ITD:limitsphysio
                        0.62
                                  0.25
                                           0.13
                                                    1.10 1.00
                                                                   2593
                                                                            2242
## Family Specific Parameters:
        Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                0.39
             0.44
                     0.03
                                         0.51 1.00
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
## Family: gaussian
   Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD * limits + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | gr(Genus, cov
     Data: forage.traits.max (Number of observations: 193)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
           total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 81)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                               0.08
                                        0.39
                                                 0.72 1.00
## sd(Intercept)
                     0.55
                                                                1448
                                                                         2177
## ~Genus (Number of levels: 29)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                        0.55
                                                 1.86 1.00
                                                                2009
## sd(Intercept)
                               0.33
                     1.11
## ~Metric2 (Number of levels: 7)
                      Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
                                             0.24
## sd(Intercept)
                          0.76
                                    0.36
                                                      1.63 1.00
                                                                     1628
                                                                              1863
## sd(ITD)
                          0.10
                                    0.09
                                             0.00
                                                      0.32 1.00
                                                                     1485
                                                                              1875
                                    0.56
                                            -0.99
                                                      0.87 1.00
                                                                     2874
                                                                              2729
## cor(Intercept,ITD)
                         -0.37
## ~spp (Number of levels: 78)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)
                     0.38
                               0.08
                                        0.24
                                                 0.54 1.00
                                                                1467
                                                                         2349
##
## Population-Level Effects:
                    Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                  0.57
                                           4.74
                                                    7.01 1.00
                                                                   2904
## Intercept
                        5.88
                        0.23
                                  0.12
                                          -0.00
                                                    0.45 1.00
                                                                   2884
                                                                            2792
## ITD
                                  0.64
                                          -2.45
                                                    0.08 1.00
## limitsphysio
                       -1.18
                                                                   3319
                                                                            3004
                                           0.20
## ITD:limitsphysio
                        0.53
                                  0.17
                                                    0.86 1.00
                                                                   2688
                                                                            2776
## Family Specific Parameters:
       Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                        0.59 1.00
                     0.04
                              0.43
                                                      1928
```

sigma

0.50

```
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
## Family: gaussian
    Links: mu = identity; sigma = identity
## Formula: log.dist ~ ITD * limits + social_tree + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 |
      Data: forage.traits.mean (Number of observations: 159)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
            total post-warmup samples = 4000
##
##
## Group-Level Effects:
## ~Authors (Number of levels: 47)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                                  0.71 1.00
## sd(Intercept)
                     0.49
                                0.10
                                         0.31
                                                                 1230
                                                                          2012
## ~Genus (Number of levels: 17)
                 Estimate Est. Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
                                         0.01
                     0.44
                                0.34
                                                  1.26 1.00
                                                                 1696
                                                                          1694
## sd(Intercept)
##
## ~Metric2 (Number of levels: 6)
                      Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)
                           0.40
                                     0.32
                                              0.02
                                                       1.23 1.00
                                                                      2455
                                                                               2305
                                                       0.51 1.00
                                                                               1831
## sd(ITD)
                           0.16
                                     0.13
                                              0.01
                                                                      1185
## cor(Intercept,ITD)
                         -0.15
                                     0.58
                                             -0.97
                                                       0.92 1.00
                                                                      2035
                                                                               2643
##
## ~spp (Number of levels: 47)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                     0.44
                                0.11
                                         0.24
                                                  0.67 1.00
                                                                 1168
## sd(Intercept)
## Population-Level Effects:
                                   Estimate Est.Error 1-95% CI u-95% CI Rhat
                                                                    6.47 1.00
## Intercept
                                       5.34
                                                 0.57
                                                          4.16
## ITD
                                       0.30
                                                 0.15
                                                         -0.02
                                                                    0.58 1.00
## limitsphysio
                                                         -2.02
                                      -0.78
                                                 0.64
                                                                    0.48 1.00
## social_treePrimitivelyEusocial
                                                 0.40
                                                         -1.88
                                                                   -0.30 1.00
                                      -1.12
## social_treeSolitary
                                      -1.13
                                                 0.39
                                                         -1.88
                                                                   -0.38 1.00
## ITD:limitsphysio
                                                                   1.07 1.00
                                       0.59
                                                 0.25
                                                          0.05
##
                                   Bulk_ESS Tail_ESS
## Intercept
                                       2526
                                                2421
## ITD
                                       1955
                                                2093
## limitsphysio
                                       3040
                                                2981
## social_treePrimitivelyEusocial
                                       2588
                                                2744
## social_treeSolitary
                                       2584
                                                2667
## ITD:limitsphysio
                                       2089
                                                2327
## Family Specific Parameters:
         Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
             0.44
                       0.03
                                 0.39
## sigma
                                          0.51 1.00
                                                        2724
                                                                  3038
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
```

scale reduction factor on split chains (at convergence, Rhat = 1).

```
## Family: gaussian
    Links: mu = identity; sigma = identity
\#\# Formula: log.dist ~ ITD * limits + social_tree + (1 | Authors) + (ITD | Metric2) + (1 | spp) + (1 | spp)
      Data: forage.traits.max (Number of observations: 193)
## Samples: 4 chains, each with iter = 2000; warmup = 1000; thin = 1;
            total post-warmup samples = 4000
##
## Group-Level Effects:
## ~Authors (Number of levels: 81)
##
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)
                                0.08
                                         0.41
                                                  0.74 1.00
                                                                 1280
                                                                          2034
##
## ~Genus (Number of levels: 29)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
##
                     0.47
                                0.32
                                         0.03
                                                  1.22 1.00
                                                                 1004
## sd(Intercept)
##
## ~Metric2 (Number of levels: 7)
                      Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                     0.35
                                              0.24
                                                        1.60 1.00
                                                                      1254
## sd(Intercept)
                           0.74
                                                                                1038
## sd(ITD)
                           0.10
                                     0.08
                                              0.00
                                                        0.30 1.00
                                                                      1770
                                                                                2133
## cor(Intercept,ITD)
                         -0.36
                                     0.56
                                             -0.99
                                                        0.87 1.00
                                                                      2494
                                                                                2772
## ~spp (Number of levels: 78)
                 Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk ESS Tail ESS
##
                                                                          2236
## sd(Intercept)
                     0.38
                                0.08
                                         0.23
                                                  0.54 1.00
                                                                 1257
## Population-Level Effects:
                                   Estimate Est.Error 1-95% CI u-95% CI Rhat
                                       6.56
                                                 0.54
                                                           5.47
                                                                    7.60 1.00
## Intercept
## ITD
                                       0.33
                                                 0.11
                                                           0.10
                                                                    0.55 1.00
## limitsphysio
                                      -1.34
                                                 0.62
                                                          -2.61
                                                                   -0.141.00
## social_treePrimitivelyEusocial
                                      -1.13
                                                 0.33
                                                         -1.76
                                                                   -0.47 1.00
## social_treeSolitary
                                      -1.10
                                                 0.32
                                                         -1.69
                                                                   -0.43 1.00
                                       0.57
                                                           0.26
                                                                    0.88 1.00
## ITD:limitsphysio
                                                 0.16
                                   Bulk_ESS Tail_ESS
## Intercept
                                       2387
                                                2577
## ITD
                                       2822
                                                2543
## limitsphysio
                                       3038
                                                2611
## social_treePrimitivelyEusocial
                                                2969
                                       2819
## social_treeSolitary
                                                2973
                                       2560
## ITD:limitsphysio
                                       2768
                                                2428
## Family Specific Parameters:
         Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
                                          0.58 1.00
## sigma
             0.50
                       0.04
                                 0.43
##
## Samples were drawn using sample(hmc). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

Discussion