Frugivore population biomass, but not density, affect seed dispersal interactions in a hyper-diverse frugivory network

Luísa Genes1\*, Gianalberto Losapio2,3, Camila I. Donatti4,5, Paulo R. Guimarães Jr.6, Rodolfo Dirzo1,7

1Department of Biology, Stanford University, Stanford, CA, USA

2Institute of Earth Surface Dynamics, University of Lausanne, Lausanne, Switzerland

3Department of Biosciences, University of Milan, Milan, Italy

4The Gordon and Betty Moore Center for Science, Conservation International, Arlington, VA, USA, 5Department of Biological Sciences, Northern Arizona University, Flagstaff AZ, USA.

6Universidade de São Paulo, Departamento de Ecologia, São Paulo, Brazil

7Stanford Woods Institute for the Environment, Stanford University, Stanford, CA, USA

**\* Correspondence:**Luísa Genes  
lgenes@stanford.edu

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Abstract

Mutualistic interactions are regulated by plant and animal traits, including, among the latter, body size and population density. In seed dispersal networks, frugivore body size determines the interaction outcome (e.g., facilitation, constraint), however species population density determines interaction probability through encounter rates. To date, most studies examining the relative role of body size and population density on seed dispersal networks have examined animal guilds encompassing a narrow range of body sizes (e.g., birds only). Given non-random, body-size dependent defaunation, understanding the relative role of these traits is important to predict and, ideally, mitigate the effects of defaunation. In the Brazilian Pantanal, we analyzed a hyper-diverse seed dispersal network composed of birds and mammals that cover a wide range of body sizes and population densities. Animal density *per se* did not significantly explain interaction patterns. Instead, population biomass, which represents the combination of body size and population density, was the most important predictor for most interaction network metrics. Population biomass was strongly correlated with body size, but not with density. Thus, larger frugivore species dispersed more plant species and had more unique pairwise interactions than smaller species. Moreover, species with larger population biomass, such as the white-lipped peccary (*Tayassu pecari*) had the strongest influence (i.e., as indicated by measures of centrality) on other species in the network and were more generalist, interacting with a broader set of species, compared to species with lower population biomass, such as the blue-crowned trogon (*Trogon curucui*). We posit that the increased abundance of small-sized frugivores resulting from the pervasive defaunation of large animals would not compensate for the loss-of-function of the latter and the inherent disruption of seed dispersal networks.

# Introduction

The Anthropocene defaunation resulting from global environmental change constitutes a driver of further biodiversity change (Dirzo et al., 2014). Large vertebrate species are more frequently affected by anthropogenic change because they are more intensively overexploited and more sensitive to disturbance than small vertebrates (Peres, 1990; Young et al., 2016). Large frugivores are potentially more important for seed dispersal network than smaller frugivores in connecting different groups of species in the network (Vidal et al., 2014), Guimarães 2020), and their disappearance can lead to changes in plant communities due to disruptions in animal and plant trait-matching (Donoso et al., 2020; Schleuning et al., 2015). .

Vertebrate population density decline leads to local extinctions of plant-animal interactions, including seed dispersal, even before species extinctions take place (Redford, 1992; Säterberg et al., 2013; Valiente-Banuet et al., 2015). Extinction of interactions may be differentially affected by traits and population characteristics of the vanishing vertebrates. For example, large mammal defaunation and its associated changes in plant-animal interactions can cascade to long-term changes in plant communities, changing the structure and diversity of regeneration understories (Dirzo and Miranda, 1990; Souza et al., 2022; Villar et al., 2020; Villar and Medici, 2021), and reducing tropical forest aboveground biomass and carbon stocks (Peres et al., 2016). However, large frugivore defaunation can also lead to ecological release of smaller frugivores that could, potentially, compensate for the lack of large vertebrates (Jansen et al., 2012; but see McConkey and Drake, 2015). If seed dispersal interaction patterns are structured by animal population density, then one would expect an ecological release to compensate for such functional roles. On the other hand, if interactions are more structured by animal body size, then compensation is unlikely. Understanding to what extent smaller-sized species may compensate for the loss of larger ones is critical to predict the effects of differential defaunation (sensu Dirzo et al., 2014) on seed dispersal networks.

Vertebrate body size regulates seed dispersal interactions mainly through energy requirements, movement, and trait-matching. Larger-sized animals generally require more fruits than smaller animals to fulfill their energy requirements (Martin, 1985), which leads to foraging on a wider number of plant species, or consuming more fruits per plant (Fleming, 1991; Palacio et al., 2016). Furthermore, large-sized frugivores can consume a wider range of plant species due to their ability of swallowing both large and small-sized seeds (Burns, 2013; Jordano, 2000). For example, small-gaped birds may only be able to disperse small seeds (e.g. Galetti et al., 2013). Moreover, larger animals can forage across larger distances, having access to a wider range of fruit species (Jordano et al., 2007). In turn, animal density is expected to affect the frequency of interactions, such that more abundant species can interact more and with more plant species (Vázquez et al., 2009, 2007). Furthermore, seed dispersal interactions may also be modulated by a combination of animal population density and body size (hereafter, population biomass). Populations with high biomass may represent very abundant species with small body size, non-abundant species with large body size, or abundant species with large body size. In non-hunted sites within the Brazilian Amazon, frugivore species with highest body size had stronger contributions to local population biomass, whereas declines in frugivore population biomass were caused by a disproportionate impact on larger-bodied frugivores, with possible consequences on seed dispersal and forest aboveground biomass (Peres et al., 2016).

Isolating the role of species density from body size in determining dispersal interaction outcomes requires observation of seed dispersal in a community that shows a natural range of density and traits, including size. However, interaction patterns have been mostly studied in communities with a low range in body size, such as bats or birds (Laurindo et al., 2020; Rezende et al., 2007). There are three potential explanations for the lack of studies in systems with a broader range in body size: (1) studies mostly take place in areas subjected to human disturbances that truncate the natural variation in body size within a community; (2) a methodological focus on specific functional guilds (such as birds and bats) due to researchers’ expertise or preference and (3) to record seed dispersal interactions from a more diverse functional guild, a suite of different methods are often required.

To address this knowledge gap, we analyzed a hyper-diverse tropical seed dispersal network that comprises a frugivore assemblage of birds and mammals with a wide range of body size and population density (Table S1) to assess the role of animal population density, body size and biomass in determining seed dispersal interaction patterns. In particular, we asked: Do, and to what extent, animal body size, population density or population biomass, explain the role of species in the interaction patterns observed in the interaction networks?

# Methods

## Study site and data collection

Data used in this study were collected in two non-defaunated sites within the Brazilian Pantanal, the largest wetland ecosystem in the world: Rio Negro (19°34′15″S, 56°14′43″W) and Barranco Alto farms (19°34′40″S, 56°09′08″W), totaling 18,500 ha. The vegetation consists of seasonally flooded savannas, semi-deciduous and gallery forests (Prance and Schaller, 1982).

Donatti et al. (2011) used various methods to detect seed dispersers and seed dispersal interactions mediated by the vertebrate frugivore assemblage at both sites. These methods included plant focal observations to record bird seed dispersal, camera trapping below fruiting trees to record mammal and bird seed dispersal and analysis of mammalian scats (Donatti et al., 2011). Vertebrate occurrence was surveyed independently from interaction observations, using line-transects as described in Peres (2000) that totaled 196 km (Donatti, 2011). Density estimates were obtained for ten mammal and six bird species (Table S1) by dividing the number of animals from a particular species observed in the area surveyed. For each animal species, the total area surveyed was computed by multiplying the distance surveyed by the average distance of animals of that particular species from the transect (Sutherland, 1996). Animal species body size was obtained from Fonseca et al. (1996), Mata et al. (2006) and Van Perlo et al. (2015), and species population biomass was calculated as a product of each species body size and its local density. As we only had density estimates for 16 animal species, we used a subset of the original network presented in Donatti et al. (2011) when analyzing the relationship between animal traits and network metrics.

**2.2. Data analysis**

To assess the relative importance of animal population density, body size and biomass in structuring seed dispersal networks, we first calculated species-level metrics based on the full Donatti et al. (2011) network comprising 46 animal species of birds, mammals, reptile and fish (excluding only the exotic feral pig *Sus scrofa*), and 46 plant species. We then computed the following species-level interaction metrics: interaction richness (i.e., the number of plant species each frugivore consumed), interaction records (i.e., the total number of feeding records for each animal species), interaction diversity (i.e., the diversity of plant species consumed by each animal species), closeness centrality (i.e., how much connected - through direct or indirect pathways - each animal species is to other species in the network), c-score (i.e. how even distributed is the interactions of a given species across all modules in the network, in which a module is a semi-independent cohesive group of interacting species) and z-score (i.e., a standardized measure of the number of interactions each species has within its own module). For these computations we used the *bipartite* package (Dormann, 2011) in R version 4.1.1 (R Core Team, 2021).

We then used such metrics as dependent variables in response to log-transformed population density, body size and biomass as predictor variables for a subset of 16 frugivore species for which population density had been estimated. We applied log-transformation to predictor variables due to data skewness and ecologically meaningful outliers. First, we assessed correlation between predictor variables using Pearson’s correlation coefficient. Population density and species body size (r=-0.32, df=14, p-value=0.2), and population density and population biomass (r=0.35, df=14, p-value=0.1) were not significantly correlated. Population biomass and species body size are correlated (r=0.74, df =14, p-value<0.001), but these two predictor variables were not simultaneously included in any model. Because metrics were calculated using the full network in Donatti et al (2011), species roles were investigated in the context of the entire sampled seed dispersal interacting community.

We used generalized linear models (GLMs) with Negative Binomial error structures for interaction richness and interaction records due to overdispersion, and Gamma error structures for interaction diversity and z-score (continuous, non-negative, and positively-skewed data), and Gaussian error structures for closeness centrality and c-score. We built models with increasing complexity, from null models with only the intercept, to models testing the interaction between body size and density. Models were fitted using R version 4.1.1 (R Core Team, 2021), and selected based on the ΔAICc < 2.0 threshold.

# Results

Within the studied seed dispersal network, frugivore species showed a wide range of population density (0.1-36 individuals/km2), body size (0.07-240 kg), and population biomass (0.1-149 kg/km2) values (Fig. 1). The set of 16 bird and mammal species included in this study dispersed 31 plant species (Fig. 2) and, notably, large-bodied species such as the tapir (*Tapirus terrestris*) and white-lipped peccary (*Tayassu pecari*) showed more frequent interactions. Indeed, according to our models, body size and population biomass were better predictors of seed dispersal interaction patterns than population density (Fig. S1), in a non-defaunated frugivore community (Fig. 3). However, relatively smaller-sized species, such as the toco toucan (*Ramphastos toco*) also interacted with a high number of plant species.

Body size (GLM, p=0.03, z=2.154, n=16, R2=0.227; AICc=101.58) and population biomass (p=0.007, z=2.674, n=16, R2=0.303; AICc=99.93) were equally good predictors of in­teraction richness (ΔAICc = 1.65; Table S2), although population biomass explained a slightly larger proportion of the response variable (R2=0.303 versus R2=0.227). Population biomass was the best predictor of interaction diversity (GLM, p=0.02, t=0.059, n=16, R2=0.415) and the c-score (GLM, p=0.02, t=0.049, n=16 R2=0.264), that represents the participation of each species in a network. A model with only opulation biomass (LM, p=0.03, t=2.295, n=16, R2=0.221) and a model that included both body size and density (LM, p=0.03, n=16, R2= 0.309) equally predicted closeness centrality, that is how connected each species is to other species in the network. Thus, as population biomass is a function body size and density, these results support the notion that total biomass is a key factor structuring the role of frugivorous species in the network is the total biomass of the population. Finally, population biomass (GLM, p=0.0111, t=0.319, n=16, R2= 0.23849) and body size (GLM, p=0.01,t=0.325, n=16 R2=0.32637; AICc=40.56) were equally good predictors of the z-score.

1. **Discussion**

Recent studies highlight the role of frugivores in ecosystem functioning, but little is known about whether and how differences in animals body size and population density explain the structure of seed dispersal networks and compensate for the defaunation of large vertebrates.In a non-defaunated landscape from the Brazilian Pantanal we examined a frugivory community that comprises a wide range of population density and body size values across 16 native vertebrate species. We found that frugivore population density itself is not a good predictor of seed dispersal patterns and seed dispersal network structure. In contrast, both body size, and population biomass (which is a combination of density and body size) were found to significantly influence seed dispersal patterns (Fig. 2). In this same community, there is a strong association between species body size and population biomass, whereas the correlation between species density and population biomass is weak. More broadly, our results indicate that large frugivores are more important for the structure of this seed dispersal network, even if these species are not abundant. In general, these species consumed more fruit species (interaction richness), consumed more fruit species in a higher frequency (interaction diversity), were more central in the interaction network (closeness centrality) and were more generalist (c- and z-score). However, beyond such general pattern, smaller-sized frugivores, such as the the chaco chachalaca (*Ortalis canicollis*) were found amongst the top-three frugivores for each of the metrics described above.

Other studies have pointed to the importance of functional traits, such as body size (e.g. Vidal et al., 2013) or neutral-based processes, such as species density (Krishna et al., 2008; Laurindo et al., 2020; Vázquez et al., 2009) in structuring species interactions. In the context of defaunation, where large-sized, and often rarer animals, tend to be extirpated in higher frequencies (Bogoni et al., 2020; Dirzo et al., 2014), and smaller-sized animals tend to become more abundant (Peres, 1990), addressing this size-biased defaunation may provide relevant insights into the potential compensatory effect of smaller animals in seed dispersal networks. In our non-defaunated seed dispersal network, there are many large-seeded plant species, which could not be dispersed by smaller frugivores if larger frugivores were extirpated (Donatti et al., 2007). The fact that density was not as important as body size or biomass in structuring interactions implies a low potential for compensatory effects. This low possibility for compensating the loss-of-function arises as abundant animals *per se* were not found to be as important to the seed dispersal patterns as species with high population biomass and high body size. In other words, having many small animals will not be enough to replace the functions once accomplished by few big animals. Such finding is of conservation significance as the lack of potential for compensatory effects in defaunated communities could cause lower dispersal and regeneration of many plant species. Examining the consistency of this finding across multiple seed dispersal networks (in conserved and differentially defaunated sites) is an aspect that warrants further research.

Out of the top three most important frugivores in each interaction pattern, only the chaco chachalaca bird is a Least Concern species according to the IUCN Red List. All other species are listed as Near Threatened, Vulnerable, or Critically Endangered. For example, population declines of large mammals, such as IUCN Vulnerable white-lipped peccaries (*Tayassu pecari*) and lowland tapir (*Tapirus terrestris*) are unlikely to be compensated for in their seed dispersal roles by abundant, but smaller animals, such as blue-crowned trogons (*Trogon curucui*). On the other hand, it would be important to examine if other types of compensatory effects might be in place where some of these large mammals experience population declines (e.g., Williams et al., 2021), as many of them are also seed predators and herbivores (e.g., Dracxler and Kissling, 2021; Mittelman et al., 2021) and some plant species may be released from these pressures, with subsequent cascading effects on the overall plant community (Martinez-Ramos et al., 2016). In addition to that, seed dispersal effectiveness is a complex process that depends on quantity and quality of dispersal and includes many interaction steps, such as the number of seeds dispersed, number of seeds dispersed per visit, gut passage effect on germination, deposition site suitability among others (Schupp et al., 2010). The interaction networks depicted in this study only consider the quantity component of seed dispersal effectiveness. Future studies that examine compensatory effects in seed dispersal networks should consider the host of other quality components of seed dispersal effectiveness to better assess the potential for functional replacements. Having said that, our results support the notion that smaller seed dispersers cannot compensate the interactions of larger-bodied vertebrates.

Given the low support for compensatory effects in this seed dispersal network, we posit that conservation actions should target areas where a wide range of frugivore functional traits is extant and promote such species reintroductions where they have been extirpated. Despite evidence provided in this study, the relative role of species density and body size to structuring interaction networks continues to be a fundamental research agenda in ecology (Guimarães, 2020). The results we uncovered in this work suggest that similar studies, comparing defaunated and non-defaunated contexts and that consider a wide-range of disperser densities and body sizes, may provide further insights on the consequences of the omnipresent size-biased defaunation that characterizes the Anthropocene.

# Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

# Author Contributions

LG, PRGJ and RD conceptualized this study. CID conducted the fieldwork and participated in former discussions. LG and GL conducted the analyses. LG and GL wrote the first draft. All authors contributed to the writing of the article and approved the submitted version.

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# Data Availability Statement

The datasets analyzed for this study can be found within the main text and supplementary material.

**Figure legends (Figures must be deleted prior to submission)**



**Figure 1.** Frequency distribution of studied frugivore population density, species body size and population biomass of frugivores from the Brazilian Pantanal, including ten mammal and six bird species.



**Figure 2.** Seed dispersal network at two nearby sites in the Brazilian Pantanal. Each green rectangle represents one plant species, and each brown rectangle represents an animal species. Grey lines represent links between species, meaning that fruits from the plant species on the left were consumed by the linked animal species on the right, and the width of the lines indicates the strength of the interaction. This network includes bird and mammalian species for which population density was estimated. Species are sorted in alphabetic order. [CAN YOU PLEASE PAINT THE ANIMAL ICONS IN BLACK, PUSH THEM A LITTLE TO THE LEFT AND INCREASE THE SIZE A LITTLE?]

**Figure 3.** Relationship for significant predictors of the structure of a seed dispersal network in the Brazilian Pantanal, according to generalized linear models. Shaded areas depict 95% confidence intervals. Body size is measured in kg, p, opulation biomass is measured in kg/kKg/m2, and population density is measured by individuals/km2. SAME ISSUE WITH ANIMAL ICONS: THE DIFFERENT SHADES OF GREY ARE VERY FAINT – AND THE BODY SIZE GRADING SCALE DOES NOT SEEM TO MATCH COLORS OF THE ICONS? Km2.

## Tables

**Table 1.** Summary of generalized linear models for predicting the effect of population density, body size and population biomass on seed dispersal network patterns. Significant variables are shown in bold, and models selected based on ΔAICc and significance are shaded.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Response variables** | **Model** | **Predictors** | **β (Estimate)** | **Standard Error** | **z-value**  **(or t-value)** | **P-value** |
| *Interaction richness* | *null* | Intercept | 2.24 | 0.15 | 14.92 | <0.001 |
|  |  |  |  |  |  |  |
|  | *density* | Intercept | 2.19 | 0.18 | 11.93 | <0.001 |
|  |  | density | 0.09 | 0.23 | 0.42 | 0.6 |
|  |  |  |  |  |  |  |
|  | *body size* | Intercept | 2 | 0.16 | 11.83 | <0.001 |
|  |  | **body size** | 0.33 | 0.15 | 2.15 | 0.03 |
|  |  |  |  |  |  |  |
|  | *biomass* | Intercept | 1.71 | 0.23 | 7.24 | <0.001 |
|  |  | **biomass** | 0.38 | 0.14 | 2.67 | 0.007 |
|  |  |  |  |  |  |  |
|  | *density + body size* | Intercept | 1.75 | 0.21 | 8.17 | <0.001 |
|  |  | density | 0.35 | 0.2 | 1.75 | 0.08 |
|  |  | **body size** | 0.44 | 0.15 | 2.82 | 0.004 |
|  |  |  |  |  |  |  |
| *Interaction diversity* | *null* | Intercept | 0.58 | 0.05 | 10.91 | <0.001 |
|  |  |  |  |  |  |  |
|  | *density* | Intercept | 0.62 | 0.07 | 8.42 | <0.001 |
|  |  | density | -0.06 | 0.08 | -0.69 | 0.5 |
|  |  |  |  |  |  |  |
|  | *density + body size* | Intercept | 0.78 | 0.1 | 7.45 | <0.001 |
|  |  | density | -0.13 | 0.08 | -1.59 | 0.1 |
|  |  | **body size** | -0.16 | 0.06 | -2.4 | 0.03 |
|  |  |  |  |  |  |  |
|  | *biomass* | Intercept | 0.8 | 0.1 | 7.58 | <0.001 |
|  |  | **biomass** | -0.15 | 0.05 | -2.59 | 0.02 |
|  |  |  |  |  |  |  |
|  | *body size* | Intercept | 0.67 | 0.07 | 8.94 | <0.001 |
|  |  | body size | -0.11 | 0.05 | -1.98 | 0.06 |
|  |  |  |  |  |  |  |
| *Interaction records* | *null* | Intercept | 3.95 | 0.27 | 14.28 | <0.001 |
|  |  |  |  |  |  |  |
|  | *density* | Intercept | 3.95 | 0.33 | 11.72 | <0.001 |
|  |  | density | -0.001 | 0.42 | -0.004 | 0.9 |
|  |  |  |  |  |  |  |
|  | *body size* | Intercept | 3.71 | 0.32 | 11.47 | <0.001 |
|  |  | body size | 0.32 | 0.3 | 1.05 | 0.2 |
|  |  |  |  |  |  |  |
|  | *biomass* | Intercept | 3.46 | 0.43 | 7.9 | <0.001 |
|  |  | biomass | 0.36 | 0.28 | 1.28 | 0.2 |
|  |  |  |  |  |  |  |
|  | *density + body size* | Intercept |  | 0.4 | 8.33 | <0.001 |
|  |  | density | 3.41 | 0.42 | 0.96 | 0.3 |
|  |  | body size | 0.47 | 0.32 | 1.47 | 0.1 |
|  |  |  |  |  |  |  |
| *Closeness centrality* | *null* | Intercept | -1.97 | 0.04 | -46.05 | <0.001 |
|  |  |  |  |  |  |  |
|  | *density* | Intercept | -2.03 | 0.04 | -42.91 | <0.001 |
|  |  | density | 0.12 | 0.05 | 2.07 | 0.05 |
|  |  |  |  |  |  |  |
|  | *body size* | Intercept | 95.49 | 9.09 | 10.5 | <0.001 |
|  |  | body size | -9.4 | 7.9 | -1.19 | 0.2 |
|  |  |  |  |  |  |  |
|  | *biomass* | Intercept | 114.67 | 12.93 | 8.86 | <0.001 |
|  |  | **biomass** | -18.39 | 7.37 | -2.49 | 0.02 |
|  |  |  |  |  |  |  |
|  | *density + body size* | Intercept | 115.16 | 12.5 | 9.21 | <0.001 |
|  |  | **density** | -26.73 | 10.78 | -2.47 | 0.02 |
|  |  | body size | -17.11 | 8.5 | -2.01 | 0.06 |
|  |  |  |  |  |  |  |
| *C-score* | *null* | Intercept | 0.41 | 0.05 | 7.55 | <0.001 |
|  |  |  |  |  |  |  |
|  | *density* | Intercept | 0.34 | 0.06 | 5.61 | <0.001 |
|  |  | density | 0.13 | 0.07 | 1.74 | 0.1 |
|  |  |  |  |  |  |  |
|  | *body size* | Intercept | 0.38 | 0.06 | 5.73 | <0.001 |
|  |  | body size | 0.05 | 0.06 | 0.82 | 0.4 |
|  |  |  |  |  |  |  |
|  | *biomass* | Intercept | 0.79 | 0.04 | 17.79 | <0.001 |
|  |  | **biomass** | -0.06 | 0.02 | -2.41 | 0.02 |
|  |  |  |  |  |  |  |
|  | *density + body size* | Intercept | 0.78 | 0.04 | 18 | <0.001 |
|  |  | **density** | -0.09 | 0.04 | -2.16 | 0.04 |
|  |  | body size | -0.04 | 0.03 | -1.54 | 0.1 |
|  |  |  |  |  |  |  |
| *Z-score* | *null* | Intercept | 0.3528 | 0.3 | 1.17 | 0.2 |
|  |  |  |  |  |  |  |
|  | *density* | Intercept | 0.4924 | 0.32 | 1.49 | 0.1 |
|  |  | density | -0.3864 | 0.41 | -0.93 | 0.3 |
|  |  |  |  |  |  |  |
|  | body size | Intercept | -0.469 | 0.34 | -1.37 | 0.1 |
|  |  | **body size** | 0.914 | 0.32 | 2.8 | 0.01 |
|  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |
|  | *biomass* | Intercept | -0.988 | 0.49 | -2 | 0.06 |
|  |  | **biomass** | 0.933 | 0.31 | 2.92 | 0.01 |
|  |  |  |  |  |  |  |
|  | *density + body size* | Intercept | -0.6642 | 0.47 | -1.4 | 0.1 |
|  |  | density | 0.2942 | 0.49 | 0.59 | 0.5 |
|  |  | body size | 1.0006 | 0.37 | 2.69 | 0.01 |