



# Social interaction, and not group size, predicts parasite burden in mammals

Juliana Lucatelli<sup>1</sup> · Eduardo Mariano-Neto<sup>1,2</sup> · Hilton F. Japyassú<sup>1,2</sup>

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## Abstract

Although parasitism is often considered a cost of sociality, the evidence is mixed, possibly because sociality is multivariate. Here we contrast the dependence of parasitism costs on major social variables such as group size and social structure, as measured by network metrics. We conduct two robust phylogenetic meta-analyses, comprising 43 published results for studies with group size and 32 results with social structure metrics. This is the first meta-analytical test of this hypothesis for mammals as a whole. Contrarily to theoretical expectations and previous meta-analyses, there is no relationship between group size and parasitism, but we find conflicting results when analysing different aspects of sociality. Our analysis reveals that social structure is connected to parasite load, possibly because contact between group members, and not group size, is linked to parasite transmission. While more intensely interconnected groups facilitate parasite transmission, large groups are frequently fragmented into smaller, weakly connected subgroups. Strong social modularisation should thus be favoured by natural selection to hamper parasite overload. Future empirical studies should focus on specific parameters of social network structure and on parasite transmissibility. If social structure can evolve fast, even culturally, then host/parasites evolutionary games enter into a whole new fast dynamics, and animal conservation studies should take advantage of this possibility.

**Keywords** Social behaviour · Social network analysis · Parasitism · Phylogenetic meta-analysis · Robust meta-analysis

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✉ Juliana Lucatelli  
julucatelli@hotmail.com

<sup>1</sup> Instituto de Biologia, Universidade Federal da Bahia, Rua Barão de Jeremoabo, 668 Ondina, Salvador 40170-115, Brazil

<sup>2</sup> Instituto Nacional de Ciência e Tecnologia em Estudos Interdisciplinares e Transdisciplinares em Ecologia e Evolução, Universidade Federal da Bahia, Salvador, Brazil

## Introduction

The evolution of sociality is a fundamental topic in behavioural research (Arnold 1990; Perrin and Lehmann 2001; van Schaik and Maria 1986), and social behaviour is certainly at the root of the success of humans as a species (Gintis 2011). Despite the positive effects of social behaviour on obtaining and allocating food resources (Blundell 2002; Creel and Creel 2002; Tennie et al. 2009), performing antipredatory behaviours (Sorato et al. 2012), and learning (Dunbar 1992, 1998), sociality also entails well known costs such as increased mate competition, reproductive suppression (Brockmann 1997), food competition (Gompper 1996), and predator attraction (Botham and Krause 2005).

An important potential adverse effect of sociality is an increase in the transmission of parasites and pathogens, a relevant issue considering that parasitism is a fundamental component of host fitness (Møller et al. 2001). The risk of parasitism can increase with sociality because it increases factors such as host proximity and contact with infected individuals or with conspecifics faeces, fecal contamination of shared food, and sexual contact (Møller et al. 1993). Parasitism is capable of causing population decline through pathological infections, threatening fragile populations, thus rendering parasite and disease management an important focus of conservation biology (Cleaveland et al. 2002). Additionally, parasitism potentially influences the evolution of social behaviour, for example: through selection of behaviours that reduce infection probability or control levels of parasite infections, such as grooming (Eads et al. 2017); dispersion; avoidance of infected areas; dominance behaviour for testing the quality of immigrants; reproductive synchrony; forced emigration; and selective, far from faeces foraging (see Møller et al. 1993 review).

Parasitism is capable of affecting host survival and reproduction (Møller et al. 2001), and larger group sizes, higher population densities, a promiscuous sexual system, social contact and colonialism are each associated with higher levels of exposure to, or transmission of, parasites (Altizer et al. 2003; Arneberg et al. 1998; Hoogland 1979; Hoogland and Sherman 1976; Johnson et al. 2004; Rifkin et al. 2012; Tella 2002). However, several studies have found that parasitism is not significantly affected by group size (Arnold and Anja 1993; Hillegass et al. 2008; Novikov et al. 2016; Zhang et al. 2010). In a comparative study, Watve and Sukumar (1995) found that among 12 species of mammals, the solitary species had higher levels of parasitism than did the gregarious ones. Furthermore, negative correlations between sociality and parasitism have been found, possibly due to decreasing infection probability within larger groups and populations (Bordes et al. 2007; Free-land 1979; Mooring and Hart 1992), or to the development of behavioural or physiological defense strategies in strongly social species (Archer et al. 2016; Bordes et al. 2007; Hart 1994; Hawlena et al. 2007; Stow et al. 2007).

Although parasitism in gregarious species can act as a selective pressure favouring the evolution of defensive strategies against parasitism (Hart 1994; Johnson et al. 2004; Hawlena et al. 2007), parasites tend to surpass such strategies in an arms race (Ezenwa et al. 2016). Thus, even if the relationship between sociality and parasitism assumes different forms in distinct species, and change over time, the general expected pattern is of greater transmissibility among more social hosts due to the higher levels of proximity and contact among individuals in larger groups.

The conflicting results among studies might partially be due to the different aspects (or variables) of social behaviour examined. To establish levels of sociality, different aspects of social behaviour have been considered, including group size (Rifkin et al. 2012; Shultz and Dunbar 2007), social network metrics (measuring aspects such as strength, reciprocity and

transitivity of social interactions; Wey et al. 2008), group composition, affiliative behaviour rate (Hillegass et al. 2008), and indexes that combine different attributes (Avilés and Harwood 2012; Shultz and Dunbar 2007). Although group size is by far the most studied aspect of sociality (Rifkin et al. 2012), considering this single aspect in isolation can sometimes be misleading, because small cohesive groups can be erroneously taken as weakly social, whereas large groups of weakly interacting individuals can be erroneously taken as highly social (Bergman and Beehner 2015; Bordes et al. 2007). Sociality is better understood as a multivariate factor (Ezenwa 2004; Pigliucci 2003; Kappeler 2019), and different aspects of sociality can potentially be associated with different ecological variables or selective pressures. For example, whereas group size should positively affect the degree of parasitism (see Rifkin et al. 2012 meta-analysis), the intensity of grooming behaviour should negatively affect the degree of ectoparasitism (Hawlena et al. 2007; Duboscq et al. 2016). The multivariate nature of sociality could thus account for the existence of conflicting empirical support concerning the effects of sociality on parasitism. Kappeler (2019) argues that to better describe and capture social complexity, aspects of social organisation (which includes group size), social structure (assessable by social interactions), sexual system, and care system should be considered. Here we advance in the direction of a more complete evaluation of the social system, including not only the most prevalent metric for sociality (group size), but also considering studies that evaluate social structure.

Sociality can be more influenced by social interactions than by group size (Griffin and Nunn 2012; Schmid-Hempel 2017; Silk et al. 2017), and group size does not necessarily reflect the levels of social cohesion and interaction within the group, as predicted by models and simulations (Nunn et al. 2015a; Sah et al. 2017, 2018). Accordingly, we investigate here the influence of group size and social structure, as measured by social network metrics, on parasitism, selecting studies that provide results for research questions at the group level. We analyse data from several independent studies and online databases, synthesising conflicting results in two meta-analyses of mammals, while testing empirically the hypothesis that social structure is a better predictor of parasitism than group size.

## Materials and methods

### Study taxon

We selected the taxon Mammalia for this study due to the existence of social, ecological and natural history databases for numerous species of this class (Jones et al. 2009; Nunn and Altizer 2005). In addition, mammals are the subjects of many biomedical and pharmacological studies that provide information on their parasites (Altizer et al. 2003). Furthermore, sociality is widely studied in mammals (e.g., Altizer et al. 2003; Arneberg 2002; Ezenwa et al. 2006; Rifkin et al. 2012).

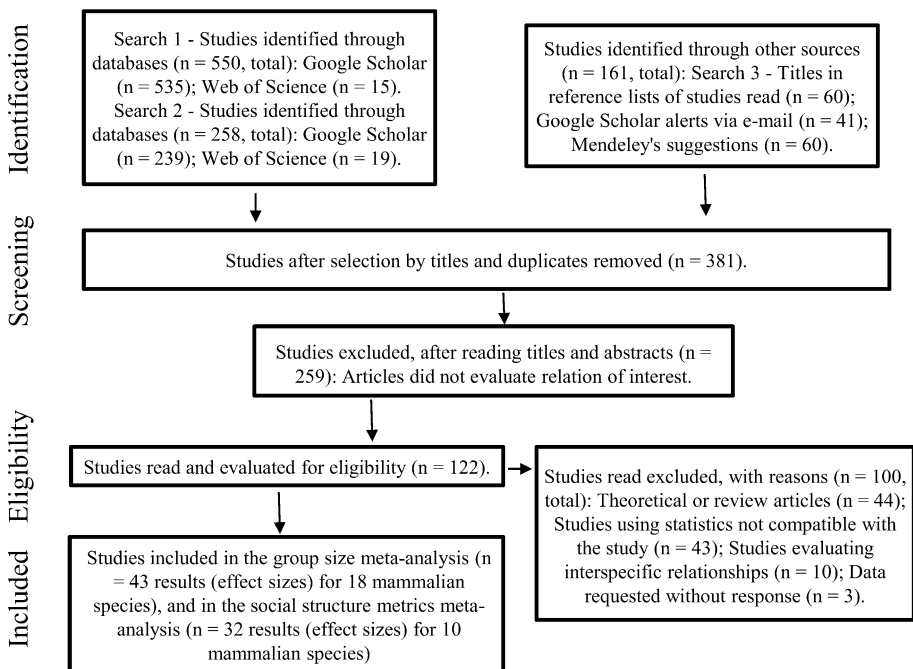
### Data collection

We tested the effects of group size and social structure on parasitism by performing two meta-analyses of multiple studies (Borenstein et al. 2009). Initially, we carried out a systematic review of studies that evaluated the relationship between sociality (independent variable) and parasitism (dependent variable). The searches were carried out in the Web of Science and Google Scholar databases and considered studies published between 1970

and 2016. In a preliminary search, which was performed on May 24, 2016 (Fig. 1), we used the keywords "(((Social\* OR gregarious\*) AND mammal\*) AND parasit\*) AND (correlation OR regression)". In this preliminary search, we identified the aspects of sociality used in the literature, allowing the configuration of the parameters of search 2, performed on July 07, 2016, which expanded the first search by including specific keywords: "(grooming rate OR contact rate OR social network analysis OR group size OR colony size OR social status OR group composition) AND mammal\*) AND parasit\* AND (correlation OR regression)."

We also screened studies identified until December 31, 2016 (search 3), based on notifications received via Google Scholar alerts of keyword matches for the first two searches and via e-mails of Mendeley's suggestions. We also screened the references of the articles retained in the previous searches to identify additional potentially useful studies. We excluded repeated articles found in different searches. The selection process is represented by the PRISMA strategy, a diagram for reporting of systematic reviews (Liberati et al. 2009), as shown in Fig. 1.

We selected published scientific papers, dissertations and theses in English (Fig. 1), and extracted the data necessary to estimate effect size and weight (correlation coefficient and sample size) for each host species. These data were obtained directly (values available explicitly in the studies), through the raw data (allowing correlation analyses to be performed), or from correlation graphs (allowing the raw data to be extracted with the Web Plot Digitizer program—Rohatgi 2016). If the required values were not provided in the study, the authors were contacted. Most of the data came from intraspecific studies, but



**Fig. 1** PRISMA strategy for meta-analyses of the relationships between parasitism and group size, or social structure, in mammals

some were extracted from interspecific studies (which evaluated the relationships among different species) that provided values for individual species. The social structure metrics used in the meta-analysis were compiled from the selected literature (Table 1).

### Correlations between sociality aspects and parasitism

We used a random effects model due to the expectation of variability among effect sizes for different studies/species. The effect sizes (correlation coefficients) were converted to Fisher's  $z$  scale, and the summary effect size for all species considered in the study was obtained along with the 95% confidence interval (Borenstein et al. 2009). From these values, we generated the forest plots (by using the "metafor" R package, Viechtbauer 2010, and R Core Team 2016) to evaluate whether group size or social interactions influence parasitism and, if so, whether the relationships were positive or negative. Following Cohen (1988), we classified effect sizes as low ( $r=0.1$ ), moderate ( $r=0.3$ ) or high ( $r=0.5$ ).

Many of the selected studies showed more than one result/effect size for the same species. To address this effect size dependency, we used a robust variance estimation (here also called robust meta-analysis), RVE (Fisher and Tipton 2015; Hedges et al. 2010). This analysis allows the use of available data sets thus avoiding information loss due to the averaging of dependent effect sizes. We used the method for correlated effects, and the analysis was adjusted for small samples (Fisher and Tipton 2015). We performed the sensitivity analyses to assess whether the actual estimate of variance was not highly sensitive to different effect size correlation ( $Rho$ ) values (Hedges et al. 2010). Since the sensitivity analyses showed that the use of different  $Rho$  values ( $Rho=0, 0.2, 0.4, 0.6, 0.8$  or  $1$ ) had practically no effect on the parameter estimates (Supplementary material 1), we used the standard value of  $Rho=0.8$ .

The phylogenetic meta-analyses were performed, along with the robust meta-analyses, to account for the dependence among the data from closely related species, which potentially have similar effect sizes. We used the method of Adams (2008), that allows to incorporate phylogenetic distance data in the meta-analyses, with the values of the terminals corrected by RVE. We pruned the phylogenies with 18 terminals (group size results, Supplementary material 2a) and 10 terminals (social structure results, Supplementary material 2b) based on the phylogenetic tree containing 5020 species of mammals (supplementary material by Fritz et al. 2009). All analyses were performed in R (R Core Team 2016) version 3.3.2 using the packages "metafor" (Viechtbauer 2010), "robmeta" (Fisher and Tipton 2015) and "grid" (to perform the meta-analysis and RVE and construct the meta-analytical graphs) and "ape" (for the phylogenetic analyses—Paradis et al. 2004). The scripts used in the analyses are available in Supplementary material 3.

### Publication bias

The tendency to publish only significant results may bias the outcome of meta-analyses (Jennions and Møller 2002). In this study, we initially used funnel plots to visually evaluate the presence of publication bias by examining the symmetry around the mean effect size (Light et al. 1994; Light and Pillemer 1984). As a complement to this analysis, we used the "trim and fill" method (Duval and Tweedie 2000a, b), which simulates the points needed to achieve symmetry of the funnel graph, thus allowing a summary effect acceptability evaluation (Borenstein et al. 2009).

**Table 1** Social structure metrics and their meanings according to their sources (studies included in this meta-analysis). Social connections between individuals in the networks were represented by interactions including mainly grooming, but also physical contact, aggression and proximity

Social structure metric	Meaning	References
Degree	Number of partners	MacIntosh et al. (2012) and Wren et al. (2016)
Strength	Intensity of interactions (time); or time percentage on social interactions	Duboscq et al. 2016; González-Hernandez et al. (2014), MacIntosh et al. (2012), Rimbach et al. (2015) and Shaith et al. (2008)
Contact or Degree	Number of interactions with other individuals	Drewe (2009), Duboscq et al. (2016), González-Hernandez et al. (2014) and Gear et al. (2013)
Betweenness	How frequently one individual is the single connection between otherwise unconnected individuals in the network	MacIntosh et al. (2012), Rimbach et al. (2015) and Vanderwaal et al. (2016)
Overall tie strength	Sum of the strength of all associations in which an individual is involved	Vanderwaal et al. (2016)
Within-clique tie strength	Sum of the strength of all associations between members of the same clique (group wherein everyone is connected to everyone)	Vanderwaal et al. (2016)
Between-clique tie strength or Weak ties	Sum of the strength of all associations between members of the different cliques	Vanderwaal et al. (2016)
Closeness centrality	Shortest path (number of "links") needed to reach all members of the network from a given individual	Rimbach et al. (2015)
In-degree or out-degree	The number of interactions/grooming received or initiated, respectively	Gear et al. (2013) and Rimbach et al. (2015)

## Effects of different aspects of sociality and parasitism

We evaluated separately two aspects of sociality (group size and social structure) that could potentially have distinct effects over parasitism. Although both group size and social structure are assessed in distinct ways in particular studies, meta-analytical studies usually zoom out from these particular methodological decisions that vary from one study to another, to focus on the more general aspects of the problem. This is a strength of meta-analysis, since the overall result will be robust to the particularities of each study (Poulin and Forbes 2011). Zooming out from these particularities implies focusing on the fundamental distinction between group size and social structure that remains across all these particular methodological decisions.

The present study is concerned with this fundamental difference, and accordingly we evaluate if these two general and distinct aspects of sociality impact parasitism in distinct directions. To test for these putatively distinct effects, we performed two separate robust phylogenetic meta-analyses, one comprising the studies that used group size metrics, and the other comprising the studies that used social structure metrics.

Considering that the studies included in our meta-analyses measured distinct metrics of parasitism (mainly richness, prevalence or abundance of parasites), distinct scales of parasitism (measured at the level of individual hosts, or at the host group level), and distinct types of parasites (endo or ectoparasites), we considered these variables as moderators (Borenstein et al. 2009), since they could potentially influence the correlation between sociality and parasitism (Ezenwa et al. 2006; Bordes et al. 2007),

A matrix of data was constructed that contained mammalian host species, study identity, type of study (intra or interspecific), order and family of each host species, sociality aspect, parasite type, parasite scale, and parasite metric. The matrix also included sample size and correlation coefficient (Pearson's  $r$  or Spearman's  $r_s$ ) information. All the data compiled in this study is available as Supplementary Material (SM4).

We performed the robust/phylogenetic meta-analyses for group size and social structure data and included the moderators variables in the models, in order to verify if the type, metric or scale of parasitism would moderate the meta-analyses (SM3).

## Results

### Social structure, and not group size, affects parasitism

Different aspects of sociality have diverging effects over parasitism. The most studied aspect of sociality, group size, does not affect parasitism ( $-0.688 \leq -0.151 \leq 0.385$ ,  $t = -0.544$ ,  $P = 0.582$ ,  $N = 43$  results from 18 investigated species). Nevertheless, social structure does have a significant, moderate to high positive effect on parasitism ( $0.178 \leq 0.381 \leq 0.583$ ,  $t = 3.684$ ,  $P = 0.000872$ ,  $N = 32$  results from 10 investigated species).

The funnel plot generated for RVE-corrected values suggests weak positive publication bias for the relationship between group size and parasitism, but this weak bias does not qualitatively change the response. Also, this funnel plot shows that there is no publication bias for the relationship between social structure and parasitism (additional data are given in Supplementary material 5a, b).

## Parasite type, metric, and scale do not moderate the correlation between sociality and parasitism

The effect of group size on parasitism does not depend on whether the parasites are endoparasites or ectoparasites ( $P=0.923$ ). Also, this effect does not depend on the metric used: parasite richness, abundance or prevalence ( $P=0.505$ ).

The effect of social structure on parasitism also does not depend on whether the parasites are endoparasites or ectoparasites ( $P=0.0756$ ). Similarly, the effect of social structure on parasitism also does not depend on whether the metric of parasitism is abundance, richness or prevalence ( $P=0.555$ ).

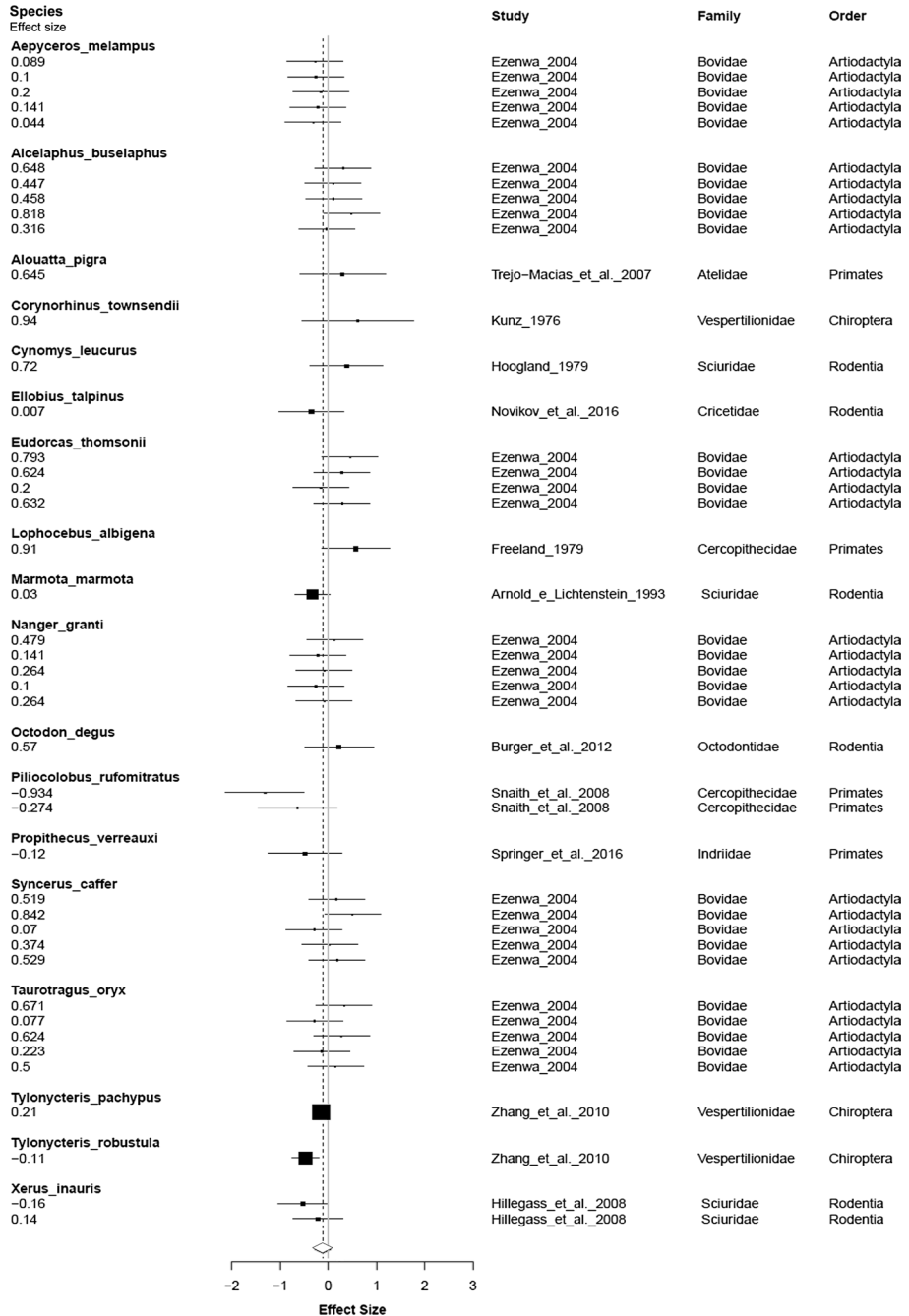
Results from analyses focusing on studies with individual scale of parasitism (one measure for each individual, or for a sample of the individuals in the group) do not differ from results with studies with group scale measurements of parasitism, such as prevalence measures (percentage of individuals infected in a group), or total richness (number of species of parasites in each group). We found that the majority of studies (29 effect sizes from 16 species of group size studies and 31 effect sizes from 9 species of social structure studies) included measures at the individual scale, against a minority of studies (14 effect sizes from 8 species of group size studies and 1 effect size from 1 species of a social structure study) focusing at the group scale. Therefore, the effect of group size on parasitism does not depend on whether the parasites are measured at individual or group scale ( $P=0.530$ ).

## Discussion

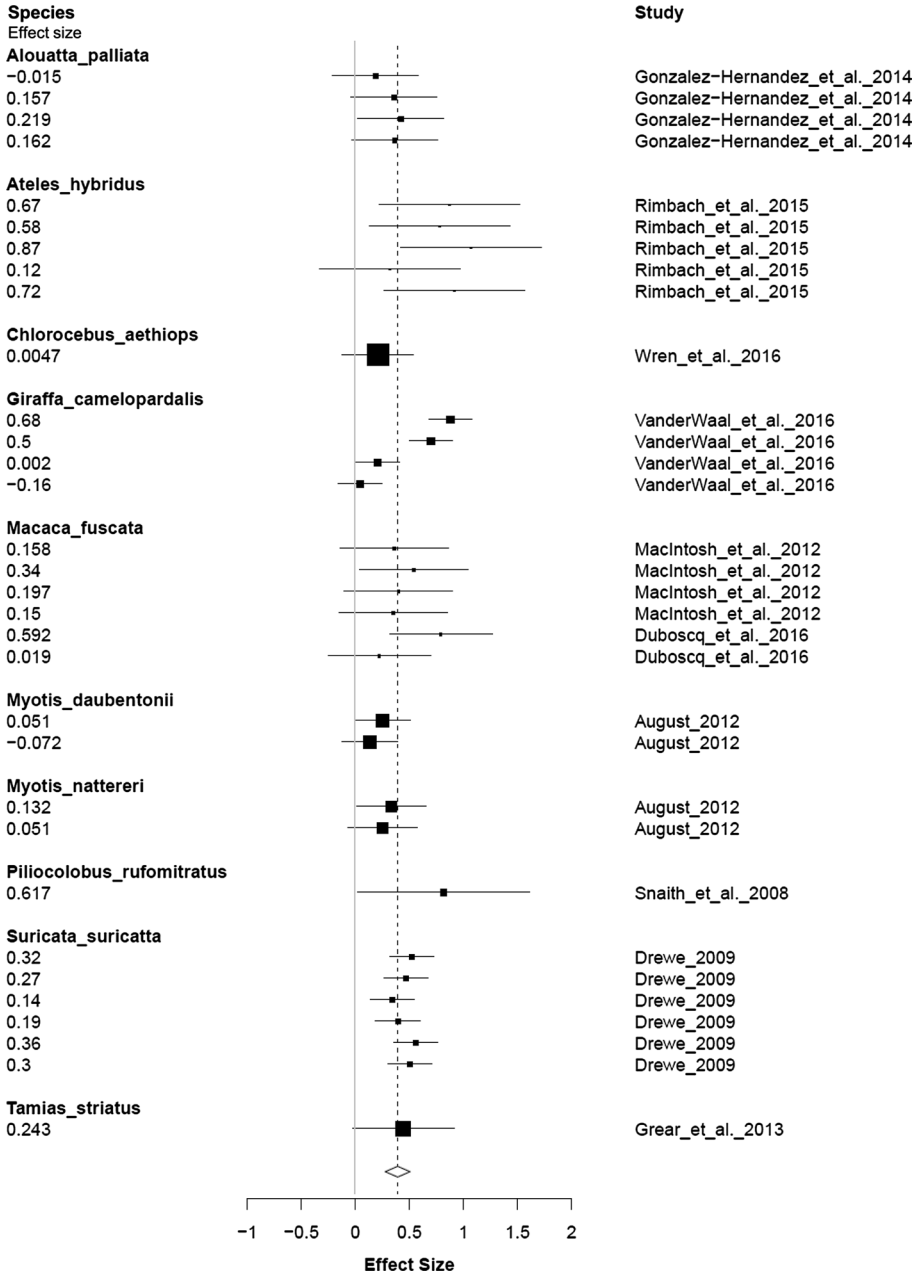
Group size, the easiest to measure, and thus most extensively studied aspect of sociality, does not predict the level of parasitism in social mammals. Although there is evidence elsewhere for a weak, but positive relationship between group size and parasitism in mammals (Cote and Poulin 1995; Rifkin et al. 2012; Patterson and Ruckstuhl 2013), our analyses, which include novel studies and correct for interdependencies within our data set (e.g. repeated studies for the same species, or multiple effect sizes for the same study, or phylogenetic dependencies between species) show no relationship between group size and parasitism (Fig. 2). Finally, our analysis shows that the social structure does predict parasitism in mammals in general (Fig. 3), in agreement with previous findings for primates (Griffin and Nunn 2012). Groups with a highly connected network of interactions between individuals are more vulnerable to parasitism than loosely connected groups. These results imply that group size is a superficial measure of sociality because it disregards social structure. For example, group living might be the result of a spatial concentration of resources (Carr and Macdonald 1986; Wright and Gompper 2005) with weak social relationships among the individuals. Even if for animals in larger groups and with few interactions there is a possibility of parasite transmission through faeces, for example, we did not find a relationship between group size and parasitism when focusing on endoparasites (the type of parasite included in the study most likely to be transmitted via faeces contamination), a result possibly explained by host strategies, such as avoiding feeding in contaminated areas (Møller et al. 1993).

Social structure is a fundamental factor affecting parasite dispersion within groups, and taking this structure into account greatly improves the prediction of parasite dynamics (Keeling and Eames 2005; MacIntosh et al. 2012; Pastor-Satorras et al. 2015). Also,





**Fig. 2** Group size has no effect over the level of parasitism, as the mean effect (dotted line) does not differ from a null effect (continuous line). The forest plot shows corrected (RVE) effect sizes (squares), confidence intervals (horizontal bars) and the summary effect size of all species (diamond, representing the robust phylogenetic meta-analysis summary effect size value), their respective references, and each species' family and order. Correlation coefficients are shown below species names



**Fig. 3** Social structure has a significant effect over the level of parasitism, as the mean effect (dotted line) differ from a null effect (continuous line). The forest plot shows corrected (RVE) effect sizes (squares), confidence intervals (horizontal bars) and the summary effect size of all species (diamond, representing the robust phylogenetic meta-analysis summary effect size value), their respective references, and each species' family and order. Correlation coefficients are shown below species names

larger groups tend to be more modularised (West 2017; Nunn et al. 2015b), and an increase in modularity would potentially reduce parasite transmissibility (Nunn et al. 2015a). Simulations show that highly modularised social contact networks with cohesive subgroups (cliques) would effectively restrict infections to a few subgroups and delay the spread of disease outbreaks (Sah et al. 2017, but see Romano et al. 2018).

Caution would be required in the direct comparison between social structure and group size results, if one considers that social structure and group size studies could differ in scale, because social structure data usually comes from single group studies, and group size data usually comes from multi-group studies. While single group studies measure individuals, multi-group studies measure groups. For example, multi-group data could indeed provide answers for population level questions, but only if the groups included in a particular the study were structured across populations, and if the experimental and analytical procedures were designed to answer population level questions. Nevertheless, the effect sizes included in our meta-analyses all come from studies focusing at the group scale, with no study designed to answer neither individual, nor population level research questions. This implies that the effect sizes derived from these original studies reflect group scale effects. Furthermore, our results seem robust also because the significant positive correlation found comes from the smaller sample of social structure studies results (32, as compared to 43 group size results), implying that social structure should indeed have a large effect (so as to be detectable even with a smaller sample).

Increased social interaction levels thus result in increased parasite pressure, and network metrics are appropriate for evaluating this relationship (Craft 2015). Although this possibility has been previously suggested through modelling (Nunn et al. 2015a) and simulation approaches (Sah et al. 2018), here we corroborate this prediction empirically for the first time through a meta-analysis including several mammal taxa. Parasitism is thus likely to be one important driver of social structure, selecting for the organisation of subgroups and for particular interaction dynamics (Nunn et al. 2015b). This is not an unfamiliar possibility, considering that grooming behaviour in primates is simultaneously a part of the social dynamics of groups (and thus an organiser of intra-group structure), and a mechanism for parasite control (McFarland 2018). Social contact network thus emerges as a main parameter controlling social group vulnerability to parasites. The insignificance of group size effects on parasitism could potentially be a side effect of the evolution of social structure in response to parasitism. For example, Snaith et al. (2008) found that larger groups of a primate species spread out more and devote less time to social interactions. If this proves to be a general rule for mammals, there would be a negative correlation between group size and social structure, due to larger and continued parasitism pressure over larger groups. Again, if this proves to be correct, parasitism would peak at intermediate group sizes, a non-linear prediction that could be tested in future empirical studies.

Our empirical result at the local, group level scale, has implications for conservation studies. First, the management of group size for conservation purposes would prove to be less efficient than the inspection of group interaction profiles, with the eventual prioritisation of parasite control interventions on more cohesive social groups. Also, if social structure can evolve quickly, even culturally (Cantor et al. 2015), then host/parasites evolutionary games enter into a whole new fast dynamics realm, potentially changing within ecological timescales, with a clear impact for animal conservation studies and modelling.

If social structure, and not group size, is a relevant factor for the evolution of the relationship between sociality and parasitism, the same could be true for the evolution of other aspects of the biology of social animals. For example, social structure not only paves the way for parasite transmission, but it also creates the roads for information transmission

within the social group (Laland and Hoppitt 2003), which includes information about resources, predators, and courtship. More broadly, empirically evaluating across taxa the relationship between sociality and the routes for the transmission of fitness relevant environmental features could reveal broad evolutionary patterns and pressures on social structure, unravelling new parameters underpinning social organisation, while identifying particular ecological and evolutionary constraints in different taxonomic groups. Pathogen and information transmission could drive the emergence of social structure in either a synergistic or an antagonistic fashion, and the details of the interaction between these interlinked factors would be decisive in the dynamics of social structure both at ecological and evolutionary timescales.

## Supplementary Material

Sensitivity analyses results; Phylogenetic trees; Scripts used in R; Data used during this study; Funnel plots.

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**Author contributions** All authors contributed to the study conception and design. Material preparation and data collection were performed by JL and analysis were performed by JL and EMN. The first draft of the manuscript was written by JL and HFJ, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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