COMMENTARIES

Measures of sociality: two different views of group size

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Most vertebrates, including humans, are gregarious to a certain degree. They tend to form shoals, flocks, coveys, herds, bands, packs, parties or colonies (hereafter: groups) of conspecific individuals. Conspecifics make up a major component of their environment thereby influencing major aspects of their lives, such as predation pressure, pathogen pressure, aggression, foraging success, metabolism and sexual selection. Consequently, sociality affects the evolution of a wide range of behavioural, morphological and life history traits (Krause & Ruxton 2002). Here, we set out to describe methods to quantify group forming tendency (i.e. sociality), to discuss controversies about their use, and to propose the use of different measures for different purposes.

Hereafter, we presume that groups are well defined and the statistical samples (or data) properly describe their populations. We do not consider differences among group members or any potential inner structure of groups. A group may consist of one or more individuals, thus a group size will be an integer ≥ 1. Under such simple circumstances, quantifying group size is a most straightforward way to characterize animal sociality. In most cases, authors do not provide raw data on the sizes of individual groups, and journal editors would also refuse to publish them. Therefore, descriptive statistics are used to summarize information about group sizes. The most frequently used group size measure is the mean $\pm$ SD. This method is only fruitful when the distribution of group size approaches normal distribution, as predicted by the optimal group size hypothesis, described in Giraldeau & Gillis (1984). However, an approximately normal distribution is very rare in avian and mammalian group size distributions. A variety of avian and mammalian group size distributions, obtained from the literature and summarized in Table 1, indicates that clumped distribution is a widespread pattern in nature. Thus, most groups are small, a few groups are large, whereas a very few of them may be extremely large (Krause & Ruxton 2002).

Measures of group size, used to quantify levels of sociality, are confused in definitions; and standard statistical methodologies of their handling are far from being appropriate and consistent. Authors often use statistical methods that presume normal distribution of data, confuse outsiders' versus insiders' view of mean group size, or neglect the ties among data points in the latter case (see below). Here, we aim to clarify group size measures and recommend appropriate statistical methodologies. First, we propose that group size measures describing groups from the outsiders' viewpoint be distinguished from those describing groups from the group members' viewpoint. Outsiders' typical measures include mean and median group sizes, as well as the shape of the group size distribution. Insiders' typical measures refer to the mean and the median crowding, where 'crowding' is the group size in which an individual lives. We recommend appropriate statistical tools to handle all these measures, while taking into

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Table 1. Group (or colony) size distribution measures of various birds and mammals

Common name	Scientific name	Sample size (number of groups observed)	Min	Median	Mean	Max	Mean crowding	Source
				Group size				
Adelie penguins, feeding flocks	Pygoscelis adeliae	553	1	1	2.0	14	3.2	Norman & Ward 1993
Adelie penguins, travelling flocks	Pygoscelis adeliae	244	1	5	5.4	26	8.3	Norman & Ward 1993
African buffalo	Syncerus caffer	157	50	150	306.1	1550	595.9	Sinclair 1977
African wild dog	Lycaon pictus	229	3	9	9.3	24	11.5	Creel 1997
Alpine marmot	Marmota marmota	250	2	4	5.0	20	6.5	Grimm et al. 2003
American bison	Bison bison	1016	1	4	5.6	38	11.9	Lott & Minta 1983
American white pelican (pairs)	Pelecanus erythrorhynchos	41	20	300	1632.9	14 900	6641.4	King & Anderson 2005
Bohor reedbuck	Redunca redunca	301	1	1	1.8	26	3.8	Wirtz & Lörscher 1983
Bonobo	Pan paniscus	99	1	5	6.7	18	9.45	White 1988
Bushbuck	Tragelaphus scriptus	69	1	1	1.5	4	1.9	Wirtz & Lörscher 1983
Canada goose	Branta canadensis	920	1	6	6.8	20	9.9	Elder & Elder 1949
Chimpanzee	Pan troglodytes verus	267	1	4	5.3	22	9.1	Tutin et al. 1983
Chinese water deer, winter	Hydropotes inermis	1080	1	1	1.6	7	2.1	Sun 2002
Common dolphin	Delphinus delphis	920	5	30	65.5	1000	219.3	Anonymous 2005
Divers	Gavia spp.	379	1	1	1.7	40	5.3	Noer et al. 2000
Glossy black-cockatoo	Calyptorhynchus lathami halmaturinus	916	1	5	7.8	60	15.9	Pepper 1996
Impala	Aepyceros melampus	1314	1	3	6.8	77	17.75	Wirtz & Lörscher 1983
Killer whale	Orca orca	424	1	4	4.2	15	5.5	Baird & Dill 1996
Kirk's dikdik	Madoqua kirki	44	1	1	1.3	3	1.5	Wirtz & Lörscher 1983
Lesser horseshoe bat, wintering	Rhinolophus hipposideros	30	1	16	43.8	204	122.1	Godlevska et al. 2005
Lesser kestrel (pairs)	Falco naumanni	51	1	2	4.7	42	16.1	Tella 1996
Mixed-species passerine flocks	Passeriformes	115	10	20	24.6	70	32.9	Hart & Freed 2003
Mountain reedbuck	Redunca fulvorufula	20	1	2	2.1	6	2.9	Wirtz & Lörscher 1983
Mouse-eared bat, wintering	Myotis myotis	21	1	14	26.8	127	77.3	Godlevska et al. 2005
Northern bobwhite quail	Colinus virginianus	378	1	11	11.0	22	12.8	Williams et al. 2003
Przewalski's gazelle	Procapra przewalskii	98	1	4	6.0	18	9.8	Lei et al. 2001
Red fox families, adults with helpers	Vulpes vulpes	14	1	2	2.6	5	2.9	Zabel 1986
Red-necked phalarope	Phalaropus lobatus	118	1	2	2.8	12	5.3	Pellinger 2004
Redshank	Tringa totanus	677	1	1	7.4	95	30.6	Cresswell 1994
Rook (pairs)	Corvus frugilegus	243	1	38	59.6	281	116.3	Debout 2003
Steenbok	Raphicerus campestris	26	1	1	1.2	3	1.3	Wirtz & Lörscher 1983
Steller sealion 2004	Eumetopias jubatus	166	1	80	174.9	1304	527.0	Fritz et al. 2006
Steller sealion 2006	Eumetopias jubatus	114	1	97.5	186.7	1319	569.2	Fritz et al. 2006
Striped dolphin	Stenella coeruleoalba	1085	5	30	57.3	800	168.8	Anonymous 2005
Thomson's gazelle	Gazella thomsonii	584	1	2	4.2	100	16.0	Wirtz & Lörscher 1983
Waterbuck	Kobus ellipsiprymnus	2082	1	3	7.1	166	24.7	Wirtz & Lörscher 1983
Whistling swan	Cygnus columbianus	735	1	3	4.2	13	6.1	Thompson & Lyons 1964

In case of aggregated distributions, the median group size is expected to be lower than the mean group size, and both these measures are expected to fall into the left part of the total range. All distributions in this data set, except for the northern bobwhite quail, fulfil these criteria (Some of the minimum and maximum values were slightly modified by rounding or pooling by the original authors and due to interpretation problems of graphical data.).

consideration the strange characteristics of these data, such as strongly skewed distributions and inherent ties in crowding data. All calculations mentioned here are supported by the software Flocker 1.0, which is available free of cost.

Outsiders' View of Group Size

Due to the highly skewed feature of group size distributions, researchers of sociality frequently face methodological problems. Some authors suggest log transformation

of raw data to achieve an approximately normal distribution of data, and then handling them with parametric statistics, such as Student's *t* test or ANOVA. Highly skewed (aggregated) distributions are, however, often impossible to transform into normal distributions, and, even when it is possible, it is hard to interpret results in terms of biology. Moreover, when mean group size is greater in one sample than in another, a contrary situation might prevail after log transformation (e.g. the means of 1, 1, 10 and 2, 3, 4 are 4 and 3, whereas the means of their log transformed values are 0.33 and 0.46, respectively).

For the analysis of non-normal data, statistics textbooks recommend the use of nonparametric methods such as the Mann–Whitney *U* test: for the comparison of two independent samples (Wilcoxon 1945; Mann & Whitney 1947). It is often claimed that the Mann–Whitney *U* test compares medians, but this is only true under some rather restrictive assumptions, like the so-called shift model (Hollander & Wolfe 1973). This model assumes that the distributions to be compared feature the same shape, only allowing for a potential shift of location, that is, the distribution functions (cdfs) of the variables to compare are $F(x)$ and $G(x) = F(x + d)$, with the null hypothesis (H_0): $d = 0$. This presumption is unrealistic when dealing with animal group size distributions.

Another usual recommendation is the exclusion of extreme data points from the analyses. In case of group size distributions, however, excluding the few large groups would cause loss of information about a large proportion or, perhaps, even the majority of individuals (see e.g. Hochachka et al. 1999). Moreover, in the case of group size distributions, extreme values are unlikely to be outliers, rather they are real values sampled from a highly skewed distribution. Therefore, it is not at all justified to omit them as outliers (Barnett & Lewis 1994).

Skewed frequency distributions are complex patterns that cannot be adequately characterized by a single descriptive statistic (see e.g. Rózsa et al. 2000). Thus, we recommend the use of the following procedures:

1. Provision of basic information, such as sample size, that is, the number of groups observed (including 'groups' consisting of single individuals).

2. Provision of the mean group size and its confidence interval (CI). Note that the mean group size, together with the number of groups, adds up to the total number of individuals in the sample. In case of heavily skewed distributions, the average group size cannot be interpreted as the typical group size contrary to our common belief that 'average' is something common and typical. The CI for the mean group size is best produced by a BCa (bias-corrected and accelerated) bootstrap procedure as proposed by Efron & Tibshirani (1993).

3. As frequency distributions tend to be skewed and often show different shapes, mean group sizes may reasonably be compared between samples by a bootstrap two-sample *t* test (Efron & Tibshirani 1993).

4. The median group size may serve as a measure of a characteristic group size in the sample. Its CI may be calculated by a method described by, among others, Rózsa et al. (2000).

5. Given that shape differences between distributions may violate the standard assumptions of the Mann–Whitney *U* test, Mood's median test is the most appropriate method to compare median group sizes across samples (Sen 1998).

6. New variants of the Mann–Whitney *U* test may be used validly for the two-sample comparison of group size, even if shape differences prevail. Here, the Brunner–Munzel test (Brunner & Munzel 2000), or the bootstrap rank Welch test (Reiczigel et al. 2005b) is proposed. They, in fact, test for stochastic equality of group sizes X and Y in two populations, that is, for H_0: $P(X < Y) = P(X > Y)$ against H_1: $P(X < Y) <> P(X > Y)$.

7. Histograms of group sizes may also be useful, providing more detailed information on group size distributions.

Insiders' View of Group Size

The major problem with group size measures is that they are often misinterpreted, since neither mean, nor median group sizes characterize typical individuals' social environments. As Jarman (1974) pointed out decades ago, average individuals live in groups larger than average, except for an unrealistic case when all groups are of equal size. A hypothetical example of this vital point is illustrated in Fig. 1. Here, groups tend to be larger in sample 1, while individuals tend to live in larger groups in sample 2. This apparent contradiction is a consequence of difference in the variance of group sizes. 'Average' individuals come from groups larger than the average group size,

	Sample 1	Sample 2
Actual group sizes	4, 5, 6	1, 4, 7
Mean (median) group size	$\dfrac{4 + 5 + 6}{3} = 5\ (5)$	$\dfrac{1 + 4 + 7}{3} = 4\ (4)$
Mean (median) size of groups as experienced by individuals	$\dfrac{4 \times 4 + 5 \times 5 + 6 \times 6}{4 + 5 + 6} = 5.13\ (5)$	$\dfrac{1 \times 1 + 4 \times 4 + 7 \times 7}{1 + 4 + 7} = 5.5\ (7)$

Figure 1. In this hypothetical example, groups tend to be larger in sample 1, while individuals tend to live in larger groups in sample 2. This apparent contradiction is a consequence of difference in the variance of group sizes. 'Average' individuals come from groups larger than the average group size, and this shift is more pronounced in the species with more variable group sizes (see Fig. 2 for more realistic examples).

and this shift is more pronounced in the species with more variable group sizes. See also Fig. 2 for more realistic examples. This phenomenon was first realized by Jarman (1974), who introduced a measure called 'Typical Group Size' to quantify group size as experienced by an average individual. He also repeated this definition in subsequent publications (Jarman & Jarman 1979; Jarman 1982). His papers became influential and intensely cited works in the field of the social organization of ungulates. However, most students of social behaviour still do not understand his main message that mean group size does not characterize the size of a group in which average individuals live.

There are at least three unlucky circumstances that contributed to the relatively poor acceptance of this groundbreaking idea. First, Jarman defined 'Typical Group Size' as the group size experienced by an average individual. This is unfortunate from a purely statistical point of view. It would have been more appropriate to define first the group size experienced by an individual (any individual). Then statistical measures, such as mean, median, variance, etc., could have been calculated from individual values. Second, the term 'Typical Group Size' is often used in a general sense without specifically referring to Jarman's definition (see e.g. Hochachka et al. 1999).

To overcome these problems, here we propose the use of the term 'crowding'. Crowding refers to group size as experienced by any individual. It equals to 1 for a solitary individual and 2 for both individuals in a group of two, etc. Thus, mean crowding equals Jarman's 'Typical Group Size'. From a technical point of view, this concept is very similar to, although not absolutely identical with, crowding definitions used in parasitology and community ecology (Read 1951; Lloyd 1967).

Finally, the major problem with Jarman's 'Typical Group Size' was the lack of appropriate statistical tools to handle this measure. The main reason for this is that crowding data inherently contain a large number of nonindependent values. A hypothetical example may provide a proper illustration of this point:

group size values: 1, 2, 3
crowding values: 1, 2, 2, 3, 3, 3
Let us eliminate one individual from the last group:
group size values: 1, 2, 2
crowding values: 1, 2, 2, 2, 2
Now let us eliminate the last group to see how data change:
group size values: 1, 2
crowding values: 1, 2, 2.

When a single individual or single group is added or eliminated, there is only one single change in group size data, while there are several parallel changes in crowding data. This means that crowding data consist of nonindependent values, or ties, which show multiple and simultaneous changes, due to a single biological event. Statistical methods currently used in zoology and sociology are incapable of handling this effect. Thus, applying standard statistical tools, such as Student's t test and ANOVA to compare crowding across samples, is obviously erroneous (see e.g. Raman 1997; Banks 2001).

We have recently proposed statistical inference methods: the construction of a point estimate, CI and
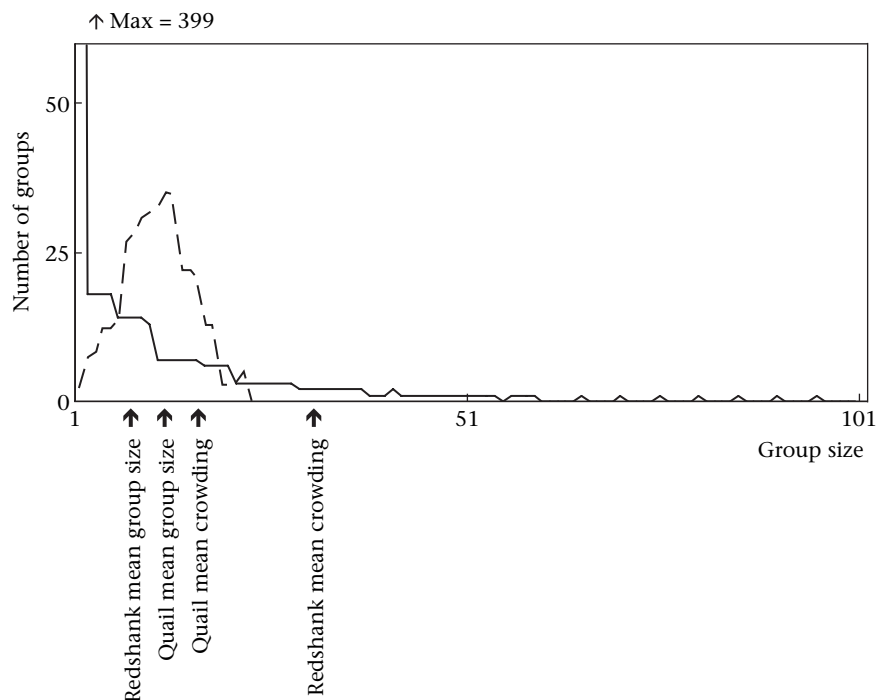

Figure 2. Frequency distributions of redshank (solid line) and bobwhite quail (dotted line) group sizes. Redshanks tend to have several small and a few large flocks. Therefore, their mean group size is lower than that of quails, which form medium-sized and less variable flocks. On the contrary, however, the few very large groups of redshanks increase their mean crowding far above that of quails. Consequently, quail groups tend to be larger than redshank groups, while redshanks tend to live in larger groups than quails.

statistical tests for crowding data elsewhere. Here, we simply recommend that interested readers find mathematical details in Reiczigel et al. (2005a). As for practical work with group size data, we recommend the following statistical procedures:

1. When describing a sample, provide the number of groups and the total number of individuals.

2. When describing a single sample, provide mean crowding and its CI. Due to the heterogeneity and the typical non-normality of group size distributions, CI construction requires the application of nonparametric methods or bootstrap techniques. As described in Reiczigel et al. (2005a), the sample mean crowding is a biased estimate of the population mean crowding. Furthermore, sample mean and sample variance of crowding are correlated. Under such circumstances, using BCa bootstrap, CI appears to be the most appropriate choice for CI construction (Efron & Tibshirani 1993).

3. A one-sample test for mean crowding may be derived from the above CI in the usual way. The null hypothesis is that crowding in the study population equals to a certain hypothetical value C_0, that is, H_0: $E(C) = C_0$ against the alternative of inequality, where $E(C)$ is the population mean of crowding. This is to be rejected at level α, if the $(1 - \alpha)$-level CI for $E(C)$ does not contain the hypothetical value C_0.

4. Similarly, an α-level two-sample test may be based on two $(1 - \alpha/2)$-level CIs. The null hypothesis is that crowding equals in the two populations, that is, H_0: $E(C_1) = E(C_2)$, against the alternative of inequality, which is to be rejected at level α, if the $(1 - \alpha/2)$-level CIs for $E(C_1)$ and $E(C_2)$ do not overlap. Especially, two samples with nonoverlapping 97.5% CIs for mean crowding provide evidence for the difference between population mean crowding at $P = 0.05$ level.

The above methods are based on a resampling procedure carried out at the level of groups rather than individuals; thus the inherent ties among individual crowding data are accounted for in the proposed analyses.

Discussion

The size of groups, flocks or colonies is a major determinant of individuals' environment, provided that we do not consider the potentially complex inner structure of groups (but see Wey et al. in press). In spite of this, current literature appears to underestimate the occurrence and magnitude of such variability, due to the lack of appropriate statistical tools to handle group size data. Most previous authors failed to differentiate between outsiders' and insiders' views of group sizes. Even those, who differentiated between these two approaches, most typically failed to apply a correct and consistent statistical methodology. In case of crowding, this methodology has not existed up until recently. That is, because the rise of computer intensive sampling methods has provided new opportunities in general (Efron & Tibshirani 1993) and also for this particular problem only recently (Reiczigel et al. 2005a).

Many authors who reported on interactions between group size and individual characters did, in fact, quantify
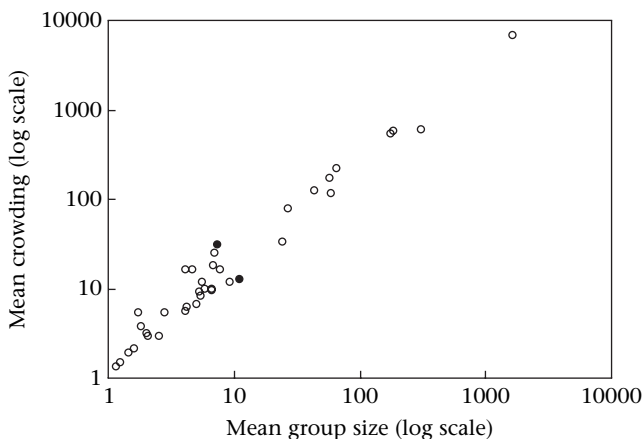
Figure 3. In a comparison across several bird and mammal species, mean group size correlates positively with mean crowding (empirical data, see Table 1 for details). The black marks represent the group size distributions of redshanks and bobwhite quails that are characterized in detail in Fig. 2.

the mean group size rather than the mean crowding. Since mean group size tends to predict mean crowding (Fig. 3), this approach may also be useful as a rough approximation. However, stronger correlation with and better predictions of animal characters may be expected from the introduction of crowding into the models to replace group size.

Note that the proposed quantification of crowding, as the size of the group where an individual lives, is not the only possibility. Any monotone increasing function of the group size may be used instead. The logarithm of group size in a few multiplicative models may turn out to be a better predictor than the group size itself. The proposed methodology also prevails in such cases.

We have done our best to clarify the difference between these two approaches, help readers formulate more specific questions about the biological causes and consequences of different types of sociality, and we have proposed statistical methods for appropriate data analysis. We also provide free access to our user-friendly software that helps nonstatistician readers carry out all the calculations mentioned above (Reiczigel & Rózsa 2006).

Finally, the question arises naturally how to assess the relationship between group size measures and other variables. If group size and another group trait are to be analysed together, there is no problem with independence, given that groups are sampled independently of each other. If group size and a character of individuals (group members) are to be analysed together, there are two possible ways to do this. The simpler one is that we carry out the analysis at the group level, that is, we characterize the groups using a summary measure (e.g. the mean) of the individual characters. If we choose to carry out the analysis at the individual level, then group size values are replicated within each group and so they are not independent. Some linear models can accommodate to such a situation (hierarchical, nested, split-plot), most of which are special cases of the generalized linear mixed model (see e.g. Agresti 2002).

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