



Specificity of grouping behaviour: comparing colony sizes for the same seabird species in distant populations

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Animal collective patterns such as group size frequency distributions often show substantial intraspecific variation, suggesting low species-specific consistency. Here, we dissect intraspecific vs interspecific components of colony size variation to estimate the repeatability (R) of colony size frequency distribution (CSFD) statistics for seabird species breeding in at least two out of four distant geographic areas of the Northern Hemisphere (21 species; 57 populations; 21 665 colonies; 9 326 479 breeding pairs). Colony sizes were highly variable both within and between species. We estimated the proportion of between-species variation using the repeatability statistic. Colony size-related statistics of CSFDs (e.g. geometric mean) showed high repeatabilities ($R = 0.73$ – 0.88), and shape-related measures ranged from null (kurtosis), moderate (fit to a log-normal distribution, $R = 0.62$) to highly repeatable (e.g. skewness, $R = 0.74$ – 0.87). We thus show that species collective patterns can be at the same time highly variable within species and a robust species-specific trait that bridge ecological spatio-temporal heterogeneities.

'The striking thing about seabird colonies, of whatever species, is the huge variation in size. It is difficult to give a typical size for any species.

Yet, [...] one could typify Guanay colonies as "huge" and Common and Flightless Cormorant colonies as "small", and the descriptions, though vague, are meaningful. Much of the same could be done for most seabirds.

J. Bryan Nelson (1980).

Consistent differences between individuals in their behaviour across time and contexts, although suspected from centuries ago (Birkhead 2008), have only recently become a hot topic in animal behaviour research, with far-reaching implications for animal ecology and evolution (Dingemans et al. 2010). Similarly, the specificity in the collective (social) behaviour of species, i.e. the consistent differences in collective patterns of species across time and contexts, was so evident to pioneering naturalists that species soon became grouped in clear-cut categories according to their social patterns (e.g. solitary vs gregarious, monogamous vs polygamous, Lott 1991). However, this became increasingly discredited when evidence accumulated showing huge variation within species, suggesting that within-species variation is not noise around fixed species features but the interesting pattern which needs to be understood (Lott 1991). This, together with the difficulties on gathering data from several species and study areas,

may explain why much less has been done during recent decades to answer whether animal collective patterns can be seen as species-specific traits. Suggesting species-specificity in collective patterns is trivial for some taxa and traits (e.g. bees build honeycombs and dragonflies do not). We here address a much less trivial question: are seabird colony sizes species-specific traits?

Group size is central to any kind of social behaviour. Describing group sizes and understanding how and why group sizes change within species across time and contexts (e.g. ecological scenarios) in a given population has received much attention (e.g. antelopes, Jarman 1974; birds, Brown and Brown 1996; ants, Gordon and Kulig 1996; spiders, Avilés and Tufiño 1998; fish, Bonabeau et al. 1999; scale insects, Vandermeer and Perfecto 2006; reviewed by Giraldeau and Caraco 2000, Krause and Ruxton 2002, Sumpter 2010). However, very little has been done to explore whether grouping behaviour differs among species. In fact, the few thorough comparative studies that tried to explain the reasons behind the differences in group sizes between species were carried out without first testing whether group sizes are indeed species-specific social traits (Brashares et al. 2000). Here we quantitatively address this seldom explored but central problem of animal collective behaviour by studying colony size frequency distributions (hereafter CSFDs) of colonial seabird species in four distant areas of the world. Disentangling

within vs between-species sources of variation will not only help to unravel the potential existence of species-specific characteristics in grouping behaviour, but would also shed light on the ecological and evolutionary conditions that determine group sizes. Large between-species variation would call for a key role of ecological or evolutionary conditions that differ between species, while larger within-species variation would suggest environmental conditions (or genetic population structure within species) as causal triggers.

Several evidences suggest a low consistency of bird species in their colony sizes (see discussion about colony definition under Methods and in Jovani et al. 2008a). Breeding bird colonies vary tremendously in size within populations, spanning several orders of magnitude in many species (Brown et al. 1990, Jovani et al. 2008a). Some species can be found breeding either solitarily or colonially only a few hundreds of meters apart (Jovani and Tella 2007) and populations can also shift from solitary to colonial breeding in consecutive years (Nuechterlein et al. 2003). Rolland et al. (1998) found bird coloniality to be a 'rather labile trait' that frequently changes states within avian phylogenies. Average species group sizes also show a very weak phylogenetic signal in different taxa, in contrast with other more 'classical' species traits such as morphology (Gittleman et al. 1996, Blomberg et al. 2003). This may not be surprising because colony sizes are not static but an emergent property of a complex network of interactions within species (e.g. conspecific attraction), between species (e.g. nest-site competition) and with the environment (e.g. climate, nest-site availability). This leads to frequent colony formation and extinction in a network of colonies connected by individual dispersal. In conclusion, current knowledge suggests group sizes could be a dynamic ecologically-driven trait of populations rather than a characteristic feature of species.

However, the introductory quotation illustrates how ornithologists and bird ecologists see colony size not only as a real species trait but as one of the key factors shaping the ecology and evolution of species (Lack 1967, 1968, Brown et al. 1990, Coulson 2002, Mitchell et al. 2004). This hypothesis is supported by inter-specific studies on colony size variation showing contrasting patterns between species when analysing a single population from each species (Götmark 1982, Brown et al. 1990, Jovani et al. 2008a). For instance, in a previous study, we reported striking differences in CSFD characteristics among 20 seabird species breeding in Britain and Ireland (Jovani et al. 2008a). The question we now address is whether such differences among species hold on larger (global) spatial scales when comparing distant populations of these same seabird species.

Advances in bird coloniality and animal grouping research suggest a matured version of this old hypothesis. Until recently, it was thought that all species displayed similar long-tailed CSFDs when displayed in standard lineal histograms, species mainly differing in the length of the tail i.e. in the size of the largest colonies of the histogram. However, using more appropriate statistical tools for highly right-skewed distributions (Pueyo and Jovani 2006), it has been recently demonstrated that superficially similar long-tailed CSFDs hide contrasting patterns, from log-normal to power law distributions (Jovani et al. 2008a). Interestingly,

these CSFDs were comprehensively described by a combination of a few statistics such as the maximum colony size or how well they fit to a log-normal distribution. Thus, here we extend the original hypothesis to several CSFD characteristics. Moreover, we take into account the effect of population size when comparing colony sizes from different populations (see Methods for a detailed explanation of the different elements of this hypothesis). Our resultant working hypothesis was that 'colonial birds have species-specific features that predispose them to show contrasting values in one or more characteristics of their CSFDs; this species-specific potential would be most clearly displayed when comparing populations above a certain threshold population size'.

Methods

Data

We gathered colony size data for 21 665 colonies (a total of 9326 479 breeding pairs) of 21 colonial seabird species from public sources (see Controlling for geographic area effects and Fig. 1 for details). Samples came from four

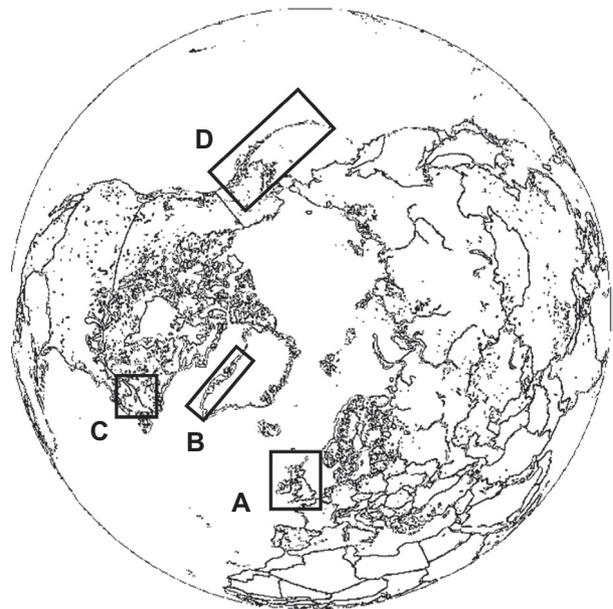


Figure 1. Data analysed: (A) Britain and Ireland, Seabird 2000 project, a collaboration between the Joint Nature Conservation Committee, Royal Society for the Protection of Birds, BirdWatch Ireland, The Seabird Group, Scottish National Heritage, Environment and Heritage Service, English Nature, Countryside Council for Wales, SOTEAG, Dept of the Environment, Heritage and Local Government and INTERREG II C (unpublished raw data; details and aggregated data in Mitchell et al. 2004 and Jovani et al. 2008a). (B) Western Greenland, a database maintained by the Dept of Arctic Environment, National Environmental Research Inst., obtained 1 March 2006. (C) St Lawrence gulf and estuary, Canada, maintained by the Canadian Wildlife Service. Obtained 19 April 2005 (Chapdelaine et al. 2005). (D) Alaska, Seabird Colonies 2000 of the Beringian Seabird Colony Catalog, maintained by the United States Fish and Wildlife Service USFWS. Obtained 6 June 2005 (Stephensen and Irons 2003).

distinct geographic regions in the Northern Hemisphere (Fig. 1). Species occurred in 2–4 of these geographic regions (median = 3) and we refer to all unique species–region combinations as ‘populations’ (57 populations in total).

Colony size characteristics

For each population, we calculated ten statistics that were selected to comprehensively describe the CSFD: 1) minimum colony size, 2) maximum colony size, 3) geometric mean, 4) coefficient of variation (CV = standard deviation/mean), 5) kurtosis (a measure of ‘peakedness’ around the mean), 6) skewness (a measure of asymmetry), 7) fit of CSFDs to a log-normal distribution as measured by the Kolmogorov–Smirnov statistic, 8) 95th percentile of the CSFD, 9) median colony size, and 10) population variability (PV, a non-parametric counterpart of CV that quantifies the mean deviation of all colony size pairs within populations; see Heath 2006 for details). All statistics (except for PV) were calculated with standard MatLab functions for parametric measures applied to \log_{10} -transformed colony sizes. PV was calculated with ver. 1.1 of variability calculator for MatLab (Heath 2006). Measures 1–3 and 8–9 are colony-size related statistics, while the others are CSFD shape-related statistics. Measures 1–7 were motivated by previous work (Jovani et al. 2008a), while 8–10 were introduced here because the non-(log)normal distribution of some CSFDs (Jovani et al. 2008a) called for non-parametric approaches. Minimum colony sizes were very low in all studied species (Supplementary material Appendix 1) thus we did not analyse its repeatability because of the lack of variability (which also implies that minimum colony size is not a species-specific trait in colonial seabirds of the Northern Hemisphere). Kurtosis, CV and fit to a log-normal distribution had a right-skewed normal distribution, and were \log_{10} -transformed to achieve normality prior to analyses.

Repeatability

Within-species repeatabilities (R) were calculated for each CSFD characteristic as $R = \sigma_{\alpha}^2 / (\sigma_{\alpha}^2 + \sigma_{\epsilon}^2)$, where σ_{α}^2 is the group (i.e. species) variance and σ_{ϵ}^2 the residual (error) variance. These variances were retrieved from a linear mixed effects model (LMM) that included species identity as a random factor and used restricted maximum-likelihood (REML) for parameter estimation (Nakagawa and Schielzeth 2010). Thus, R tells us about the strength of the differentiation among species (σ_{α}^2) relative to the total variation. The total variation encompasses the variance within species (i.e. between populations of each species; σ_{ϵ}^2) and the variance between species (σ_{α}^2).

The effect of population size

Studies on group size frequency distributions need to control for population density (although this has rarely been done; Krause and Ruxton 2002, but see Beauchamp 2011). Put simply, a penguin population with some hundreds of breeding pairs can not have colonies of thousands of hundreds of nests even if the same species shows such huge colonies elsewhere. Our working hypothesis, however,

was not about how large colonies are according to population size, but rather whether species show consistent patterns of colony sizes. Thus, we were not trying to ‘control for’ population size in the traditional way (e.g. by studying the residuals of CSFD characteristics with population size), but we instead studied the change in the species-specificity of CSFD characteristics (measured by the repeatability R) when analysing subsets of populations with different minimum population size thresholds. For colony size-related variables (e.g. geometric mean) we used (nested) subsets of populations with more than 10, 100, 1000 or 10000 nests, and for CSFD shape-related variables (e.g. CV) we used thresholds of 25, 50, 75 or 100 colonies. We used different thresholds because colony sizes are closely linked to population size but not necessarily so to the number of colonies, while a minimum number of colonies is indispensable to accurately estimate the shape-related measures of CSFDs. For example, a population with 1000000 nests in five colonies does not allow the calculation of an accurate measure of skewness, but offers relevant data about the maximum colony sizes that the species can reach.

Controlling for geographic area effects

Data from Britain and Ireland were obtained from Seabird 2000 (data from 1998–2002), where specific methodologies for each species were designed to obtain a snapshot of colony sizes (see Mitchell et al. 2004 and Jovani et al. 2008a for methodological details). Available data for the other geographic areas (Greenland, Canada and Alaska) were in the form of colony catalogues. These are permanently updated datasets that provide information on the most recent known size of colonies. Thus, the temporal window of these catalogues is larger and the sources of information more heterogeneous than those of Seabird 2000. Moreover, census methods could vary among different localities (even within localities through time, space or surveyors), thus potentially introducing noise to the data. For instance, defining colonies is a difficult task (Coulson 2002, Jovani and Tella 2007) and largely dependent on subjective decisions. For the Seabird 2000 project we used the ‘sub-site’ (i.e. stretches of coastline of around 1 km in length) as previously done elsewhere (see details in Jovani et al. 2008a and Supplementary material Appendix 1), and we analysed colony sizes as reported for the other three populations. CSFDs from the Seabird 2000 proved to be robust against different colony definitions (see Electronic Appendix in Jovani et al. 2008a). In any case, consistent differences between localities (both methodological and environmental) would go against species-specific CSFDs patterns, thus making our study conservative with respect to species-specific patterns. These potential methodological differences could homogenise colony sizes of species occurring in the same geographic areas and could also introduce statistical noise. Also, ecological factors known to shape colony sizes could differ widely across the different study areas, introducing systematic differences in colony sizes. Therefore, we also re-analysed our data introducing the geographic area as a factor (adjusted repeatabilities, Nakagawa and Schielzeth 2010). An increase in the estimated repeatability when including the geographic area factor would indicate

a mixture of systematic ecological idiosyncrasies or methodological biases occurring in the different study areas and affecting simultaneously colony sizes of all the species living in the same area.

Results

Only kurtosis had very low and non-significant repeatabilities in all our analyses [R mean (range) = 0.03 (0–0.11); all $p > 0.12$]. All other studied CSFD characteristics had larger repeatability estimates, which substantially increased when analysing sets of populations of an increasing size [mean (range) ΔR from lowest to highest thresholds = 0.217 (0.030–0.522); paired t -test, $t = 5.927$, $DF = 15$, $p < 0.0001$; Supplementary material Appendix 2]. Introducing geographic area as a factor slightly increased R estimates [mean (range) $\Delta R = 0.059$ (–0.057–0.223); paired t -test, $t = 5.043$, $DF = 31$, $p < 0.0001$; Supplementary material Appendix 2]. Below, and in the Discussion, we focus on the most powerful analyses done for each variable (Fig. 2), i.e. introducing the geographic area as factor, and applying the highest population size thresholds (see Fig. 2 legend for sample sizes).

Colony-sizes varied in several orders of magnitude within populations (Supplementary material Appendix 1). Moreover, different populations of the same species showed contrasting values for all studied variables (Fig. 3). However, values from populations of the same species were much more similar than those of different species (Fig. 3). Accordingly, 95% CI of repeatability estimates for all variables were well above zero, demonstrating that they were statistically significant at $\alpha = 0.05$ (Fig. 2). Repeatability estimates were all moderate to high, with five out of the eight studied variables showing repeatabilities above 0.8 (Fig. 2).

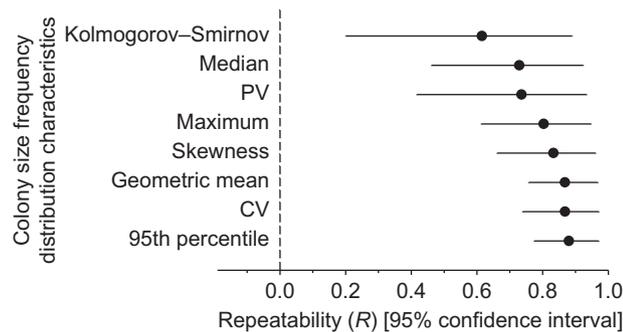


Figure 2. Species repeatability estimates (error lines show 95% CI) on different features of colony size frequency distributions (CSFDs) calculated from species with $> 10\,000$ nests (for size-related variables) or > 100 colonies (for CSFD shape-related characteristics; see Methods for details). PV stands for population variability (Methods). Sample sizes for colony size-related variables were 27 populations of 11 species. For CSFD shape-related variables sample sizes were 24 populations of 11 species. See Supplementary material Appendix 2 for all R estimates calculated with different methods and data thresholds.

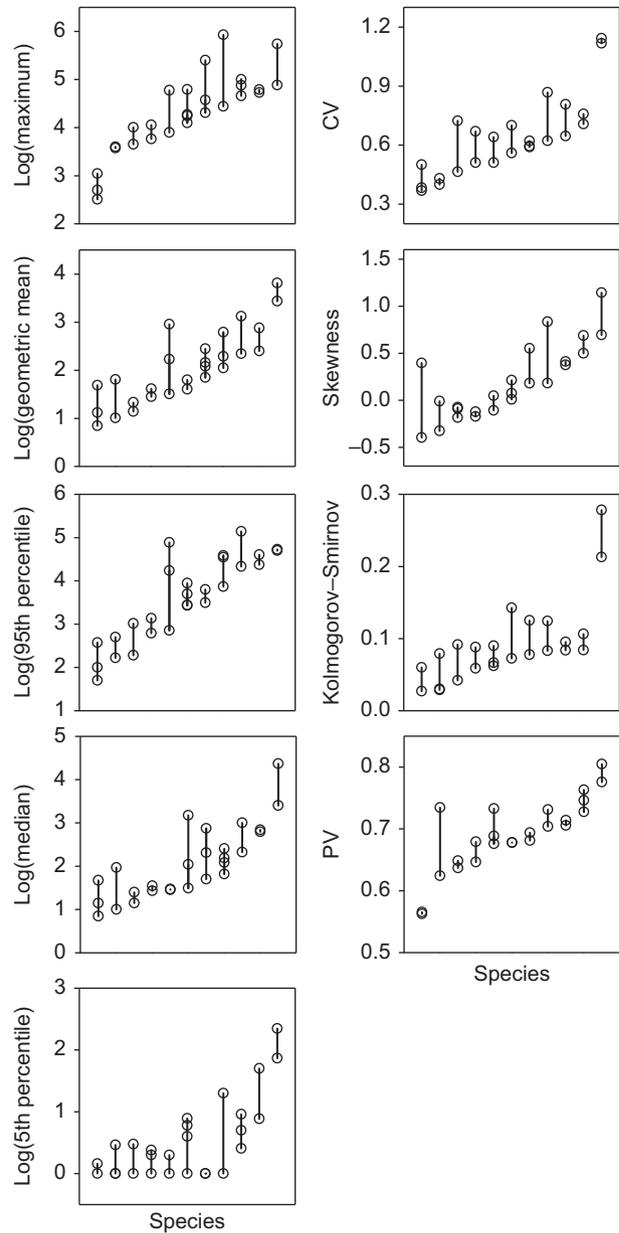


Figure 3. Colony size frequency distribution (CSFD) characteristics. Lines link populations (open circles) of the same species. Species are ordered according to the displayed variable (i.e. species position differ between panels; see Supplementary material Appendix 1 for a detailed account of CSFD statistics for each measured variable). For colony size-related variables (A–C) populations with $> 10\,000$ nests are plotted; for shape-related variables (D–F) populations with > 100 colonies are used.

Discussion

Most of the population patterns extracted from CSFDs hold when comparing spatially distant populations of same species: colony size-related measures (e.g. 95th percentile), the shape of CSFDs (e.g. skewness), and colony size variation (e.g. CV) all showed very high repeatability estimates ($R > 0.8$). In other words, more than 80% of between-population variance in many CSFD features was explained

by species identity. Therefore, although colony size variation within species was substantial, it did not erode species-specific differences on CSFD characteristics, but colony size variation was in fact a very species-specific trait.

In a previous study on 20 seabird species breeding in Britain and Ireland we revealed important differences in the kurtosis of their CSFDs (Jovani et al. 2008a). In the spatially extended analysis that we present here, we have found that kurtosis of CSFDs is not significantly species-specific when analysed across distant parts of the world. Thus, differences on the collective patterns of species in a given area can be misleading when generalized to the species as a whole, even when such differences between species are substantial in the sample area. The moderate repeatability of the fit of CSFDs to a log-normal distribution is also informative, by showing that species move to some extent along the power law-log(normal) continuum (Jovani et al. 2008a). This idea is supported by a study on lesser kestrels *Falco naumanni*, where a population showing a power law CSFD in a given year, increasingly shifted to a 'truncated power law' throughout an eight-years study period, becoming closer to a right-skewed log-normal distribution (Jovani et al. 2008b).

Overall, our study supports the old idea that bird species greatly differ in colony sizes, expanding it to several different CSFD characteristics. These patterns were especially apparent when analysing subsets of large populations, showing that species have a potential to create contrasting CSFDs, and that these differences become more pronounced when populations increase their population sizes. Interestingly, this occurs despite the multiple ways in which the studied areas differ in their present and historical ecological and human-mediated factors. Thus, species-specific CSFDs are not only species-specific features but really robust characteristics that bridge ecological spatio-temporal heterogeneities. Understanding which is/are the most relevant species-specific features that create these species-specific colony sizes would be a necessary next step on the understanding of group living in birds.

We visualise three non-mutually exclusive kinds of hypotheses. First, species-specificity in collective behaviour may be the simple additive outcome of individuals of different species behaving differently in non-social tasks. For instance, it may occur that different species show different CSFD characteristics because species (all individuals within each species) show contrasting foraging behaviours, allowing species to hold different colony sizes according to appropriate food availability (Coulson 2002, p. 101). Second, it could be that species show some species-specific social behaviour that lead to species-specific emergent colony size patterns; e.g. different conspecific attraction (colony size preferences). And third, individuals of all species could have the same (i.e. not species-specific) individual behaviour (e.g. to breed in the largest colony available). Under this scenario, species-specific CSFD characteristics would be driven by other processes such as environmental factors constraining colony sizes in a species-specific way (e.g. because of species-specific nesting microhabitat selection). Interestingly, different CSFD characteristics (e.g. geometric mean, CV) may, at first, seem to require different explanations. However, in a previous study (Jovani et al. 2008a)

we found a high correlation between most of the retrieved measures, thus holding some promise that much of CSFD patterns can be explained by a handful of variables. This encourages restarting the pioneering research by David Lack (1967, 1968) on the causes and consequences of species-specific colony size variability across species with currently available comparative methods and huge colony size datasets.

Behavioural traits, including collective behaviours such as coloniality in birds (Rolland et al. 1998) and generally group sizes in several taxa (Gittleman et al. 1996) are among the most evolutionarily labile species traits (Mayr 1963, Blomberg et al. 2003) and those showing larger intraspecific plasticity (Lott 1991; e.g. colony sizes, Brown et al. 1990, Jovani et al. 2008a). However, we have found robust specificity in colony sizes despite potentially important differences in the ecological scenarios inhabited by distant populations of same species. Therefore, we suggest that animal collective behaviours could be, at the same time, highly variable within-species and part of the social phenotypic specificity of species.

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Supplementary material (Appendix J5643 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.