

# Functional relationship between group size and population density in Northwest Atlantic seabirds

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**ABSTRACT:** In many bird societies, group size results from the fusion and fission of existing groups. Group size dynamics should ideally be investigated in a population-level context since population density is likely to influence the rate of encounter between individuals and thus the value of joining or leaving groups. However, few studies have documented the shape of the functional relationship between group size and population density. The functional relationship can be of 2 types: (1) a strictly increasing function reflecting random joining and leaving, and (2) a saturating function indicating a preference for a range of group sizes so that a large increase in population density results primarily in more groups rather than larger groups. Using at-sea survey data from 2006 to 2010 in the Northwest Atlantic, I documented a saturating functional relationship between group size and population density in 5 species of seabirds and a strictly increasing function in 2 other bird species. The results suggest that upper limits to group sizes may be common in seabirds, perhaps reflecting feeding competition in larger groups.

**KEY WORDS:** Atlantic seabirds · Feeding competition · Group size · Population density

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## INTRODUCTION

Many species of animals forage in groups. Group living has been thought to increase foraging efficiency and protection against predators (Krause & Ruxton 2002). However, living in groups is also associated with costs such as increased foraging competition. The balance of costs and benefits associated with the size of a group should favour the evolution of an optimal group size (Pulliam & Caraco 1984). Nevertheless, as long as individuals benefit from joining a group of optimal size, group size is expected to increase beyond the optimal group size to an equilibrium value where joining ceases to be beneficial (Sibly 1983, Clark & Mangel 1986). While evolutionary thinking suggests that group size should be narrowly constrained between an optimal and equilibrium value, many species commonly show a tremendous range of aggregation sizes suggesting that our understanding of the factors that regulate group size dynamics is far from complete (Krause & Ruxton 2002).

In social systems with fluid group membership, group size results from the fusion and fission of existing non-territorial groups (Croft et al. 2003, Ramos-Fernandez et al. 2006, Pays et al. 2007, Fortin et al. 2009). Thus, such dynamics should ideally be investigated in a population-level context (Caraco 1980). Population density, defined as the number of individuals that occur in a given area and interact with each other, should be taken into account when investigating group size dynamics because population density influences the potential rate of encounter between individuals, and thus the relative value of joining and leaving groups, constraining the maximum realized group size. Documenting the relationship between group size and population density is therefore important to understand group size dynamics and the underlying dispersion of prey resources.

The functional relationship between group size and population density can conceivably take 2 forms. In the simplest scenario, groups form by random joining and splitting and individuals show no preference for

groups of a given size. In such a case, group size is expected to increase monotonically with population density (Caughley 1964, Bonabeau et al. 1999). In the alternative scenario, individuals show a preference for certain group sizes due to the balance of ultimate costs and benefits. As population density increases, group size is first expected to increase linearly given that at low densities few individuals are available to form groups and groups are not expected to be large. Group size will increase with population density until the preferred size is attained, beyond which any increase in population density should lead to the formation of more groups rather than larger groups (Krause & Ruxton 2002, Beauchamp & Fernández-Juricic 2005).

Many empirical studies in fluid societies have shown that an increase in population density leads to an increase in group size (e.g. Spinage 1969, Wirtz & Lorschler 1983, Gerard et al. 2002), although this is not always the case (Leuthold & Leuthold 1975, Alonso et al. 1987, Pinto et al. 1993, Hart & Freed 2003). A limitation of most of these studies is that changes in group sizes have been documented over a limited range of population densities, often limited to 2 different population densities, making it difficult to establish the functional relationship. In those species with sufficient variation to judge the shape of the functional relationship between group size and population density, strictly linear relationships have been documented (Taylor 1982, 1983, Southwell 1984, Barrette 1991, Lawes & Nanni 1993, Borkowski 2000). Conversely, a saturating function has been documented in only a few species thus far (Johnson 1983, Toigo et al. 1996).

Perhaps even more daunting for the interpretation of the data so far is the fact that population density may be correlated with other ecological factors that are directly responsible for changes in group size. For instance, population density may be higher in years with larger food supply, and group size may be larger in those years simply because patches of food are richer and not because population density is higher (Wirtz & Lorschler 1983, Lawes & Nanni 1993). Additionally, the same species can reach different population densities in different habitats due to features, such as habitat openness, which may vary among habitats and act directly on group size (Leuthold & Leuthold 1975, Gerard et al. 2002). While the manipulation of population density represents the best experimental option (Morgan & Fernández-Juricic 2007), it is not feasible with larger species and under certain field conditions. A major challenge, therefore, is to provide effective control for extraneous factors potentially correlated with population density and group size.

My objective was to establish the functional relationship between group size and population density. Specifically, I examined which of the above 2 types of

functional relationship was more relevant in several species of seabirds for which data on group sizes are available over a wide range of population densities. To address the issues raised earlier, I documented the functional relationship over a wide range of population densities while controlling statistically for ecological factors potentially correlated with population density or group size. The prediction was that the relationship between group size and population density would reach a plateau if individuals showed a preference for groups of certain sizes.

## MATERIALS AND METHODS

I used the Eastern Canada Seabirds at Sea (ECSAS) survey database of the Canadian Wildlife Service, Environment Canada. Surveys from 2006 to 2010 ranged from 40 to 60° N and from -70 to -41° W. During these surveys, group sizes of flying birds and of birds on the water were gathered systematically within 300 m of the ship using a standardized methodology (Gjerdrum et al. 2011) agreed upon for seabird surveys (Barbraud & Thiebot 2009). Briefly, birds on the water are recorded continuously, but flying birds are recorded using a number of instantaneous snapshots covering both the side and the front of the vessel. Survey results from this area have been used earlier to estimate population densities and to describe species distributions and habitats (e.g. Huettmann & Diamond 2001, 2006).

In these at-sea surveys, the behaviour of birds on the water has not always been noted, and it is generally not known if these birds aggregated over food resources or were simply resting. Time of day and the geographical location of the sampling point at the beginning of each 5–10 min interval are also provided in the dataset. Encountering a flock is quite a rare event and most 5–10 min bins are empty. A flock was defined as an aggregation of 2 or more birds flying or occurring together on the water, generally within meters of one another. Flocks were considered discrete units and were not aggregated in any bins. Mixed-species flocking can occur when 2 or more species are aggregated. I calculated the percentage of sightings involving mixed-species flocking, but group sizes for each species involved were treated separately.

I restricted the analysis to winter surveys (from October to March), thus avoiding major fluctuations in group sizes related to breeding and migration. The 7 most common seabird species included in the analysis were black-legged kittiwake (BLKI) *Rissa tridactyla*, dovekie (DOVE) *Alle alle*, great black-backed gull (GBBG) *Larus marinus*, greater shearwater (GRSH) *Puffinus gravis*, herring gull (HERG) *L. argentatus*,

northern fulmar (NOFU) *Fulmarus glacialis* and thick-billed murre (TBMU) *Uria lomvia*. For each survey, I calculated the encounter rate as the total number of birds of 1 species recorded during a survey divided by the length of the survey in km. Population density was obtained by multiplying encounter rate by the total width of the observation window around the survey vessel, namely 0.3 km.

Group size distributions are generally heavily skewed to the right. Given that the variance of group size for each species was much larger than the mean, 2 types of models are appropriate to model the distribution of group sizes (details below), namely the negative binomial model and the power law model. Using Akaike's Information Criteria and likelihood ratio tests, the power law model provided an equal or better fit to the data than the negative binomial model, and was thus used to evaluate the effect of population density on group size (Beauchamp 2011).

Truncated power law models were fitted to the data using maximum likelihood estimation. The dataset consists of a sequence of sightings where group size is  $>1$  since groups of size 0 are unobserved. The probability density function (pdf) for the power law determines the probability of observing a group of any particular size. There are  $i = 1, 2, \dots, n$  sightings and  $Y_i$  is the  $i^{\text{th}}$  sighting and  $j = 1, 2, \dots$  are the possible values for  $Y_i$ . The power law model has 1 parameter,  $\alpha$  (Clauset et al. 2009), and the pdf is given by:

$$\Pr(Y_i = j | Y_i > 0) = j^{-\alpha} / [\zeta(\alpha, 1)] \quad (1)$$

where  $\zeta(\alpha, 1) = \sum(k + 1)^{-\alpha}$  and the summation for  $k$  (an integer value) is taken from 0 to infinity.

The model was fitted separately for each species and for each type of group (flying or on the water). Maximum likelihood estimation requires determination of the log-likelihood function, which was obtained from the literature (Clauset et al. 2009). For a given species/group type, the log-likelihood is calculated over all sightings, and maximum likelihood estimation provides an estimate for the unknown parameter,  $\alpha$ .

The statistical model to determine the effect of population density on group size included a random effect associated with the cruise ID. Because survey cruises differed in length and occurred at different times of the season or in different years, mean group size is expected to vary from one survey to another, and the random factor was used to model this extrinsic variability. In addition to the random factor, the model included the following fixed factors: population density, the squared value of population density, time of day (categorised as before or after noon) and season (winter: January, February or March; Fall: October, November or December). The squared value for popu-

lation density allows to model non-linear effects on group size thus creating a quadratic function of population density. When statistically non-significant, the squared value for population density was removed from the model. Time of day and season were included since they may influence mean group size. The procedure Nlmixed from SAS v9.2 was used to develop these models and to test for statistical significance. I used the general likelihood function for the dependent variable.

This procedure models the effect of each independent variable, such as population density, on the power law parameter ( $\alpha$ ). The  $\beta$  coefficient provided by the model determines the magnitude of changes in the value of  $\alpha$  in response to changes in the independent variable. The interpretation of a negative value for the  $\beta$  coefficient, for instance, is that  $\alpha$  decreases with an increase in the value of the independent variable so that the distribution of group sizes is shifted toward larger values.

If the functional relationship between group size and population density is saturating, the distribution of group sizes will be shifted to larger values as density increases but will stabilize when density is higher. To obtain an estimate of what would be a typical group size at these larger densities, I calculated mean crowding, the mean size of groups as experienced by an individual (Reiczigel et al. 2008), for each species at each density. Mean crowding, rather than the median or the mean, is more likely to reflect the size of groups that an average individual experiences. With the NLin procedure in SAS, I then used a non-linear segmented regression with 2 parts, namely a quadratic function of density below a threshold density and a constant value (the asymptote) beyond, to obtain an estimate of the asymptote for each species.

## RESULTS

I obtained data from 41 survey cruises with a median transect length of 236 km (range: 13 to 1732 km). Estimates of population density and mean crowding along with the prevalence of solitary sightings and mixed-species flocking are provided in Table 1 for each species.

For groups on the water, the functional relationship between group size and population density was statistically significantly saturating for BLKI, DOVE, HERG, NOFU, and TBMU (Table 2). Group size increased linearly with population density in the GBBG and GRSH but with no apparent saturation (Table 2). For flying groups, a statistically significant saturating function was only documented in BLKI and NOFU (Table 2). Fig. 1 illustrates the relationship between group size

Table 1. Population density (ind. km<sup>-2</sup>) and group size estimates for 7 seabird species in the Northwest Atlantic in 2006–2009. Mean crowding: mean size of groups as experienced by individuals (ind.)

Species	Population density		Groups on water		Flying groups		Sightings of mixed-species flocks (%)		
	No. of cruises	Median density <sup>a</sup> (min–max)	No. of sightings	Mean crowding (min–max)	Sightings of 1 ind. (%)	No. of sightings		Mean crowding (min–max)	Sightings of 1 ind. (%)
Black-legged kittiwake	38	0.11 (0.0035–2.5)	234	192.3 (1–500)	41.5	969	11.7 (1–80)	73.3	1.8
Dovekie	30	0.12 (0.0023–0.81)	966	5.3 (1–50)	57.4	626	11.3 (1–50)	39.6	0.75
Great black-backed gull	36	0.018 (0.0014–0.18)	218	26.9 (1–70)	57.3	262	1.9 (1–10)	87.0	5
Greater shearwater	19	0.16 (0.0013–0.95)	117	36.3 (1–100)	52.1	1010	25.1 (1–175)	60.8	2.5
Herring gull	24	0.022 (0.0004–0.29)	87	43.9 (1–106)	60.9	206	2.0 (1–14)	87.9	4.8
Northern fulmar	36	0.18 (0.0015–1.2)	637	48.2 (1–250)	48.7	1484	8.8 (1–55)	60.0	1.3
Thick-billed murre	29	0.093 (0.0017–0.22)	689	4.8 (1–35)	61.3	262	21.9 (1–100)	59.9	0.53

<sup>a</sup>When at least 1 bird was detected during a survey

on the water and population density in NOFU, with a statistically significant saturating function, and in GRSH, with a strictly linear function.

The random variance component was not statistically significant in most models, and was assumed to be negligible in TBMU where the random effect could not be fitted (Table 2). A statistically significant seasonal effect on group size occurred in BLKI and GBBG with winter counts lower than fall counts (Table 2). Statistically significant diurnal differences occurred in BLKI, GBBG, DOVE and NOFU, with generally lower counts in the afternoon (Table 2).

For those species showing a saturating functional relationship between group size on the water and population density, the non-linear regression of mean crowding on population density revealed varying asymptotic mean crowding values among species, which were generally low for the 2 species of pursuit divers, namely DOVE and TBMU, and higher for the other species foraging mainly at or near the surface (Table 3).

## DISCUSSION

Using a wide range of population densities, and controlling statistically for potential differences in group size among surveys, seasonal and time-of-day effects, I documented a saturating functional relationship between group size and population density in several species of Northwest Atlantic seabirds, especially for groups on the water as opposed to flying groups. In 2 species, the functional relationship for groups on the water was a strictly increasing function of population density. The variance component associated with individual cruises was often small, suggesting that extrinsic variability in group size among surveys was generally small.

An initial increase in group size with population density was expected given that at low densities, group sizes are small due to scarcity of available individuals. In contrast to the prediction from the random model of joining and splitting, group size reached an asymptote at higher densities in several species suggesting that increases in population density at this point caused mostly an increase in the number of groups rather than an increase in group size, as suggested earlier (Krause & Ruxton 2002, Beauchamp & Fernández-Juricic 2005). These results suggest that a preferred range of group sizes exists in many species of seabirds. As discussed below, groups on the water probably feed, and it is conceivable that an increase in group size can lead to an increase in feeding competition.

DOVE is a pursuit-diving species (Montevecchi & Stenhouse 2002) that is known to aggregate in large

Table 2. Parameter values for the power law model fitted separately for groups on the water and flying for 7 species of Northwest Atlantic seabirds in 2006–2009

Model parameter	Flying groups		Groups on water	
	$\beta$ (SE)	p	$\beta$ (SE)	p
<b>Black-legged kittiwake</b>				
Intercept	2.96 (0.19)	<0.0001	2.44 (0.31)	<0.0001
Population density	-2.35 (0.68)	0.001	-2.71 (0.88)	0.005
Population density squared	0.79 (0.28)	0.008	0.88 (0.37)	0.02
Time of day (PM vs. AM)	-0.40 (0.15)	0.01	-0.74 (0.27)	0.01
Season (winter vs. fall)	0.72 (0.22)	0.003	-0.21 (0.26)	0.43
Variance related to cruise ID	0.13 (0.079)	0.12	0.18 (0.097)	0.08
<b>Dovekie</b>				
Intercept	1.75 (0.16)	<0.0001	2.45 (0.21)	<0.0001
Population density	-0.88 (0.46)	0.07	-4.30 (1.49)	0.008
Population density squared	–	–	4.79 (1.87)	0.02
Time of day (PM vs. AM)	0.20 (0.089)	0.03	0.095 (0.11)	0.41
Season (winter versus fall)	0.084 (0.22)	0.39	0.088 (0.20)	0.66
Variance related to cruise ID	0.12 (0.06)	0.06	0.098 (0.056)	0.09
<b>Great black-backed gull</b>				
Intercept	3.78 (0.41)	< 0.0001	2.50 (0.24)	<0.0001
Population density	-1.04 (3.73)	0.78	-2.75 (1.33)	0.048
Population density squared	–	–	–	–
Time of day (PM vs. AM)	-0.16 (0.36)	0.66	0.34 (0.17)	0.048
Season (winter versus fall)	-0.78 (0.60)	0.20	-0.84 (0.24)	0.002
Variance related to cruise ID	0	1	0	1
<b>Greater shearwater</b>				
Intercept	2.10 (0.17)	< 0.0001	1.72 (0.17)	<0.0001
Population density	0.13 (0.45)	0.78	-1.27 (0.27)	0.001
Population density squared	–	–	–	–
Time of day (PM vs. AM)	0.051 (0.088)	0.57	0.58 (0.22)	0.03
Season (winter versus fall)	One season mostly	–	One season mostly	–
Variance related to cruise ID	0.12 (0.091)	0.21	0	1
<b>Herring gull</b>				
Intercept	3.58 (0.50)	<0.0001	3.17 (0.61)	<0.0001
Population density	-0.091 (6.99)	0.99	-28.52 (11.38)	0.02
Population density squared	–	–	90.11 (39.79)	0.04
Time of day (PM vs. AM)	-0.25 (0.49)	0.61	-0.27 (0.57)	0.64
Season (winter vs. fall)	0.92 (1.35)	0.51	-0.19 (0.69)	0.79
Variance related to cruise ID	0	1	0.35 (0.38)	0.36
<b>Northern fulmar</b>				
Intercept	3.02 (0.23)	<0.0001	2.29 (0.17)	<0.0001
Population density	-6.12 (1.54)	0.0003	-3.14 (0.95)	0.002
Population density squared	4.20 (1.35)	0.004	2.02 (0.81)	0.02
Time of day (PM vs. AM)	0.32 (0.075)	0.0001	-0.082 (0.10)	0.42
Season (winter vs. fall)	0.11 (0.31)	0.73	0.015 (0.27)	0.96
Variance related to cruise ID	0.35 (0.14)	0.01	0.098 (0.052)	0.07
<b>Thick-billed murre</b>				
Intercept	3.19 (0.40)	<0.0001	3.03 (0.24)	<0.0001
Population density	-14.29 (5.59)	0.01	-15.04 (3.57)	<0.0001
Population density squared	42.59 (20.91)	0.04	53.85 (14.19)	0.0002
Time of day (PM vs. AM)	-0.38 (0.20)	0.06	-0.24 (0.15)	0.10
Season (winter vs. fall)	0.24 (0.30)	0.42	0.34 (0.14)	0.02
Variance related to cruise ID	Assumed equal to 0	–	Assumed equal to 0	–

densities (>1000 ind. km<sup>-2</sup>) at frontal systems (Follestad 1990). In the winter surveys reported here, densities were much lower and in line with those reported earlier for the Northwest Atlantic (Brown 1988). A saturating functional relationship between group size and population density was documented along with a small

mean crowding value at higher densities suggesting constraints on upper foraging group sizes. While research suggests that diving species may benefit from foraging with companions on evasive prey (Götmark et al. 1986), it is also the case that when large numbers are present, foraging success may decrease due to

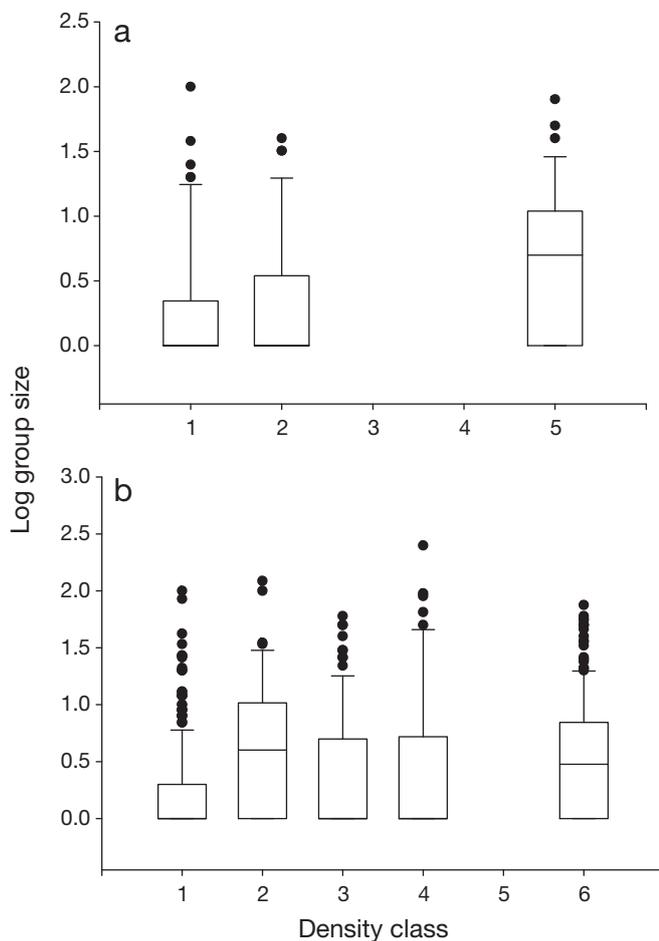


Fig. 1. Increases in group size on the water as a function of population density in (a) greater shearwater (GRSH) and (b) northern fulmar (NOFU) in the Northwest Atlantic. Group sizes are on logarithmic scale and the following population densities have been regrouped (Class 1: ]0, 0.2], Class 2: ]0.2, 0.4], Class 3: ]0.4, 0.6], Class 4: ]0.6, 0.8], Class 5: ]0.8, 1], Class 6: ]1+). Bottom and top of box: 25th and 75th percentile, respectively. Line within box: median. Whiskers extend to 1.5 times the inter-quartile range. Dots: outliers

interference competition (Beauchamp 1998, Lewis et al. 2001, Davoren et al. 2003). In the case of DOVE, competition must come mostly from conspecifics given that mixed-species flocking was rare for this species. Few studies of diving behaviour and prey capture are available in this species (Harding et al. 2009), and more research is needed to document the purported changes in feeding success as a function of group size. Along with TBMU and the gull species, this species was found alone frequently on the water, which is consistent with the competition hypothesis.

TBMU, like the DOVE, is a pursuit-diver (Gaston & Hipfner 2000) and a saturating functional relationship between group size and population density was also documented along with a small mean crowding values at higher densities. As in DOVE, few instances of mixed-species flocking occurred in this species suggesting that competition would be limited to conspecifics. Variation in diving behaviour in this species has been related to intraspecific competition for mobile prey (Paredes et al. 2008). This may explain why of all species, TBMU was found alone most often. Intraspecific competition for food was also suggested for a closely related species (Davoren et al. 2003).

NOFU and BLKI showed a saturating functional relationship like the 2 pursuit-diving species but with a much higher asymptotic group size at higher population densities. NOFU uses a variety of foraging techniques, but foraging is usually done near the surface (Hatch & Nettleship 1998). Very large flocks have been observed when fulmars feed on schooling fishes (Hobson & Welch 1992). Similarly, very large flocks of kittiwakes, which also forage near the surface, occur at sea (Hatch et al. 2009) and individuals are known to use conspecifics to locate patches of food (Bayer 1983). It would appear that the type of prey and foraging of these 2 species are amenable to much larger group sizes and that competition only probably takes place in larger groups and at higher population densities. Competition for kittiwake is

Table 3. Fit of the non-linear model between mean crowding on the water and population density for 7 species of seabirds in the Northwest Atlantic in 2006–2009

Species	Foraging type	Range of population densities (min–max)	Range of mean crowding (min–max)	% of explained variance	Rounded asymptote estimate <sup>a</sup>
Dovekie	Diver	0.0038–0.81	1–25.7	20	8
Thick-billed murre	Diver	0.0017–0.22	1–16.8	15	5
Great black-backed gull	Surface feeder	0.0014–0.18	1–37.2	–	–
Greater shearwater	Shallow diving	0.013–0.95	1–88.2	–	–
Herring gull	Surface feeder	0.0012–0.29	1–83.4	45	37
Northern fulmar	Surface feeder	0.0034–1.22	1–121.2	52	64
Black-legged kittiwake	Surface feeder	0.0034–2.5	1–378.3	86	408

<sup>a</sup>Only provided for species where the functional relationship between group size and population density was saturating

often caused by the presence of kleptoparasitic gull species (*Larus* spp) (Maniscalco et al. 2001), but this is probably not very frequent here given that mixed-species flocking was relatively rare for kittiwake. Intraspecific competition for food in kittiwake has been suggested as a result of a reduction in prey availability near the surface caused by the presence of conspecifics (Ainley et al. 2003), which may explain why kittiwakes do not always join other feeding flocks (Irons 1998). Perhaps because of these benefits of foraging in groups, fewer individuals occurred alone on the water in these 2 species.

The 2 gull species, HERG and GBBG, are surface dippers but are also known to scavenge food resources produced by other gulls or other species (Pierotti & Good 1994, Good 1998). Mixed-species flocking, which may provide opportunities for scavenging, was the most common in these 2 species. Foraging success has been shown to increase with group size in a species of gull foraging in small groups in an enclosure (Götmark et al. 1986), but competition could become apparent in the field at larger group sizes. For instance, arrival of a gull species to a mixed-species flock often reduces the foraging success of species that arrived earlier (Sealy 1973, Hoffman et al. 1981, Camp-huysen & Webb 1999), which would make larger aggregations of gulls less attractive and partly explain a saturating functional relationship. Similarly, GBBG are often dominant over HERG in foraging interactions (Rome & Ellis 2004) and if larger groups of HERG attract more GBBG, the success of herring gulls in larger flocks may be compromised, thus selecting against larger formations. It is not clear why a saturating functional relationship was not documented in GBBG despite much overlap in population density and group sizes with the herring gull but the issue could be settled with a larger sample size for these 2 species.

GRSH is a shallow-diving species (Ronconi et al. 2010) and is known to join flocks of conspecifics and other species (Haney et al. 1992), which is compatible with the finding that this species occurred in large groups and quite often in the presence of other species. No saturating functional relationship was documented for this species during the winter surveys despite the fact that the range of population densities was quite large in comparison to other species in the data set. It is possible that competition only arises in this species at larger densities. In the tropics, GRSH occurs in very large flocks over large schools of fish (Duffy 1989), and in the Northwest Atlantic, they are often drawn to foraging marine mammals (Pierotti 1988). It is perhaps the case that competition for food may be negligible in such aggregations. An alternative hypothesis is that some of the groups recorded during the surveys were not foraging but resting instead, which would reduce the scope for a saturating functional relationship.

It is somewhat surprising that a saturating functional relationship between group size and population density was documented in flying groups of some species given that such groups are not competing for resources. Nevertheless, I note that in contrast to groups on the water, group size in flying groups was correlated with population density in fewer species. Flying groups may form after a foraging group has been disturbed. Therefore, the saturating function relationship documented for groups on the water can transfer to some extent to flying groups as well.

Documenting the functional relationship between group size and population density has both fundamental and practical relevance. (1) Probability of individual survival is often influenced by group size since both predator detection and food intake rate can be directly related to variation in group size (Williams et al. 2003, Watson et al. 2007). Therefore, knowledge of the functional relationship between group size and population density becomes an important tool to model future changes in population sizes that arise from group-size related changes in predation risk and food intake rate in the habitat where the relationship was documented. (2) Since many anthropogenic changes influence population density, for instance through habitat fragmentation (Fernández-Juricic 2000, van Houtan et al. 2006), it might be easier to predict future changes in population density knowing in which type of groups individuals are most likely to be found and how they survive in such groups.

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#### LITERATURE CITED

- Ainley DG, Ford RG, Brown ED, Suryan RM, Irons DB (2003) Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. *Ecology* 84: 709–723
- Alonso JC, Alonso JA, Veiga JP (1987) Flocking in wintering common cranes *Grus grus*: influence of population size, food abundance and habitat patchiness. *Ornis Scand* 18: 53–60
- Barbraud C, Thiebot JB (2009) On the importance of estimating detection probabilities from at-sea surveys of flying seabirds. *J Avian Biol* 40:584–590
- Barrette C (1991) The size of Axis deer fluid groups in Wilpattu National Park, Sri Lanka. *Mammalia* 55:207–220
- Bayer RD (1983) Black-legged kittiwake feeding flocks in Alaska: Selfish/reciprocal altruistic flocks? *J Field Ornithol* 54:96–99
- Beauchamp G (1998) The effect of group size on mean food intake rate in birds. *Biol Rev Camb Philos Soc* 73:449–472
- Beauchamp G (2011) Fit of aggregation models to the distribution of group sizes in Northwest Atlantic seabirds. *Mar Ecol Prog Ser* 425:261–268

- Beauchamp G, Fernández-Juricic E (2005) The group-size paradox: effects of learning and patch departure rules. *Behav Ecol* 16:352–357
- Bonabeau E, Dagorn L, Féron P (1999) Scaling in animal group-size distributions. *Proc Natl Acad Sci USA* 96: 4472–4477
- Borkowski J (2000) Influence of the density of a sika deer population on activity, habitat use, and group size. *Can J Zool* 78:1369–1374
- Brown RGB (1988) Oceanographic factors as determinants of the winter range of the dovekie (*Alle alle*) off Atlantic Canada. *Colon Waterbirds* 11:176–180
- Camphuysen CJ, Webb A (1999) Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. *Ardea* 87:177–198
- Caraco T (1980) Stochastic dynamics of avian foraging flocks. *Am Nat* 115:262–275
- Caughley G (1964) Social organization and daily activity of the red kangaroo and grey kangaroo. *J Mammal* 45: 429–436
- Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. *Theor Popul Biol* 30:45–75
- Clauset A, Shalizi CR, Newman MEJ (2009) Power-law distributions in empirical data. *SIAM Rev* 51:661–703
- Croft DP, Arrowsmith BJ, Bielby J, Skinner K and others (2003) Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos* 100:429–438
- Davoren GK, Montevecchi WA, Anderson JT (2003) Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Mar Ecol Prog Ser* 256:229–242
- Duffy DC (1989) Seabird foraging aggregations: a comparison of two southern upwellings. *Colon Waterbirds* 12:164–175
- Fernández-Juricic E (2000) Forest fragmentation affects winter flock formation of an insectivorous guild. *Ardea* 88: 235–241
- Follestad A (1990) The pelagic distribution of little auk (*Alle alle*) in relation to a frontal system off central Norway, March/April 1988. *Polar Res* 8:23–28
- Fortin D, Fortin ME, Beyer HL, Duchesne T, Courant S, Dancoise K (2009) Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. *Ecology* 90:2480–2490
- Gaston AJ, Hipfner JM (2000) Thick-billed murre. In: Poole A (ed) *The birds of North America Online*, Vol 497. Cornell Lab of Ornithology, Ithaca, NY
- Gerard JF, Bideau E, Maublanc ML, Loisel P, Marchal C (2002) Herd size in large herbivores: Encoded in the individual or emergent? *Biol Bull* 202:275–282
- Gjerdrum C, Fifield DA, Wilhelm SI (2011) Eastern Canada seabirds at sea (ECSAS) standardized protocol for pelagic seabird surveys from moving and stationary platforms. Tech Rep. Canadian Wildlife Service, Ottawa
- Good TP (1998) Great black-backed gull. In: Poole A (ed) *The birds of North America Online*, Vol 330. Cornell Lab of Ornithology, Ithaca, NY
- Götmark F, Winkler DW, Andersson M (1986) Flock-feeding on fish schools increases individual success in gulls. *Nature* 319:589–591
- Haney JC, Fristrup KM, Lee DS (1992) Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scand* 23:49–62
- Harding A, Egevang C, Walkusz W, Merkel FR, Blanc S, Grémillet D (2009) Estimating prey capture rates of a planktivorous seabird, the little auk (*Alle alle*), using diet, diving behaviour, and energy consumption. *Polar Biol* 32:785–796
- Hart PJ, Freed LA (2003) Structure and dynamics of mixed-species flocks in a Hawaiian rain forest. *Auk* 120:82–95
- Hatch SA, Nettleship DN (1998) Northern fulmar. In: Poole A (ed) *The birds of North America Online*, Vol 361. Cornell Lab of Ornithology, Ithaca, NY
- Hatch JJ, Robertson GJ, Baird HP (2009) Black-legged kittiwake. In: Poole A (ed) *The birds of North America Online*, Vol 92. Cornell Lab of Ornithology, Ithaca, NY
- Hobson KA, Welch HE (1992) Observations of foraging Northern Fulmars (*Fulmarus glacialis*) in the Canadian High Arctic. *Arctic* 45:150–153
- Hoffman W, Heinemann D, Wiens JA (1981) The ecology of seabird feeding flocks in Alaska. *Auk* 98:437–456
- Huettmann F, Diamond AW (2001) Seabird colony locations and environmental determination of seabird distribution: a spatially-explicit breeding seabird model for the Northwest Atlantic. *Ecol Modell* 141:261–298
- Huettmann F, Diamond AW (2006) Large-scale effects on the spatial distribution of seabirds in the Northwest Atlantic. *Landscape Ecol* 21:1089–1108
- Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79: 647–655
- Johnson CN (1983) Variations in group size and composition in red and Western grey kangaroos, *Macropus rufus* (Desmarest) and *M. fuliginosus* (Desmarest). *Aust Wildl Res* 10: 25–31
- Krause J, Ruxton GD (2002) *Living in groups*. Oxford University Press, Oxford
- Lawes MJ, Nanni RF (1993) The density, habitat use and social organisation of Dorcas gazelles (L.) in Makhtesh Ramon, Negev Desert, Israel. *J Arid Environ* 24:177–196
- Leuthold W, Leuthold BM (1975) Patterns of social grouping in ungulates of Tsavo National Park, Kenya. *J Zool* 175: 405–420
- Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412:816–819
- Maniscalco JM, Ostrand WD, Suryan RM, Irons DB (2001) Passive interference competition by glaucous-winged gulls on black-legged kittiwakes: a cost of feeding in flocks. *Condor* 103:616–619
- Montevecchi WA, Stenhouse IJ (2002) Dovekie. In: Poole A (ed) *The birds of North America Online*, Vol 701. Cornell Lab of Ornithology, Ithaca, NY
- Morgan T, Fernández-Juricic E (2007) The effects of predation risk, food abundance, and population size on group size of brown-headed cowbirds (*Molothrus ater*). *Ethology* 113:1173–1184
- Paredes R, Jones IL, Boness DJ, Tremblay Y, Renner M (2008) Sex-specific differences in diving behaviour of two sympatric Alcini species: thick-billed murres and razorbills. *Can J Zool* 86:610–622
- Pays O, Benhamou S, Helder R, Gerard JF (2007) The dynamics of group formation in large mammalian herbivores: an analysis in the European roe deer. *Anim Behav* 74: 1429–1441
- Pierotti RJ (1988) Associations between marine birds and mammals in the Northwest Atlantic. In: Burger J (ed) *Seabirds and other marine vertebrates*. Columbia University Press, New York, NY, p 31–58
- Pierotti RJ, Good TP (1994) Herring gull. In: Poole A (ed) *The birds of North America Online*, Vol 124. Cornell Lab of Ornithology, Ithaca, NY
- Pinto LPS, Costa CMR, Strier KB, da Fonseca GAB (1993) Habitat, density and group size of primates in a Brazilian tropical forest. *Folia Primatol (Basel)* 61:135–143

- Pulliam HR, Caraco T (1984) Living in groups: Is there an optimal group size? In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell, Oxford, p 122–147
- Ramos-Fernandez G, Boyer D, Gomez V (2006) A complex social structure with fission–fusion properties can emerge from a simple foraging model. *Behav Ecol Sociobiol* 60: 536–549
- Reiczigel J, Lang Z, Rozsa L, Tothmeresz B (2008) Measures of sociality: two different views of group size. *Anim Behav* 75:715–721
- Rome MS, Ellis JC (2004) Foraging ecology and interactions between herring gulls and great black-backed gulls in New England. *Waterbirds* 27:200–210
- Ronconi RA, Ryan PG, Ropert-Coudert Y (2010) Diving of great shearwaters (*Puffinus gravis*) in cold and warm water regions of the South Atlantic Ocean. *PLoS ONE* 5:e15508
- Sealy SG (1973) Interspecific feeding assemblages of marine birds off British Columbia. *Auk* 90:796–802
- Sibly RM (1983) Optimal group size is unstable. *Anim Behav* 31:947–948
- Southwell CJ (1984) Variability in grouping in the eastern grey kangaroo, *Macropus giganteus*. I. Group density and group size. *Aust Wildl Res* 11:423–435
- Spinage CA (1969) Territoriality and social organization of the Uganda defassa waterbuck *Kobus defassa ugandae*. *J Zool* 159:329–361
- Taylor RJ (1982) Group size in the eastern grey kangaroo, *Macropus giganteus*, and the wallaroo, *Macropus robustus*. *Aust Wildl Res* 9:229–237
- Taylor RJ (1983) Association of social classes of the wallaroo, *Macropus robustus* (Marsupialia; Macropodidae). *Aust Wildl Res* 10:39–45
- Toigo C, Gaillard JM, Michallet J (1996) La taille des groupes: un bioindicateur de l'effectif des populations de bouquetin des Alpes (*Capra ibex ibex*)? *Mammalia* 60:463–472
- van Houtan KS, Pimm SL, Bierregaard RO, Lovejoy TE, Stouffer PC (2006) Local extinctions in flocking birds in Amazonian forest fragments. *Evol Ecol Res* 8:129–148
- Watson M, Aebischer NJ, Cresswell W (2007) Vigilance and fitness in grey partridges *Perdix perdix*: the effects of group size and foraging-vigilance trade-offs on predation mortality. *J Anim Ecol* 76:211–221
- Williams CK, Lutz RS, Applegate RD (2003) Optimal group size and northern bobwhite coveys. *Anim Behav* 66: 377–387
- Wirtz P, Lorsche J (1983) Group sizes of antelopes in an East African National Park. *Behaviour* 84:135–156

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