

How Might Family and Flock Size be Related?

- See the document `geese001` for a previous version of what I expected to observe in the species.
- See `geese002` for a summary of data collection on Kolguyev.
- See `geese003` for a summary of the conditions on the wintering grounds.
- See `geese004` for a summary of how expectations held up to observations.

A summary of group living

Abundance is related to resources

It is widely accepted that abundance is driven by the levels of relevant resources. At the species assemblage level, the number of niches is one of the most basic predictors of richness. Other factors that influence richness as well as abundance are intra- and inter-species interactions. Within species, the abundance of individuals is predicted by the size of the ecological niche, which, like the number of niches available to an assemblage, is a function of environmental variables. In the case of most animals - consumers - the deciding variable is vegetation cover, which is a good proxy for availability and quality of nutrition. Vegetation cover is a most useful metric, for it can be remotely sensed, allowing for the survey of large areas. In addition, it is itself a response to a number of other variables - temperature and water availability foremost, but also less easily or frequently measured phenomena, such as photoperiod, pollutant concentrations, landscape management and the like. As such, it serves as a convenient abstraction of these others, the interactions between which are usually complex and indirect.

Why animals live in groups

Animals in abundance usually live in groups, and the costs and benefits of group living are well studied. See Krause and Ruxton (2002) for a very comprehensive look at the topic. The benefits especially are frequently emphasised. Quantitatively, the time (and hence energy) expended on some behaviours shows a negative density dependence - the per-capita cost of these behaviours decreases with group size. Anti-predator vigilance is often cited as an example. Fewer animals spend less of their time in vigilance behaviours in large groups when compared to small ones, with the 'many-eyes' and encounter-dilution mechanisms the two causes most

commonly held to underlie the effect. Roberts (1996) discusses how findings in favour of one mechanism could also favour the other, but the net result is that animals (and birds are especially well studied when it comes to this question) spend less time on vigilance. Grouping benefits are also accrued outside a time-budget framework. The per-capita costs of a purely physiological activity – thermogenesis during sleep – are reduced simply by the proximity of group members, allowing for a sharp increase in the wintertime energy savings of colony-nesting African Striped mice as compared to solitary nesting conspecifics (SCANTLEBURY et al. 2006). On the other hand, one of the most significant costs of grouping is held to be the transmission of disease causing pathogens, but Côté and Poulinb (1995) seem to believe pathogens exert conflicting pressures on groups.

*Grouping benefits **and** hinders some behaviours*

Some activities, like foraging and parasite/predator avoidance, become both easier and more difficult as the size of a group increases. In the case of foraging, per-capita costs are reduced in those groups where the resource cannot be easily detected, accessed or processed by a single individual alone, cooperation proving effective in these processes. Examples at two extremes are most pack-living canids, which regularly take prey many times their size (Creel and Creel 1995), and colonial leaf-cutter ants, which would be unlikely to individually maintain a nearly agricultural system based on fungi (Mueller et al. 2001). Predator **avoidance** is also helped by larger groups – predators are detected earlier, more accurately, and better avoided by a number of proposed mechanisms; Krause and Ruxton (2002) presents these mechanisms in full. However, foraging in groups also results in increased competition for resources, and per-capita resource availability is reduced. This applies especially to grazers foraging on a resource patch, which may incur costs in both competing and moving between patches, since a finite patch will be exhausted more quickly by a large group. Anti-predator defence might be increased by group living, but the detectability of large groups is also higher, and they are more profitable for predators to attack. The tradeoff is well captured in the ‘encounter-dilution’ model.

Groups form from simple local rules

Animal groups may also form in the apparent absence of resources or threats, and yet present complex structure. Such structure emerges from individuals following a limited number of very simple rules in their interactions with each other. For example, theoretical models have shown that under only two imperatives – to maintain a minimum distance from a neighbour, while aligning oneself with the neighbour’s direction of movement

– individual fish in a three-dimensional space formed up to four distinct group structures as parameters controlling their tendencies to avoid and align with neighbours were tweaked (Couzin et al. 2002). This model was validated in lab experiments, where fish formed three kinds of groups: an unorganised ‘swarm’, a highly polarised (or aligned) state, and a torus, or doughnut with the fish milling around a hollow centre. The formation of these structures was most strongly predicted by the number of fish in the group, with larger groups forming a ‘milling’ state more frequently than any other (Tunstrøm et al. 2013). Fish schools forming such groups are also observed in the wild and are indeed a staple of documentaries. Simple rules governing grouping have implications even at larger spatial scales. In models, when only a small proportion of the group has both information about resources and a poor tendency to align with other members, these informed and independent individuals move towards resources. Other group members follow in keeping with the tendency to align. Such a mechanism might underlie such large scale phenomena as animal migrations (Gueron and Levin 1993, Couzin et al. (2005)).

Groups are often heterogeneous

Even in the simplest theoretical models, those that draw the attributes of equivalent group members from a normally distributed pool, the groups formed may show considerable heterogeneity as Parrish et al. (2002) discuss. This results in the formation of gradients within groups, with the positions of group members predicted by certain traits. This may be extreme enough to cause the emergence of leaders, as Sueur (2010) show in relation to nutrient needs. Conversely, certain areas in a group are hypothesised as being more advantageous to occupy. The Hamiltonian ‘selfish herd’ model, for example, predicts that individuals will try to occupy the centre of a herd, or a position close to other animals, since this reduces their risk of being targeted by predators (Hamilton 1971). This prediction has been found to hold in fish schools wherein all but one members of the group were habituated to ‘Schreckstoff’, a substance that naturally enters the water only when a fish is injured, for example, by a predator. This indicator of predator presence induces fear responses in fish. The naive individual, while initially occupying a random position, manoeuvred itself such that it was not on the group periphery when the substance was introduced into the water (Krause 1993).

Grouping rules have a physiological basis

The emergence of observed generalised ‘rules’ for group formation has its basis in the physiological costs and benefits associated with spatial pattern-

ing. While protection from predation risk, such as in a Hamiltonian herd, is a major driver, one major component of the costs of grouping is intra-group agonistic interactions. These are widely held to increase with group density, and might be between individuals, or between family units, or some generalised social unit, as reported in gulls (Ewald et al. 1980). Group structure, then, is often determined by the interaction between the stresses and resultant energy costs of performing and fending off aggressive behaviours, and the other benefits gained by group living. For example, colonies of nesting seabirds have inter-nest (and thus, inter-family) distances that are considered to be a function of each family needing 'its own space'. This need is however modulated by the evident benefits conferred by a dense colony against predation on eggs and young by nest-raiders. In colonies that face a lower predation risk, nests are spaced widely apart; see a similar idea in Oro (1996) and Massaro et al. (2001). Similar effects result from yet more experiments with fish: real predators, attacking virtual prey dots each with their own quantitative traits determining the tendencies to avoid and align, selected against solitary movement and also against the adoption of tortuous, or less directed, movement (Ioannou et al. 2012).

What do grouping animals maximise?

Grouping, then, is modulated by the balancing of multiple demands, and groups don't always appear to structure themselves as would be expected from model predictions. An individual's preference of position in a group is usually based on more than one attribute of the space. A more comprehensive model of grouping would include:

- The benefits against predation,
- The costs in terms of scramble competition¹, and,
- The costs in terms of interference competition², quantified as fights or agonistic interactions.

While the Hamiltonian selfish herd confers benefits from predation to central individuals, it also likely exposes them to competition and expensive fights. Individuals would then be expected to identify group zones in which they gain energy on the whole, and attempt to stay in those zones.

Black et al. (1992) studied wintering Barnacle goose flocks showed that the net energetic value of occupying a position on the group periphery is however not significantly different from occupying a position in the centre. Position in the flock was indeed found to be a function of social dominance, the cost of vigilance, and competition for resources. Dominance, or success in interference competition, was seen to have a clear positive dependence on the size of the social unit. Families dominated in fights, challenging more often and winning more challenges. Pairs dominated singles, with single

¹ Maximising resource intake by maximising resource discovery, ie, 'scrambling' to find resources.

² Maximising resource intake by maximising access to resources, ie, 'interfering' with others' access to resources.

juveniles worst off. The flock edge was more risky, with increased vigilance behaviours and hurried feeding, but also more profitable, since scramble competition at the edge was lower, and resources higher, as compared to the dense centre of the flock where resources were quickly depleted. Barnacle goose flocks then have three zones: the periphery, the rich but risky periphery dominated by families, the quickly depleted but safe centre, and the completely depleted trailing edge. This is also likely to apply to geese in general.

What do geese select for?

How individuals choose groups

Given this limited introduction to animal group behaviours, we can make some rough guesses about *how* an individual goose would choose a group to join. An individual choice is made to minimise energy expenditure and maximise fitness³. The choices made by individuals are capable of biasing the choices of group members – to whom the same options have subsequently been offered – in favour of the most recent previous choice. Simultaneously, the choice made by an individual is affected by the number of individuals making the same choice. This quorum sensing has been shown in experiments to allow groups to make faster and more accurate decisions, for example in scenarios of predation risk. Such a mechanism is likely to underlie most decisions animals make to join groups. Assuming a uniform distribution of resources across a landscape, or a lack of information about the location of resources, a lone goose would select for:

- A group of a size approaching the threshold at which anti-predator benefits are conferred by some mechanism, and,
- A group in which its agonistic interactions (and hence energy expended) are minimised.

Given that millions of geese descend on the wintering grounds each year, it is likely that finding a flock of a suitable size is not a difficult task for geese. One could expect that the distribution of flock sizes is a normal one, in which the mean flock size is close to the threshold of predator-avoidance⁴.

³ This varies with the sex, social condition, and age of the individual being considered. Goose families appear willing to invest considerable energy to acquire forage, reducing short-term fitness, but probably increasing long-term fitness in the form of further successful breeding seasons.

⁴ One could expect at least two thresholds in flock size: a minimum predator-avoidance size, and an optimum size where competition costs \leq vigilance benefits.

Conjectures

Agonistic interactions in a flock are driven by the size of social units

Within a forming flock, agonistic interactions might be expected to increase solely with group size, but Amano et al. (2006) report that in Whitefront flocks in Japan, such interactions did not increase significantly with group size alone. The study did not appear to consider group composition, however. It is possible that in goose flocks, the absolute number of aggressions is driven by the mean size of its social units. As Black et al. (1992) have shown in Barnacle geese, agonistic interactions are largely due to large social units, or families, which have the highest rank in the dominance hierarchy. This increase is supported by a drop in the per-capita costs of aggression as social unit size grows. This is because most of the costs are borne by the guarding male or parents, but also because juveniles of families also play some supporting role in determining the outcome of challenges⁵. As the area occupied by a social unit, and the breadth of its wavefront of advance increases, its movement is both more disruptive to other geese in a flock, and is also more likely to encounter disruptions in the form of resting or foraging geese that are trying to maintain their position at the front of an advancing, or diffusing, flock.

⁵ Per-capita aggression costs vs. proportion of male involvement is likely to have a trough at a point where the male does most of the fighting but the rest of the family helps.

Agonistic interactions are driven by the number of large social units

Next, one could expect that agonistic interactions in a flock rise with the number of families. Assuming a constant mean family size of n juveniles with two parents, the area occupied by this social unit of $n+2$ geese is larger than that of smaller social units, ie, pairs or singles. The path of their advance is also wider and results in more aggressive behaviours. By the same mechanism as above, families, which don't usually separate within a flock⁶, would be expected to cause more disruption and in general impose more costs on their neighbours.

⁶ Johnson and Raveling (1988) and Jónsson and Afton (2008) report otherwise in wintering non-Anser geese, but Black et al. (1992) supports this view.

The claim is that an individual goose would choose to join a flock which has few, and small, families.

Flocks form around family groups

Elder and Elder (1949) reported that in a large goose, the Canada goose (*Branta canadensis*), flocks are in fact composed of family groups, and that flock sizes are thus often multiples of the mean family size in this species. The main point here is that families are the basic unit of goose organisation, and precede flock formation⁷, and provide a core around which other geese

⁷ Miller and Dzubin (1965) find that individually released family members regroup.

may group. This is borne out by personal observations of Whitefronts from the breeding grounds on Kolguyev. The size of flocks, if they could even be called that, was never above 100 individuals. 'Flocks' were composed of loose groups of families and pairs. Chronologically too, the idea that families form before flocks is supported by the way in which the migrating flock forms, which is probably by the agglomeration of groups of geese that have bred and are in families of some size, and of groups of single or paired geese that did not breed.

From the point of view of competition, families and single geese or pairs likely select for different attributes in flocks. Since families both incur lower per-capita costs of aggression, as well as win fights and thus gain access to better nutrition, they can afford to seek out flocks and intra-flock positions that maximise their energy intake, ignoring the rule of conflict minimisation. This freedom, as well as some small benefit of being in a group, allows families more freedom in which, if any, flock they join.

The second claim is that flocks form around families.

Given these lines of reasoning, it appears that instead of families being socially weak units that are pushed to the margins of flocks, the opposite is true. Families are dominant units, monopolising the edge, and free to make choices regarding flock membership. This should lead us to believe that instead of family sizes being influenced by flock sizes, the opposite is true. The size and number of families in a flock affect the cost of flocking with them, and so likely affect to some extent the formation of flocks around them.

This might explain why larger families of wintering Whitefronts are seen in smaller flocks.

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