FLOCK SIZE MEASURES OF MIGRATING
LESSER WHITE-FRONTED GEESE *ANSER ERYTHROPUS*

Lengyel, Sz.[1], Tar, J.[2] and Rózsa, L.[3]

[1]Department of Ecology, University of Debrecen, H-4032 Debrecen, Egyetem tér 1, Hungary
[2]Hortobágy National Park Directorate, H-4024 Debrecen, Sumen u. 2, Hungary
[3]Ecology Research Group, MTA-ELTE-MTM
H-1088 Budapest, Baross u. 13, Hungary, E-mail: lajos.rozsa@gmail.com

Migrating in flocks has various benefits but also incurs costs, which depend on the conditions individuals experience in flocks of various sizes. Here we quantified such conditions by using recently developed methods to measure crowdedness in animal groups using data on flock sizes of the endangered Fennoscandian population of the globally threatened Lesser White-fronted Goose *Anser erythropus*. Data were gathered on migration in Hortobágy National Park (E Hungary) between 1994 and 2006. Data on 548 sightings of the species suggested that the distribution of flock sizes was skewed and that flock sizes were significantly larger in the autumn than in the spring. Despite this difference, mean crowding values, i.e., the group size in which an average individual occurs, were remarkably similar in the spring and in the autumn. These results show that even though flock size varied seasonally, the social environment experienced by the average individuals was surprisingly stable across seasons. Such stability can be important in the consistency of the benefits and costs of migrating in flocks. Our results also draw attention to the importance of quantifying crowdedness in animal groups as these measures can provide information different from those provided by looking at mean group size alone.

Key words: mean group size, flocking behaviour, crowding

INTRODUCTION

Many birds migrate in flocks. Flocking during migration can have several advantages to individuals. First, knowledge on migration routes and staging sites can be shared among individuals, and navigation can be improved in groups (SIMONS 2004, CODLING *et al.* 2007). Second, flocking behaviour may also enhance the efficiency of finding patchily distributed food resources at staging sites (BEAUCHAMP 1998), and may improve innovative capabilities to discover new sources of food (LIKER *et al.* 2009). Third, grouping decreases predation pressure per individual via increased vigilance or a dilution effect (HAMILTON 1971, BEAUCHAMP & RUXTON 2008). Finally, flying in groups can have aerodynamic benefits leading to more efficient energy use (HEDENSTROM & ALERSTAM 1995). However, flocking can also have negative effects on individuals. For example, living in large flocks increase aggression and intraspecific competition and may provide greater exposure to parasites or disease vectors (KRAUSE & RUXTON 2002, WHITEMAN & PARKER

2004, BEAUCHAMP 2007). Therefore, it is of conservation and ecological interest to understand whether individuals experience different crowdedness conditions in different-sized flocks as these experiences may be directly related to the costs and benefits of flock formation.

The Lesser White-fronted Goose *Anser erythropus* is the smallest species in the genus *Anser*. Lesser White-fronted Geese breeds in the sub-arctic zone from northern Fennoscandia to eastern Siberia and migrate long distances to Greece, Turkey, Iran, Iraq (populations west of the Ural Mountains) and to China (populations east of the Ural Mountains). The species is globally threatened, being recognised as vulnerable by the IUCN Species Survival Commission (2006). Two of the three wild subpopulations declined significantly in the 20th century, and the Fennoscandian population, the smallest of the three, continues to decline at a rate of c. 5% per year. The genetically distinct Fennoscandian population is now estimated at 20 breeding pairs or 60–80 total individuals at most (AARVAK *et al.* 2009).

The Fennoscandian population migrates from the breeding grounds in northern Norway to wintering sites in Greece, Bulgaria and Turkey through the Kanin Peninsula (northern Russia), western Estonia, and Hortobágy, a major stopover site in Eastern Hungary. Lesser White-fronted Geese spend up to two months in Hortobágy National Park during autumn migration and one month during the spring migration. During staging at this site, Lesser White-fronted Geese use fishponds and marshes as night roosting sites and alkali grasslands and arable lands as feeding sites (LENGYEL *et al.* 2009). On migration, Lesser White-fronted Geese tend to be social, though single individuals may also frequently occur. Single individuals or small flocks occur mainly in Hortobágy National Park, and scarcely in other parts of Hungary, such as the Fertő–Hanság and the Kiskunság National Parks.

The aim of our present study is to quantify the flocking behaviour of Lesser White-fronted Geese observed at Hortobágy from the autumn of 1994 to the winter of 2006. Lesser White-fronted Geese prefer to feed, move and roost in flocks formed by conspecifics. Flock members exhibit highly coordinated behaviours, thus flocks are rather well defined in the field. Lesser White-fronted Geese flocks or single individuals may also join flocks of other goose species. In Hortobágy, Lesser White-fronted Geese move around in homogeneous flocks in the spring migration and early autumn staging and associate with flocks of other geese – Greylag Goose *Anser anser* and Greater White-fronted Goose *Anser albifrons* – in late autumn staging. However, Lesser White-fronted Geese individuals behave and move as a group even in larger goose flocks and behaviours are much less coordinated across species. The Hortobágy staging site offers a good opportunity to study flocking behaviour because Lesser White-fronted Geese are free to use spatially

distinct roosting and feeding sites scattered over vast areas, which increases the chances for variation in flocking behaviour.

MATERIALS AND METHODS

For the sake of mathematical simplicity, we defined 'flock' as one or more conspecific individuals occurring at the same place at the same time and exhibiting coordinated behaviours. 'Same place' was defined as one roosting or feeding site and 'same time' was defined as the same day. A flock observed at the same place on two consecutive observation periods was considered as two separate data points (see potential non-independence problems discussed below). Spring and autumn seasons were treated separately.

Data on group sizes were obtained from a database on Lesser White-fronted Geese observations, which included all reliable observations (n = 897) of the species in the Hortobágy area between 1905 and 2006. The database was compiled by the Hortobágy Environmental Association from a detailed survey of the literature and from data on Lesser White-fronted Geese occurrences provided by national park rangers and field ornithologists. Observation effort has varied greatly in the period covered by the database as interest in the species grew considerably in parallel with its global decline starting in the 1950s and 1960s. The current system of Lesser White-fronted Geese monitoring was launched in 1994 and it involves detailed searches of the most important roosting and feeding sites for Lesser White-fronted Geese at least once a week during the months Lesser White-fronted Geese are potentially present in the Hortobágy area (March-May in spring, September-December in autumn). To make our conclusions robust to variation in observation effort, we used data only from the period 1994–2006, when observation effort could be considered similar across years. We did not log-transform data because values varied only across two orders of magnitude (1–110).

Statistical analyses were first focused on the mean and median of flock sizes, i.e., the arithmetic mean and the median of group sizes calculated across flocks as data points. Secondly, we also quantified crowding, i.e., the group size in which an actual individual occurs. Thus mean crowding equals the arithmetic mean of group sizes calculated across individuals as data points. This measure was defined as 'typical group size' by Jarman (1974) and 'individual group size' by Jovani & Mavor (2011). For example, a sample of three flocks with flock sizes 1, 4 and 7 is characterized by the mean group size (1+4+7) / 3 = 4 and a mean crowding (1*1+4*4+7*7) / (1+4+7) = 5.5

Naturally, average individuals occur in groups larger than the mean group size, and the magnitude of this difference is a function of the variability of group sizes.

Mean crowding is particularly hard to handle statistically; the major problem is the inherent non-independence of data points. When handling crowding measures, one has to be aware of the links among individual data points. For example, when an individual leaves a flock of 10, then crowding will change from 10 to 1 for this particular bird, and also from 10 to 9 for the 9 other birds. Similarly, when an observer observes – or fails to observe – a flock of 10 birds, then 10 data points are added or missed in parallel with each other. Thus, crowding data exhibit several coordinated changes due to a single biological event. We followed the statistical methodology described by Reiczigel et al. (2008) to control for these types of non-independence as implemented in their free software (Reiczigel & Rózsa 2006).

It is very likely in our data set that the same individuals and the same flocks have been recorded several times at different places and/or at different times. Here we do not control for such potential pseudoreplication in the sense of Hurlbert (1984). However, this problem is rather small from a biological point of view, because our observations practically cover the whole Fennoscandian popula-

tion of Lesser White-fronted Geese and thus our statistics serve a purely descriptive rather than predictive function. Thus we cannot and do not claim that unknown members or flocks of the same population would exhibit similar flocking behaviours. Confidence intervals (CI) refer to a 95% probability.

RESULTS

Our data set summarizes 144 observations of flocks or single individuals in the spring period that cover a total of 2 465 individuals. In the autumn period, a total of 404 observations covered a total of 9 091 birds. As already emphasized above, this is far above the true population size, since the same flocks could have been recorded several times.

As it is a usual characteristic of avian flocking behaviour (JOVANI & MAVOR 2011), flock sizes exhibited an aggregated (skewed) distribution pattern, i.e., most flocks were small, a few were large, and a very few were very large (>100 birds). Group sizes were more variable in the spring than in the autumn, the variance-to-mean ratio was 21.42 in the spring and 15.98 in the autumn. A test for stochastic equality (REICZIGEL *et al.* 2005) indicates that the flock size distributions differed significantly between the two seasons (Brunner-Munzel test $P = 0.0002$, bootstrap test with 2000 replications, $P = 0.0000$).

Mean group size was lower in the spring and higher in the autumn (17.1, CI: 14.43 – 20.44 and 22.5, CI: 20.66 – 24.31, respectively) and this difference was
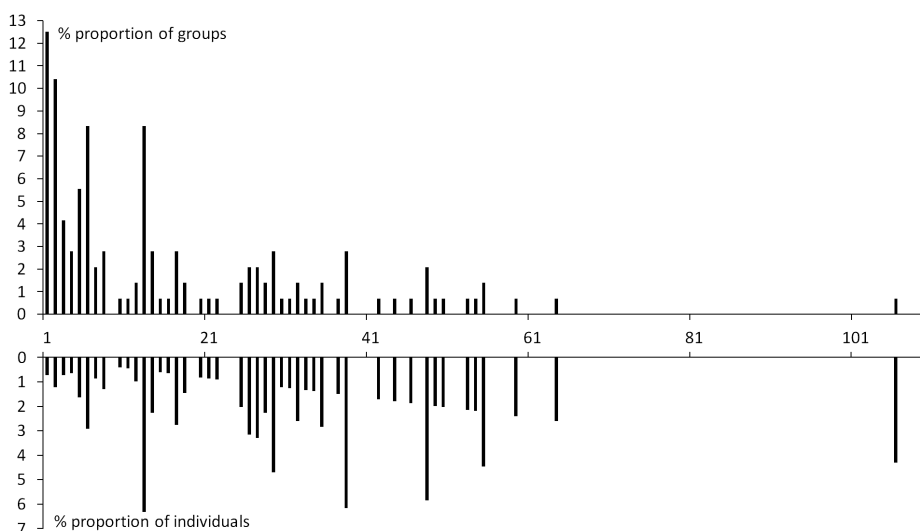

Fig. 1. The distribution of Lesser White-fronted Geese flocks (above) and individuals (below) among flock size categories in the spring at Hortobágy, 1994–2006

highly significant (bootstrap two-sample t-test, t = 2.905, 2000 replications, two-sided $P = 0.0045$). Similarly, median group sizes were lower in the spring than in the autumn (11.5, CI: 6 – 13 and 19, CI: 18 – 21, respectively), and this difference was also highly significant (Mood's median test, exact two-sided $P = 0.000$) (Figs 1 & 2).

In contrast, mean crowding values, i.e., the group size in which an average individual occurs, were remarkably identical in the spring and in the autumn (38.44, CI: 31.55 – 50.33 and 38.39, CI: 35.42 – 41.87), and did not differ statistically ($P > 0.05$).

DISCUSSION

We quantified flock size measures of spring versus autumn migratory Lesser White-fronted Geese in eastern Hungary. Our results show that Lesser White-fronted Geese flocks tend to be larger in the autumn than in the spring, and that the autumn flocks are also less variable in their size. Consequently, the average individuals' social environment – as expressed by the surrounding flock size – was surprisingly stable across seasons. We emphasize that the statistics described above are of descriptive nature. As the data practically cover the whole Fennoscandian Lesser White-fronted Geese population, there is no biological relevance to speculate about the predictive value of these statistics.
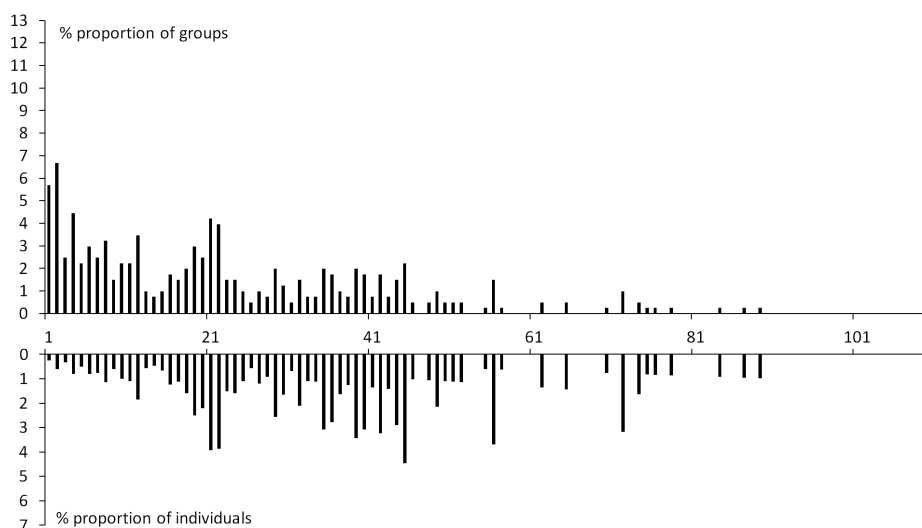

Fig. 2. The distribution of Lesser White-fronted Geese flocks (above) and individuals (below) among flock size categories in the autumn at Hortobágy, 1994–2006

Measures of sociality in migrating Lesser White-fronted Geese in Eastern Hungary are likely to be shaped by strong environmental limitations. Firstly, flock size cannot grow to high levels (say, hundreds) simply because of the absence of excess individuals. It seems likely that in the few cases where flock sizes exceeded 100 individuals (e.g. in 1996); practically the whole Fennoscandian Lesser White-fronted Geese population was observed in a single flock. Secondly, the spatial distribution of food resources is likely to affect the spatial dispersion of feeding flocks. One can conceivably argue that feeding efficacy can be higher in smaller flocks than in large ones, thus pressure to exhibit optimal foraging tactics increase the chance that a large flock would break down into several small groups. Finally, predation pressure is likely to have an opposite effect. Flocking birds often rely on a dilution effect against predation, i.e. they prefer larger groups so as to minimize predation threat per individual (HAMILTON 1971). Indeed, natural predators such as eagles, falcons, canids etc. are often present in the staging habitats (TOLVENEN *et al.*, TAR, J. – unpubl. data), and hunting pressure is still significant on Lesser White-fronted Geese at some sites during migration (ØIEN *et al.* 2009).

To summarise, we believe that the quantitative measures of Lesser White-fronted Geese flocking behaviour at Hortobágy are shaped by effects if population size, optimal foraging and predation pressure. Future changes in any of these effects would probably cause significant shifts of these measures. Our current effort was to provide quantitative baseline values that enable future detection of any such changes.

<center>*</center>

<center>REFERENCES</center>

AARVAK, T., LEINONEN, A., ØIEN, I. J. & TOLVANEN, P. (2009) Population size estimation of the Fennoscandian Lesser White-fronted Goose based on individual recognition and colour ringing. Pp. 71–75. *In:* TOLVANEN, P., ØIEN, I. J. & RUOKOLAINEN, K. (eds): *Conservation of the Lesser White-fronted Goose on the European migration route. Final report of the EU LIFE-Nature project,* WWF Finland Report 27 and Norwegian Ornithological Society Report 1–2009, Helsinki.

BEAUCHAMP, G. (1998) The effect of group size on mean food intake rate in birds. *Biological Reviews* **73**: 449–472.

BEAUCHAMP, G. (2007) Competition in foraging flocks of migrating semipalmated sandpipers. *Oecologia* **154**: 403–409.

BEAUCHAMP, G. & RUXTON, G. D. (2008) Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks. *Animal Behaviour* **75**: 1837–1842.

CODLING, E. A., PITCHFORD, J. W. &, SIMPSON, S. D. (2007) Group navigation and the "many-wrongs principle" in models of animal movement. *Ecology* **88**: 1864–1870.

HAMILTON, W. D. (1971) Geometry for the selfish herd. *Journal of Theoretical Biology* **31**: 295–311.

HEDENSTROM, A. & ALERSTAM, T. (1995) Optimal flight speed of birds. *Philosophical Transactions of the Royal Society B* **348**: 471–487.

HURLBERT, S. H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**: 187–211.

IUCN SPECIES SURVIVAL COMMISSION (2006) *IUCN 2006 Red List of Threatened Species.* IUCN, Gland. 191 pp.

JARMAN, P. J. (1974) The social organisation of antelope in relation to their ecology. *Behaviour* **75**: 215–268.

JOVANI, R. & MAVOR, R. (2011) Group size versus individual group size frequency distributions: a nontrivial distinction. *Animal Behaviour* **82**: 1027–1036.

KRAUSE, J. & RUXTON, G. D. (2002) *Living in groups.* Oxford University Press, New York, 210 pp.

LENGYEL, S., TAR, J. & ECSEDI, Z. (2009) Space use and exposure of Lesser White-fronted Geese to hunting in the Hortobágy region (Eastern Hungary). Pp. 53–60. *In:* TOLVANEN, P., ØIEN, I. J. & RUOKOLAINEN, K. (eds): *Conservation of the Lesser White-fronted Goose on the European migration route. Final report of the EU LIFE-Nature project,* WWF Finland Report 27 and Norwegian Ornithological Society Report 1–2009, Helsinki.

LIKER, A. & BÓKONY, V. (2009) Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 7893–7898.

ØIEN, I. J., AARVAK, T., EKKER, M. & TOLVANEN, P. (2009) Mapping of migration routes of the Fennoscandian Lesser White-fronted Goose breeding population with profound implications for conservation priorities. Pp. 12–15. *In:* TOLVANEN, P., ØIEN, I. J. & RUOKOLAINEN, K. (eds): *Conservation of the Lesser White-fronted Goose on the European migration route. Final report of the EU LIFE-Nature project,* WWF Finland Report 27 and Norwegian Ornithological Society Report 1–2009, Helsinki.

REICZIGEL, J., LANG, Z., RÓZSA, L. & TÓTHMÉRÉSZ, B. (2008) Measures of sociality: two different views of group size. *Animal Behaviour* **75**: 715–721.

REICZIGEL, J. & RÓZSA, L. (2006) *Flocker 1.1: A software to quantify and compare statistical measures of groups size.* Distributed by the authors, http://www.zoologia.hu/flocker/flocker.html [accessed 03 January 2012]

REICZIGEL, J., ZAKARIÁS, I. & RÓZSA, L. (2005) A bootstrap test of stochastic equality of two populations. *The American Statistician* **59**: 156–161.

SIMONS, A. M. (2004) Many wrongs: the advantage of group navigation. *Trends in Ecology & Evolution* **19**: 453–455.

TOLVANEN, P., AARVAK, T. & ANUFRIEV, V. (2009) Lesser White-fronted Goose survey on Kanin Peninsula, Russia, in September 2008. Pp. 40–43. *In:* TOLVANEN, P., ØIEN, I. J. & RUOKOLAINEN, K. (eds): *Conservation of the Lesser White-fronted Goose on the European migration route. Final report of the EU LIFE-Nature project,* WWF Finland Report 27 and Norwegian Ornithological Society Report 1–2009, Helsinki.

WHITEMAN, N. K. & PARKER, P. G. (2004) Effects of host sociality on ectoparasite population biology. *Journal of Parasitology* **90**: 939–947.