

FACEBOOK FOR GEESE:

The causes and consequences of non-random social associations in a group forager

SUBMITTED BY MATTHEW JOHN SILK TO THE
UNIVERSITY OF EXETER

AS A THESIS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN
BIOLOGICAL SCIENCE, OCTOBER 2014

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.



Abstract

The application of social network analysis in animals has facilitated research into dynamic fission-fusion social systems. These have important implications for the evolution of individual social behaviour, and for population-level processes such as information transfer and disease dynamics. This thesis explores the assumptions behind using networks to study animal social systems in projects using individual-marking or biologging. It then applies these methods to study social structure in a study population of a long-distance migrant, the light-bellied brent goose. It provides new insights about the causes and consequences of social structure, and individual social strategies, in a fission-fusion social system in the context of a migratory cycle. We show that social networks have a strong spatial structure, but with additional non-randomness once these spatial constraints have been accounted for. However, individual social associations are seasonally dynamic. These social structures, and their seasonal dynamics, are highly stable between years. Furthermore, non-random associations have important implications for foraging success. Individuals foraging in more familiar flocks are able to spend more time feeding, and less time involved in aggressive interactions or vigilant. This results in social network position influencing the ability of some individuals to gain body condition during spring staging and leave for breeding grounds in better condition. These results highlight the importance of understanding social networks when investigating individual time-budgets in social foragers. They also emphasise the importance of establishing the link between individual status and social network position before drawing any conclusions about the role of social network position in explaining differences in fitness between individuals in fission-fusion social systems.

Acknowledgements

Certainly, none of this would have been possible without the help of Stuart Bearhop, who has always been full of ideas, supportive and, most importantly, patient when things sometimes went wrong. Tom Tregenza has always been great at stepping in to help out when needed, often with very little warning. Darren Croft has also provided great input throughout, even if often restricted to meetings as I rushed through Exeter to and from fieldwork. I feel I should include Andrew Jackson here as well, who has was a massive help at the start of my modelling work, and somehow taught me R just by sitting and watching him work for a couple of days (still haven't quite worked out how that happened...). I would also like to thank Pete Robertson at FERA for providing some useful thoughts at various points and MD Sharma for providing me computer space without which some of my analysis would have been impossible. I have been lucky enough to work in a fantastic research group – I gained an enormous amount from sitting through many a very lengthy research group meeting, even if it didn't always feel like it at the time! Finally (academically at least), I certainly wouldn't be where I am now without the enthusiasm and careful guidance of Nick Davies, Rose Thorogood, Maggie Couvillon, and especially Stu Sharp as an undergrad student. Before working with all of you I certainly could have envisaged myself here now.

The success of my fieldwork wouldn't have been possible without everyone in the Irish Brent Goose Research Group, especially to Graham McElwaine and Kendrew Colhoun who have been a massive help throughout (although I'm pretty sure that Graham won't be that sad if the thousands of resightings associated with my research stop for a little while at least!). Pat and Dick Watson, and Cian and Rachel Merne have both been fantastic to me throughout my times in Dublin, and helped out a great deal with everything. Niall Tierney is another person I want to mention. He must have been present at almost every canon-net catch we attempted, even when luck wasn't on our side. Thanks also to Kerry Mackie and Alan Lauder for being willing to give up time to be the men in charge of the gunpowder when Stu wasn't around. If I listed everyone else that helped out at canon-net catches or sent in resightings that were used in my project I would very quickly run out of space, but I feel very lucky to have done all of my winter fieldwork in Dublin with so many enthusiastic people helping out or even just stopping to chat to

me in the street. Also a massive thank you to Agnes, Alison, Andy, Ant, Darragh, Ed, Emma, Freydis, Ian, Matt, Niall, Rafael, Richard, Stephen and Tom (alphabetical order seemed like the only fair way) who have all been great help with my own data collection at various points. You were all brilliant; especially those of you who managed to get up at hideous times in the morning in Iceland for weeks at a time with (largely) minimal complaint! I also want to thank Niall K, Sean, Clare amongst many others for being crucial in keeping me sane during my stays in Dublin, and Óli in Iceland for being so keen to introduce me to so many of my favourite things to eat.

In the end though most of my last three years have been spent in Falmouth, and there are a lot of people to blame for the last three years being so much fun. First and foremost I want to thank James Duffy for being able to put up with living me for more than two years now. I also owe a huge amount to Bea and Stephen Downing who have been very supportive friends for my entire time in Cornwall. I also want to say a massive thank you to everyone who made the farmhouse such a great place to work, especially Bea, Julian, Robin and Lindsay who I've shared the most fun office with pretty much ever since I can remember! Also to everyone else who have been awesome friends for the last few years, especially Siobhan (and her constant reminders of Dublin), Sheridan, Chris, Phil, Mitch and Jenni who have been around ever since the beginning, and all of those who I've now known nearly that long - Dave, Sean, Lucy, Mikey, Sarah and Sarah. More generally it wouldn't have been the same without all the fantastic people I've kayaked with, climbed with, cycled with, walked with, birdwatched with or played football with, and sometimes even found time to go to the pub with over the last few years – I couldn't mention everyone who's made my time down here so brilliant.

Finally, I'd like to thank my parents. I am pretty sure they are at the very least partly to blame for my love of the natural world, and certainly all of their help and support over the years made a massive contribution to me being here writing this.

*I decided on that evening
That I was through with sitting still
I stood up and started moving
With a childlike fascination
For those doors that don't have locks
And the stairways that were blocked
So I dug through the obstruction
Put my fist around the railing
And each step was far apart
And far away from steps before it
And the air was getting thinner
Until I couldn't breathe at all
And if I happened to look behind me
There were miles and miles of stairs
Enough so I couldn't see the doorway
But I knew that it was there
And on the last step I was dizzy
Because there were stairs in all directions
But I found another door
And through the door there was the attic
Without old clothes
Without a ceiling
Everything had opened wide
Into the jaws of something bigger
Finally it had found me
The answer, the feeling, and the truth:

That I'm small*

Contents

ABSTRACT	3
ACKNOWLEDGEMENTS	4
CONTENTS	7
LIST OF TABLES	13
LIST OF FIGURES	14
AUTHOR'S DECLARATION	17
1. GENERAL INTRODUCTION	19
1.1 Living in groups: how animal sociality really works	20
1.2 The evolution of fission-fusion social systems	21
1.3 The evolution and development of social structure in fission-fusion societies	22
1.4 Repeated interactions, familiarity and cooperation	23
1.5 Consequences of social structure in fission-fusion societies	25
1.5.1 Individual-level effects of fission-fusion dynamics	26
1.5.2 Population-level consequences of fission-fusion dynamics	27
1.6 Using social networks	28
1.7 Study system	30
1.8 Thesis Outline	33
2. THE IMPORTANCE OF FISSION-FUSION SOCIAL GROUP DYNAMICS IN BIRDS	35
2.1 Abstract	36
2.2 Introduction	37

2.2 The Social Environment and Fission–Fusion Dynamics	42
2.2.1 Stochastic fission–fusion	42
2.2.2 Long-term stable associations	43
2.2.3 Kinship	45
2.2.4 Phenotypic assortment	47
2.3 The Ecological Environment and Fission–Fusion Dynamics	49
2.3.1 Spatial variation in the environment	50
2.3.2 Temporal variation in the environment	50
2.3.3 Unpredictable events	54
2.4 Researching Fission–Fusion Dynamics in Birds	54
2.4.1 Using social networks	55
2.4.2 Migration and spatio-temporal variation in social dynamics	56
2.4.3 Using experiments to understand avian social dynamics	57
2.4.4 Observational studies and the investigation of large-scale natural systems	58
2.4.5 Collective behaviour and avian social dynamics	59
2.5 Anthropogenic Impacts on Fission–Fusion Dynamics	60
2.6 Conclusions	61
3. THE CONSEQUENCES OF UNIDENTIFIABLE INDIVIDUALS FOR THE ANALYSIS OF AN ANIMAL SOCIAL NETWORK	63
3.1 Abstract	64
3.2 Introduction	65
3.3 Methods	71
Generation of population	71
Generation of social groups	72
Construction of social networks	73
Definition of identifiable individuals	74
Calculation of network metrics	75
Statistical analysis	75

3.4 Results	76
Precision	76
2. Accuracy	80
3. Bias	81
3.4 Discussion	84
Accuracy of individual-level metrics	85
Precision of individual-level metrics	85
Individual-level metrics in small partial networks	86
Applications and further work	89
Conclusions	90
4. THE EFFECTS OF CORRECTING FOR GROUP SIZE DURING SOCIAL NETWORK CONSTRUCTION	91
4.1 Abstract	92
4.2 Introduction	93
4.3 Methods	97
Within Flock Simulations	97
Population-level Simulations	99
Statistical Analysis	105
4.4 Results	106
Within Flock Simulations	106
Population-level Simulations	109
4.5 Discussion	120
Using group size corrections for natural systems	122
The effect of metric choice	122
Preferred associations and alliances	124
Epidemiological networks	125
Information transfer	126
A better understanding of within group dynamics	127

5. SOCIAL AND SPATIAL EXPLANATIONS FOR DYNAMIC SOCIAL INTERACTIONS IN A MIGRATORY WILDFOWL POPULATION	129
5.1 Abstract	130
5.2 Introduction	131
5.3 Methods	135
Study system	135
Data collection	136
Spatial analysis	137
Social network analysis	138
Construction of null networks	141
Statistical analysis	142
5.4 Results	145
5.5 Discussion	158
Individual social strategies in a dynamic fission-fusion social system	160
The consequences of fission-fusion sociality in the context of migration	162
Conclusions	163
6. FAMILIARITY BREEDS CONTENT: THE IMPORTANCE OF SOCIAL CONTEXT IN EXPLAINING GROUP FORAGING BEHAVIOUR	165
6.1 Abstract	166
6.2 Introduction	167
6.3 Methods	171
Study system	171
Social network analysis	171
Behavioural Data Collection	173
Statistical Analysis	175
6.4 Results	178
What makes aggression more likely?	178

What influences the amount of time individuals spending in aggressive interactions?	178
What influences the proportion of time individuals spend vigilant?	181
Does this have knock-on implications for foraging success?	185
6.5 Discussion	187
Stable social associations, dominance hierarchies and reduced aggression	187
Aggression and social monitoring	188
Social associations and reduced social vigilance	190
The social environment, individual time-budgets and fitness	191
Conclusions	193
7. SOCIAL NETWORK POSITION AND BODY CONDITION IN A HIGHLY DYNAMIC FISSION-FUSION SOCIAL SYSTEM	195
7.1 Abstract	196
7.2 Introduction	197
7.3 Methods	201
Study system	201
Data collection	202
Social network analysis	203
Construction of null networks	203
Spatial analysis	204
Statistical analysis	205
7.4 Results	207
7.5 Discussion	218
Social status and social network position	219
Social network position and foraging success	221
Statistical approaches to network analysis	223
Conclusions	224
8. GENERAL DISCUSSION	225
8.1 Overview	226

8.2 Using association-based social networks in natural systems	226
8.3 Fission-fusion dynamics in a migratory species	229
8.4 Space use, repeated interactions and stable social hierarchies	231
8.5 The individual in a complex social world	234
8.6 Concluding remarks	236
REFERENCES	238

List of tables

Table 2.1. Examples of research into avian sociality	41
Table 3.1. Details of the five key network metrics used in Chapter 3	69
Table 3.2. Reliability of network metrics in partial networks of two different sizes	78
Table 3.3. Bias in metric estimates in partial networks of two different sizes	83
Table 4.1. The parameterisation of potential group size corrections applied in Chapter 4	101
Table 4.2. A summary of the key qualitative results for population-level simulations by correction type	119
Table 5.1. Sample sizes for social network construction and home range area calculations	138
Table 5.2. Details of the key network metrics used in Chapter 5 and what they measure at an individual and population level	140
Table 5.3. A summary of the relationship between individual utilisation distributions and social association strength in the six staging periods studied	149
Table 5.4. Descriptive network-level statistics for five of the networks investigated	154
Table 6.1. Explanatory variables used in mixed models in Chapter 6, how they were used in the models and the reasons for their inclusion	177
Table 6.2. Explanatory variables present in the top model set for the four behavioural models constructed in Chapter 6, the importance of the models they are contained in and the estimate	180
Table 7.1. The effect size of sex, social status and number of resightings on social network position in observed and randomised networks	209
Table 7.2. The model estimates and associated standard errors for terms not containing social network information in a linear mixed-effects model for API scores	214
Table 7.3. Summary of model estimates for the effect of network metrics and interactions containing network metrics on departure body condition in the observed network and randomised networks	215
Table 7.4. Summary of model estimates for the effect of network metrics and interactions containing network metrics on daily rate of change in body condition in the observed network and randomised networks	216

List of figures

Figure 1.1. Considering some implications of dynamic social systems on ecology	25
Figure 1.2. A proposed relationship for the link between social structure in staging populations and fitness in light-bellied brent geese	32
Figure 2.1. The social network structure of different social systems	38
Figure 3.1. Group size distributions for observed and simulated data	69
Figure 3.2. The proportion of juveniles in observed and simulated populations	70
Figure 3.3. Family sizes in observed and simulated populations	72
Figure 3.4. The relationship between partial network size and metric reliability in simulated populations	77
Figure 3.5. The relationship between partial network size and metric accuracy in simulated populations	82
Figure 4.1. The relationship between group size and association strength for four potential group size corrections	102
Figure 4.2. A comparison of negative exponential and inverse corrections	102
Figure 4.3. The effect of the relationship between group density and group size on the probability of two individuals interacting in a group	107
Figure 4.4. The effect of inter-individual interaction distances on the probability of individuals interacting in groups of different sizes	108
Figure 4.5. The relationship between the probability of two individuals interacting and group size in groups of highly mobile foragers	109
Figure 4.6. The effect of applying different group size corrections on the mean of four key network metrics	110
Figure 4.7. The effect of applying different group size corrections on the coefficient of variation of four key network metrics	111
Figure 4.8. The regression slope for the relationship between values of individual network metrics when different group size corrections are used	115
Figure 4.9. The strength of correlation between values of individual network metrics when different group size corrections are used	116
Figure 5.1. A typical social network from a light-bellied brent goose staging population	146
Figure 5.2. A comparison of network-level metrics in observed and randomised networks	147
Figure 5.3. The relationship between association strength in intertidal and terrestrial networks during winter staging	151

Figure 5.4. Changes in associations between intertidal and late winter networks	152
Figure 5.5. The relationship between association strength during late winter and spring networks for individuals recorded in both study areas in 2012	155
Figure 5.6. Inter-annual social community dynamics in observed and randomised networks	157
Figure 6.1. An illustration of scores of aggression intensity in light-bellied geese	174
Figure 6.2. The relationship between mean aggression intensity and the proportion of time spent in agonistic interactions in foraging light-bellied brent geese	179
Figure 6.3. The relationship between the proportion of time an individual spends vigilant and the amount of aggression it receives in light-bellied brent geese	182
Figure 6.4. The relationship between vigilance rate and the mean individual-level association strength in flocks of light-bellied brent geese varying in mean flock-level association strength	183
Figure 6.5. The relationship between mean flock-level association strength and the proportion of time an individual spends vigilant for light-bellied brent geese varying in social strategy	184
Figure 6.6. The relationship between within flock association strengths and time spent foraging in light-bellied brent geese	186
Figure 7.1. The relationship between social status and utilisation distribution area	210
Figure 7.2. The relationship between social status and betweenness	210
Figure 7.3. The effect of social status on API scores in spring staging light-bellied brent geese	212
Figure 7.4. The effect of sex on API scores in spring staging light-bellied brent geese	213
Figure 7.5. A comparison of the effect of mean association strength on body condition during spring staging in the observed and randomised networks	217
Figure 8.1. A framework for a better understanding of the relationship between conditional traits and social network position for individuals in a fission-fusion social system	234

Author's declaration

During the research contributing to this thesis MJS was supported by a FERA seedcorn grant awarded to Stuart Bearhop, and the University of Exeter. Simulation-modelling work was completed by MJS with the initial help of Andrew Jackson (Trinity College, Dublin). All statistical analysis was completed by MJS with some input from Stuart Bearhop, Darren Croft, Ian Cleasby and David Fisher. All chapters in this thesis were written by MJS, with Stuart Bearhop, Tom Tregenza, Darren Croft, Andrew Jackson and David Fisher commenting on initial drafts.

Data used in spatial and social network analysis were collected by MJS (with the assistance of many people mentioned in the acknowledgements) and taken from the Irish Brent Goose Research Group resightings database. Behavioural observations were conducted by MJS with the assistance of Richard Price, Stephen Lang, Edward Burrell, Anthony Schultz, Tom Bodey and Rafael Matias.

With these exceptions, I declare that the work contained in this thesis is my own and has not been submitted for any other degree or award.

Chapter 2

Silk M.J., Croft D.P., Tregenza T. and Bearhop S. The importance of fission-fusion social group dynamics in birds. *Ibis*, **156**, 701-715.

Chapter 3

Silk M.J., Jackson A.L., Croft D.P., Colhoun K. and Bearhop S. The consequences of unidentifiable individuals for the analysis of an animal social network. *Submitted to Animal Behaviour*.

Chapter 4

Silk M.J., Croft D.P., Jackson A.L. and Bearhop S. Correcting for group size in the construction of animal social networks. *In preparation for submission to Behavioural Ecology and sociobiology*.

1. General Introduction



1.1 Living in groups: how animal sociality really works

Many animals live in groups. Understanding the costs and benefits of living in groups has been a major focus of behavioural ecology research for many years (Krause & Ruxton 2002). However, it is in recent years that major progress has been made in exploring the true complexity of this phenomenon. Historically, the concept of sociality was rather static. A lot of work focussed on identifying optimum group sizes, the number of individuals at which the benefits of being a member of the group were outweighed by the costs (Brown 1982; Pulliam & Caraco 1984; Rasa 1989; Williams, Lutz & Applegate 2003), and evolutionarily stable group sizes (Pulliam & Caraco 1984; Parrish & Edelstein-Keshet 1999), where the benefits obtained by an individual joining a group are outweighed by the costs of joining it (Parrish & Edelstein-Keshet 1999). However, the costs and benefits of sociality are unlikely to remain similar through space and time. This means that grouping behaviour is often highly spatiotemporally dynamic (Couzin 2006; Aureli *et al.* 2008; Couzin & Laidre 2009; Sueur *et al.* 2011b), and results in the vast majority of animal social systems displaying some of form fission-fusion dynamics (Aureli *et al.* 2008; Sueur *et al.* 2011b), in which groups frequently split up and join together. Dynamic social systems have numerous implications for population-level processes (disease: Hamede *et al.* 2009, information transfer: Aplin *et al.* 2012; Claidiere *et al.* 2013; Webster *et al.* 2013) and individual strategies (Croft *et al.* 2006; McDonald 2007; Oh & Badyaev 2010; Aplin *et al.* 2012; Aplin *et al.* 2013; Wey *et al.* 2013), and therefore have a major impact on social evolution (Connor *et al.* 1998; Couzin 2006).

1.2 The evolution of fission-fusion social systems

Dynamic social systems will evolve when there is temporal or spatial variability in the environment (Sueur *et al.* 2011b). This drives changes in the relative costs and benefits of grouping and alters the social decisions that individual animals make. For animals in social groups or aggregations there is a consensus cost associated with maintaining cohesion with a group (Conradt & Roper 2000; Conradt & Roper 2005). This occurs as a consequence of an individual having to behave differently to how it would in a non-social context (and thus not maximise its energy intake) in order to behave synchronously and remain within a group if other individuals in the group have different requirements (Conradt & Roper 2000; Calhim, Shi & Dunbar 2006; Michelena *et al.* 2006). When the costs of maintaining cohesion exceed the benefits then individuals may leave the group or the group may fragment; a fission event. Fission of a larger group into a number of subgroups is especially likely when there are multiple individuals in a group sharing a characteristic that increases the relative benefit or reduces the relative cost of interacting with other similar individuals. These social factors can include kinship, phenotypic similarities or advantages related to familiarity or repeated interactions.

Fission-fusion dynamics will occur when environmental variability favours a flexible strategy. For example, spatial variation in the environment is likely to lead to the evolution of fission-fusion social systems (Sueur *et al.* 2011b). However, if levels of spatial variability are too high then groups or subgroups may segregate completely along environmental gradients (e.g. Conradt, Clutton-Brock & Guinness 2000) and changes in social associations will be infrequent. This means that fission-fusion dynamics are most likely to evolve at intermediate levels of environmental heterogeneity (Sueur *et al.* 2011b), an idea

that is beginning to receive some theoretical (Hancock, Milner-Gulland & Keeling 2006; Ramos-Fernández, Boyer & Gómez 2006) and empirical (Chapman, Chapman & Wrangham 1995; Lehmann, Korstjens & Dunbar 2007; Fortin *et al.* 2009; Bercovitch & Berry 2010; Cortes-Avizanda *et al.* 2011) support. Temporal heterogeneity in the environment will also promote fission-fusion dynamics, and again understanding its influence on social decision-making is key to understanding how fission-fusion will occur. Predictable temporal changes to the environment are more likely to result in the evolution of flexible social strategies, as when temporal changes are unpredictable the costs of leaving a group become larger and the benefits of using social information increase, increasing the benefits of maintaining cohesion (Sueur *et al.* 2011b). This means that fission-fusion dynamics commonly occur across cycles, whether they be seasonal (Bos, Van De Koppel & Weissing 2004; Wittemyer, Douglas-Hamilton & Getz 2005; Amano *et al.* 2006), diel (Ratchford & Eggleston 2000; Kerth, Ebert & Schmidtke 2006; Kerth 2010; Kerth, Perony & Schweitzer 2011) or tidal (Fleischer 1983; Inger *et al.* 2006a; Beauchamp 2010).

1.3 The evolution and development of social structure in fission-fusion societies

Fission-fusion social systems frequently generate population social structures in which patterns of associations are not random (Croft *et al.* 2005; Pike *et al.* 2008; Carter *et al.* 2009; Croft *et al.* 2009; Aplin *et al.* 2012; Mourier, Vercelloni & Planes 2012; Aplin *et al.* 2013; Carter *et al.* 2013). These social structures can arise for numerous reasons, and teasing apart how these

societies are structured is a vital step in understanding the social and ecological mechanisms that drive fission and fusion in the first place. Determining the scale over which interactions occur is a key step. Spatial constraints are often an important driving force in determining who interacts with whom in dynamic social systems (Mourier, Vercelloni & Planes 2012; Carter *et al.* 2013; Garroway, Bowman & Wilson 2013; Shizuka *et al.* 2014). Space and social interactions are closely interlinked, and in species that are highly site faithful, may be difficult to distinguish. After all, an individual may use an area because of the individuals it interacts with in that area, or interact with individuals because they share the areas it uses. Therefore, in cases where animals live in fission-fusion societies and exploit limited home ranges, shared utilisation distributions are likely to be important factors influencing social associations (Mourier, Vercelloni & Planes 2012; Shizuka *et al.* 2014). Fission-fusion social structures will further develop to be non-random in situations where there are benefits to be obtained from interacting repeatedly with the same individuals. Genetic (Wolf & Trillmich 2008; Carter *et al.* 2013) or phenotypic similarities (Croft *et al.* 2005) are likely to be of key importance in this process, but it is possible for these advantages to accrue solely as a function of increased familiarity. It is the latter of these mechanisms that is the primary motivation for much of this work.

1.4 Repeated interactions, familiarity and cooperation

Even when individuals are not related or assorted by phenotypic differences there can be considerable benefits of interacting repeatedly with the same individuals that could drive the development of non-random social structures. It has been demonstrated theoretically that both direct (van Veelen

et al. 2012) and generalised (van Doorn & Taborsky 2012) reciprocity are more likely to evolve in non-random social structures. van Veelen *et al.* (2012) showed that, even within systems where social interactions were fairly fluid, some population structure could favour the evolution of direct reciprocity. Whilst the importance and prevalence of direct reciprocity in non-human animals remains unresolved (Clutton-Brock 2009), this work does suggest that any mechanism that imposes social assortment could promote cooperative behaviour or increase other benefits associated with having interacted previously with other group members.

Increased familiarity will influence a wide range of social behaviours in a large diversity of species (Griffiths *et al.* 2004; Kavaliers, Colwell & Choleris 2005; Carter *et al.* 2009; Gaynor & Cords 2012; Kurvers *et al.* 2013), in particular being likely to increase the efficiency of social foraging (Griffiths *et al.* 2004) by reducing levels of aggression (Johnsson 1997; Utne-Palm & Hart 2000) and vigilance (Carter *et al.* 2009; MacIntosh & Sicotte 2009; Gaynor & Cords 2012). A key mechanism for reduced aggression in populations where repeated interactions are frequent is the formation of dominance hierarchies (Hsu, Earley & Wolf 2006). These have been widely studied in systems with highly structured patterns of social interactions (e.g. Frank 1986; Bergman *et al.* 2003), but the extent to which they can persist and the magnitude of their influence on behaviour when social interactions are more fluid has received little empirical attention. Even small changes in the social behaviour of individuals could result in substantial effects of familiarity on individual time budgets due to the way these changes in social behaviour are likely to scale-up to collective group-level patterns (Marshall *et al.* 2012). It is only after considering the social

context of these changes and their impact on collective behaviour that the full extent of differences on individual time budgets can be appreciated.

1.5 Consequences of social structure in fission-fusion societies

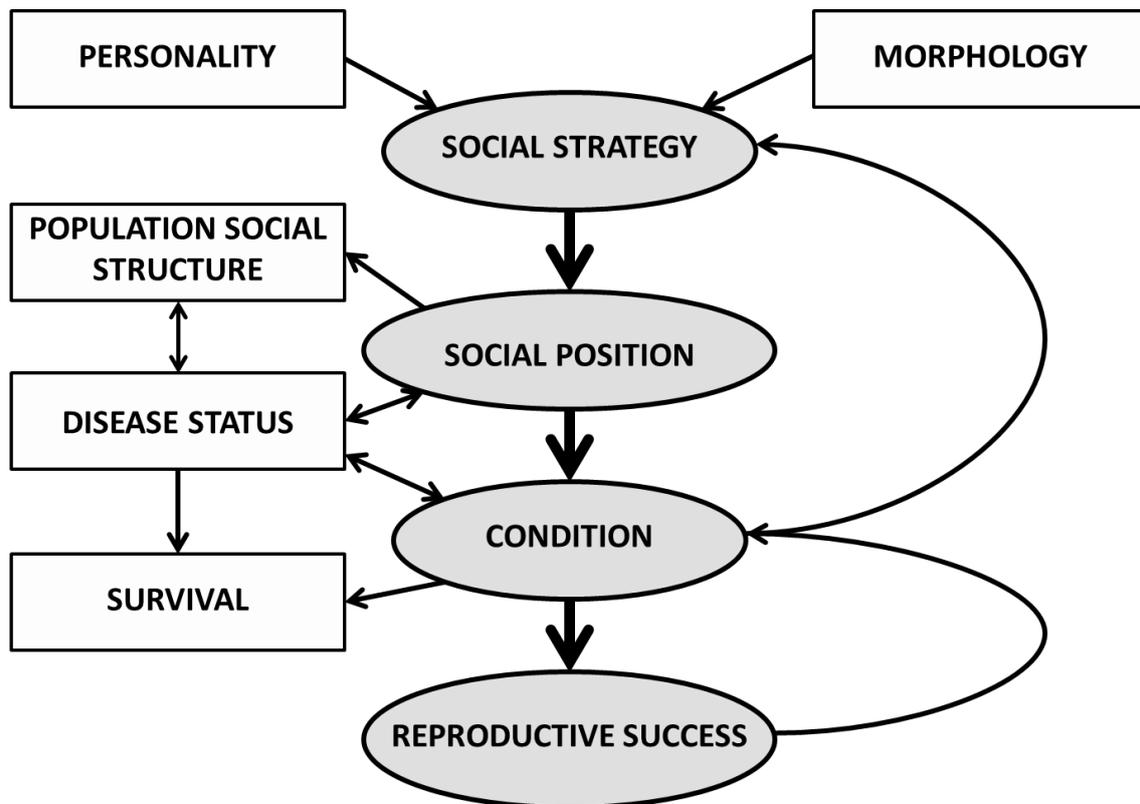


Figure 1.1. Considering some implications of dynamic social systems on ecology

The causes and (some examples of) effects of social network position in animals. The flow chart demonstrates the complex, dynamic nature of individual social network position and its relationship to both fixed (personality and morphology) and conditional (body condition and reproductive success) individual traits.

1.5.1 Individual-level effects of fission-fusion dynamics

Understanding social structure and variation in individual strategies within specific fission-fusion social systems will be critical to understanding the impact they have (Fig. 1.1). Phenotypic variation between individuals, especially in behavioural (personality) traits, will result in variation in the optimal social strategy for an individual. For example, bold and shy domestic sheep *Ovis aries* have been found to differ in their grouping preferences (Michelena *et al.* 2010). Furthermore, social strategy in a fission-fusion social system is a plastic trait by definition. This means individual social strategies are likely to be temporally dynamic as a function of their status or condition (Weber *et al.* 2013; Goldenberg *et al.* 2014), or in response to changes in the ecological environment (Fortin *et al.* 2009; Bercovitch & Berry 2010; Cortes-Avizanda *et al.* 2011). However, despite this, at an individual-level variation in social strategy is likely to be closely tied to reproductive success (McDonald 2007; Formica *et al.* 2012; Wey *et al.* 2013). This relationship is anticipated to be both causative and consequential. Individuals that are more successful or have higher social status can be more selective in the social associations they form and are less likely to have their social interactions imposed upon them. Being able to be more selective with social associations will result in more of the benefits discussed in the previous sections being accrued, with positive effects on fitness and survival expected to occur as a result.

1.5.2 Population-level consequences of fission-fusion

dynamics

The social structure of fission-fusion social systems will also have an important effect at a population level, especially on information transfer and epidemiology (Fig. 1.1). The diffusion of social information through a population will depend on the social structure of that population (Claidiere *et al.* 2013), with the likelihood of individuals obtaining that information linked to their position in that social structure (Aplin *et al.* 2012; Claidiere *et al.* 2013). Understanding information transfer in this way could have important implications in understanding the spread of particular behaviours through a population (Franz & Nunn 2009; Claidiere *et al.* 2013; Webster *et al.* 2013; Boogert *et al.* 2014). This knowledge might be particularly beneficial in cases when these new behaviours result in human-wildlife conflict. For example, in bottlenose dolphins *Tursiops aduncus* individuals were more likely to begin accepting food hand-outs, a potentially harmful behaviour, if they associated more frequently with individuals that already performed this behaviour (Donaldson *et al.* 2012).

Knowledge of the spatiotemporal dynamics of social structure is also likely to be greatly beneficial in understanding how parasites and pathogens might spread through a population (Hamede *et al.* 2009; Craft *et al.* 2011; Danon *et al.* 2011; Bull, Godfrey & Gordon 2012). In this case, being able to predict the effects of social structure at any one time and how this social structure changes across time will both be of utmost importance. Hamede *et al.* (2009) demonstrated the value of understanding patterns of social interactions in understanding patterns of disease spread by using social contact networks to explain the spread of devil facial tumour disease in Tasmanian devils *Sarcophilus harrisii*. In this example, this knowledge was used to highlight

conservation issues as this disease has caused a drastic population decline (McCallum *et al.* 2009). However, this is not the only possible application of a better understanding of epidemiology in dynamic animal social systems. Disease transfer in animals can lead to major human-wildlife conflicts (Chen *et al.* 2005; Donnelly *et al.* 2005; Woodroffe *et al.* 2006), and work describing how disease and social position covary (Weber *et al.* 2013), and how this may change with different management approaches (Carter *et al.* 2007; McDonald *et al.* 2008; Beeton & McCallum 2011) can be of great value to managing disease in these populations. Additionally, many animal populations are important vectors of zoonotic diseases and a better knowledge of temporal dynamics of social structure in these species would contribute to an understanding of how they will influence the global spread of these diseases. A prime example is the case of avian influenza. Wildfowl species are considered key vectors of this virus (Chen *et al.* 2005; Hoyer *et al.* 2011; Dijk *et al.* 2014), and as many possess highly dynamic fission-fusion social systems and are migratory over long distances, an improved understanding of the dynamics of their social system across the annual cycle is imperative.

1.6 Using social networks

Social networks provide an invaluable tool in describing social structure in animal populations, and quantifying the social position or strategy of individuals within these social systems (Croft, James & Krause 2008; Wey *et al.* 2008; Sih, Hanser & McHugh 2009). Social networks are now widely used for socio-ecological research in animals, especially those with dynamic social systems (Connor, Heithaus & Barre 2001; Croft *et al.* 2005; Aplin *et al.* 2012;

De Silva & Wittemyer 2012; Farine, Garroway & Sheldon 2012; Mourier, Vercelloni & Planes 2012; Shizuka *et al.* 2014). A social network is a graph in which nodes represent individuals, and nodes are connected by edges (lines) if individuals are observed to have interacted or associated. Whilst some social networks are based on direct observations of interactions (Madden *et al.* 2009; Madden *et al.* 2011; Dey *et al.* 2013; Tóth *et al.* 2014), the majority of animal social networks are association-based and use the gambit of the group assumption (Whitehead & Dufault 1999; Croft, James & Krause 2008). Gambit of the group assumes that meaningful social relationships can be deduced from observations of spatiotemporal co-occurrence. Networks can be binary (either individuals are connected or not), but frequently edges are weighted by the strength or frequency of interactions between individuals. Weighted networks tend to be preferred as they carry more information about the social interactions that have occurred (Franks, Ruxton & James 2010; Farine 2014), but have previously been more complex to analyse (Croft, James & Krause 2008).

Social network analysis (SNA) can be used to quantify either network-level properties that describe social structure at a population level, or node-level measures that describe the social position of a given individual. At an individual level network metrics can describe the centrality of a node to a network (degree: Bonacich 1972, eigenvector centrality: Bonacich 1987; Bonacich 1991, betweenness: Freeman 1977), properties of the connections it forms (coefficient of variation in degree, mean association strength: Barrat *et al.* 2004) or how clustered it is in the network (measures of local transitivity: Watts & Strogatz 1998). Combined, these metrics can provide a very detailed picture of an individual's social position. The mean and variance of many of these metrics can also be used to describe the structure of the network as a whole.

Additionally, the density of edges, average path length (Wey *et al.* 2008) or various algorithms that can detect cliques or communities within the network (e.g. Girvan & Newman 2002; Newman & Girvan 2004) can also help describe the social structure of a population.

With careful analysis, taking into account the non-independence of individuals co-occurring in networks, node-level metrics can be especially useful descriptors of the social strategy an individual uses. This makes it possible to correlate individual social strategies with social status (Madden *et al.* 2011), age (Wey & Blumstein 2010; Madden *et al.* 2011), sex (Wolf *et al.* 2007), personality (Croft *et al.* 2009; Aplin *et al.* 2013; Wilson *et al.* 2013) and reproductive success (Formica *et al.* 2012; Wey *et al.* 2013) to better understand how and why individuals vary in these strategies. Meanwhile network-level measures allow us to develop an understanding of how different fission-fusion social systems are structured, and how this in itself may influence how information is used, how disease is transferred or why particular social strategies arise in the first place. The rapid progress being made in the study of dynamic social systems would not be possible without SNA.

1.7 Study system

This research was completed on a long-term study population of light-bellied brent geese *Branta bernicla hrota*. The East Canadian High Arctic (ECHA) population of this species breeds in the Canadian arctic, with its breeding range centred on Ellesmere, Axel Heiberg, Bathurst and Devon Islands (Robinson *et al.* 2004). The entire population undertakes a transatlantic migration in August/September and May/June, spending the winter around the

coasts of Western Europe. Whilst there are small wintering populations in Normandy, the Channel Islands and scattered up the west coast of Great Britain, the vast majority of the population winters around the coast of Ireland. During migration periods birds stage on the west coast of Iceland between the Reykjanes Peninsula and Breiðafjörður. These staging areas are particularly important in spring when they are used for a period of 3 - 6 weeks in late April and May.

The species is coastal and historically fed almost exclusively on marine resources (Robinson *et al.* 2004). However, in many parts of its wintering range individuals now feed on these intertidal areas in the autumn and early winter, before moving on to terrestrial grasslands when these resources are exhausted. Light-bellied brent geese are highly social foragers during winter and spring staging and roost communally, forming a highly dynamic fission-fusion social system. The annual cycle of this population is highly time constrained, and foraging behaviour during winter and spring staging is of vital importance in determining reproductive success through carry-over effects (Inger *et al.* 2010). Furthermore, individual site use is culturally inherited and individuals are highly site faithful (Harrison *et al.* 2010). Together, these aspects of this species' ecology are likely to make the social context of an individual's behaviour during these periods highly important (Fig. 1.2).

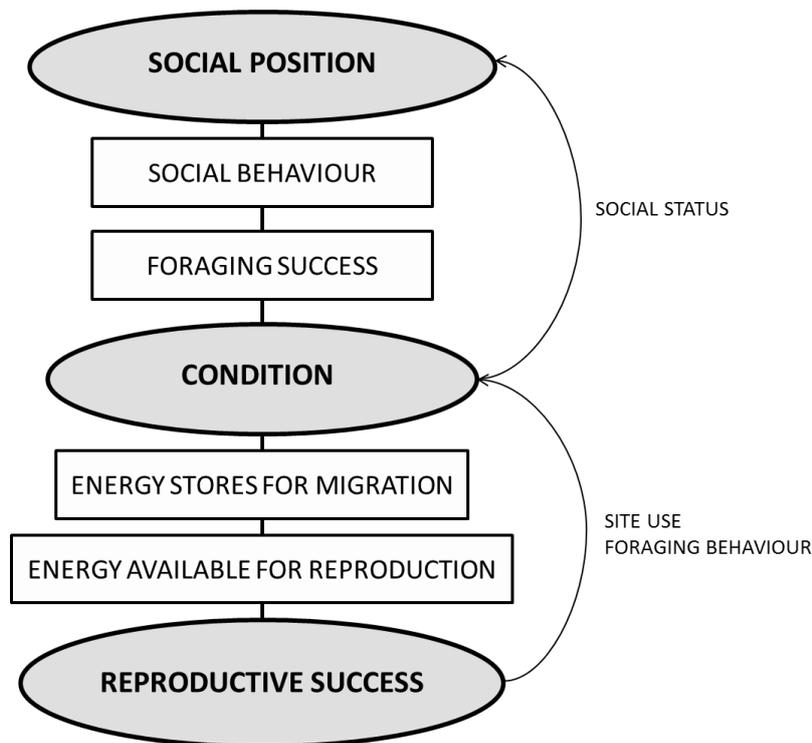


Figure 1.2. A proposed relationship for the link between social structure in staging populations and fitness in light-bellied brent geese

Social network position is predicted to influence individual reproductive success by being an important mediator of social behaviour in foraging groups. The species is a capital breeder and links between body condition during non-breeding periods and reproductive success has already been established (Inger *et al.* 2010). Reproductive status (dominance) and condition are predicted to feedback on social network position in these populations.

The two study populations used for this project were in Dublin Bay in eastern Ireland during winter staging and on the Álftanes Peninsula in southwest Iceland during spring staging. Both of these areas are key staging sites with populations of several thousand individuals. They contain a high proportion of colour-ringed birds (around 10% of all individuals) relative to other parts of the population, and a high density of volunteer observers to provide additional information to the Irish Brent Goose Research Group (IBGRG) database. In addition feeding sites in these staging areas are well defined and

mapped, facilitating incorporation of information in the resightings database into this research.

1.8 Thesis Outline

The main focus of this thesis is to investigate the causes and consequences of variation in population social structure and individual social strategy in a dynamic fission-fusion social system. Studies of fission-fusion dynamics have been unusual in avian study systems and in Chapter 2 I review the existing evidence for fission-fusion social dynamics in birds, highlighting the social and ecological mechanisms that are likely to be particularly pertinent to avian study systems. The review focuses on the use of social network approaches in avian study populations in further developing our understanding on the processes key in dynamic social systems. Within this, the potential role of migration as a key influence on social dynamics in birds is particularly emphasised.

In Chapters 3 and 4 I use a similar simulation-based approach to test two of the key assumptions made when constructing social networks using association data. Animal social networks constructed using association data often use only a sample of individuals from the population, especially when individuals must be captured to be made identifiable. Our study population presents a clear example of this. In Chapter 3 I use a simulated fission-fusion population parameterised using light-bellied brent geese to explore the consequences of building partial networks from a subsample of the population on the accuracy, reliability and bias of individual network metrics. Chapter 4 focuses instead on the gambit of the group assumption that co-occurrence in a

social group constitutes a meaningful social interaction. Intuitively, the strength of this assumption would be expected to vary with group size, with co-occurrence in a larger group being less likely to indicate that two individuals have interacted. I first use simple models of animals moving in a group to demonstrate how susceptible this relationship is to variation in group density, changes in individual movement and the stability of social groups. I then go on to test the consequences of using corrections designed to control for this effect when constructing social networks in simulated populations parameterised using light-bellied brent goose data.

In Chapter 5 I use social network analysis to investigate the causes and seasonal dynamics of social structure in light-bellied brent geese. The particular focus is on the relative importance of spatial constraints and the social factors additional to this. The inter-annual stability of social structures and changes in social relationships during winter and spring staging are also investigated. Chapter 6 explores the idea that there may be advantages to interacting repeatedly with the same individuals. I investigate social foraging behaviour, asking how familiarity with flock-members, alongside other social and environmental covariates, may influence key aspects of social behaviour that trade-off with foraging success. Chapter 7 returns to a more network-centric approach, but focussed at an individual-level. I attempt to explain differences in social position among individuals before going on to explore the impacts of these differences on body condition during spring staging (and thus fitness). Chapter 8 integrates these ideas to discuss the key aspects of fission-fusion sociality in this study system, and its wider implications for our understanding of the development and evolution of social structure in dynamic social systems more generally.

2. The importance of fission-fusion social group dynamics in birds



2.1 Abstract

Almost all animal social groups show some form of fission–fusion dynamics, whereby group membership is not spatio-temporally stable. These dynamics have major implications at both population and individual levels, exerting an important influence on patterns of social behaviour, information transfer and epidemiology. However, fission–fusion dynamics in birds have received relatively little attention. We review the existing evidence for fission–fusion sociality in birds alongside a more general explanation of the social and ecological processes that may drive fission–fusion dynamics. Through a combination of recent methodological developments and novel technologies with well-established areas of ornithological research, avian systems offer great potential to further our understanding of fission–fusion social systems and the consequences they have at an individual and population level. In particular, investigating the interaction between social structure and environmental covariates can promote a deeper understanding of the evolution of social behaviour and the adaptive value of group living, as well as having important consequences for applied research.

2.2 Introduction

Group living is widespread in animals, including birds (Krause & Ruxton 2002). It can evolve for many reasons, most frequently through the benefits of reduced predation risk or improved foraging success. Animal social groups usually form when the benefits of association exceed the competitive and health costs of existing close to other individuals (Krause & Ruxton 2002). The relative importance of these costs and benefits in driving group dynamics is highly dependent on the environment and the condition or phenotype of a given individual (Conradt & Roper 2000; Fortin *et al.* 2009). This means that sociality is often spatio-temporally dynamic (Lehmann, Korstjens & Dunbar 2007; Sueur *et al.* 2011b), and that highly stable groups are the exception rather than the rule (Jacobs 2010). The extent of changes in group cohesion and composition define the extent of fission–fusion social dynamics in any particular system (Fig. 2.1; Aureli *et al.* 2008).

To benefit from social cohesion, individuals in a group must be able to reach a consensus decision (Conradt & Roper 2005). Fission happens when a full consensus is not reached and either individuals leave groups separately as a result of combined decisions (Conradt & Roper 2005) or larger groups divide into smaller subgroups when only a partial consensus occurs (Couzin 2006). These processes could occur as a result of active decision-making processes, but are more generally a result of individuals following social interaction rules. These rules may include processes of attraction, alignment and repulsion that regulate inter-individual distances without requiring complete knowledge of the global environment (Camazine 2003). They are likely to vary between individuals (Couzin & Krause 2003; Kurvers *et al.* 2010), and to co-vary with the social and ecological environment (Hoare *et al.* 2004). Similar processes will be

important when groups or individuals rejoin during fusion events (e.g. Elgar 1986). Both active decision-making and interaction rules are strongly influenced by a combination of social and environmental factors, making a consideration of the relative costs and benefits during fission and fusion events fundamental to understanding their occurrence.

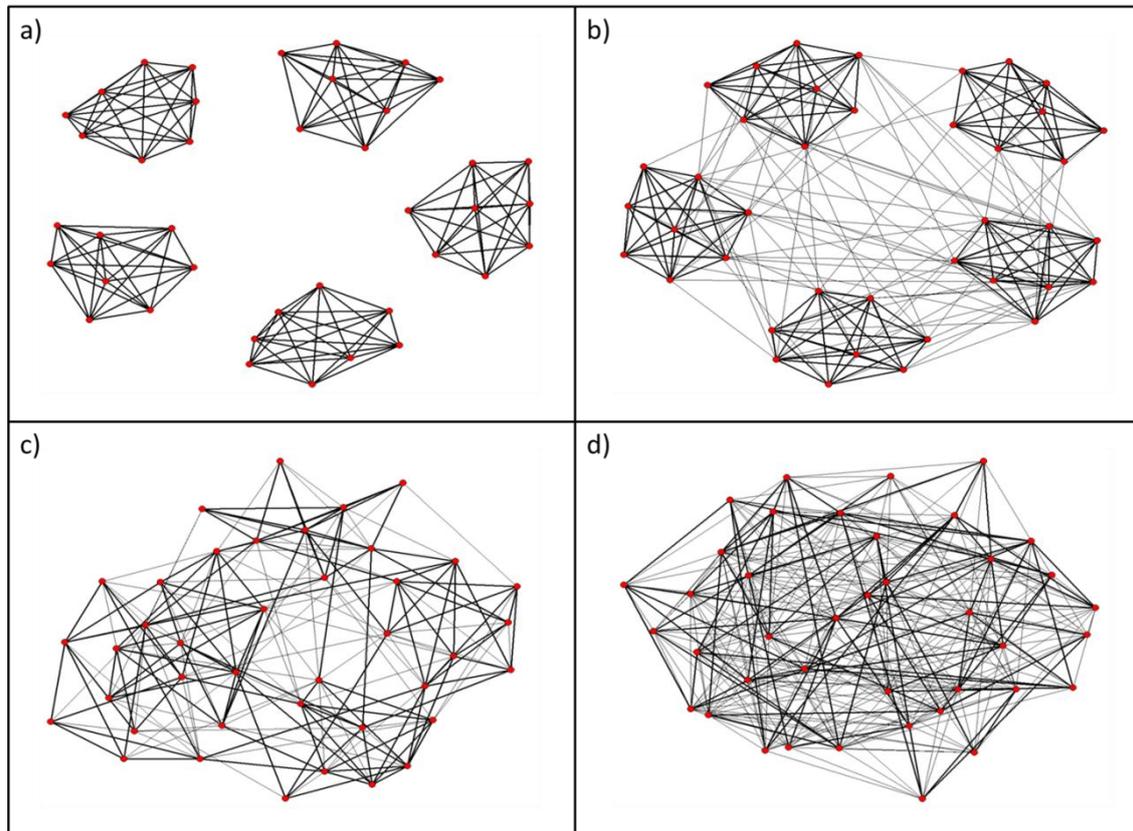


Figure 2.1. The social network structure of different social systems

Social networks for (a) stable social groups with no fission–fusion and very limited movement of individuals between groups; (b) highly structured fission–fusion social system with predictable subgroups formed during fission events; (c) fluid fission–fusion social system with some degree of social preferences driving the underlying structure; (d) highly fluid fission–fusion social system with random social interactions. Thicker lines are representative of stronger social associations.

Fission-fusion dynamics are likely to have important implications for the evolution of social behaviour (Kutsukake 2006; Kerth 2008; Harrison, Sciberras & James 2011; Micheletta *et al.* 2012), information transfer (Sueur *et al.* 2011b; Aplin *et al.* 2012; Claidiere *et al.* 2013) and the spread of parasites (Danon *et al.* 2011; Bull, Godfrey & Gordon 2012). Therefore, considering social interactions in a fission-fusion context is fundamental to generalising our understanding of the ecology, evolution and conservation of social animals. Studying fission-fusion systems improves our understanding of the social and environmental factors that cause social groups to vary in size, and also of how individual differences can influence interaction rules and social decisions.

Fission-fusion dynamics are found in a wide range of species and taxonomic groups (e.g. Guppies *Poecilia reticulata*: Croft *et al.* 2003, bats: Kerth, Ebert & Schmidtke 2006, birds: Aplin *et al.* 2012 and American Bison *Bison bison*: Fortin *et al.* 2009). Ramos-Fernández, Boyer and Gómez (2006) demonstrated that fission-fusion sociality could arise from a relatively simple agent-based foraging model under certain levels of environmental heterogeneity, suggesting that fission-fusion sociality could be taxonomically widespread in animals that experience these environments. There has been a historical focus on social dynamics in highly cognitive species (primates: Chapman, Chapman & Wrangham 1995; Lehmann, Korstjens & Dunbar 2007; Asensio, Korstjens & Aureli 2009; Henzi *et al.* 2009, dolphins: Connor, Heithaus & Barre 2001; Lusseau 2007; Wiszniewski, Allen & Möller 2009, elephants: Wittemyer, Douglas-Hamilton & Getz 2005; Archie, Moss & Alberts 2006). The highly structured fission-fusion dynamics in these systems are likely to be influenced by derived levels of social intelligence, and thus not reflect the full extent of the variability of fission-fusion dynamics more generally. Aureli *et al.*

(2008) suggested considering instability in social dynamics on a complex, multi-dimensional scale, and to do this requires a considerable extension of the social systems investigated.

Given the large amount of bird-focussed socio-ecological research (Table 2.1), it seems likely that avian social systems could contribute greatly to our understanding of fission-fusion dynamics using comparative, observational and experimental approaches with both intra- and inter-specific groups. Recent methodological developments and advances in technology that simplify the collection and analysis of data from large numbers of individuals simultaneously are now making this feasible. We outline the likely social mechanisms (long-term stable associations, kinship and phenotypic assortment) that influence fission and therefore social structure in birds using evidence from studies of birds and of better studied taxonomic groups, the latter being used to guide suggestions for additional work in avian systems. We focus on how these social mechanisms influence fission events, as much of the literature on the social mechanisms contributing to social structure has focussed on this process. We link this to existing evidence for fission-fusion sociality in birds, with the role of the ecological environment in avian fission-fusion dynamics being discussed broadly. Finally we suggest methods for further research into avian fission-fusion social systems using ringing studies, highlighting areas of study that particularly suit avian study systems. We aim to emphasise the great potential for ornithological research to further our knowledge of fission-fusion social dynamics, and consequently our understanding of social evolution, and individual social strategies and decision-making more generally.

Area of research	Selected avian examples	Literature
Anti-predator benefits	Group size and vigilance in many species	reviewed in Beauchamp 2008
Foraging benefits	Barnacle Goose <i>Branta leucopsis</i> Cliff Swallow <i>Hirundo pyrrhonata</i> Common Starling <i>Sturnus vulgaris</i>	Drent & Swierstra 1977 Brown 1988 Templeton & Giraldeau 1996
Thermoregulatory benefits	Long-tailed Tits <i>Aegithalos caudatus</i>	McGowan <i>et al.</i> 2006
Costs	Cliff Swallow <i>Hirundo pyrrhonata</i> finches <i>Fringilla sp.</i> Common Redshank <i>Tringa totanus</i> Common Blackbird <i>Turdus merula</i>	Brown & Brown 1986 Lindström 1989 Cresswell 1994 Cresswell 1998
Intra-group social dynamics	Barnacle Goose <i>Branta leucopsis</i> Scaly-breasted Munia <i>Lonchura punctulata</i>	Black <i>et al.</i> 1992; Kurvers <i>et al.</i> 2009 Flynn & Giraldeau 2001
Collective behaviour	Common Starling <i>Sturnus vulgaris</i>	Ballerini <i>et al.</i> 2008; Cavagna <i>et al.</i> 2010

Table 2.1. Examples of research into avian sociality

2.2 The Social Environment and Fission–Fusion

Dynamics

The individual decisions and social mechanisms that govern patterns of fission-fusion are integral to the social dynamics and structures that occur in these systems (Fig. 2.1). Many key social processes are likely to vary greatly along the gradient from structurally stable (Fig. 2.1b) to highly fluid social systems (Fig. 2.1d), and this may have further consequences for the range of successful individual strategies. Partial consensuses are particularly important in fission-fusion dynamics. For a partial consensus, and thus a fission event, to occur there must be variation in the costs and benefits of forming social associations with other group members. Therefore, although fission could occur stochastically, partial consensuses are typically driven by shared characteristics, including long-term stable associations, kinship and phenotypic assortment. These characteristics can alter interaction rules, influence the probability of activity synchrony between individuals (Conradt 1998; Conradt & Roper 2000) or reduce the costs associated with maintaining social cohesion.

2.2.1 Stochastic fission–fusion

Group fission could arise stochastically with no predictable sub-group composition resulting. This is most likely to occur as a result of social interaction rules, and will be of most significance when variation in the costs and benefits of interacting with different subsets of individuals is limited. It is possible for groups of individuals following basic interaction rules to fragment due to the inherent stochastic nature of these interaction rules and motion, especially when all members of a group are not within each other's radius of attraction or alignment

(Couzin & Krause 2003). This is because individuals outside these zones do not interact with each other directly. As group sizes get larger, more individuals lie outside each other's radius of alignment or attraction and stochasticity increases. Therefore larger groups are more likely to fragment (Couzin & Krause 2003), even in the absence of any substantial changes in social and foraging behaviour in a group.

The concept of subgroup composition being driven by a stochastic process represents a null model against which to compare partial consensus hypotheses. Additionally, stochasticity could have important consequences for population social structure in its own right. There is evidence for random, non-stable social associations in shorebirds (Myers 1983; Conklin & Colwell 2008) resulting in social dynamics that are highly fluid (Fig. 2.1d). Although this is not direct evidence that stochastic fission-fusion occurs, it is suggestive that it may occur frequently in these systems.

2.2.2 Long-term stable associations

There are likely to be specific benefits of interacting repeatedly with the same set of individuals in dynamic social systems. These include the modification of social behaviour due to increased familiarity (Griffiths *et al.* 2004), and co-operative behaviour (Croft *et al.* 2006; Ryder *et al.* 2011), including both direct (van Veelen *et al.* 2012) and generalised (van Doorn & Taborsky 2012) reciprocity.

Familiarity

Work on other taxa has demonstrated that social behaviours influenced by familiarity include aggression (Johnsson 1997; Utne-Palm & Hart 2000), vigilance (Kutsukake 2006; Carter *et al.* 2009; MacIntosh & Sicotte 2009), social learning (Lachlan, Crooks & Laland 1998; Swaney *et al.* 2001; Ward, Hart & Krause 2004; Kavaliers, Colwell & Choleris 2005) and co-operative behaviour (Croft *et al.* 2006; Gilby & Wrangham 2008). This modification of behaviour affects individual time budgets and foraging success (Griffiths *et al.* 2004), altering the benefits of maintaining cohesion with different individuals. This is likely to make group and sub-group composition more predictable and result in a population social structure that deviates from random (Fig. 2.1c). For example, in captive barnacle geese *Branta leucopsis*, mutually familiar individuals associated preferentially, thus generating non-random social networks (Kurvers *et al.* 2013).

However, avian examples of the importance of familiarity in influencing social behaviour in a fission–fusion context are limited. Cristol (1995) found that familiarity with the most dominant individual positively affected an individual's position in a social hierarchy in flocks of dark-eyed juncos *Junco hyemalis* that had recently undergone fusion. Support is also provided by the effect of familiar neighbours on social behaviour and reproductive success in great tits *Parus major* (Grabowska-Zhang, Sheldon & Hinde 2012; Grabowska-Zhang, Wilkin & Sheldon 2012). Although not occurring in a fission-fusion context, this demonstrates that familiarity can alter social behaviour in birds.

Alliances

Alliances are two or more animals behaving so that they encounter resources together and co-operate in competition for these resources with other conspecifics (Connor & Whitehead 2005), and so can be considered a specialised form of long-term stable association. The best examples of alliances in avian social structures are lek-mating systems of manakins (Pipridae) in which alliances between males in courtship displays form the basis of a complex social structure (McDonald 2009; Ryder *et al.* 2011). In corvids, (Fraser & Bugnyar 2012) found evidence of reciprocity of social support in northern ravens *Corvus corax*, with individuals that engaged in affiliative relationships being more successful in competing for food (Braun & Bugnyar 2012). Further work on social structure in corvids would allow fission-fusion dynamics in a highly cognitive bird species to be compared to similarly cognitively advanced mammals (e.g. Connor, Heithaus & Barre 2001; Connor 2007; Lehmann, Korstjens & Dunbar 2007; Asensio, Korstjens & Aureli 2009).

2.2.3 Kinship

Kin structure may be important in driving social interactions (Hatchwell 2010), and thus patterns of fission-fusion. The indirect fitness benefits obtained by interacting with related rather than unrelated individuals are likely to increase the relative benefits of social cohesion, for example by reducing aggression (Gompper, Gittleman & Wayne 1997; Beisner *et al.* 2011) or facilitating social learning (Kavaliers, Colwell & Choleris 2005). This may alter social interaction rules and increase the probability of consensus. For example, Kurvers *et al.* (2013) found preferential assortment with kin in captive barnacle geese using social network analysis (SNA), indicating that individuals were much more likely

to forage in groups with related individuals. Some additional evidence is also available from wild populations. In common eiders *Somateria mollissima*, sub-groups arriving back at the colony were more related to each other than the colony average (McKinnon, Gilchrist & Scribner 2006). This suggests that foraging sub-groups and thus fission-fusion dynamics in this population were partly determined by genetic relatedness. Similarly, in bell miners *Manorina melanophrys*, which have a structured, multi-tiered fission–fusion social system, high levels of kin structure were found in colonies, with coterie of related individuals associating preferentially but often forming flocks with other colony members (Painter *et al.* 2000). Few other studies explicitly link relatedness and fission-fusion dynamics in birds.

Kinship has also been shown to increase within-flock social cohesion in both house sparrows *Passer domesticus* (Tóth *et al.* 2009) and greylag geese *Anser anser* (Frigerio, Weiss & Kotrschal 2001), supporting the theoretical work of Aureli *et al.* (2012), who predicted that inter-individual distances in fission–fusion groups should be influenced by social factors. It seems likely that birds found closer together within a flock would be more likely to maintain cohesion when fission occurs, as levels of social attraction to closer individuals is likely to be higher (Couzin & Krause 2003). However, the only evidence for relatedness directly underlying fission events is from primates, in which kinship and inter-individual distance at the time of fission were important in explaining sub-group composition in rhesus macaques *Macaca mulatta* (Sueur, Petit & Deneubourg 2010). Avian research makes it possible to test further the importance of kinship in fission events in socio-ecologically similar, highly structured fission-fusion social systems such as those likely to be found in corvids (e.g. Braun & Bugnyar

2012; Fraser & Bugnyar 2012) or some co-operative species (Painter *et al.* 2000; Browning *et al.* 2012).

2.2.4 Phenotypic assortment

Phenotypic assortment can affect the probability of a consensus occurring because of a range of benefits of being in groups with similar individuals, of which the best studied are the oddity effect and activity synchrony. Here we focus on activity synchrony, as research into the oddity effect – predator preference for prey that stand out in a group – typically requires group choice experiments (Engeszer, Ryan & Parichy 2004; Wong & Rosenthal 2005; Blakeslee *et al.* 2009; Rodgers, Kelley & Morrell 2010), which are very scarce in birds. If phenotypic assortment is important during fission, then it is likely to be important in determining social structure within a population, as there should be significantly more similarity within rather than between the sub-groups that form. This would also be apparent as a result of increased positive assortativity (Newman 2002) of similar phenotypes within social networks constructed for these populations (e.g. Farine 2014).

Activity synchrony

Differences between individuals will lead to differences in their requirements and behaviour (Conradt 1998). Thus, phenotypic differences between individuals, both morphological and behavioural, can increase the probability of groups fragmenting as a result of differences in social interaction rules between phenotypes (Couzin & Krause 2003), reduced activity synchrony (Conradt 1998; Conradt & Roper 2000; Michelena *et al.* 2006) that increases

the costs of remaining together in a group, and potentially also differences in micro-habitat preferences (Conradt, Clutton-Brock & Guinness 2000; Conradt *et al.* 2001).

The importance of physical phenotypes

Theoretical work modelling movement and interaction rules in groups of fish has demonstrated the importance of differences in physical phenotypes in fission (Couzin & Krause 2003). For example, in models in which groups of fish consisted of two phenotypes differing in swimming speeds, fission occurred more rapidly than when all fish were similar. However, empirical evidence for the importance of activity synchrony in group cohesion of morphologically similar individuals is currently restricted to mammals (Conradt & Roper 2000; Calhim, Shi & Dunbar 2006; Michelena *et al.* 2006). Approaches that relate group size to activity synchrony and the probability of fission events in birds would help to understand the role of these processes. Mixed-species flocks perhaps offer the greatest potential, as differences between species could be seen as representing an extreme case of phenotypic divergence. For example, Farine and Milburn (2013) noted that individuals in mixed-species flocks frequently shifted their individual foraging niches towards those of associates. If future studies were able to quantify the cost of this process, and the effect on the maintenance of activity synchrony, then mixed-species flocks could be fundamental to improving our knowledge of how these processes contribute to fission-fusion dynamics.

The importance of behavioural phenotypes

Personality differences between individuals would also be expected to influence their social decision-making (Michelena *et al.* 2010; Webster & Ward 2011; Wilson *et al.* 2013) or the interaction rules followed by individuals (Michelena *et al.* 2010), and thus patterns of sub-group cohesion. One method available for investigating this is to look for positive assortativity of personalities within a social network. A good example of the potential of this approach is provided by a recent study of great tits, which found that individuals with less exploratory phenotypes were found in less central positions in a network and formed more stable social associations than those that were more exploratory, indicating considerable variation in social strategies (Aplin *et al.* 2013).

2.3 The Ecological Environment and Fission–Fusion

Dynamics

Sueur *et al.* (2011b) suggested that fission-fusion dynamics are most likely to evolve in systems with intermediate spatial variability and predictable temporal variability in the environment. Although little studied, there is evidence that fission-fusion dynamics occur in birds. More generally, some life-history traits of birds, such as colonial nesting (Rolland, Danchin & Fraipont 1998), communal roosting (Beauchamp 1999) and the formation of moulting ‘superflocks’ (e.g. Fox & Salmon 1994) will inherently lead to fission-fusion social dynamics at different timescales.

2.3.1 Spatial variation in the environment

The predictions of Sueur *et al.* (2011b) about how spatial variation in the environment influences social dynamics are supported by theoretical (Hancock, Milner-Gulland & Keeling 2006; Ramos-Fernández, Boyer & Gómez 2006) and empirical work on mammals (Chapman, Chapman & Wrangham 1995; Lehmann, Korstjens & Dunbar 2007; Fortin *et al.* 2009; Bercovitch & Berry 2010), which finds that patchy environments are important in driving fission-fusion dynamics. Birds frequently occupy large home-ranges and many species are migratory, offering suitable study systems through which to expand on our understanding of the role of the spatial heterogeneity in the environment. A good example is provided by the effect of resource availability on aggregative behaviour in black kites *Milvus migrans* and Egyptian vultures *Neophron percnopterus* (Cortes-Avizanda *et al.* 2011). Both species are migratory scavengers, breeding in Europe and moving to the Sahel during winter. In Europe, food resources are scarce, resulting in aggregations of individuals, whereas in the Sahel, carcasses are widely available and aggregative behaviour is highly unusual. Thus, only where there is spatial variability in the environment does fission-fusion occur.

2.3.2 Temporal variation in the environment

Although spatial variability in the ecological environment can be important, temporal heterogeneity is the principal factor driving the occurrence of fission-fusion in most systems. In avian systems, variation in the environment across seasonal, diel and tidal cycles is most important in generating fission-fusion dynamics.

Seasonal cycles

Seasonality in social dynamics is widespread in birds (Helm, Piersma & Van der Jeugd 2006). Resource availability is one of the most important factors limiting group size (Krause & Ruxton 2002) and in many systems it varies predictably, with climatic shifts between seasons providing the required conditions for the evolution and occurrence of fission-fusion dynamics (Sueur *et al.* 2011b). For example, in dark-bellied brent geese *Branta bernicla bernicla* flock sizes increase as spring progresses, reflecting a seasonal increase in primary productivity, and resulting in increased benefits to foraging in larger groups due to improved grazing efficiency in shorter swards (Bos, Van De Koppel & Weissing 2004). In contrast, in greater white-fronted geese *Anser albifrons*, flock sizes decrease during winter staging as resource depletion results in increased competition for resources (Amano *et al.* 2006). Differences in resource availability will also cause switches in resource exploitation, and this may also be expected to result in fission-fusion dynamics. For example, Japanese cormorants *Phalacrocorax capillatus* form larger groups when foraging on ephemeral epipelagic prey than when foraging inshore on benthic prey (Watanuki *et al.* 2004). Evidently differences in resource exploitation have major implications for avian sociality, and therefore seasonal instability in group sizes should be widespread.

Life-history constraints, particularly moulting behaviour and reproductive strategy, can also be fundamental in driving seasonal fission-fusion dynamics. Some of the most spectacular examples across an annual cycle occur in colonial breeding species, especially seabirds, in which large aggregations occur during the breeding season, but individuals are often dispersed and much

less social at other times of year (Haney, Fristrup & Lee 1992). Seasonality of social behaviour also occurs in passerines, although typically these species are more social during the non-breeding season (Morse 1970; Griesser *et al.* 2009; Browning *et al.* 2012). For example, in co-operatively breeding apostlebirds *Struthidea cinerea* and chestnut-crowned babblers *Pomatostomus ruficeps*, non-breeding flocks are larger and formed of several co-operatively breeding units (Griesser *et al.* 2009; Browning *et al.* 2012), resulting in fission-fusion social dynamics across an annual cycle. Moulting often leads to increased aggregation in many bird species, especially waterbirds (Geldenhuys 1981; Fox & Salmon 1994), also resulting in considerable seasonal variation in social dynamics. This could be of significance when considering social interactions on a large spatial scale, and may be a vital consideration in understanding disease dynamics in these systems. In a similar way it might be important to consider the impact of migration on social dynamics, as this will be another life-history trait that influences social dynamics across an annual cycle (e.g. Cortes-Avizanda *et al.* 2011). All of these life-history constraints alter the costs and benefits of interacting with other individuals and are thus fundamental in driving fission-fusion dynamics across larger temporal scales.

Diel cycles

Variation in the ecological environment across a diel cycle leads to differences in predator and prey communities over the course of a day, resulting in changes to foraging–predation risk trade-offs and thus behaviour (Lima & Bednekoff 1999; Sih, Ziemba & Harding 2000), including grouping decisions (Creel & Winnie Jr 2005). Fission-fusion dynamics of communal roosting are well documented in bats (Vonhof, Whitehead & Fenton 2004; Popa-Lisseanu *et*

al. 2008; Kerth, Perony & Schweitzer 2011) and spiny lobsters (Ratchford & Eggleston 2000), and as communal roosting is widespread in birds (Beauchamp 1999), it is likely to be a fundamental driver of social structure in avian populations. For example, communal roosts of common starlings *Sturnus vulgaris* are formed by the aggregation of foraging flocks (Carere *et al.* 2009). Additionally, differences between individuals in their body condition across a diel cycle may also alter the foraging-predation risk trade-off, resulting in variation in social interaction rules between individuals, or variation in social decision-making in a way that may contribute further to patterns of fission-fusion social dynamics.

Tidal cycles

Many bird species, especially shorebirds and wildfowl, exploit intertidal resources, and therefore fission-fusion dynamics may be driven by tidal cycles. For foraging shorebirds the main effect of high tides will be to reduce the area of available resources and increase aggregation size (Fleischer 1983), although as tides rise and birds are forced to forage closer to terrestrial habitats, changes in predation risk will also influence grouping decisions (Beauchamp 2010). Light-bellied brent geese *Branta bernicla hrota* forage on terrestrial grasslands at high tide when intertidal resources are not available, resulting in increased risk of predation and therefore increases in flock size (Inger *et al.* 2006a). For most species using intertidal areas, the tidal cycle is a major driver of social dynamics.

2.3.3 Unpredictable events

Unpredictable or non-cyclic changes to the environment can also contribute to the occurrence of fission-fusion social dynamics. Differences among individuals alter the relative costs and benefits of remaining with a social group after environmental change, so such events can be important in triggering both fission and fusion of groups. This can result in less predictable environmental changes having predictable consequences for social dynamics. For example, army ant swarms in the Neotropics create an unpredictable food resource that results in aggregations of some bird species, especially obligate ant-following species, a process that results in fission-fusion social dynamics (Willson 2004).

2.4 Researching Fission–Fusion Dynamics in Birds

Fission-fusion dynamics in birds are likely to be highly variable and frequently different from those in other vertebrate groups due to birds' mobility and tendency to migratory behaviour. Approaches that describe the spatio-temporally dynamic social structures will be particularly important in describing patterns of social associations in birds, with a more experimental approach being particularly beneficial in investigating why they occur. Further development of theoretical ideas, especially of how fission-fusion dynamics might depend on landscape use and migratory behaviour in large-scale natural systems, would complement these methodological developments closely and may be particularly valuable to epidemiological or conservation research through a predictive modelling approach.

2.4.1 Using social networks

SNA is a tool to describe social systems and reveal their underlying dynamics (Croft, James & Krause 2008; Wey *et al.* 2008; Sih, Hanser & McHugh 2009). Social network approaches use a series of observations of individually recognisable animals to construct a population-wide pattern of social associations using information provided by social interactions or co-occurrence in groups (Croft, James & Krause 2008). This makes it possible to visualize and quantify patterns of social associations and elucidate a population's social structure (Fig. 2.1), even when only a small proportion of the population is individually identifiable (Chapter 3), suggesting that SNA will be applicable to colour-ringing studies (e.g. Farine & Milburn 2013).

Using SNA makes it possible to establish the frequency and importance of stable associations in avian societies, especially when spatial constraints are imposed (Wolf *et al.* 2007; Mourier, Vercelloni & Planes 2012; Pinter-Wollman *et al.* 2013) or home or foraging range information incorporated into permutation tests for network structure (e.g. Carter *et al.* 2009). Additionally, the use of SNA in population-wide, individual-marking studies in avian systems provides an opportunity to investigate the role of phenotypic assortment (including in mixed-species study systems) or kinship in more fluid fission-fusion societies, the latter provided genetic data are also available.

Understanding social structure in fission-fusion systems will be particularly beneficial in recognising the consequences for parasite transmission and information transfer. For example, Aplin *et al.* (2012) demonstrated that greater connectivity in a social network was correlated with the likelihood of an individual finding a new foraging patch in mixed-foraging flocks of tits. Similar social network studies in other taxa have revealed the importance of these

approaches in understanding the spread of parasites and disease (e.g. Hamede *et al.* 2009; Bull, Godfrey & Gordon 2012). Many bird species represent significant reservoirs of zoonotic diseases, so using social network approaches to further our knowledge of how social dynamics in these species influence patterns of epidemiology will be insightful. For example, research into the transmission of avian influenza has highlighted the importance of social aggregations and population density in explaining inter-individual transmission (Gaidet *et al.* 2012), and it seems likely that an improved understanding of social structure and dynamics could further explain these patterns. Interestingly, the prevalence of the influenza virus was linked to density at a community rather than a species level, perhaps emphasising the importance of developing mixed-species network approaches.

2.4.2 Migration and spatio-temporal variation in social dynamics

Considering spatio-temporal variation in social dynamics will also be important to understanding the population-level processes outlined above. This is especially true for migratory species, whose differences in staging areas and foraging sites might alter the social dynamics that occur (e.g. godwit foraging densities: Gill, Sutherland & Norris 2001). Social network approaches have been used to investigate temporally dynamic network structures (Henzi *et al.* 2009; Cantor *et al.* 2012; Pinter-Wollman *et al.* 2013), so tools to assess the temporal dynamics of avian social structures are available. Given that migratory species are of great interest from a disease perspective (Hoye *et al.* 2011) and to conservation (Vickery *et al.* 2014), and that many aspects of staging ecology

are still poorly understood (Warnock 2010), investigating social network dynamics across the annual cycle in these species could provide some important insights. By using the temporally dynamic network approaches introduced above, it should be possible to determine the stability of social structures, and even social associations themselves across the annual cycle. This clearly has major implications for understanding disease dynamics and social evolution. Predictions that the likelihood of associations persisting between seasons in these systems depends on the strength of associations, relatedness, shared use of staging areas, overall migration strategies or the properties of the social system itself could all be tested in avian systems.

2.4.3 Using experiments to understand avian social dynamics

The methods outlined above will provide valuable insights into understanding how life-history traits and ecology can influence fission-fusion sociality, but experimental approaches will be needed to develop a finer-scale understanding of the mechanisms that drive their occurrence. The use of both passerine (Templeton & Giraldeau 1996; Livoreil & Giraldeau 1997) and non-passerine (Tome 1988; Guillemain, Fritz & Blais 2000) study systems to assess individual decision-making by artificially manipulating resource availability has already proved productive, and extending this to test decision-making in a social context could aid understanding of how variation in the environment can cause fission-fusion sociality. Aplin *et al.* (2012) manipulated the distribution of food resources by moving sunflower feeders to novel random locations while investigating the role of social structure in influencing information transfer, and similar experimental manipulations could be used to improve our understanding of the ecological drivers of fission-fusion sociality in birds. SNA could be used to

compare patterns of sociality between treatments that varied in the distribution of resources, an approach that could be compared directly with the predictions made by Sueur *et al.* (2011b) about the importance of intermediate levels of spatial heterogeneity in the environment in the evolution of fission-fusion. Mixed-species study systems may also offer particular potential in these respects, especially when the species involved vary in their foraging preferences. It may be possible to develop an even more fine-scale understanding of the role of the ecological environment as a driver of fission and fusion processes if mixed-species systems are studied under closely controlled conditions. Altering the ecological environment in ways that affected different species in contrasting ways is likely to be a powerful method to improve our understanding of fission-fusion.

2.4.4 Observational studies and the investigation of large-scale natural systems

The results of experimental investigations could be further supported with evidence from observational studies conducted in natural systems, especially in long-term colour-ringing or bio-logging studies. Particularly suitable systems include wildfowl or shorebirds, in which fission-fusion dynamics are already known to occur and colour-ringing schemes are widespread. However, some passerine study systems are also likely to be suitable for this research (Mcgowan *et al.* 2007; Farine & Milburn 2013), especially when reality mining (Krause *et al.* 2013) of bio-logging data can be used (e.g. Aplin *et al.* 2012; Aplin *et al.* 2013). The contribution of this approach is likely to be increased by including study systems where fission-fusion involves mixed species flocking,

such as shorebirds (Colwell 2010) or tits (Farine, Garroway & Sheldon 2012). By recording flock sizes in different environments exploited by a single population or community it should be possible to demonstrate the importance of spatio-temporal variation in the environment on variation in group size. Furthermore, by investigating marked individuals, the role of social decision-making could be investigated more thoroughly. In particular, personality variation has previously been linked to differences in social network position (Croft *et al.* 2005; Croft *et al.* 2009; Krause, James & Croft 2010; Aplin *et al.* 2013), but the mechanisms that result in this have received little attention and would be a profitable area of ornithological research. Finally, in many bird species levels of aggression (Inger *et al.* 2006a) and vigilance (Beauchamp 2008) in foraging flocks are high, and in systems with fluid fission-fusion dynamics considerable variation in within-flock familiarity is likely. Classical observational studies that use focal and scan sampling of behaviour and are given a social context by complementary social network information could thus be highly informative. These social behaviours are observed readily in many birds, meaning avian systems are likely to offer excellent potential for how familiarity may influence social and foraging behaviour and therefore patterns of stable associations in natural systems.

2.4.5 Collective behaviour and avian social dynamics

Bird populations also provide a good opportunity to improve our understanding of the interaction rules that will be important mechanisms in driving fission and fusion in avian social systems. Ballerini *et al.* (2008) showed that observations of collective behaviour could be used to deduce interaction rules in flocks of common starlings, and by developing these approaches further

it will be possible to identify how interaction rules co-vary with the social and ecological environment as well as recognizing the consequences of this variation on fission-fusion dynamics themselves. By using comparative observational studies (Carere *et al.* 2009) alongside novel experimental designs in intra- and inter-specific study systems, ornithological research could contribute to understanding the link between interaction rules, intra-group collective behaviour and population-level fission-fusion social dynamics.

2.5 Anthropogenic Impacts on Fission–Fusion

Dynamics

It is likely that anthropogenic habitat change could have a considerable impact on avian social systems. Perhaps the most important drivers will be habitat degradation, fragmentation and loss, increased disturbance and the provision of novel food resources (e.g. supplementary feeding). Understanding human impacts on avian social dynamics, and the effect this has on individuals, could be important in understanding the response of species to increasing anthropogenic pressures and in improving conservation strategies. Habitat degradation alters social dynamics in a comparative study of mixed-species flocks in urban and forest environments in Malaysia (Lee *et al.* 2005), and supplementary feeding reduces the tendency of varied tits *Parus varius* to join mixed-species flocks, thus altering social dynamics (Kubota & Nakamura 2000). However, although human influence on social dynamics in birds is likely to be very widespread, few studies explicitly link anthropogenic factors with fission-fusion dynamics. Again, as illustrated by the available examples, using systems

with mixed-species flocking is likely to present a particularly good opportunity for research into the anthropogenic effects on fission-fusion dynamics. Specifically, it could be predicted that the response to anthropogenic change may vary between species according to differences in their ecology.

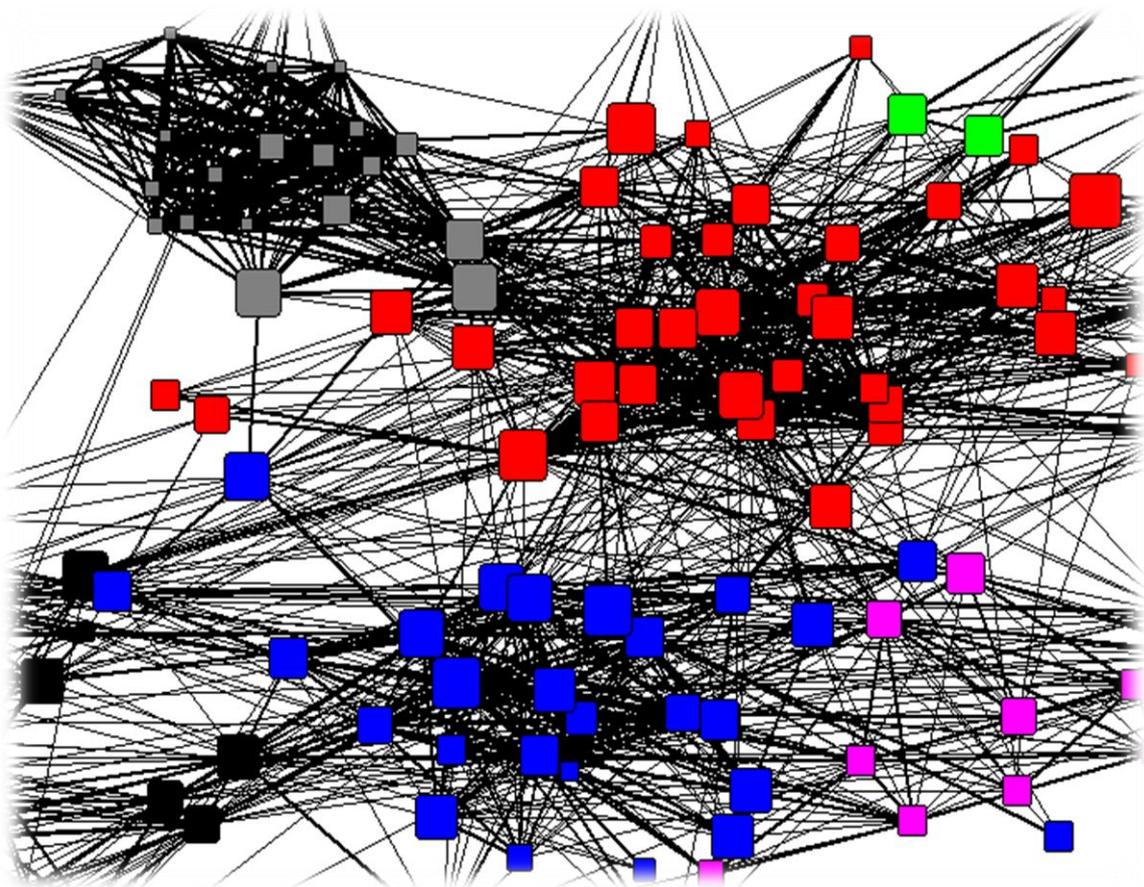
2.6 Conclusions

Fission-fusion dynamics are widespread in birds. Social structure in avian fission-fusion systems depends on the ecological determinants that drive these social dynamics and the social mechanisms that govern combined and partial consensus decision-making during fission events. Our understanding of these social mechanisms in avian social structures remains limited. SNA provides an ideal tool for improving our knowledge of dynamic social systems in birds, especially given the abundance of ongoing studies using uniquely identifiable individuals. Development of socio-ecological approaches in ornithological research offers great potential for furthering understanding of these social systems.

By studying social dynamics in fission-fusion social systems, it will be possible to understand more fully the importance of the social environment and population social structure in governing patterns of social behaviour, disease dynamics and information transfer. Considering these key consequences of fission-fusion sociality has numerous applications in developing a broader understanding of social evolution and decision-making, as well as in conservation and epidemiology. In particular, an improved understanding of social structure dynamics in migratory populations would be of great value, as

many of these populations are of conservation interest or may act as important vectors for diseases.

3. The consequences of unidentifiable individuals for the analysis of an animal social network



3.1 Abstract

The use of social network analysis is pervasive in understanding animal social systems, and is used to provide information about how individuals vary in their social strategy. Many long-term studies comprising uniquely marked individuals use social network analysis as an analytical tool. However, the assumption that it is possible to make inferences using network metrics calculated using a subset of the population has yet to be tested in an animal social network. We use a simulation study of networks derived from random social interactions in a typical fluid fission-fusion social system to determine the precision and accuracy of measures of individual social position based on incomplete knowledge. We show that individual social positions measured in partial social networks correlate strongly with positions in the full social network. This result is resilient to changes in network density and becomes stronger as the size of the simulated population is increased. The choice of network metric has an important effect on the precision of partial networks only when they include a small subset of the population. This work demonstrates that valid inferences about individual social position and strategy can be made using partial networks in animal social networks that are not highly structured. However, some caution is required using particular metrics when a low proportion of the population is identifiable. We also recommend extending this approach across a range of social network structures, as this will have important consequences for the use of social network analysis in a wide-range of long-term study systems.

3.2 Introduction

Social network analysis (SNA) is now widely used to study animal social behaviour (Wey *et al.* 2008; Sih, Hanser & McHugh 2009; Farine, Garroway & Sheldon 2012; Pinter-Wollman *et al.* 2013), and is fast developing beyond being a descriptive tool to become fundamental in quantifying behavioural interactions and their subsequent consequences in a wider social context (Sueur *et al.* 2011a; Formica *et al.* 2012; Dey *et al.* 2013; Kohn *et al.* 2013; Wey *et al.* 2013). There is a growing focus on understanding how an individual's personality, phenotype and condition interact to influence its social decision-making and social strategy (Croft *et al.* 2005; Croft *et al.* 2009; Aplin *et al.* 2013; Wilson *et al.* 2013). By studying variation in individual social position, it is possible to make inferences about both the mechanisms that drive population social structure in a study system (Connor, Heithaus & Barre 2001; Wittemyer, Douglas-Hamilton & Getz 2005; Stanley & Dunbar 2013), and the consequences of following particular social strategies for individual fitness (McDonald 2007; Formica *et al.* 2012; Wey *et al.* 2013). Extracting individual-level metrics from networks is therefore a major application of SNA in behavioural ecology, and being able to apply network analysis to infer individual social behaviour in a wide range of systems becomes highly significant.

Social position has been linked to home range (see Pinter-Wollman *et al.* 2013 for a review), social status (Sueur & Petit 2008), age (Patriquin *et al.* 2010), sex (Gilby & Wrangham 2008; Carter *et al.* 2013), genetic relatedness (Archie, Moss & Alberts 2006; Carter *et al.* 2013; Schülke, Wenzel & Ostner 2013), ability to acquire social information (Aplin *et al.* 2012; Claidiere *et al.* 2013), disease status (Weber *et al.* 2013) and reproductive success (Wey *et al.* 2013) in recent empirical investigations. Additionally, there has been increasing

recent interest in social network position as a personality trait or part of a wider behavioural syndrome (Krause, James & Croft 2010; Wilson *et al.* 2013). The role of these potential factors in influencing social position, and the consequences to an individual of that social position can be investigated using a simple correlative approach at an individual level (Formica *et al.* 2012; Wey *et al.* 2013). This makes data from many marking or tagging projects highly valuable in generalising our understanding of what processes drive individual social strategies and social evolution in many types of fission-fusion social system, and how this then contributes to variation in overall population social structure.

Historically SNA was largely limited to systems where all (or the vast majority of) individuals in a system are individually identifiable (Connor, Heithaus & Barre 2001; Croft *et al.* 2005; Drewe, Madden & Pearce 2009; Ramos-Fernández *et al.* 2009). However, it is now increasingly used in a wide range of long-term ecological studies where this is not the case. In particular, there are now many examples of social networks being used in study populations where individuals are only identifiable once captured and tagged, a restriction that can substantially reduce the identifiable component of the population (Hamede *et al.* 2009; Oh & Badyaev 2010; Aplin *et al.* 2012; Farine & Milburn 2013; Weber *et al.* 2013). This is of concern because social networks are relational data, and the relations among the members of a sample will only be a subset of their full set of relationships (Alba 1982; Croft, James & Krause 2008). This means that it could be expected that relational data responds more unreliably to sampling from a population than other data types, as missing individuals may exert a strong influence on the social measures of individuals sampled.

This issue has been investigated elsewhere in the social networks literature (Borgatti, Carley & Krackhardt 2006; Lee, Kim & Jeong 2006; Stumpf & Thorne 2006). With the primary focus of these studies to explore the accuracy of network-level measures (Borgatti, Carley & Krackhardt 2006; Lee, Kim & Jeong 2006; Frantz, Cataldo & Carley 2009), node-level metrics have been largely ignored. The presence of unidentifiable individuals is directly analogous to random node sampling (Lee, Kim & Jeong 2006). Lee, Kim and Jeong (2006) explored structural properties of random node sampling at a network level and found that whilst the degree exponents of sampled networks were inaccurate relative to the real network, the changes were predictable suggesting that relative values of node-level metrics have the potential to remain similar. In support of this, Stumpf and Thorne (2006) found that inferences could be made using subsamples of molecular networks generated through random node sampling, suggesting that partial networks could provide useful information if relative values rather than accurate values of node-level metrics are required.

Despite this finding, the effect of using “partial networks” constructed using a random subset of the population on the on the properties of individual metrics in animal social networks has received little attention (Croft, James & Krause 2008; Cross *et al.* 2012a). Franks, Ruxton and James (2010) investigated how various network properties depended upon the number of censuses and the proportion of individuals sampled in each census. They concluded that the former was more important, and that network-level properties were fairly resilient to a low number of individuals being detected on each census. Whilst this focuses more on the concept of the detectability of identifiable individuals rather than the effects of unidentifiable individuals, it

does perhaps suggest that there is potential for social network studies to make valid inferences using only a sample of the population.

In this study we use a simulated fluid fission-fusion social structure parameterised using a long-term study of light-bellied brent geese *Branta bernicla hrota* to investigate how properties of the social network vary as the proportion of identifiable individuals in the population changes. Light-bellied brent geese are a species with typical fluid fission-fusion dynamics with considerable spatiotemporal variation in group sizes (Fig. 3.1). The outcome of this is a fairly well connected social network but variation among individuals in social network positions, making it possible to test structural hypotheses at an individual-level. We examine how changing proportions of identifiable individuals in a population alters the relationship between an individual's apparent network metrics and its real social metrics (i.e. network metrics when the entire population consists of identifiable individuals).

We look at a selection of key social metrics to determine whether the choice of network metric in a given study could affect the accuracy and precision of the conclusions that can be drawn. We investigate four of the most commonly used measures of centrality and one commonly used measure of transitivity (Table 3.1), which combined provide a range of important measures of social position. This study represents a first attempt to apply a simulation-based approach to understanding the effects of random node deletion to an animal social system, and should serve to highlight the importance of understanding the consequences of this more widely in a greater range of social systems.

Metric	Type	How is it calculated?	What does it measure?
Degree	Centrality	A count of the number of individuals a focal individual is connected to in the network	The number of social connections an individual has
Strength	Centrality	A sum of the total weight of all a focal individual's connections in the network	Accounts for the value of the connections an individual has as well as the number of individuals it is connected
Betweenness	Centrality	A count of the number of shortest paths between other individuals in the network that pass through a focal individual	The importance of an individual in connecting different parts of the network
Eigenvector centrality	Centrality	The focal individual's value in an eigenvector that corresponds to the maximum eigenvalue from the network in matrix form	The influence of an individual in the network, taking into account its second-order connections
Clustering Coefficient	Transitivity	The proportion of individuals connected to the focal individual that are inter-connected themselves	The embeddedness of individual within its social clique

Table 3.1. Details of the five key network metrics used in Chapter 3

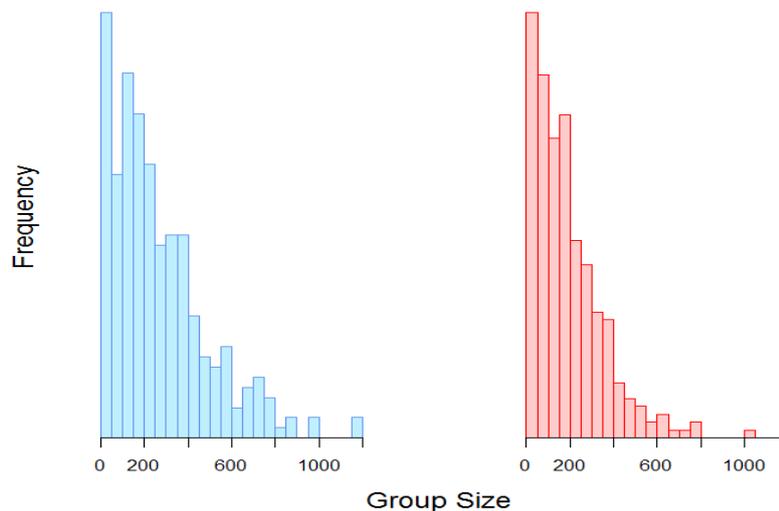


Figure 3.1. Group size distributions for observed and simulated data The group size distribution of the Dublin staging population of ECHA light-bellied brent geese in Jan-Mar 2012 (blue bars, left) plotted against an example histogram of the corresponding negative binomial group size distribution used in our models (red bars, right).

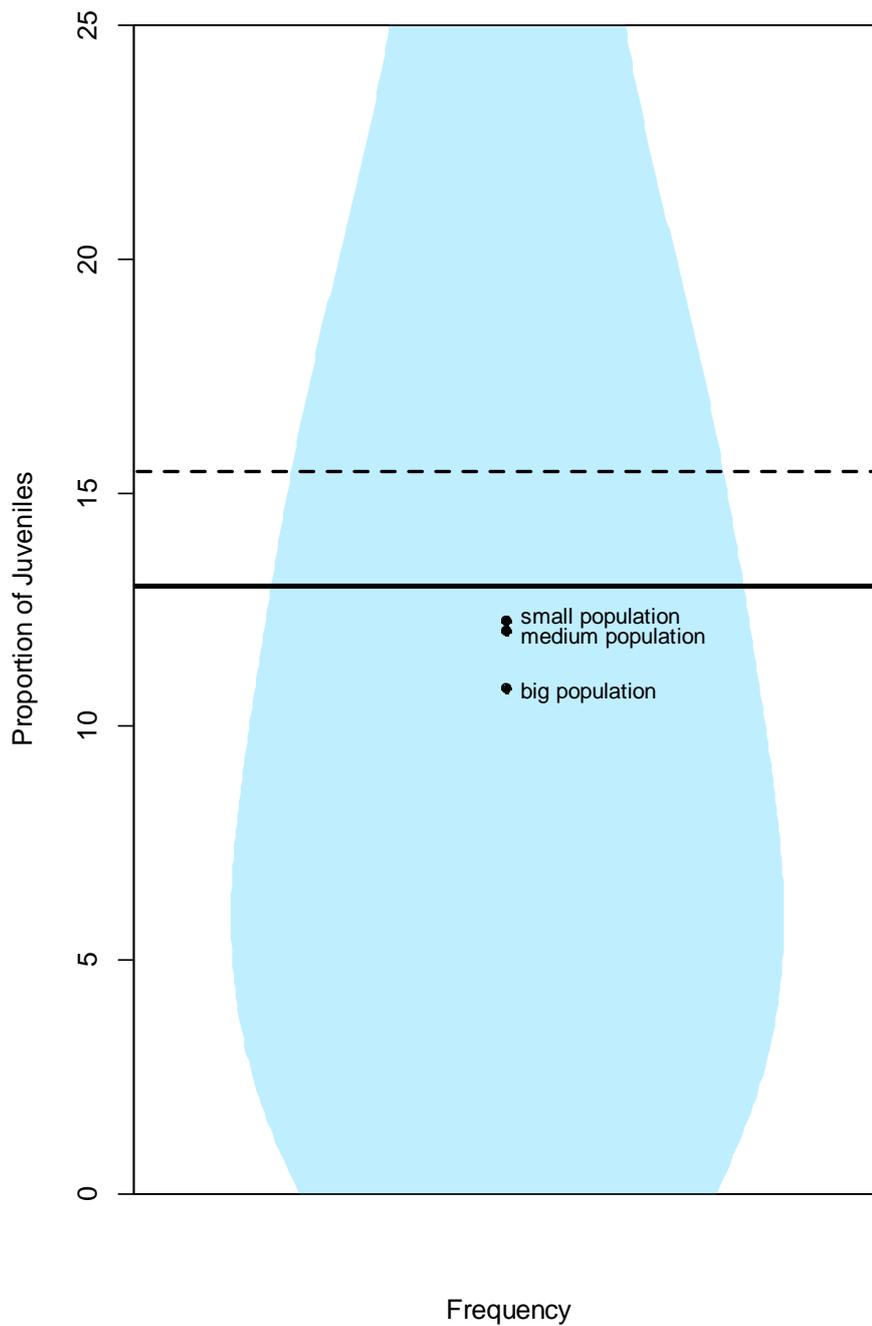


Figure 3.2. The proportion of juveniles in observed and simulated populations

The distribution of annual variation in the proportion of juvenile ECHA light-bellied brent geese (blue shaded area) based on data available in Madsen, Cracknell and Fox (1999). The median of this distribution is represented by the solid black line and the mean by the dashed black line. The proportion of juveniles present in our three simulated populations are shown using labelled points and fall between the median and peak of the frequency distribution.

3.3 Methods

Generation of population

The simulated populations of light-bellied brent geese analysed in this study were generated using data from a long-term ecological study on the Irish wintering population of this sub-species.

1. Three simulated populations of geese containing 308, 591 and 978 individuals were generated. The three population sizes used were selected to represent a range of realistic population sizes likely to be used in long-term studies. These populations were formed of family units, where a family unit was defined as an unpaired individual, a non-reproductive pair or family (parents with dependent juveniles). Family units remained together throughout the sampling process.
2. The frequency of family units (Fig. 3.2) and the number of juveniles in each family (Fig. 3.3) were specified from distributions based on real data. The number of juveniles in each family was generated using a binomial distribution that produced family sizes to that in the Irish Brent Goose Research Group database, with the proportion of juveniles generated
3. Each individual and family unit were assigned a unique identity for use in social group generation and subsequent social network construction.

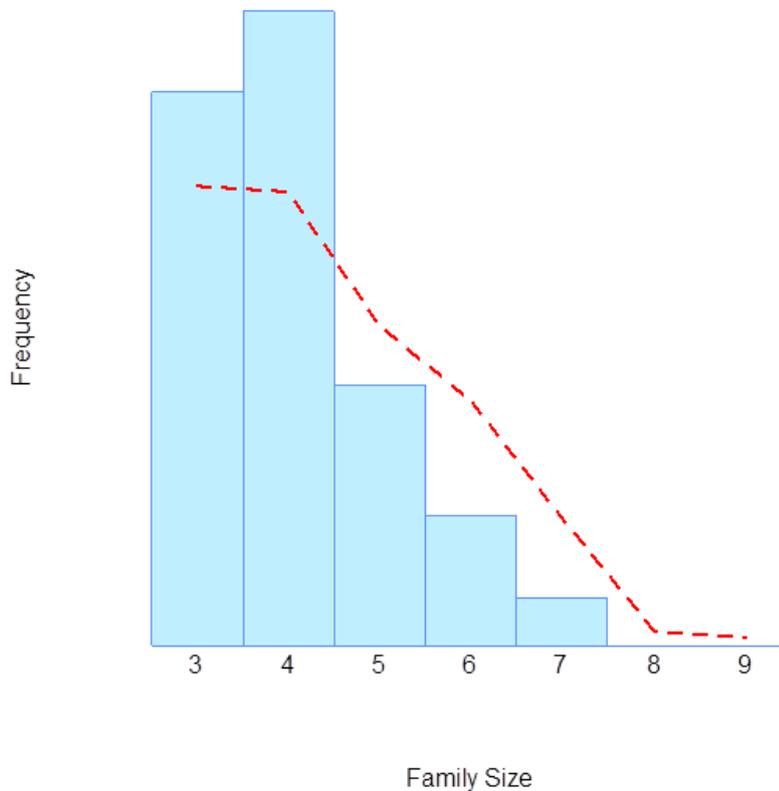


Figure 3.3. Family sizes in observed and simulated populations

The distribution of the number of juveniles in a family group in the Irish wintering population of ECHA light-bellied brent geese (red dashed line) plotted against an example histogram of the simulated binomial distribution used in our models.

Generation of social groups

At each iteration of the algorithm the population was split into different social groups. Social groups were assigned at a family unit level to ensure that family units remained cohesive as observed in the real data. The group-size distribution for these groups was based on fitting a negative binomial distribution to real data from a focussed socioecological study of the Dublin wintering population in Jan-Mar 2012 (Fig. 3.1) with size = 1.4 and $\mu = \text{population}/10$.

1. All family units in the population were randomly ordered.
2. A group size was determined randomly from the negative binomial distribution outlined above, with the population size used to calculate μ equalling the number of family units in the population.
3. The corresponding number of family units was taken from the reordered population set.
4. Steps 2) and 3) were repeated until the total number of family units allocated equalled or just exceeded the number of family units in the population.
5. If the latter case was true, this last group was not included and any remaining family units were allocated randomly to groups already created.

Each of the three populations were randomly split into social groups using this method at each time step in a series of 5 or 10 time steps to provide the association information used to generate social networks of two different densities. Using this number of time steps was sufficient to generate considerable variation in edge weight whilst preventing networks from being completely connected, as this would impact on the ability to use certain key network metrics to differentiate between the social position of individuals in binary networks.

Construction of social networks

Social networks were constructed using the gambit of the group assumption (Whitehead & Dufault 1999; Croft, James & Krause 2008; Franks, Ruxton & James 2010), with edges connecting individuals that had co-occurred in the same social group. Both weighted and binary association matrices were

calculated so that we were able to test both weighted and binary network metrics. Repeating the sampling process for different numbers of time steps allowed us to monitor the effect of network (edge) density on the robustness of our conclusions.

Definition of identifiable individuals

Simulations were run for each combination of the three population sizes and two network densities (six in total), then analysed with five different levels of assigned marking effort (90%, 70%, 50%, 30%, 10% of individuals made identifiable). Individuals were made identifiable at random, and individuals that had not been made identifiable were removed from the association matrix to create a partial network containing only identifiable individuals. This process is outlined in more detail below. 10 repeats of each level of marking effort were run, generating 50 partial networks for each of the six full networks.

To assign individuals as identifiable:

1. Each individual was assigned a number from a random uniform distribution between 0 and 1.
2. Individuals with a number equal to or lower than the assigned marking effort was defined as identifiable.
3. To generate variation between replicates in the identity and precise number of individuals made identifiable steps 1) and 2) were repeated 10 times to produce 10 different subsets of the original network.

Calculation of network metrics

For each combination of identifiability, population size and network density, measures of strength, degree, binary betweenness, binary eigenvector centrality and weighted clustering coefficient (Table 3.1) were calculated for each node in the full network and each of the 50 partial networks (300 partial networks in total).

Statistical analysis

1. Precision: Correlation coefficients between network metric values in each partial network and the corresponding full association matrix were calculated. This approach (rather than matrix correlation methods) was used so that the slope of the regression could be calculated to provide information on accuracy (below). For each level of marking effort in each run of the simulation (30 in total; five levels of marking effort in six runs of the simulation for different population sizes and network densities), the mean and variance of the 10 correlation coefficients generated was calculated for each network metric. These values were then used to illustrate how marking effort, population size and network density affect the precision of estimates of each network metric in partial networks. This enabled us to investigate how the proportion of individually identifiable individuals in a population may affect our ability to use that partial network to infer their real social position.
2. Accuracy: The mean slope of the regression was calculated for each of the five network metrics for each level of marking level in each run of the simulation. The slope of the regression describes how the value (rather

than its relative value) of network metrics calculated in each partial network is related to the value in the real network. This was used to illustrate the effect of marking effort on the accuracy with which different network metric values in a partial network estimated an individual's real network metric values.

3. Bias: The relationship between the real (simulated) social positions and y residual (both its actual value and the magnitude of this value) of an individual was then found for each regression. This enabled us to detect any potential bias towards individuals in particular social positions having their network metrics under- or overestimated when using partial networks to infer social position.

Generation of the simulated populations and all SNA was carried out using R 2.15.1 (R development Core Team 2014). Network analysis used the packages tnet (Opsahl 2009) and igraph (Csardi & Nepusz 2006).

3.4 Results

Precision

The results for the small and large populations are presented in figure 4. The mean correlation between partial and full networks declines non-linearly and the variance in the correlation coefficients calculated increases non-linearly as the proportion of identifiable individuals decreases (Fig. 3.4, Table 3.2). The precise nature of these changes depends on the size of the simulated population, the density of the social network and network metric being investigated (Fig. 3.4, Table 3.2).

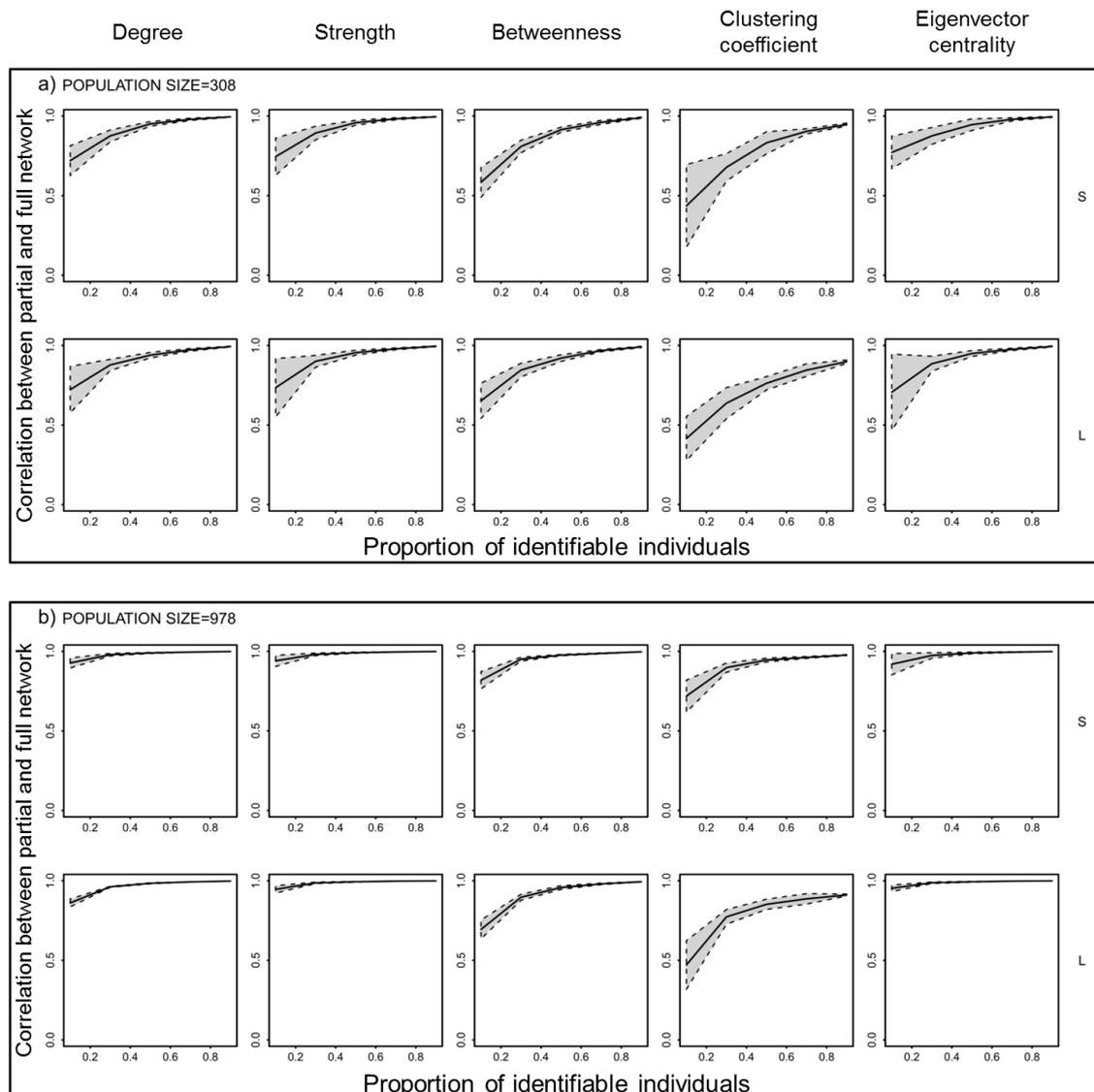


Figure 3.4. The relationship between partial network size and metric reliability in simulated populations

The relationship between the proportion of identifiable individuals and the correlation between five different social metrics in the partial social network (containing only these individuals) and full network in two simulated populations of different sizes (our small and large populations). The S and L panel for each population refers to the 5 time step and 10 time step sampling process used when generating networks and represents networks of different densities. Solid black lines join the mean correlation coefficients at each level of marking effort, with the light grey area bordered by a dashed line joining the mean \pm standard deviation at each level of marking effort.

Partial Network	Metric	Small		Medium		Large	
		Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
10%	Degree	0.72	0.09	0.83	0.09	0.93	0.03
10%	Strength	0.74	0.12	0.86	0.08	0.94	0.04
10%	Betweenness	0.58	0.09	0.70	0.05	0.82	0.05
10%	Clustering coefficient	0.44	0.26	0.56	0.15	0.72	0.10
10%	Eigenvector centrality	0.77	0.10	0.85	0.11	0.92	0.07
50%	Degree	0.95	0.01	0.98	0.002	0.99	0.003
50%	Strength	0.96	0.02	0.99	0.002	0.99	0.003
50%	Betweenness	0.91	0.02	0.95	0.01	0.98	0.004
50%	Clustering coefficient	0.83	0.07	0.94	0.01	0.95	0.01
50%	Eigenvector centrality	0.95	0.04	0.99	0.002	0.99	0.01

Table 3.2. Reliability of network metrics in partial networks of two different sizes

The mean correlations and variance in correlation coefficients between the partial and full networks when 10% and 50% of individuals are identifiable for low density networks in all three populations (small, medium, large).

Population size

An interaction between population size and the proportion of individuals in the partial network is important in explaining the correlation between metric values in a partial network and their corresponding values in the full network (Fig. 3.4). As the size of the simulated population increases (c.f. top two and bottom two rows of panels of Fig. 3.4), the magnitude of the changes to the mean and variance decrease, especially when the proportion of identifiable individuals in the population is low (upper two rows). The results for the small and large populations are shown, with the middle population being intermediate in this effect. This pattern was similar for all metrics investigated, although the scale of the effect did vary. This suggests that the use of partial networks to infer individual social network positions is more precise in larger study populations.

Network density

Network density (number of time steps) generally had a limited effect on the precision of inferences from partial networks. However, estimates of clustering coefficient from high density partial networks were consistently less precise in all population sizes (Fig. 3.4). Additionally, there was increased variance in the precision of partial networks at low marking efforts in the smallest population size investigated (Fig. 3.4).

Network metrics

The correlation of all network metrics between the partial and full network declined as the proportion of individuals included in the partial network decreased. For all metrics there was also a clear change in the relationship when the partial network contained fewer than approximately $1/3$ of individuals,

below which correlation coefficients declined more rapidly. However, there was substantial variation between different network metrics (compare across columns of Fig. 3.4) in the extent of these changes. When 50% or more individuals in the population were identifiable, the values for all network metrics in partial networks were correlated very closely with the simulated real situation (Table 3.2). Measures of centrality (degree, strength and eigenvector centrality) in partial networks remained highly correlated with those in the full network even when only 10% of individuals in the population were identifiable for all population sizes investigated (Table 3.2). The strength of correlations for betweenness and clustering coefficient declined much more substantially, especially in the smaller population sizes used (Table 3.2). For clustering coefficient in particular, there was also a substantial increase in variance, indicating a lack of reliability in values in a partial network (Table 3.2).

2. Accuracy

Network metrics and network density

The relationship between the number of identifiable individuals in a population and the accuracy with which individual metrics in a partial network estimated the real situation was highly dependent on the network metric being used (Fig. 3.5). The accuracy of degree (not illustrated as the results obtained were nearly identical to strength) and strength decreased linearly in direct proportion to the proportion of identifiable individuals in the population (Fig. 3.5a). In contrast, the accuracy of eigenvector centrality did not depend on marking effort in any networks, although the estimates from partial networks tended to be more accurate in high density networks (Fig. 3.5d). For both

betweenness (Fig. 3.5b) and clustering coefficient (Fig. 3.5c) the effect of the proportion of identifiable individuals on the accuracy of estimates from partial networks is strongly influenced by the density of the network being studied. Estimates of betweenness remained highly accurate at all levels of marking effort in low density networks, but accuracy declined in direct proportion to marking effort in high density networks. Contrastingly, the accuracy of clustering coefficient declined in proportion to marking effort in low density networks and was independent of marking effort in high density networks, most likely as a result of the network being close to fully connected. This also seemed to make the accuracy highly dependent on the size of the simulated population (Fig. 3.4d). These problems serve to highlight a key issue with the use of clustering coefficient for association data, in which networks are often highly connected.

3. Bias

The effect of social position

Correlations between an individual's real (simulated) social position and the magnitude of its y residuals for the relationship between that and its position in a partial network were weak for all network metrics in all runs of the simulation. The effects sizes of this relationship for cases in which 10% and 50% of individuals are identifiable are presented in Table 3.3. This implies that the effect of an individual's social position on the reliability of using a partial network to infer its real social position is minimal regardless of population size, network density or the proportion of marked individuals in the population.

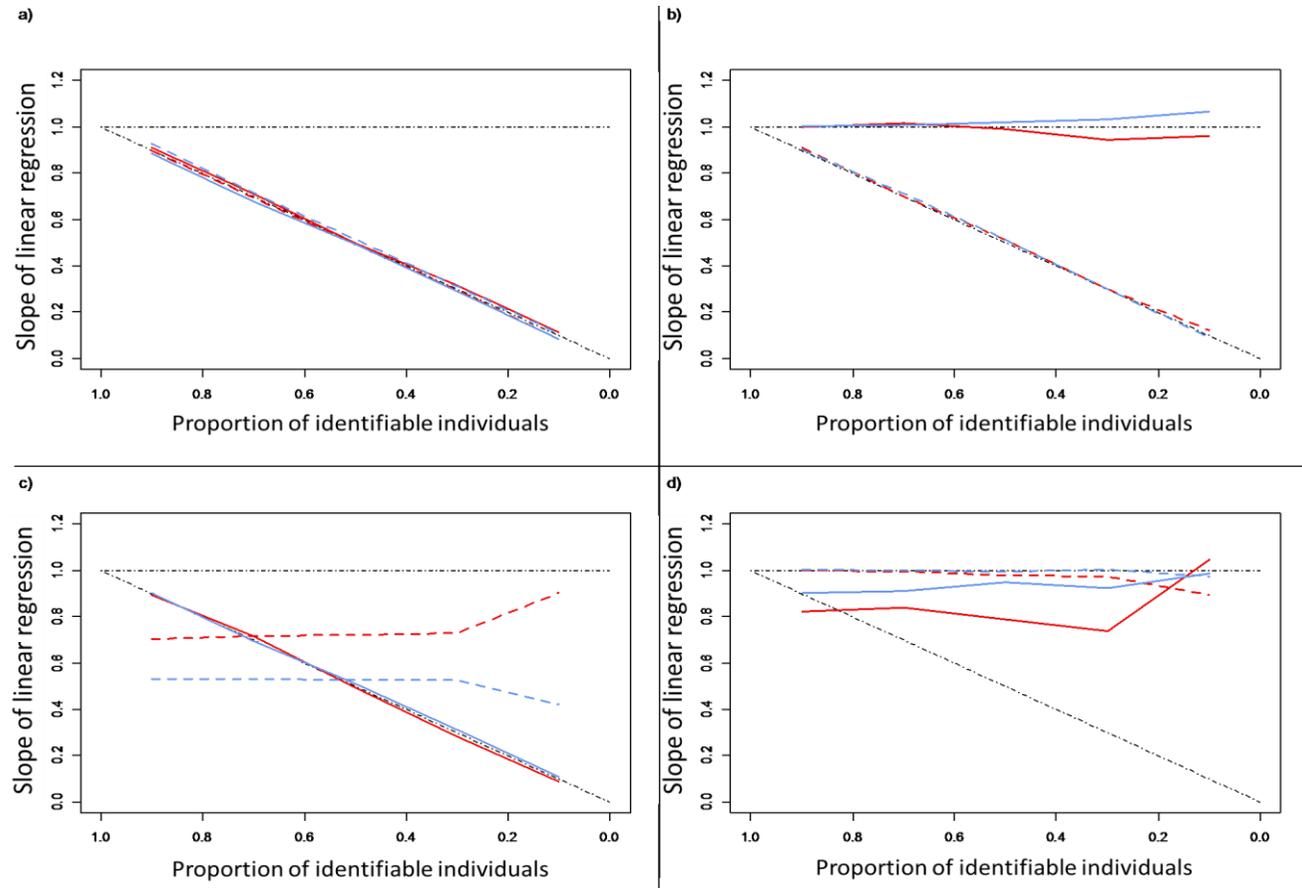


Figure 3.5. The relationship between partial network size and metric accuracy in simulated populations

The relationship between the proportion of identifiable individuals in a partial network and the slope of the linear regression for four different social metrics: a) strength, b) betweenness, c) clustering coefficient and d) eigenvector centrality. Solid lines represent low density networks (5 time steps) and dashed lines high density networks (10 time steps). Blue lines represent the small population and red lines represent the large population. In a) lines are jittered to enable them to be distinguished. The dot-dash black lines represent the case when accuracy is independent of the proportion of identifiable individuals ($y = 1$) and the case when accuracy decreases linearly with the proportion of identifiable individuals in a partial network ($y = 1 - x$).

Partial Network	Metric	Small		Medium		Large	
		Low density	High density	Low density	High density	Low density	High density
10%	Degree	-0.006	-0.008	-0.001	-0.005	-0.001	-0.009
10%	Strength	0.001	-0.002	0.003	0.001	0.002	-0.0001
10%	Betweenness	0.018	0.003	0.016	0.004	0.009	-0.002
10%	Clustering coefficient	-0.185	0.208	-0.108	0.033	0.007	-0.036
10%	Eigenvector centrality	0.032	-0.0409	0.0507	0.023	0.033	0.005
50%	Degree	-0.005	-0.012	-0.003	-0.012	-0.005	-0.012
50%	Strength	0.007	0.007	-0.003	0.002	0.001	0.001
50%	Betweenness	0.021	0.007	0.027	-0.002	0.010	0.001
50%	Clustering coefficient	0.032	0.051	0.007	0.008	0.005	0.018
50%	Eigenvector centrality	0.027	0.032	0.009	0.010	0.007	0.003

Table 3.3. Bias in metric estimates in partial networks of two different sizes

The mean effect sizes of “real” network metric value on the y residual of the relationship between individual network metric values in partial and full networks in high and low density networks when 10% and 50% of individuals are identifiable in all three populations (small, medium, large).

3.4 Discussion

Concerns have been expressed on the reliability of using social networks constructed using a subset of the population (Croft, James & Krause 2008; Cross *et al.* 2012b). However, the impact of using these “partial networks” in lieu of full information to infer individual social network metrics has yet to be investigated in animal social networks. Whilst studies looking at this process of random node sampling (Lee, Kim & Jeong 2006), have occurred elsewhere in the social networks literature they have not focussed on the ability to make predictions about individual-level network metrics. This study investigated how the precision and accuracy of social metrics calculated using SNA are affected by varying the proportion of individually identifiable individuals in a simulated network parameterised using a dynamic social system. The results indicate that, contrary to previous expectations, in social networks based on highly fluid social interactions it is possible to make precise inferences about individual social position when not all individuals in a population are individually identifiable (i.e. partial networks). Significantly, there was an increase in reliability as the simulated population grew in size. Thus, in study populations with broadly similar social dynamics, the results obtained using partial networks can be useful, especially when the study population is relatively large. Previous work elsewhere in the social network literature has demonstrated the potential for changes in network structure to influence the consequences of sampling from a network (Frantz, Cataldo & Carley 2009), so a crucial next step will be to extend these results to more highly structured animal social networks.

Accuracy of individual-level metrics

Some network metrics remain accurate in partial networks, or are inaccurate in a predictable manner, even when a low proportion of a population is identifiable. The strong relationship between the proportion of identifiable individuals and the accuracy with which simple centrality measures (degree and strength) predict the actual value of an individual's centrality is notable, as it means it is likely to be possible to correct for this effect if the level of marking effort in a population is known. It is also clear that measurements of eigenvector centrality remain similar regardless of the proportion of a population in a partial network, so that these values could be universally considered fairly accurate. However, for both betweenness and clustering coefficient there is a complex interaction between marking effort and network density that would make using corrections to estimate an individual's real values for these metrics highly unreliable in natural study populations.

Precision of individual-level metrics

It is the conclusions we can draw about the precision of network metrics calculated from partial networks that are most important. Both the precision of the predictions made using partial networks, and the lack of bias caused by variation in metric values are highly resilient to the number of identifiable individuals in the population, even when as few as 10% of individuals in a population are individually identifiable. If half or more of the individuals in a population can be recognised then all five of the social network metrics investigated can be used informatively with high levels of confidence in all population sizes investigated. Below this level of marking effort, simple

measures of centrality remain the most reliably precise at all population sizes, whilst betweenness and clustering coefficient become consistently less precise in the predictions they produce. This effect is more pronounced in high density networks for clustering coefficient. Whilst the mean correlations between partial networks and the real situation remain relatively strong even for these metrics; the high levels of variation that occur around these values would mean their use as predictive measurements of individual social position for single networks would have a high risk of being unreliable. As a result care is advised in selecting which social metrics should be used in these circumstances, especially in small study populations.

Individual-level metrics in small partial networks

This work reveals differences between social metrics in their precision when a low proportion of individuals in a population are identifiable (30% or less). Whilst basic measures of centrality remain highly informative when few individuals in the population are individually identifiable, the precision of betweenness and clustering coefficient decline considerably if the study population is relatively small. It is clear that in larger study populations this effect is of less importance, although the reliability of using clustering coefficient remains low in high density networks due to the lack of variation in values of this metric. It is likely that these measures perform far less well in small populations and marginally less well in large populations as connections between other individuals in the network are of more significance, thereby enhancing the issues associated with sub-sampling relational data (Alba 1982; Croft, James & Krause 2008). Measures of betweenness, for example, can be highly dependent on the presence or absence of a single edge. Clustering coefficients

are based on how well inter-connected first-order connections are, and therefore will also vary in precision based on what subset of these nodes is sampled. The additional effect of network density on the reliability of using clustering coefficient explained by a lack of variation between individuals in the network, highlight issues with the use of clustering coefficient in association-based networks. Finding a measure of weighted transitivity that better accounts for the weighting of edges would, therefore, be highly beneficial in analysing networks such as these.

These two metrics that perform less well are integral in understanding some key aspects of an individual's social position. Betweenness measures the importance of an individual in connecting different parts of the network by measuring the number of shortest paths between other individuals that pass through it (Freeman 1977; Wey *et al.* 2008). This makes it a key metric to investigating the spread of disease or information through a network (Hamede *et al.* 2009; Aplin *et al.* 2012). For example, in many epidemiological studies, individuals with high betweenness are termed super-spreaders (Craft *et al.* 2011; Weber *et al.* 2013). In contrast, the clustering coefficient (Watts & Strogatz 1998) measures the embeddedness of an individual within its local network structure, so could be important in considering repeat social interactions and familiarity (Croft, James & Krause 2008; Wilson *et al.* 2013). An individual with a high clustering coefficient is likely to react repeatedly with the same set of individuals and they are likely to have interacted previously with each other, considerably altering the dynamic of the social environment in a group.

Given the unreliability of these metrics as indicators of real social position in small partial networks, finding alternative metrics or combinations of metrics

that do not display these properties to corroborate any inferences made would be beneficial. For clustering coefficient, one very basic measure that offers some potential is the mean and coefficient of variation of the weight of an individual's network connections. Repeated interactions with individuals will typically result in more highly weighted connections than for a socially mobile individual, as well as having a higher clustering coefficient. This will result in individuals that tend to interact with the same subset of other individuals having a higher mean and more variable weight of social associations. Given the high precision of both degree and strength at all proportions of identifiable individuals, this method offers particular promise as an alternative to the more susceptible clustering coefficient metric. Finding an alternative social measure for betweenness is more complicated. Whilst betweenness is often weakly correlated with both degree and eigenvector centrality, it captures properties that neither of these measures do. An individual with high betweenness will almost certainly have high degree and/or eigenvector centrality, but an individual with high degree or eigenvector centrality does not necessarily have high betweenness. One possible alternative may be to use flow betweenness instead (Freeman, Borgatti & White 1991; Weber *et al.* 2013). This measures the proportion of total paths between all pairs of nodes passing through a focal node, and thus seems likely to be less susceptible to reductions in the proportion of identifiable individuals in a population. Additionally, measuring the efficiency of an individual's egonetwork (Hanneman & Riddle 2005) may provide some idea of the importance of an individual in connecting different parts of a network, and as a more simple measure is also less likely to be affected by missing individuals than betweenness. Determining how other less susceptible measures can be used to give an equivalent social measure to betweenness

and clustering coefficient would enable additional key social network questions to be addressed confidently using limited partial networks even in small populations.

Applications and further work

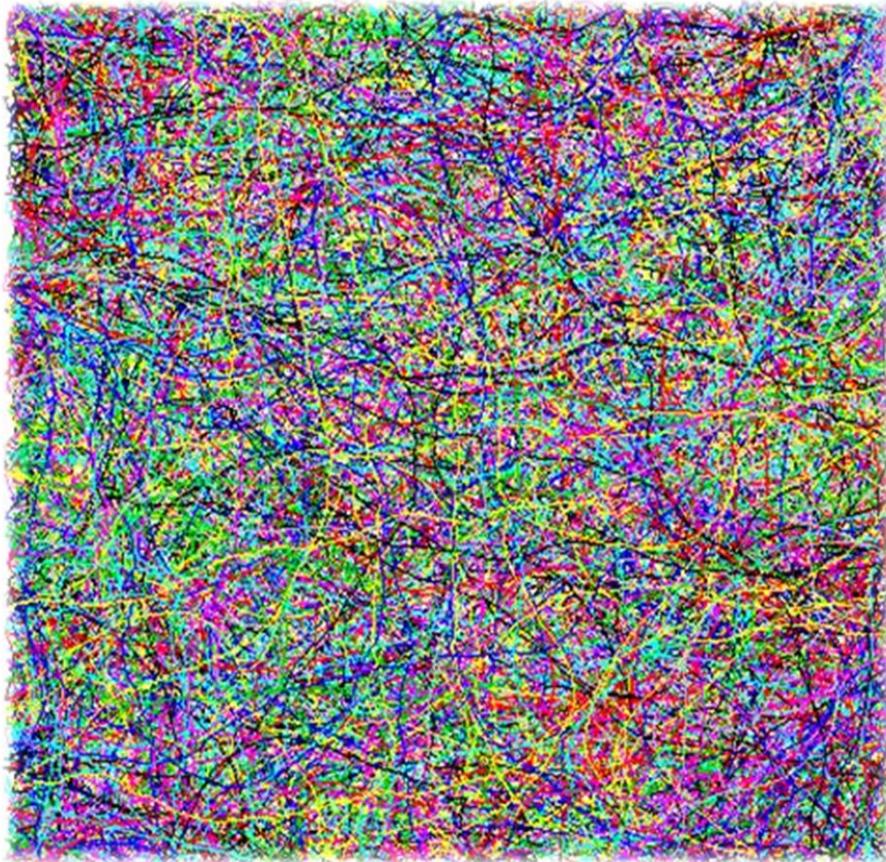
Whilst this research is based on a system parameterised using a single species, there is no reason that these conclusions should not hold more generally for other fluid fission-fusion social systems. The social networks generated in this study varied in their density (the number of completed edges), and individual social network metrics were also highly variable. Furthermore, the light-bellied brent geese used as a model system form a highly fluid fission-fusion social system (Chapter 5) are typical of many similar social foragers (Sundaresan *et al.* 2007; Conklin & Colwell 2008; Aplin *et al.* 2012). As such, the study should be seen as an important starting point in researching the potential of using SNA in animal populations where a substantial proportion of individuals are not individually identifiable. Further work generalising these conclusions across a range of biologically meaningful network structures is likely to prove highly rewarding. Varying network topologies have certainly been found to influence the accuracy of network-level metrics (Frantz, Cataldo & Carley 2009), so may have an adverse effect on the precision of individual-level metrics as well. Thus it could be speculated that the different properties of these types of network may make inferences made about individual social positions more susceptible to sub-sampling effects. However, this is difficult to predict with any certainty. Therefore, investigating similar questions about “partial networks” in more highly-structured social systems, such as those found in

primates (Lehmann & Dunbar 2009) and dolphins (Connor, Heithaus & Barre 2001; Lusseau 2003; Cantor *et al.* 2012) would be especially beneficial.

Conclusions

By influencing behavioural traits, foraging success and disease status, social network position will often be fundamental in determining body condition, stress levels (Brent *et al.* 2011), and ultimately reproductive success (McDonald 2007; Formica *et al.* 2012; Wey *et al.* 2013). In this regard, demonstrating the potential of using social network approaches in systems where many individuals are not identifiable is highly important. This work used a process of random social interactions in a simulated population of a model species with highly fluid fission-fusion dynamics, typical of many social animals, and therefore our conclusions about the use of partial networks will be widely applicable for many species with dynamic social systems. Additionally we highlight that the influence of network topology on the ability to use node-level measures to predict social position - rather than measuring accuracy of network-level properties – has received little attention in the broader networks literature. Therefore, further work extending this research into more highly structured networks remains of great importance, and clearly has important applications for the analysis of animal social networks.

4. The effects of correcting for group size during social network construction



4.1 Abstract

Social network analysis is now a widely used tool in animal behaviour. Many animal social networks are constructed using the gambit of the group assumption. This assumes that meaningful patterns of social relationships can be inferred from recording co-occurrence of individuals in groups without measuring direct interactions. Clearly the validity of this assumption will vary with group size, and it has been suggested that correcting for group size when calculating association strength could be a solution for this. Here we study a variety of potential methods for making such corrections, demonstrating their potential utility using the results of a simple agent-based model of movement within a group. We then test the effect of using these corrections on key population-level and individual-level social metrics in simulated populations parameterised using a typical fluid fission-fusion social system. The results demonstrate that the use of these corrections can drastically alter the structure of the social network and the inferences made about the social position of individuals within the network. As a result we provide guidance on the most sensible way of using group size corrections. We suggest that this should rely on pre-existing knowledge of intra-group dynamics in a system and the questions being asked using network analysis. We would recommend a cautious application of such corrections in situations where meaningful interactions are unlikely in large groups, for example transmission of parasites by contact or social learning by demonstration, with the nature of the correction used being determined by the structure and behaviour of social groups in a specific system.

4.2 Introduction

The social environment that an animal finds itself in exerts a huge influence on the decisions it makes (Salomon 2009; Jacobs *et al.* 2011; Miller *et al.* 2013), underpinning behaviour (Croft *et al.* 2006; Blumstein, Wey & Tang 2009; Marshall *et al.* 2012) and consequently its condition and fitness (McDonald 2007; Formica *et al.* 2012; Wey *et al.* 2013). Furthermore there is increasing evidence that social environments vary considerably among individuals according to the social strategies they use, which are often mediated via differences in morphological (Croft *et al.* 2005) or behavioural (Pike *et al.* 2008; Croft *et al.* 2009; Krause, James & Croft 2010; Wilson *et al.* 2013) phenotypes. As such, improving our knowledge of how interaction rules, phenotypic variation, behaviour and social context are interlinked is now considered highly important in understanding the evolution of social behaviour and social systems (Sueur *et al.* 2011b; Silk *et al.* 2014).

Social network analysis (SNA) is becoming a key tool in the understanding of the interaction between an individual's behaviour and its social environment (Krause, Lusseau & James 2009; Sih, Hanser & McHugh 2009). It allows the interpretation of social interactions with other individuals in a wider social context (Croft, James & Krause 2008; Sih, Hanser & McHugh 2009), and enables both broad-scale (at a population level) and fine-scale (within groups) social structures to be elucidated in dynamic social systems (Croft, James & Krause 2008; Pinter-Wollman *et al.* 2013). The construction of social networks requires that an interaction between two individuals is defined (Whitehead 1997; Croft, James & Krause 2008). In a limited number of cases specific behavioural interactions can be observed and recorded (Madden *et al.* 2009; Madden *et al.* 2011; Dey *et al.* 2013; Tóth *et al.* 2014), however in many systems social

interactions are inferred from information on group composition using the assumption that co-occurrence in a group constitutes a meaningful interaction - the gambit of the group (GoG) assumption (Whitehead & Dufault 1999). Whilst the potential flaws in this assumption have been extensively discussed (Croft, James & Krause 2008; Franks, Ruxton & James 2010), there is still some debate as to how best to proceed in situations when it is violated.

One of the biggest issues relates to group sizes, which often vary substantially in natural systems, and are highly likely to influence the viability of GoG. The strength of the assumption that co-occurrence in a group constitutes a meaningful interaction is likely to be weakened considerably in larger groups as the probability of two individuals interacting, or the importance of this interaction when it occurs, is likely to be considerably reduced. However, the extent to which the GoG assumption changes with group size might be dependent on intra-group dynamics. In particular, GoG may be less affected by changes in group size when groups are more stable, individuals more mobile within groups or individuals can interact over great distances as these are all traits that increase the probability of individuals interacting in larger groups.

Correcting for the effects of group size on the probability of any two individuals interacting may have major implications for SNA in weighted networks that have yet to be considered. In particular, giving greater importance to the co-occurrence of individuals in small groups will reduce the overall connectedness of networks and thus would be expected to increase in the mean and variation of average path length (average number of edges between any pair of individuals in the network; Wey *et al.* 2008) and betweenness (the number of shortest paths between other individuals passing through each individual in the network; Freeman 1977) in networks. If this increased

cliquishness of networks does occur, it may also have an effect on measures of transitivity (a measure of how clustered together individuals tend to be within the network; Watts & Strogatz 1998) and community structure. It is also likely that basic centrality measures, such as strength (the aggregate weight of all edges connected to an individual; Barrat *et al.* 2004) and eigenvector centrality (a measure of an individual's influence in the network based on its number of second-degree connections; Bonacich 1972), in corrected networks are lower on average. Additionally, individual network metrics may differ depending on the correction employed. The role of gregariousness in influencing individual network metrics has been commented on previously (Godde *et al.* 2013). Individuals that are more frequently found in larger groups will typically occupy different social network positions and differ in certain network metric values. Therefore, counteracting the impact of variation in gregariousness by using group size corrections may result in individual network metrics describing different social properties in networks constructed using different corrections by reducing the impact of differences between individuals in gregariousness. This would result in weak correlations between the values of individual network metrics in networks constructed using different group size corrections.

Croft, James and Krause (2008) suggested correcting for group size within association indices using $\frac{1}{Group\ size-1}$ when calculating them. This was based on the methods used by Newman (2001) when constructing collaboration networks of scientists. Subsequently, a small number of empirical studies have implemented this group size correction (Darden *et al.* 2009; Edenbrow *et al.* 2011). The use of a group size correction, as suggested by Croft, James and Krause (2008), is an intuitive method for reducing this effect. However, despite this, its use in social network studies has remained limited and the

consequences of using such a correction have remained untested. We employ a simple agent-based model to demonstrate the potential importance of using a range of corrections for group size when defining social interactions using association-based methods. These models assume individuals move randomly with respect to each other, but vary in the movement rules that individuals follow, inter-individual interaction distances and the amount individuals move within a group. We will use the outcomes of this within-group approach to suggest how these novel potential corrections that could be used in natural systems, in addition to the $\frac{1}{Group\ size-1}$ correction suggested previously.

We then generated a simulated population with fluid fission-fusion dynamics to investigate the consequences of using these different types of corrections on the properties of the social network itself and also the social network position of individuals within the network as measured by a range of key network metrics. Fission-fusion social dynamics typify animal social systems (Couzin & Laidre 2009), and examples where these dynamic social systems are fluid and dominated by relatively weak social associations would be expected to be widespread (Silk *et al.* 2014). Our simulated population was parameterised using a long-term study system of light-bellied brent geese *Branta bernicla hrota* (Inger *et al.* 2006b; Harrison *et al.* 2010; Inger *et al.* 2010). This system was selected as a basis for the simulated population as it represents a good example of a dynamic social system, with considerable spatiotemporal variation in group sizes at different times of day, season and year (Irish Brent Goose Research Group unpublished data), making it an excellent example of a system in which employing group size corrections may be particularly important to understanding the true social structure of a population. This work represents a first attempt to describe the effect of using

corrections for group size when constructing social networks using GoG, with the results from the simulations being used to guide suggestions for how these methods may be developed in the future.

4.3 Methods

Within Flock Simulations

A simple agent-based model was used to model interactions between individuals in different sized groups. Individuals were modelled as particles moving within a confined region that was related to the size of the group. Three conditions were used to determine the size of the region: i) fixed density, in which the size of the area increased linearly with group size, ii) increased density (asymptotic), in which the size of the area increased in proportion to the square root of the group size and iii) reduced density, in which the size of the area increased in proportion to the flock size to the power of 1.25. The former relationship may be expected when patches are small. However, when available space is not limited the latter relationship is likely to occur, as when groups get larger more individuals lie outside each other's interaction distances resulting in reduced cohesion (Couzin & Krause 2003). Simulations were completed in groups of between 20 and 200 individuals to represent a fairly typical range of group sizes expected in dynamic social systems. For each combination of conditions (density, duration, interaction distance) and group size the simulation was repeated five times.

Movement

At time $(t) = 0$ all individuals in the group were assigned to random coordinates and randomly selected an initial direction of movement (between 0° and 359° unless it was in close proximity to the bounds of the region – see below). All individuals then moved one body length in this direction. At subsequent time steps each individual randomly selected a movement direction within 20° of its current bearing, unless it was in close proximity to the bounds of the region in which case it was randomly assigned a movement direction to keep it within the bounded area. This process was repeated for predefined number of time steps for each group size and distance matrices between all individuals were calculated at each time step. The number of time steps was varied in different runs of the simulation to investigate how differences in the amount individuals moved could influence within group interactions. The durations used were 500, 2000 and 5000 time steps. These durations were defined to represent a range of realistic intervals over which groups might persist in fission-fusion systems

Social Network Analysis

At $t=0$ the mean distance between individuals in the distance matrix was calculated. All individuals closer than a predefined number of body lengths were defined as having interacted. This interaction distance was varied between different runs of the simulation to determine the impact it had on within group interactions. The interaction distances used were 3, 10 and 20 body lengths. The shortest interaction distance represents a distance over which behavioural interactions between dyads of individuals are likely to operate, while an interaction distance of 20 body lengths could be seen as representing the case

when group-level behaviour or the transmission of certain parasites was being considered. Individuals that had interacted were assigned a value of one in an association matrix created for the group. All other individuals were assigned a value of zero. At each subsequent time step this process was repeated and the association matrices summed and then made binary. This resulted in a final association matrix that recorded whether or not all dyads of individuals in the group had interacted (according to the above definition) at any point during the simulation.

The “connectedness” of all individuals was then calculated using the equation $\frac{\text{degree}}{\text{group size}-1}$. This metric ranges between 0 and 1 depending on the proportion of other individuals in the network a focal individual is connected to. The network-level mean of this metric for each run of the simulation was calculated and plotted against group size to illustrate the relationship between group size and the likelihood of two individuals being involved in a meaningful social interaction.

Population-level Simulations

Generation of population

The simulated populations of light-bellied brent geese analysed in this study were generated using data from a long-term ecological study on the Irish wintering population of this sub-species (see Chapter 3). Ten simulated populations of geese containing 100 family units were generated. A family unit was defined as an unpaired (unassociated) individual, a non-reproductive pair or family (parents with dependent juveniles) (Inger *et al.* 2006b; Inger *et al.* 2010). The frequency of family units and the number of juveniles in each family

were specified from distributions based on real data (Chapter 3). Populations consisted of 20 unassociated individuals, 60 non-reproductive pairs and 20 families. Each individual and family unit were assigned a unique identity for use in social group generation and network construction.

Generation of social groups

Social groups were assigned over five time steps. At each time step the population was split into different social groups. The group size distribution for these groups was based on real data from a focussed socioecological study of the Dublin wintering population in Jan-Mar 2012 (Chapter 3). This distribution was a negative binomial distribution (size = 1.4, μ = population/10). Social groups were assigned at a family unit level to ensure that family units remained cohesive units.

1. All family units in the population were randomly ordered.
2. A group size was determined randomly from the negative binomial distribution outlined above, with the population size used to calculate μ equalling the number of family units in the population.
3. The corresponding number of family units was taken from the resampled list of family units.
4. Steps 2) and 3) were repeated until the total number of family units allocated equalled or exceeded the number of family units in the population.
5. If the latter case was true, this last group was not included and any remaining family units were allocated randomly to groups already created.

Equation: $AI = \frac{1}{1 + e^{a((GS-1)-b)}}$								
Method	Correction type	Correction shape	Parameter <i>a</i>		Parameter <i>b</i>			Correction ID
1	Uncorrected	Constant	-10^{19}		0			A
2	Linear	Linear decrease	10^{-4}		$\frac{population}{2}$			B
3	Inverse	Negative exponential	$\frac{24}{population}$	$\frac{12}{population}$	0			a ₁ : F a ₂ : J
4	Threshold	Negative sigmoidal	$\frac{24}{population}$	$\frac{12}{population}$	$\frac{population}{2}$	$\frac{population}{4}$	$\frac{population}{8}$	a ₁ : C,D,E a ₂ : G,H,I

Table 4.1. The parameterisation of potential group size corrections applied in Chapter 4

The parameterisation of the ten potential correction models applied (pairwise combinations of parameter a and parameter b within each row) using a single overall equation. Columns 1-3 provide broader details on each correction model used.

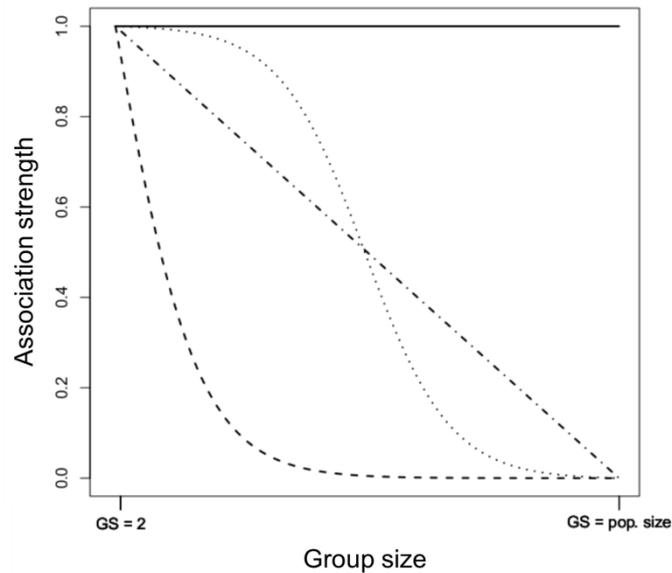


Figure 4.1. The relationship between group size and association strength for four potential group size corrections

The proposed relationship between group size and the association index assigned for each of the four types of correction model used: uncorrected (solid line), linear correction (dot-dash line), threshold model (dotted line) and negative exponential model (dashed line)

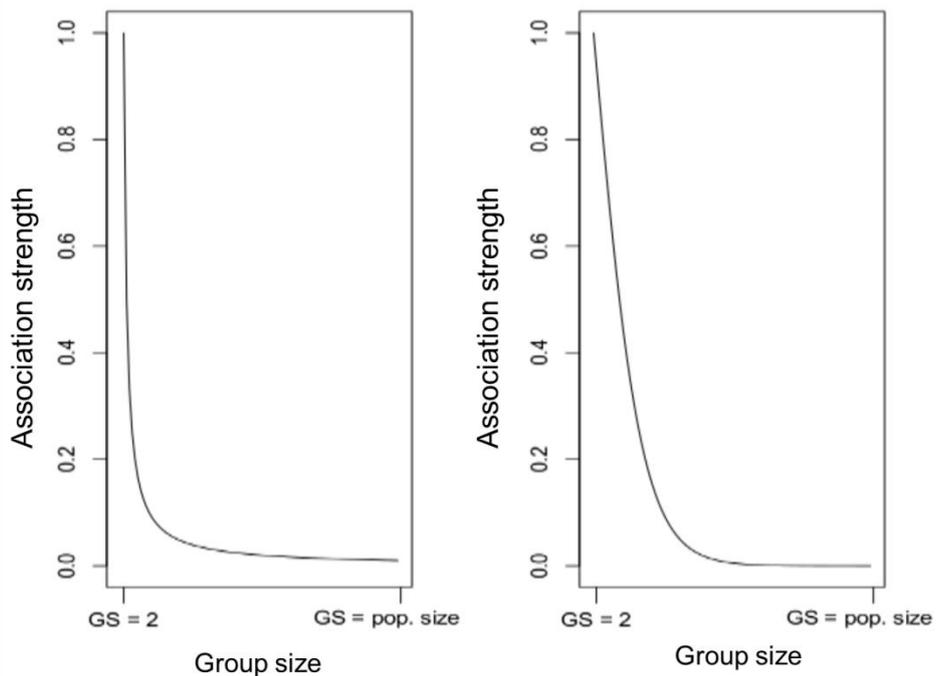


Figure 4.2. A comparison of negative exponential and inverse corrections

The proposed relationship between group size and the association index assigned for (left) the inverse correction suggested by Croft et al. (2008) and (right) a negative exponential correction with parameter a set to $24/\text{population size}$.

Social network construction

Social networks were then constructed using GoG, with association indices being corrected by one of four types of correction (Table 4.1, Fig. 4.1). As well as uncorrected networks (A) and corrections equivalent to $\frac{1}{Group\ size-1}$ corrections (F and J), a linear correction (B) and threshold models, in which interaction strengths declined at a particular threshold value (C, D, E, G, H and I) were also tested. These latter two types were added as two intuitive forms that this relationship could take. The linear decrease assumes that increases in group size reduces the probability of two individuals interacting meaningfully but that the rate of change in this probability remains independent of group size. The threshold models assume that individuals may be able to interact with most or all of the other individuals in a group up until a particular group size at which the probability of interactions declines rapidly. This might occur for example if individuals in larger groups behave differently to individuals in smaller groups. The choice of these correction types was also supported by the results of the within group simulations, where all four types were found to be appropriate depending on the intra-group dynamics.

For each of correction types 2, 3 and 4 the association index of two individuals co-occurring in a group varied between one, when groups comprised only two individuals, to zero when a group comprised every individual in a population. For correction types 3 and 4 parameter a (see Table 4.1) was set at two different values. This altered the steepness of the threshold over which interaction strength declined with group size. For the larger value of a the reduction in interaction strength occurred rapidly over a small range either side of where the threshold was set (parameter b). For the smaller value of a this change was more gradual. The larger value for a was chosen to result in a

relationship similar to that obtained using the $\frac{1}{Group\ size-1}$ correction first suggested by Croft, James and Krause (2008) (Fig. 4.2).

1. Method 1 involved using no group size correction, with the co-occurrence of two individuals in a group of any size resulting in an association index value of 1.
2. Method 2 applied a linear correction for the effect of group size on association strength.
3. Method 3 applied a negative exponential correction with two possible threshold gradients (parameter a ; table 1). The steeper of these was designed to be similar to the $\frac{1}{Group\ size-1}$ correction currently used (Fig. 4.2).
4. Method 4 applied a threshold model, in which the association index of two individuals co-occurring in a group declined rapidly once a group contained a fixed proportion of the population. Method 4 was repeated with the threshold (parameter b ; see Table 4.1) set at $1/2$, $1/4$, and $1/8$ of the population size. Two threshold gradients were also used for each threshold level of method 4 resulting in six possible corrections.

The sum of these association indices then provided a weighted social network for each method that was used in further analyses.

Calculation of social metrics

For each network generated, individual node metrics and overall mean network-level metrics were calculated for degree (Croft, James & Krause 2008), strength (Barrat *et al.* 2004), betweenness (Freeman 1977), eigenvector centrality (Bonacich 1972) and clustering coefficient (Watts & Strogatz 1998).

These metrics were selected as being representative of a range of different network-level and individual-level social properties, as well as having widespread usage in the animal social network literature.

Statistical Analysis

Network level metrics

The mean and coefficient of variation of each of the five key network metrics at a network level was calculated for each social network. This enabled differences in the properties of networks constructed using each of the ten group size corrections to be compared.

Individual level metrics

For each network metric linear models were constructed between individual metrics for each pairwise combination of group size corrections within each run of the simulation. The correlation coefficient (r), regression slope and intercept were extracted from these models. The distribution of these parameters between different runs of the simulation were then used to show the similarity of the network metrics calculated for each individual when group size was corrected for in different ways.

Generation of the simulated population and all SNA was carried out using R 3.0.2 (R development Core Team 2014). Network analysis used the packages tnet (Opsahl 2009) and igraph (Csardi & Nepusz 2006).

4.4 Results

Within Flock Simulations

Simple models of random movement within a flock indicate that a range of corrections may be required depending on the intra-group dynamics and interaction distances present in a study system (Fig. 4.3, 4.4, 4.5). When interaction distances are high, groups are stable (longer simulation durations) or group density increases as groups get larger then not correcting for group size effects is likely to be appropriate (Fig. 4.5). However, as interaction distances get smaller and groups become more ephemeral (shorter simulation durations), the likelihood of group size having no or limited effects on the probability of two individuals interacting becomes increasingly small, especially when larger groups are less densely packed (Fig. 4.3). The gradient of the correction depends somewhat on the interaction distance used (Fig. 4.4) and the relationship between group size and density (Fig. 4.3), and is likely to approach linear in relatively stable groups of highly mobile animals especially when group density increases with group size. In intermediate cases where group density is approximately constant, within group interactions are highly dependent on interaction distances and group stability (Fig. 4.4). With small interaction distances and low simulation duration the mean connectedness of within group networks followed a negative exponential decrease as group size increased. However, as these values increased a negative sigmoidal relationship between group size and mean connectedness, in which interaction probability was initially stable and then declined rapidly at a threshold group size, was typical (Fig. 4.4b, 4.4c). These thresholds were steeper when interaction distances were small and approached linear in cases when individuals could interact over long distances.

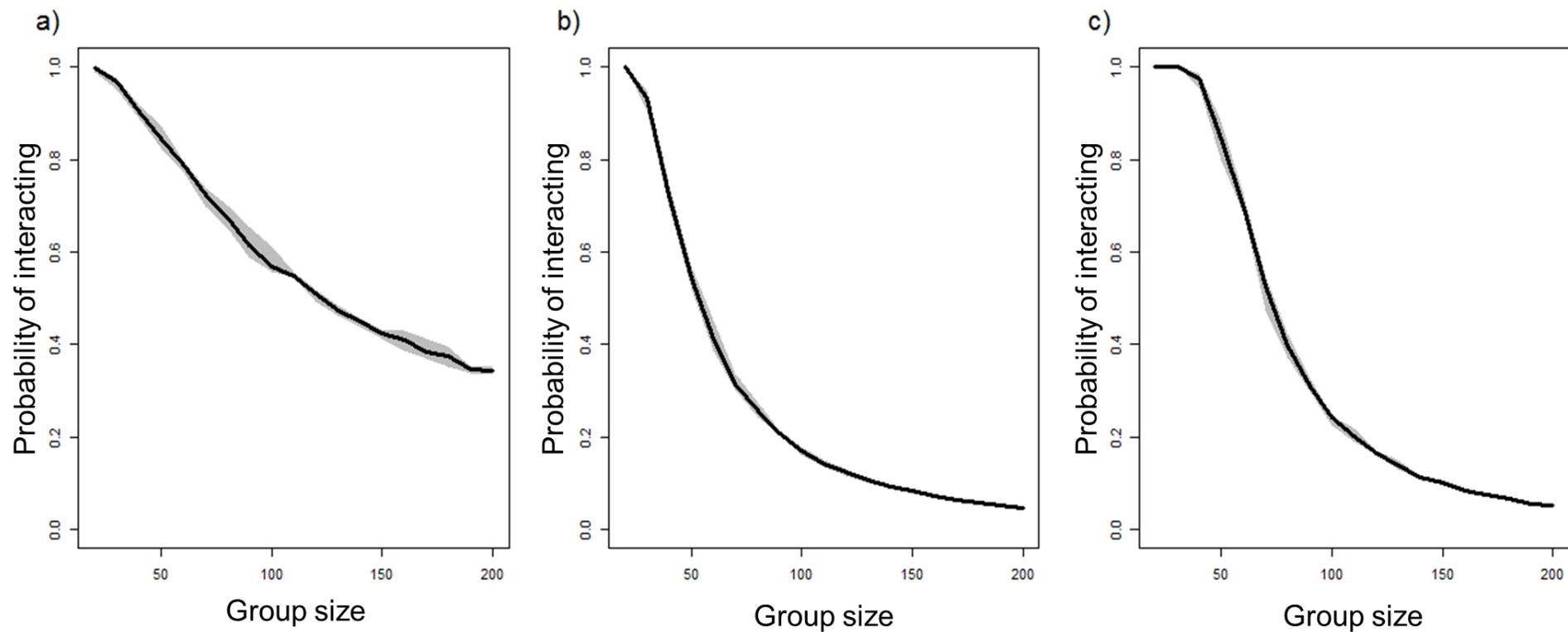


Figure 4.3. The effect of the relationship between group density and group size on the probability of two individuals interacting in a group

The relationship between group size and the mean interaction probability of dyads for three groups varying in their relationship between group size and density: a) group density increases with group size, in b) group density is independent of group size and c) group density reduces with group size. These results are for runs of the simulation with simulation duration fixed at 2000 time-steps and interaction distance fixed at 3 body lengths. Black lines join the mean “mean connectedness” at each group size. Grey shading represents the range of five runs of the simulation.

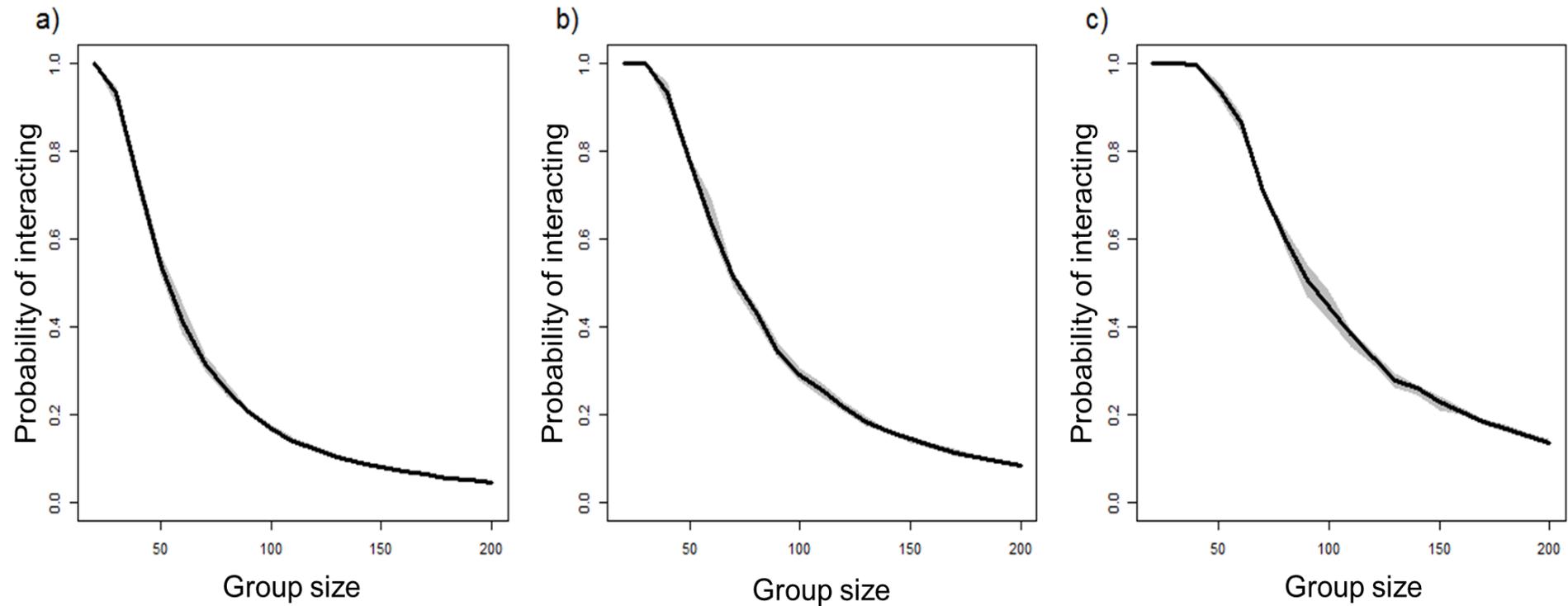


Figure 4.4. The effect of inter-individual interaction distances on the probability of individuals interacting in groups of different sizes

The relationship between group size and the mean interaction probability of dyads for three groups varying in their inter-individual interaction distances: a) three body lengths, b) 10 body lengths and c) 20 body lengths. These results are for runs of the simulation with simulation duration fixed at 2000 time-steps and group density independent of group size. Black lines join the mean “mean connectedness” at each group size. Grey shading represents the range of five runs of the simulation.

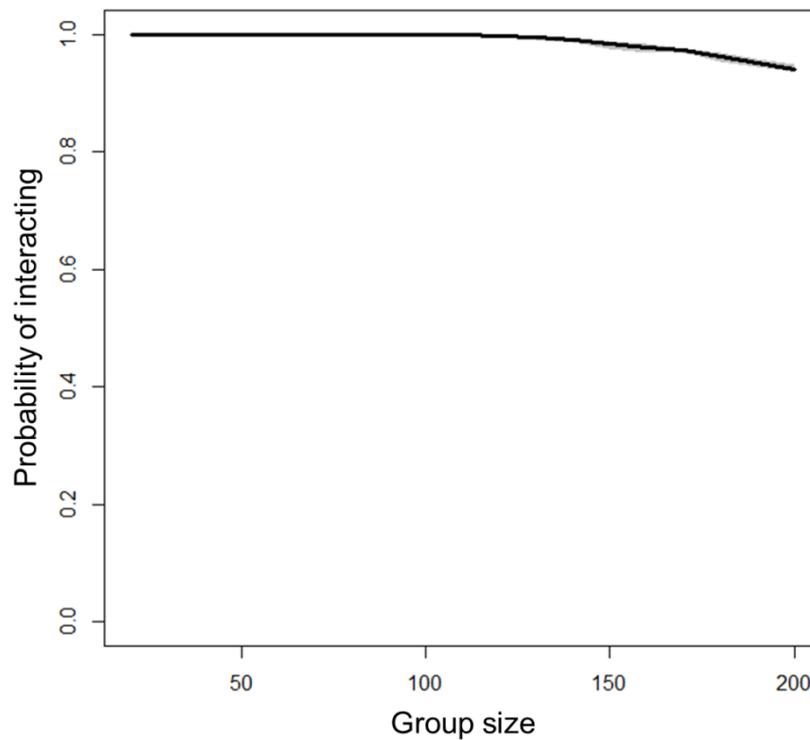


Figure 4.5. The relationship between the probability of two individuals interacting and group size in groups of highly mobile foragers

The relationship between group size and the mean interaction probability of dyads when groups were stable or highly mobile ($t=5000$), group density increased with group size and inter-individual interaction distances were high (20). The black line joins the mean “mean connectedness” at each group size. Grey shading represents the range of five runs of the simulation.

Population-level Simulations

Network level metrics

The effect of using different corrections on the mean and variation of network level metrics varied considerably depending on the network metric of interest and type of correction used (Fig. 4.6, Fig. 4.7). Qualitative descriptions of the key results are also included in Table 4.2.

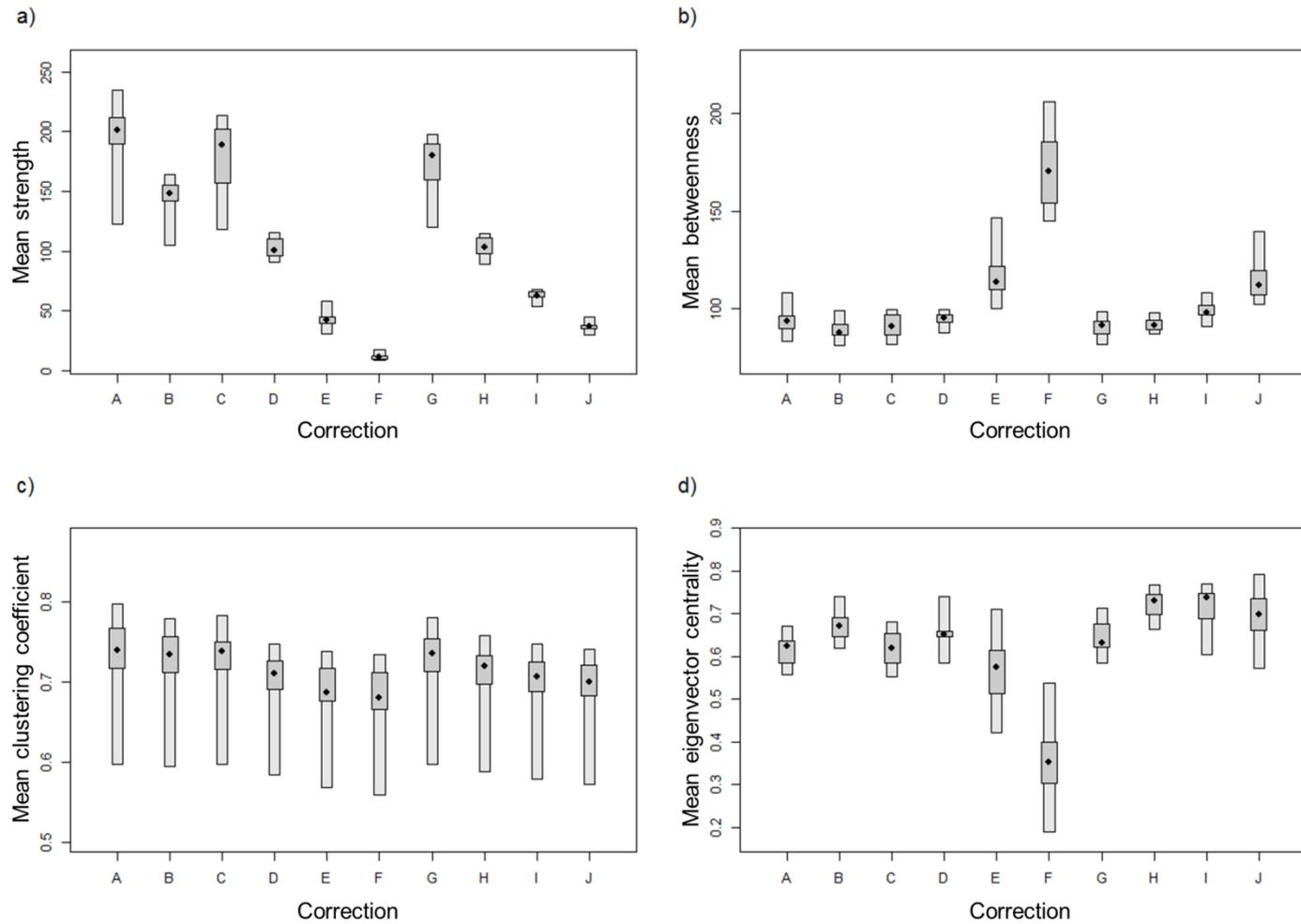


Figure 4.6. The effect of applying different group size corrections on the mean of four key network metrics

The effect of the correction applied on social network construction on network-level means for four different network metrics: a) strength, b) betweenness, c) clustering coefficient and d) eigenvector centrality. The black point represents the median value, the dark grey box the interquartile range and the light grey box the range from the 10 runs of the simulation.

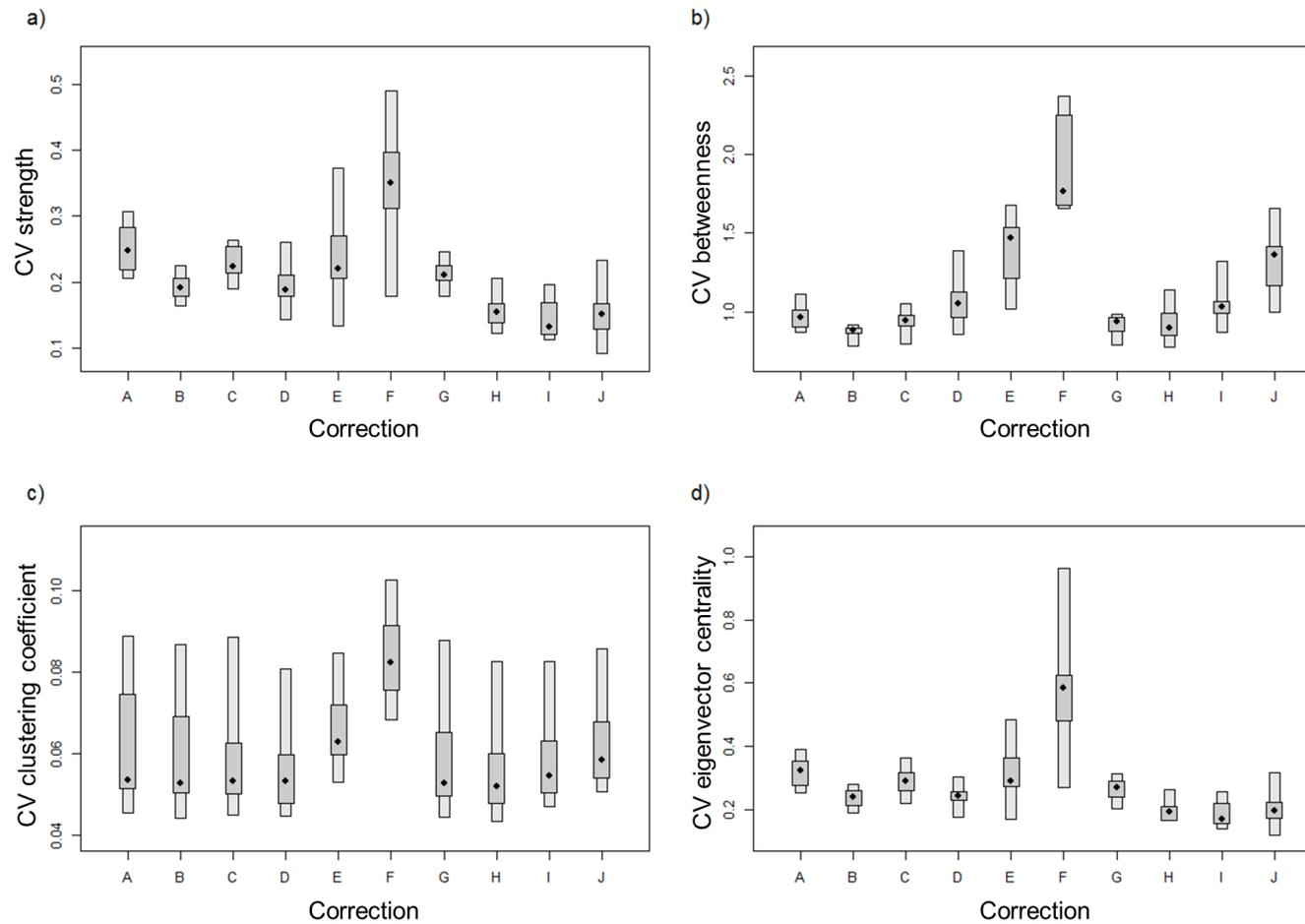


Figure 4.7. The effect of applying different group size corrections on the coefficient of variation of four key network metrics

The effect of the correction applied on social network construction on network-level coefficients of variation for four different network metrics: a) strength, b) betweenness, c) clustering coefficient and d) eigenvector centrality. The black point represents the median value, the dark grey box the interquartile range and the light grey box the range from the 10 runs of the simulation.

Linear Correction

Linear corrections (B) produced network properties similar to uncorrected networks with little difference in the mean or variance in any metrics measured. There was a slight decrease in mean strength (Fig. 4.6a) indicating a reduction in the importance of gregariousness in influencing this measure. The coefficient of variation of all centrality measures (Fig. 4.7) also showed a slight reduction suggesting a stabilising effect of using this correction, presumably also on the influence of gregariousness on these measures.

Threshold models

Mean values of strength (Fig. 4.6a) inevitably declined as stronger corrections were used (thresholds tending towards zero D, E, H and I) due to the adjustments of the association index values used when calculating the networks. There is also an increase in the mean betweenness (Fig. 4.6d) and increase in the coefficient of variation for all metrics (Fig. 4.7) suggesting a less well connected network. Whilst this result is apparent with both a steep threshold (high value of a) and more shallow threshold (low value of a), it is very restricted in the latter case. In fact, whilst the patterns are qualitatively similar for betweenness and clustering coefficient at both threshold gradients (c.f. D and E versus H and I across panels b and c), for strength and eigenvector centrality networks corrected with a shallow threshold are more similar to uncorrected and linear corrected networks (c.f. H and I versus other correction types across panels a and d). When the threshold was set at high values (C and G) the networks produced were, as would be predicted, very similar to uncorrected networks as the threshold was set above the size of most groups.

Inverse corrections

Networks constructed using inverse corrections were the most different to uncorrected networks. Network-level means of all centrality measures (strength, betweenness and eigenvector centrality) were substantially altered when a steep threshold (higher value of α) was used (Fig. 4.6; F all panels), and this pattern persisted for strength and betweenness with a less steep threshold (Fig. 4.6; J all panels). Mean strength and mean eigenvector centrality were reduced when an inverse correction was used, whilst mean betweenness increased. The variation in network metrics was also higher when the threshold was steep (Fig. 4.7; F all panels), and this pattern remained qualitatively similar for strength (Fig. 4.7a) and betweenness (Fig. 4.7b) when a more shallow threshold was used in the inverse model. The increase in variance of betweenness (Fig. 4.7b) and clustering coefficient (Fig. 4.7c) are particularly noticeable relative to other correction types (especially when a steep threshold was used - F versus J). This is strongly indicative that there is reduced connectivity and a much stronger community structure to the networks produced with these corrections. Increased variance in betweenness points to there being a small number of nodes which many shortest paths between individuals in the network pass through. Similarly, the fact that the mean clustering coefficient stays the same whilst the variation increases points to some individuals having higher and some individuals lower values of this metric, a pattern indicative of a more sub-divided network.

Individual level metrics

Figure 4.8 shows the values for regression slopes between individual network metrics in each of the corrected networks with the same values in the uncorrected network for the 10 runs of the simulation. The extent of this decrease varies considerably between different network metrics. Figure 4.9 shows the correlation strengths of these relationships. The key qualitative results are outlined in table 4.2. For clustering coefficient (Fig. 4.8c) the decrease is sufficiently small to make little qualitative difference. An individual's clustering coefficient in any particular network is likely to be predictive of its clustering coefficient in any other network. However, for other network metrics (Figs. 4.8a, 4.8b and 4.8d) the same is not true, and values for a metric in a given network are only predictive in a subset of the other networks.

Linear corrections

It is clear that for all metrics networks in which a linear correction is applied (B) correlate strongly with the uncorrected network. The steepness of the regression slope varies between metrics (Fig. 4.8). For clustering coefficient and eigenvector centrality it is close to one suggesting that the values themselves are very similar to those in the uncorrected networks. For strength and betweenness this not the case, implying that using a linear correction reduces the influence of gregariousness on these measures.

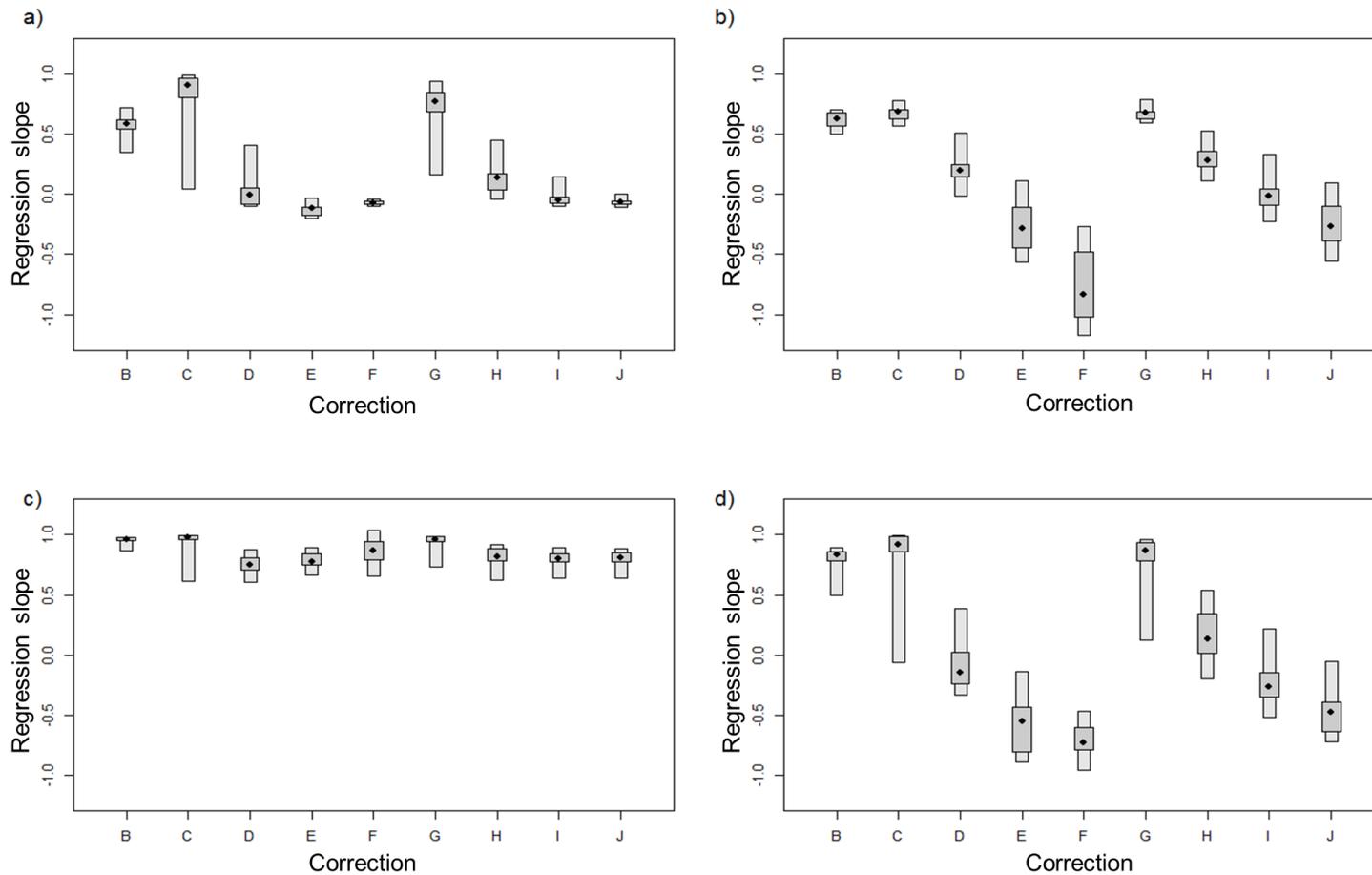


Figure 4.8. The regression slope for the relationship between values of individual network metrics when different group size corrections are used

The regression slope for the linear relationship between individual network metrics in 9 social networks in which association indices have been corrected for group size effects (B-J) and the case in which no correction has been employed (A) for four different network metrics: a) strength, b) betweenness, c) clustering coefficient and d) eigenvector centrality. The black point represents the median value, the dark grey box the interquartile range and the light grey box the range from the 10 runs of the simulation.

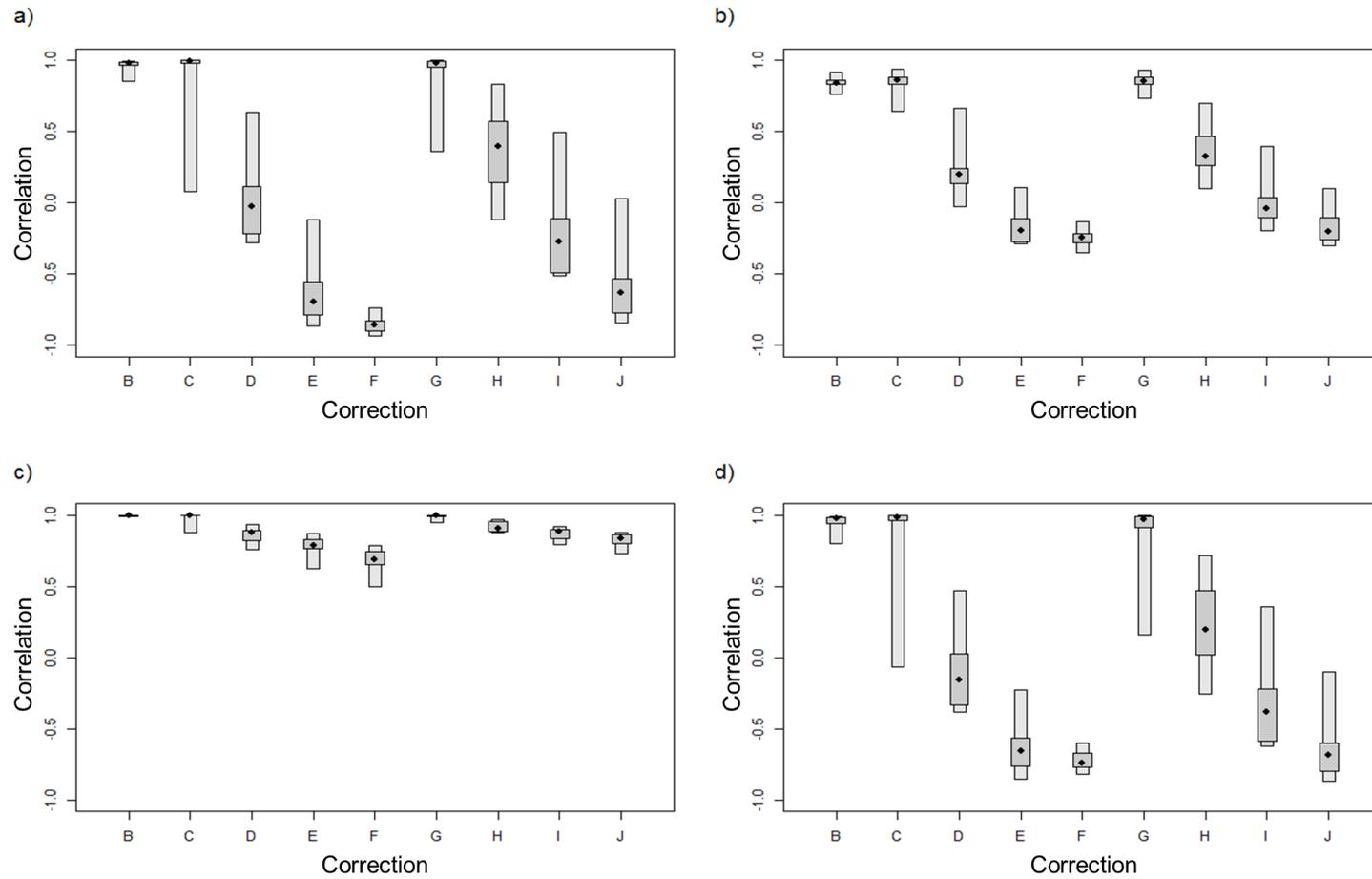


Figure 4.9. The strength of correlation between values of individual network metrics when different group size corrections are used

The correlation of individual network metrics in 9 social networks in which association indices have been corrected for group size effects (B-J) with the case in which no correction has been employed (A) for four different network metrics: a) strength, b) betweenness, c) clustering coefficient and d) eigenvector centrality. The black point represents the median value, the dark grey box the interquartile range and the light grey box the range from the 10 runs of the simulation.

Threshold models

When a threshold model is applied with a high threshold (C and G) individual level metrics correlate strongly with those in the uncorrected network. However, the strength of this correlation decreases as the threshold shifts towards zero (Fig. 4.9) and the slope of the regression becomes considerably smaller than one (Fig. 4.8). For all measures of centrality, intermediate threshold levels result in networks that are uncorrelated with and have intermediate regression slopes to both uncorrected networks and those corrected with the inverse model. The regression slope of strength declines at a slower rate than those for betweenness and eigenvector centrality, however this is likely to be related to the big changes apparent in network-level means of this metric (Fig. 4.6). The strength of correlations and regression slopes also become highly variable between different runs of the simulation indicating that the effect of using these corrections on measures of individual social position is unpredictable at these intermediate levels. When the threshold is close to zero (corrections E and I) the outcome is qualitatively very similar to that obtained by using inverse corrections and is discussed below. Changing the steepness of the threshold makes little qualitative difference to these results (compare C,D,E to G,H,I in each panel), although there is a slight reduction in the rate of decrease in regression slopes for betweenness in particular (Fig. 4.8d).

Inverse corrections

The correlation with uncorrected networks is lowest in the negative exponential models (F and J). Changing the steepness of the threshold makes little qualitative difference to these results (compare F to J in each panel). For

strength (Fig. 4.9a) and eigenvector centrality (Fig. 4.9d) the correlation between the inverse models F and J (as well as threshold models with a low threshold; E and I), and uncorrected networks becomes strongly negative. For betweenness (Fig. 4.9b) the negative correlations are weaker, and correlations are close to zero or only slightly negative. The pattern for the slopes of the relationship is slightly altered. As thresholds at or close to zero the slope of the regression for strength tends towards zero (Fig. 4.8a) indicating that measures of strength in the uncorrected network are not predictive of measures of strength in the corrected network. For betweenness (Fig. 4.8b) and eigenvector centrality (Fig. 4.8d) the regression slopes approaches minus one. This means that high values of one of the metrics in the uncorrected network would predict low values in one of the corrected networks and vice versa. As a result all of these basic centrality measures may be measuring different things depending on how group size is corrected for when networks are constructed, with the reduced effect on the regression slope for strength likely to be caused by the considerable reduction in mean strength in corrected networks.

Correction	Network mean	Network-level variation	Regression
B	slight reduction for strength slight increase for eigenvector centrality	slight reduction for strength slight reduction for betweenness slight reduction for eigenvector centrality	positive relationship for strength and betweenness highly positive relationship for clustering coefficient and eigenvector centrality
C	all metrics similar to uncorrected	all metrics similar to uncorrected	highly positive relationship for strength, clustering coefficient and eigenvector centrality positive relationship for betweenness
D	reduction for strength	slight reduction for strength slight reduction for eigenvector centrality	no relationship for strength, betweenness and eigenvector centrality highly positive relationship for clustering coefficient
E	considerable reduction for strength increase in betweenness	increase for betweenness slight increase for clustering coefficient	no relationship for strength negative relationship for betweenness and eigenvector centrality highly positive relationship for clustering coefficient
F	considerable reduction for strength considerable increase for betweenness	increase for strength considerable increase for betweenness increase for clustering coefficient increase for eigenvector centrality	no relationship for strength highly negative relationship for betweenness negative relationship for eigenvector centrality highly positive relationship for clustering coefficient
G	all metrics similar to uncorrected	slight reduction for strength slight reduction for betweenness slight reduction for eigenvector centrality	highly positive relationship for strength, clustering coefficient and eigenvector centrality positive relationship for betweenness
H	reduction for strength slight increase for eigenvector centrality	reduction for strength slight reduction for eigenvector centrality	no relationship for strength, and eigenvector centrality weak positive relationship for betweenness highly positive relationship for clustering coefficient
I	considerable reduction for strength slight increase for eigenvector centrality	reduction for strength slight reduction for eigenvector centrality	no relationship for strength, and betweenness weak negative relationship for eigenvector centrality highly positive relationship for clustering coefficient
J	considerable reduction for strength slight increase for betweenness slight increase for eigenvector centrality	reduction for strength slight increase for betweenness slight reduction for eigenvector centrality	no relationship for strength weak negative relationship for betweenness negative relationship for eigenvector centrality highly positive relationship for clustering coefficient

Table 4.2. A summary of the key qualitative results for population-level simulations by correction type

Results for network-level properties are in columns one and two. Results for individual network metrics are in column three.

4.5 Discussion

Variation in group sizes generates an important problem when social networks constructed using GoG are used to study social interactions in a population (Croft, James & Krause 2008; James, Croft & Krause 2009; Godde *et al.* 2013). The strength of the assumption is likely to vary in groups of different sizes as the probability of meaningful interactions between individuals changes (James, Croft & Krause 2009). We have shown that within group interactions are highly variable even when only basic agent-based models of random movement are used; depending on the aggregation size and density, inter-individual interaction distances and movement rules. This has implications for the probability of two individuals in a group interacting, and therefore how group size corrections should be employed when constructing social networks. Furthermore, the application of these corrections to network data generated from random social interactions in a simulated population of light-bellied brent geese made considerable qualitative and quantitative differences to the structure of social networks and the position of individuals within them. As a result we would recommend a careful consideration of the questions being asked and the likely intra-group dynamics of a study population before group size corrections are used during social network construction, as this will influence how the validity of the gambit of the group assumption is influenced by group size. We provide guidance on this process later in the discussion.

Using our simulations of within group movement we demonstrated that in groups varying in these properties the probability of interaction could be independent of group size, decline linearly (or nearly so) as group size increased, undergo an exponential decrease similar to the relationship produced using a $\frac{1}{Group\ size-1}$ correction, and follow a threshold model where the

likelihood of interaction changed substantially around a threshold group size. This was despite the fact that only random movement models were used. Variation in the relationship between the probability of interactions and group size were highly dependent on the exact nature of the intra-group dynamics, especially inter-individual density and interaction distances.

The effect of using these different potential corrections during social network construction varied substantially. Using a linear correction for group size resulted in little change from uncorrected networks. However, network-level metrics were very different when a negative exponential was used or as the threshold group size in method 4 tended to zero. These networks typically had much higher mean betweenness, lower eigenvector centrality and much more variation in all metrics measured. These results suggest that networks constructed with these group size corrections are less well connected and more cliquish. This effect was particularly strong when the rate at which values of the association index declined with group size was higher.

Correcting for group size effects also had a considerable effect on individual level network metrics. Centrality measures in networks constructed using inverse models or threshold models close to zero had a negative relationship to the same measures in uncorrected networks, indicating that they were measuring different social properties to each other. This negative relationship between measures in inverse or threshold corrected networks and uncorrected networks was particularly strong for eigenvector centrality, where there was a strong correlation (Fig. 4.9d) on a highly negative regression slope (Fig. 4.8d). Strength also had a strong negative correlation between networks constructed using these corrections compared to the uncorrected network (Fig. 4.9a), but the slope of the regression was closer to zero (Fig. 4.8a). Corrections

at intermediate thresholds were typically not correlated with either uncorrected networks or networks corrected with low thresholds, and applying a linear correction resulted in individual metrics that correlated with those in the uncorrected network. These patterns were, however, highly variable.

Using group size corrections for natural systems

It is clear that the use of group size corrections has a fundamental effect on SNA, whether the focus is at the population level or individual level. In particular, the method most similar to that suggested in recent literature (Darden *et al.* 2009; Edenbrow *et al.* 2011) typically resulted in the biggest changes from the conventional approach to network construction without a group size correction. Therefore, researchers should justify their choice of group size correction carefully based on their knowledge of intra-group dynamics in their study system or the questions they are asking using SNA. This requires a consideration of what aspect of behaviour or ecology is being investigated using networks, which metrics are being used to achieve this and system-specific patterns of intra-group dynamics.

The effect of metric choice

It is clear that different network metrics respond differently to the use of group size corrections, and this may also want to be accounted for when choosing metrics to use in investigations of animal social structure or interpreting the results obtained. For example, the mean eigenvector centrality varies less between different group size corrections than strength at a network level. This indicates that differences in group size have more of an effect on

measures of strength, and that care should be taken when interpreting values of this metric depending on how it is being used. Strength in an uncorrected network therefore measures the gregariousness of individuals as much as providing information on the weight of preferred associations. Increased gregariousness at a population level would also be expected to reduce variation in metrics at a network-level, and this is particularly evident for betweenness. Betweenness measured in corrected networks tends to be higher and more variable. This is indicative of it being better able to capture variation between individuals in how important they are in connecting different components of the network when used in networks corrected using threshold or inverse corrections.

This variation between individual metrics is also likely to be driven to some extent by the influence that individual differences in gregariousness have on their value (Godde *et al.* 2013). For example, strength in particular is highly dependent on the number of individuals in each group that an individual finds itself in. The role of gregariousness in influencing SNA has been investigated in the calculation of half weight association indices (HWI), and an improved association index developed that accounts for the effect of gregariousness (HWIG; Godde *et al.* 2013). This may provide an alternative approach, however it does not directly control for the effect of group size on the strength of GoG, and as such the need to further develop and understand methods of group size correction during social network construction in natural systems is still a priority. For example, it may be interesting to explore how the answers achieved using social network methods vary according to the corrections made, and how this depends on the aspect of behaviour or ecology being studied.

Preferred associations and alliances

Networks constructed with negative exponential or low threshold group size corrections generated more strongly structured networks, as evidenced by increased variation in all key network metrics. This could be of great use to researchers using SNA to develop an idea of social preferences. For example, social networks have often been used to study alliances (Connor, Heithaus & Barre 2001; Lusseau 2003; McDonald 2007; McDonald 2009; Wiszniewski, Brown & Möller 2012; Kurvers *et al.* 2013), and placing more emphasis on interactions in small groups might provide a more powerful approach for detecting alliances and long-term stable associations as strong associations are intuitively more likely to persist in smaller groups.

Familiarity and social preferences are also important in modulating numerous social behaviours (Johnsson 1997; Croft *et al.* 2006; Gilby & Wrangham 2008; Carter *et al.* 2009; MacIntosh & Sicotte 2009), and therefore using group size corrections to increase the importance of interactions in small groups is also likely to be a potentially important consideration in studies that link animal behaviour and social networks (Croft *et al.* 2006; Carter *et al.* 2009; Croft *et al.* 2009; Aplin *et al.* 2013). However, the precise nature of the behaviour investigated should be considered before applying group size corrections in these cases. By using a group size correction to obtain this information, greater emphasis is placed on the importance of interactions in small groups. This is something that will be important in the study of some social behaviours, but less so if familiarity or repeated interactions influence these behaviours at a group-level or alter patterns of collective behaviour. It also minimises the influence of individual variation in gregariousness in a similar manner to Godde *et al.* (2013), and therefore the importance of these

differences in gregariousness in understanding the behaviour being investigated should also be a consideration.

Epidemiological networks

For other uses of social networks it is understanding interaction distances, and how inter-individual density covaries with group size that is most important. The most obvious example here is networks used to explain epidemiological processes (Hamede *et al.* 2009; Danon *et al.* 2011; Bull, Godfrey & Gordon 2012; Weber *et al.* 2013). It is highly likely that meaningful interaction distances vary greatly between pathogens, and this will influence how networks should be constructed. Often disease transfer requires close contact between individuals (Hamede *et al.* 2009; Weber *et al.* 2013), and as a result the probability of meaningful interactions occurring would be reduced considerably in larger groups, and the use of corrected networks may be advisable. However, other pathogens may be infective over much greater distances, or have longer transmission periods, considerably reducing the impact of increases of group size on the probability of interaction. An extreme example illustrating how this might occur is work by Godfrey *et al.* (2009) which demonstrated that a transmission network constructed by connecting individuals that had shared a refuge within 24 hours was a good predictor of parasite transmission in gidgee skinks (*Egernia stokesii*). This work clearly highlights the potential importance of shared space use in the spread of some parasites, and therefore how using uncorrected networks constructed using GoG will be useful in some epidemiological networks.

Information transfer

Another important use of networks in ecology has been to understand patterns of information transfer (Aplin *et al.* 2012; Claidiere *et al.* 2013; Atton *et al.* 2014; Boogert *et al.* 2014). For example, (Aplin *et al.* 2012) found that individual centrality measures in uncorrected networks predicted how quickly individuals would find novel food resources. In this situation, where centrality measures will describe gregariousness and the tendency of individuals to move between groups, using uncorrected networks is likely to be more informative than using networks that greatly reduce the importance of weak interactions. Patch discovery will occur at a group level, so considering the likelihood of interactions within a group is of very limited importance. However, when the focus of information transfer is at a smaller scale, the group size effect becomes more important. For example, social learning can often occur through an individual observing a demonstrator (Heyes 1994; Kavaliers, Colwell & Choleris 2005; Aplin, Sheldon & Morand-Ferron 2013), and an interaction of this nature will be more likely in smaller groups. In addition, empirical work has often demonstrated the importance of familiarity in social learning (Ward, Hart & Krause 2004; Kavaliers, Colwell & Choleris 2005; Atton *et al.* 2014), which furthers the importance of generating more structured networks that place greater emphasis on interactions in small groups. In this area of research it may even be possible to exploit the different information provided by uncorrected and corrected networks to provide some idea of how information transfer occurs. If close interactions or interactions with familiar individuals are important to the process, it would be predicted that group size corrected networks would better predict patterns of information transfer.

A better understanding of within group dynamics

Results from our population-level simulations demonstrate the major impact correcting or not correcting for group size can have on the outcomes of SNA, as well as highlighting how correcting networks may be a powerful way of answering important research questions in a network context. Without knowing how individuals move and interact within groups, and how these interactions differ between different ecological processes of interest, it is impossible to be sure how the effect of group size should be corrected for. By using a basic agent-based model we have demonstrated how differences in movement parameters, flock density and interaction distances can substantially alter how changes in group size affect the probability of individuals interacting in a group. Even with models that solely consider random motion, several possible relationships emerged varying from the probability of interaction being independent of group size to there being a rapid negative exponential decrease in interaction strength as group size increased. One key finding was the relative importance of the relationship between group size and density in influencing how interaction probabilities declined with group size. Further work focussed on understanding intra-group dynamics would therefore also be highly beneficial, especially in exploring the role of random versus non-random movement rules in affecting these processes.

Agent-based models of collective motion are becoming increasingly well-developed (Couzin *et al.* 2002; Couzin & Krause 2003; List, Elsholtz & Seeley 2009; Cavagna *et al.* 2010; Bode, Wood & Franks 2011; Sueur, Deneubourg & Petit 2011; Ioannou, Guttal & Couzin 2012; Miller *et al.* 2013), and developing a framework in which these can be applied to parameterise intra-group social dynamics in different systems would further improve our knowledge of when

and how to use group size corrections when constructing social networks. In particular, by adding basic interaction rules based upon attraction, alignment and repulsion (Couzin & Krause 2003), and potentially varying these rules according to social preferences or past interactions (Bode, Wood & Franks 2011) it should be possible to model a wide range of biologically realistic scenarios. If these more complex agent-based models of collective motion can be developed in a way to make them widely applicable simply with system-specific parameter changes, then these models will be incredibly powerful in directing future methods of social network construction.

5. Social and spatial explanations for dynamic social interactions in a migratory wildfowl population



5.1 Abstract

Many animals form dynamic fission-fusion social systems with the resultant patterns of social associations being fundamental in determining many key ecological phenomena, such as disease dynamics and the benefits of group foraging. The roles of spatial and social factors in determining this social structure will be an important influence on the temporal dynamics of the social associations that result. However, these spatio-temporal dynamics remain poorly understood, especially in migratory populations. We use social network analysis to describe the spatio-temporal dynamics of social structure and stable social associations in a migratory wildfowl population. We demonstrate that high levels of site fidelity are fundamental in driving the generation of non-random social structures in this system, and that low levels of adult dispersal result in population social structures that show high inter-annual stability. However, we show that a purely spatial explanation for these patterns of social interactions is not satisfactory, with individuals forming stronger associations with fewer individuals than purely spatial patterns of interactions would predict. Furthermore, these social associations are somewhat stable throughout staging periods, even when individuals move to exploit different resources. Despite there being considerable evidence for stable associations persisting both within single staging periods and between years, there is no evidence for stable social bonds persisting throughout each annual cycle. This research raises interesting questions about how the evolution of limited dispersal and site fidelity might be closely interlinked with the development of long-term stable social associations, as well as having important implications for understanding of disease dynamics in migratory populations.

5.2 Introduction

Fission-fusion social systems, in which group sizes and membership are spatio-temporally dynamic (Couzin 2006; Couzin & Laidre 2009; Sueur *et al.* 2011b), are widespread in animals (Sueur *et al.* 2011b; Silk *et al.* 2014). Patterns of social interactions in these dynamic fission-fusion societies are often highly complex (Wittemyer, Douglas-Hamilton & Getz 2005; Couzin 2006; Pinter-Wollman *et al.* 2013; Silk *et al.* 2014), and are greatly dependent on individual differences (Wilson *et al.* 2013) as well as variation in the social and ecological environment (Sueur *et al.* 2011b). Fission-fusion social dynamics, and the strategies of individuals within them, are likely to have a major influence on several key population level processes. For example, information transfer has been closely linked to social structure in squirrel monkeys (Claidiere *et al.* 2013), and variation in individual social strategy influences the rate at which this information is acquired in mixed-species social systems of passerines (Aplin *et al.* 2012). These population-level processes will be highly dependent on the temporal dynamics of fission-fusion social structures (Pinter-Wollman *et al.* 2013). However, despite this there has been little research into the temporal dynamics of fission-fusion societies in animals (see Pinter-Wollman *et al.* 2013). Temporal social dynamics are likely to be especially pronounced in migratory species, as variation in the ecological environment across the migratory cycle of these species will alter the social dynamics that result (Cortes-Avizanda *et al.* 2011). Understanding social dynamics across the annual cycle of these populations will have important implications in understanding social behaviour and epidemiology. The latter has important applications as migratory populations are of particular interest from a disease perspective (Chen *et al.*

2005; Hoyer *et al.* 2011), and the social dynamics that occur across the annual cycle will be fundamental in underpinning their epidemiology.

Space use plays an important role in structuring social interactions in many fission-fusion systems (Wolf & Trillmich 2008; Mourier, Vercelloni & Planes 2012; Carter *et al.* 2013; Shizuka *et al.* 2014), but its role is particularly interesting in migratory populations. Migratory populations occupy different areas at different points of their migratory cycle and yet often display limited dispersal and high levels of site fidelity (Hansson *et al.* 2002; Winkler *et al.* 2004; Harrison *et al.* 2010; Buchanan *et al.* 2012). This creates several possible scenarios for the persistence of social structures and individual-level patterns of social associations across annual cycles and between years. If adult dispersal is constrained then patterns of social associations within staging periods would be expected to persist between years. However, empirical evidence for this is scarce with only one recent social network example from a fission-fusion population. Golden-crowned sparrows *Zonotrichia atricapilla* maintain social associations between years in a complex fission-fusion social system during winter staging with both spatial and social explanations being important (Shizuka *et al.* 2014). Equally little empirical research has investigated the persistence of non-family social associations across the annual cycle of migratory species. The limited evidence available, from greater snow geese *Anser caerulescens atlantica* (Desnoyers, Gauthier & Lefebvre 2012) and humpback whales *Megaptera novaeangliae* (Valsecchi *et al.* 2002), points to social associations not persisting between different points of the migratory cycle. However, no studies have considered social associations within the context of the population social structure at multiple points in the annual cycle of a migratory species. This will be important as an understanding of the relative

role of spatial constraints in explaining non-random patterns of social associations within staging periods, and their dynamics across the annual cycle, would provide valuable insights into the evolution of social behaviour and social systems in migratory populations. In particular, dynamic patterns of social associations would be expected to have a major influence on changes in social foraging behaviour across the annual cycle in these systems.

Non-random social associations in fission-fusion social systems are suggested as being key in determining beneficial alterations to social foraging behaviour in such systems (Silk *et al.* 2014). There is widespread empirical evidence for previous social associations among group members - familiarity - reducing aggression (Johnsson 1997; Utne-Palm & Hart 2000; Griffiths *et al.* 2004) and vigilance (Roberts 1988; Carter *et al.* 2009; MacIntosh & Sicotte 2009; Gaynor & Cords 2012), and thus increasing foraging efficiency (Griffiths *et al.* 2004). Increased familiarity as a result of repeated previous social interactions can alter behavioural interactions between both kin (e.g. Frommen & Bakker 2004, Edenbrow & Croft 2012) and non-kin (Kurvers *et al.* 2013), and is likely to be especially pronounced when social hierarchies are important mediators of social behaviour in foraging groups, as they will be stabilised by repeat interactions between individuals (Utne-Palm & Hart 2000; Hsu, Earley & Wolf 2006). The benefits of interacting with familiar individuals can be accrued irrespective of the process that drives previous interactions, so in this regard non-random social structures driven entirely by spatial factors would still have a beneficial effect on social behaviour. However, it would be expected that the benefits obtained would be further enhanced if additional social factors contributed to generating repeated interactions, meaning that patterns of space use and the development of non-random social associations will be very closely

linked. This will be especially important in the context of migration. However, without an understanding of what drives the temporal dynamics of social associations in these populations, it is not possible to fully recognise their influence on social behaviour in foraging groups.

We use a social network approach to investigate social dynamics at multiple points in a migratory cycle for the first time using staging populations of the east Canadian high arctic (ECHA) population of light-bellied brent geese (*Branta bernicla hrota*). Using a social network approach enables us to quantify individual social network positions and place them in the context of social interactions at a population level. This population is migratory and exhibits a highly dynamic fission-fusion social system during winter and spring staging. Individuals roost communally in intertidal areas before forming large, ephemeral flocks feeding on intertidal areas or coastal terrestrial grasslands. Membership of these foraging flocks is highly dynamic and small groups or individuals frequently move between different foraging groups. However, despite the high turnover rate of membership of foraging flocks, they typically show low levels of dispersal and high levels of site fidelity in site choice during these staging periods (Harrison *et al.* 2010). Additionally, dominance hierarchies remain important in driving social behaviour within these groups (Inger *et al.* 2006a).

We explore the role of social and non-social processes in explaining social network structure at different stages of the annual cycle of this species. First we investigate the factors shaping non-random social structure in winter and spring staging populations. We predict that spatial constraints will be important in driving much of the coarse-level social network structure in these populations, but that additional social factors will also be important at finer-scales meaning that networks differ from those constructed using models that

account for only these spatial factors. In particular, we hypothesise that individuals form preferred associations that result in them forming fewer but stronger associations than predicted by null models. We then explore how social associations change within a winter staging period as individuals move from intertidal to terrestrial foraging. If preferred social associations are important in determining social network structure, then social networks would be predicted to be correlated between these two foraging periods even once spatial factors have been accounted for. We then use data from our winter and spring staging populations to compare the population-level social structure between seasons and examine the persistence of social associations across the migratory cycle. It is predicted that high levels of site fidelity in staging site selection may limit the importance of social preferences driving migration strategies, and thus that persistent social associations among different staging seasons would be infrequent (Harrison *et al.* 2010). Finally, we determine the inter-annual stability of social associations within each staging period, predicting that pairs (dyads) of individuals will tend to remain in the same social network communities due to the benefits obtained from site fidelity and repeated interactions with other individuals. Together these approaches will provide us a better insight into the temporal dynamics of social structure and patterns of individual social associations in a migratory population.

5.3 Methods

Study system

Data were collected in winter and spring staging populations of ECHA light-bellied brent geese between January 2012 and December 2013. The study

populations used were Dublin Bay, Ireland (winter) and Alftanes, Iceland (spring). In these populations ~10% of geese were marked with alphanumeric-coded colour leg-rings that made them uniquely identifiable. This enabled social and spatial information about these ringed individuals to be gathered in both populations. Previous work has demonstrated the potential to use partial networks based on small samples of a population (Chapter 3). Sites were selected as a result of being important winter and spring staging sites for this population, having a relatively high proportion of marked individuals and a high density of volunteer observers to provide supplementary data.

Data collection

Data collection was split into three periods: early winter (EW; 1st November – 31st December), late winter (LW; 16th January – 16th March) and spring (S; 29th April - 29th May). Data were collected for each staging period was collected in two years (EW: 2012 and 2013, LW: 2011 and 2012, S: 2011 and 2012). The principal observer (MJS) was present for the majority of each of these study periods but additional data submitted to the Irish Brent Goose Research Group (IBGRG) resightings database by highly experienced observers were also used to supplement these observations for each winter study period, but not for spring staging periods. For records from volunteer observers, only observations of terrestrial foraging flocks were included due to it being easier to define distinct foraging locations for these records.

The principal observer and team conducted observations in a structured manner. During spring staging observations were conducted on a fixed route three times on each day that observers were present. This ensured all sites were visited regularly and that observations of social associations were

conducted over a timeframe which made them independent observations. Observations during early winter staging were conducted on intertidal sites two hours either side of low water and at terrestrial sites at other times. Observations during winter staging periods were conducted on a more opportunistic basis, but all core sites were visited on at least one occasion each day. Additional data collected along with the individual ring combinations were date, time, location and flock size. It was also noted whether flocks were observed feeding on terrestrial, saltmarsh or intertidal areas. Family bonds (i.e. partners and offspring) were also recorded where possible. Individuals were classified as being adults in family groups (with a count of juveniles), paired adults, unpaired adults, juveniles in family groups or unassociated juveniles. Assignment to families required individuals to be found in close proximity and exhibit spatially and temporally coordinated movements (Inger *et al.* 2006a). Duplicated records were removed from the data used to construct social networks.

Spatial analysis

Location data associated with each resighting of an individual was used to provide home (foraging) range information for that individual. For winter staging periods this was done separately for intertidal and terrestrial foraging behaviour as well as for the entire dataset. Home range areas were only generated for individuals that had been resighted 10 or more times to increase confidence of home range estimates. Home ranges were calculated using bivariate normal kernels in the package `adehabitatHR` (Calenge 2006) in R 3.1.1 (R development Core Team 2014) for all of these individuals that were observed at more than one distinct location (sample sizes are available in Table

5.1). Home range overlaps were calculated by computing the volume of the intersection of two home ranges (method “VI” in adehabitatHR). This measure of overlap was selected as it has previously been demonstrated to be the most robust method with small sample sizes of relocations (Fieberg & Kochanny 2005). Home range centroids were determined by calculating the mean x and y coordinates for all resightings of an individual. A distance matrix of distances between home range centroids was then computed. As we were only interested in the extent of home range overlap and the distance between home range centroids we made no effort to control for the effect of the number of resightings on individual home range areas. However, when only individuals resighted 10 or more times were included, this effect was minimal.

Population	Staging period	Year	Size of network	Resighted >10 times (individuals for which home range area calculated)	Resighted >5 times
Dublin	EW	2012	369	185 (184)	280
Dublin	EW intertidal	2012	239	25 (-)	92
Dublin	EW	2013	317	92 (71)	232
Dublin	LW	2012	449	199 (197)	315
Dublin	LW	2013	429	214 (214)	316
Iceland	S	2012	373	225 (218)	307
Iceland	S	2013	339	213 (195)	270

Table 5.1. Sample sizes for social network construction and home range area calculations

Social network analysis

Social networks were constructed by assuming that two individuals that co-occur in a foraging group were associated (Whitehead & Dufault 1999). Distinct foraging groups were defined using a chain rule (Croft, James & Krause 2008) that defined individuals as being in distinct groups if there was a separation of 50 metres (a distance based on preliminary observations and previous literature: e.g. Pays *et al.* 2007) or more or they were split by an

artificial barrier (e.g. a road or fence-line). This information was used to construct social networks for the overall dataset, and in the case of EW data, separately for intertidal and terrestrial observations.

Social networks were constructed for each study period. Networks were created using half weight association indices (HWI; Whitehead 2008). HWI matrices were calculated to account for it being more likely that two geese were encountered in the same group. No group size corrections were used in the calculation of these metrics as geese are fairly mobile within foraging groups, making it likely that the GoG is appropriate in almost all group sizes encountered (Chapter 4). Social networks containing all observations from a study period were constructed for each of the six periods (see Table 5.1 for the size of networks constructed). Additionally, a seventh network for early winter staging in 2012/2013 was constructed using only data from intertidal foraging sites.

From these networks a range of key individual-level and population-level network metrics were calculated. Node-level metrics calculated and the reasons for their use are summarised in Table 5.1. To compare the inter-annual stability of networks the “fastgreedy” community detection algorithm in the R package igraph (Csardi & Nepusz 2006) was used to assign individuals to communities. The number of communities was determined by optimisation of modularity scores, which measure the relative number of connections formed within and between social communities. This algorithm was used as it was time-efficient relative to betweenness-based methods and never failed to run in simulated datasets (this was an occasional problem when using eigenvector-based methods). The results obtained in the observed datasets were, however, robust to the choice of community detection algorithm.

Metric	How is it calculated?	What does it measure at an individual level?	What does it measure at a network level?
Degree	A count of the number of edges connected to a node	The number of social associations an individual has	Gives an idea of the density of connections in the network
Strength	A sum of the total weight of all edges connected to a node	The total value of all the connections an individual has	Network-level mean describes typical gregariousness and association weight
Mean association strength	Mean weight of all edges attached to a node	The frequency with which an individual interacts with the same individuals	Network-level mean association strength provides a measure of mixing or structure in the network
Coefficient of variation	Coefficient of variation of an individual's associations to all other individuals in the population	Provides a measure of the strength of individual social preference. Few, strong connections will result in a high value. Lots of weak connection will result in a low value	Mean provides an alternative measure of network density and structure
Betweenness	The number of shortest paths passing through a node	A measure of how important an individual is in connecting different parts of the network	Network-level mean and variation in betweenness help describe how structured a network is
Eigenvector centrality	The node's value in the eigenvector corresponding to the maximum eigenvalue from the association matrix	A measure of the importance of an individual in the network – its second order centrality	Network-level mean describes how well-connected the network is

Table 5.2. Details of the key network metrics used in Chapter 5 and what they measure at an individual and population level

The variation in all network-level metrics can be used to describe variation in individual social strategies.

Construction of null networks

Null models for social network structure were constructed using two methods to enable us to test the importance of spatial constraints in driving patterns of social associations. In method A individuals were re-assigned to groups randomly. In method B the locations of all groups were also maintained from the observed data, and individuals could only be re-assigned to a group if they had occurred at that location in the real dataset. This applied a spatial constraint on the ability of individuals to form social associations in this set of null models. Method B, therefore, represents an expectation of the social structure that would result if social associations existed purely as a function of spatial constraints on the probability of co-occurrence in a social group. Thus, any additional variation is explained either by very fine-scale patterns of space use or social factors, two processes that are likely to be inherently related.

Both methods involved re-assigning individuals to groups, with the number and size of groups maintained from the observed data. The order of individuals and groups was randomised before each re-assignment. For both methods individuals could also only be assigned to a group once. If individuals remained at the end of the re-assignment process that couldn't be assigned to any of the remaining groups they were added to a randomly selected existing group that re-assignment rules allowed them to occur in. This resulted in some groups differing in size from their corresponding groups in the observed dataset. However, these changes had a negligible effect on the data structure, especially as there were a variable proportion of ringed birds in each flock in the observed dataset anyway.

For each type of null model 1000 random sets of social information were generated and used to construct social networks to be compared to the observed network for each study period.

Statistical analysis

All analyses were conducted in R 3.1.1 (R development Core Team 2014) unless otherwise stated.

1. The role of spatial and social factors in social structure

In order to test whether social network structure was non-random relative to the assumptions of random social interactions, the mean and variance of a selection of key network-level metrics (Table 5.1) in observed networks were compared to the equivalent values in null models constructed without spatial constraints (method A). Observed networks were then compared to the equivalent values in null models constructed with spatial constraints (method B). This made it possible to determine whether the observed social networks differed from those expected from random social interactions constrained by individual home ranges.

Matrix regression tests were then conducted in the sna package (Butts 2008; Butts 2014) to test the relationship between social association strength (using HWI association matrices) in the observed networks and home range overlap and distance between home range centroids. Models were fitted using ordinary least squares and their statistical significance tested by using QAP

permutation tests to generate confidence intervals (Dekker, Krackhardt & Snijders 2007).

2. Temporal stability of social structures within staging periods

Data from the 2012/2013 winter staging period (the winter for which we had high resolution data from both study periods) were used to quantify the similarity of social associations between intertidal EW and LW networks. This approach used networks containing only individuals that occurred in both the intertidal EW (five or more resightings) and LW periods (10 or more resightings). A lower threshold was used for intertidal networks as less data were available, and birds showed higher levels of site fidelity during this period. Matrix regression methods (see above) were employed to determine the stability of social associations between these periods by modelling how association strength and distance between home range centroids during intertidal foraging explained association strength and home range overlap in the LW period. Distance between centroids was used for intertidal data, as high levels of site fidelity meant many individuals used only one intertidal site, preventing a home range from being calculated. Using this measure also limited the effect that using a smaller number of relocations for this dataset might have. A random individual from each pair was excluded from these analyses if both members of a pair were colour-ringed. Otherwise there would be multiple measures from a single family, which are known to act as a single cohesive unit in this species (Inger *et al.* 2006a; Harrison *et al.* 2010). If social associations during intertidal foraging are maintained later in the winter then they would be predicted to improve model fit when modelling association strength more than when modelling home range overlap of the LW data. In addition, the frequency

of dyads in which connections were a) maintained, b) gained or c) lost between intertidal EW and LW networks was calculated to establish the nature of changes in social associations between these periods.

3. Changes in social structure across the annual cycle

Population-level network metrics (see Table 5.1) were used to compare social networks constructed for each section of the annual cycle. Networks constructed for intertidal foraging flocks during the EW period, terrestrial foraging flocks during LW and the overall dataset for the S period were compared. A descriptive rather than statistical approach was used as differences in network size and composition complicates informative statistical analysis (Croft, James & Krause 2008). The persistence of social associations between winter and spring staging was also tested for both 2012 and 2013 using mantel tests in the package *vegan* (Oksanen *et al.* 2013) on the two pairs of association matrices of individuals observed five or more times in each staging period. As previously, one individual from a pair was excluded from these analyses if both members of a pair were colour-ringed.

4. Inter-annual stability of social network structure

Community assignment data were used to test the stability of social relationships between years. Only individuals resighted 10 or more times in both years (148 individuals for LW, 151 individuals for S) were used in the final analysis to ensure confidence in their social position. For LW and S periods all dyads were scored as being in the same or a different community in each year; being assigned a one if they were in the same community or a zero if not.

These values were placed in an n by n matrix, with n corresponding to the number of individuals in the analysis. The two matrices corresponding to each year (2012 and 2013) were then summed for each staging period. This resulted in all dyads having a score of two (occurred in the same community in both years), one (occurred in the same community in only one year) or zero (occurred in the same community in neither year). The same process was then repeated in 100 pairs of random (method A) and spatially-constrained random (method B) networks for each staging period of interest, to generate a predicted normal distribution under these two scenarios. The frequency of individuals sharing a community in both years, just one year or in neither year in the observed networks was then compared to these normal distributions. Tests for significance were performed by calculating Z-scores, with p values adjusted following the Bonferroni correction for multiple testing.

5.4 Results

1. The role of spatial and social factors in generating social structure

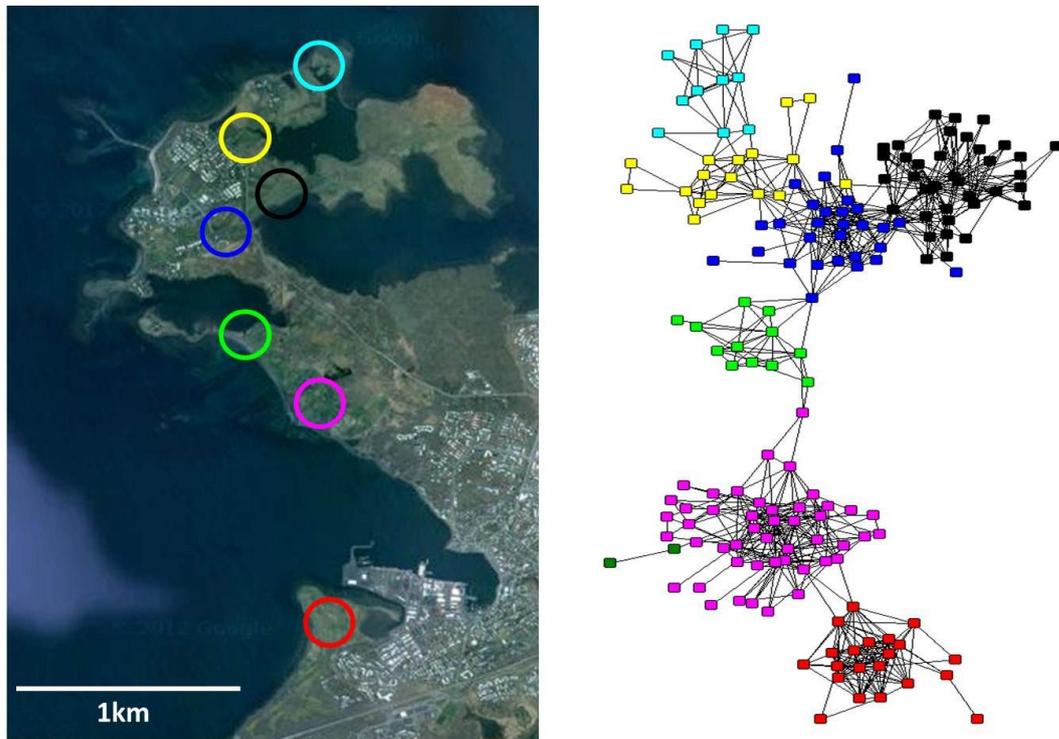


Figure 5.1. A typical social network from a light-bellied brent goose staging population
 Edges have been filtered to only connect individuals that have co-occurred on 5 or more occasions. Colours represent social communities as assigned by the Girvan-Newman algorithm in NetDraw. Coloured circles on the satellite image map the corresponding social communities to their broad geographic locations.

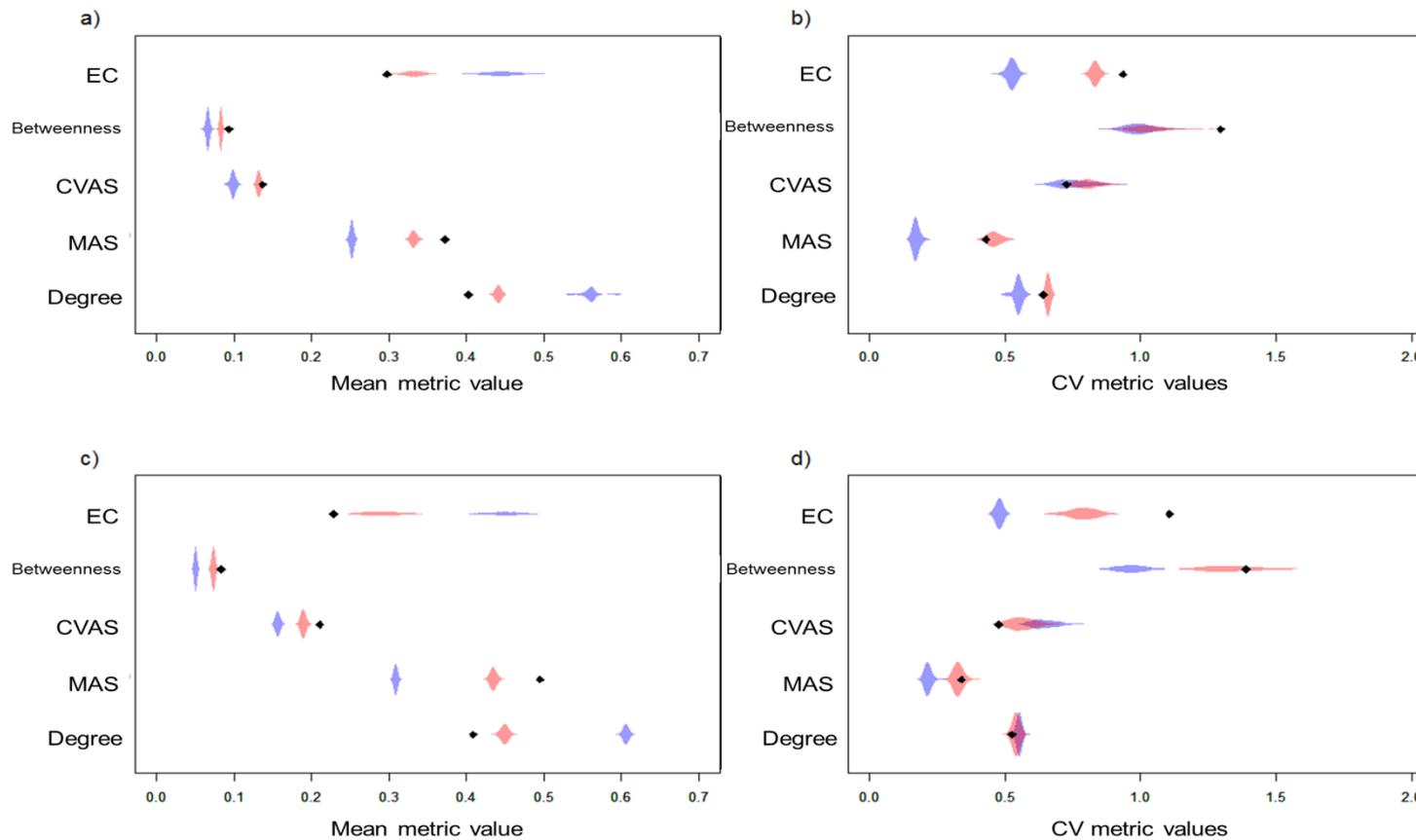


Figure 5.2. A comparison of network-level metrics in observed and randomised networks

The mean and coefficients of variation of five key network metrics for the Dublin late winter network (a and b) and Iceland spring network (c and d) in 2012. Mean network metrics are represented as a proportion of the maximum observed measurement of that metric in a given network to enable them to be presented on the same scale. Black points represent values obtained from the real, observed network, blue distributions represent the values obtained from 1000 randomised null networks and the red distributions represent the values obtained from 1000 spatially constrained null networks. EC is eigenvector centrality, CVAS is the coefficient of variation of association strength (including all possible associations) and MAS is mean association strength.

Light-bellied brent goose social networks display a non-random social structure (Fig. 5.1, Fig. 5.2) in all staging periods. Association strength in all observed networks was closely correlated with home range overlap. Models containing just an effect of home range overlap were better supported than models containing just distance between home range centroids or a combination of the two in all staging periods (Table 5.3, and see Table 5.1 for sample sizes). These spatial relationships explained between 33.9 and 56.7% of variation in social association strength, indicating that non-spatial factors must also be important in explaining social network structure in all staging periods.

In all periods randomised networks constructed with spatial constraints provided a better description of network properties than those constructed without spatial constraints (Fig. 5.2). However, observed networks were still different from these spatially constrained null networks, providing further evidence for the importance of non-spatial factors. In observed networks individuals tended to form fewer but stronger associations than predicted by either set of null networks (e.g. Fig. 5.2a and 5.2c). Observed networks generated from terrestrial foraging data also tended to have higher mean betweenness and lower mean eigenvector centrality than predicted by either set of null networks (Fig. 5.2a and 5.2c), but this pattern did not persist in EW networks when many birds were foraging predominantly intertidally (e.g. comparison to spatial null networks: betweenness $Z=0.01$, $p=0.99$; eigenvector centrality $Z=-1.74$, $p=0.082$). This suggests that variation in space use is more important in explaining betweenness values when birds are foraging intertidally, with additional factors important during terrestrial foraging. Variation in network metrics tended to be similar between observed networks and the spatially-

constrained null models (Fig. 5.2b and 5.2d). However, in terrestrial networks eigenvector centrality was more variable than in null networks, indicating the individuals were more variable in their second-order connectivity than expected even in spatially-constrained null networks.

Population	Staging period	Year	Best model	r ²	F	Effects size of home range overlap
Dublin	EW	2012	home range overlap only	0.339	10200	0.285
Dublin	EW	2012	distance between centroids only	0.270	6238	NA
Dublin	EW	2012	overlap and distance	0.380	5167	0.252
Dublin	EW	2013	home range overlap only	0.377	1503	0.339
Dublin	EW	2013	distance between centroids only	0.228	733	NA
Dublin	EW	2013	overlap and distance	0.381	765.9	0.302
Dublin	LW	2012	home range overlap only	0.366	11130	0.302
Dublin	LW	2012	distance between centroids only	0.287	7769	NA
Dublin	LW	2012	overlap and distance	0.377	5851	0.236
Dublin	LW	2013	home range overlap only	0.567	29820	0.390
Dublin	LW	2013	distance between centroids only	0.416	16200	NA
Dublin	LW	2013	overlap and distance	0.567	14920	0.379
Iceland	S	2012	home range overlap only	0.417	16900	0.273
Iceland	S	2012	distance between centroids only	0.122	3273	NA
Iceland	S	2012	overlap and distance	0.417	8450	0.273
Iceland	S	2013	home range overlap only	0.430	14280	0.270
Iceland	S	2013	distance between centroids only	0.141	3107	NA
Iceland	S	2013	overlap and distance	0.430	7143	0.272

Table 5.3. A summary of the relationship between individual utilisation distributions and social association strength in the six staging periods studied

The results of the three models tested is presented, with the best model in bold.

2. Dynamics of social networks during winter staging

Social associations present during intertidal foraging persisted during the LW period when individuals foraged on terrestrial grasslands ($r^2=0.150$, $F=152.4$, $n=42$, $p<0.001$; Fig. 5.3). This resulted in some stability in social interactions throughout a staging period. When social relationships in LW were modelled with social associations and intertidal home range information from EW intertidal foraging as explanatory variables (for 42 individuals for which sufficient information was available), both were found to be significant in the final model ($r^2=0.286$, $F=173.4$; association strength $p=0.045$, distance between centroids $p<0.001$). When the same explanatory variables were used to explain home range overlap in LW (for the same 42 individuals) only home range information had a significant effect ($r^2=0.371$, $F=254.9$; association strength $p=0.601$, distance between centroids $p<0.001$), demonstrating that previous social associations formed during intertidal foraging were important to some extent in explaining social associations later in the staging period, but home range overlap was independent of previous associations. The change in foraging strategy from intertidal to terrestrial feeding did result in a change in the population social structure. LW networks tended to be less highly structured (LW network density = 0.044, EW intertidal network density = 0.026), with many associations in LW networks being newly formed (Fig. 5.4).

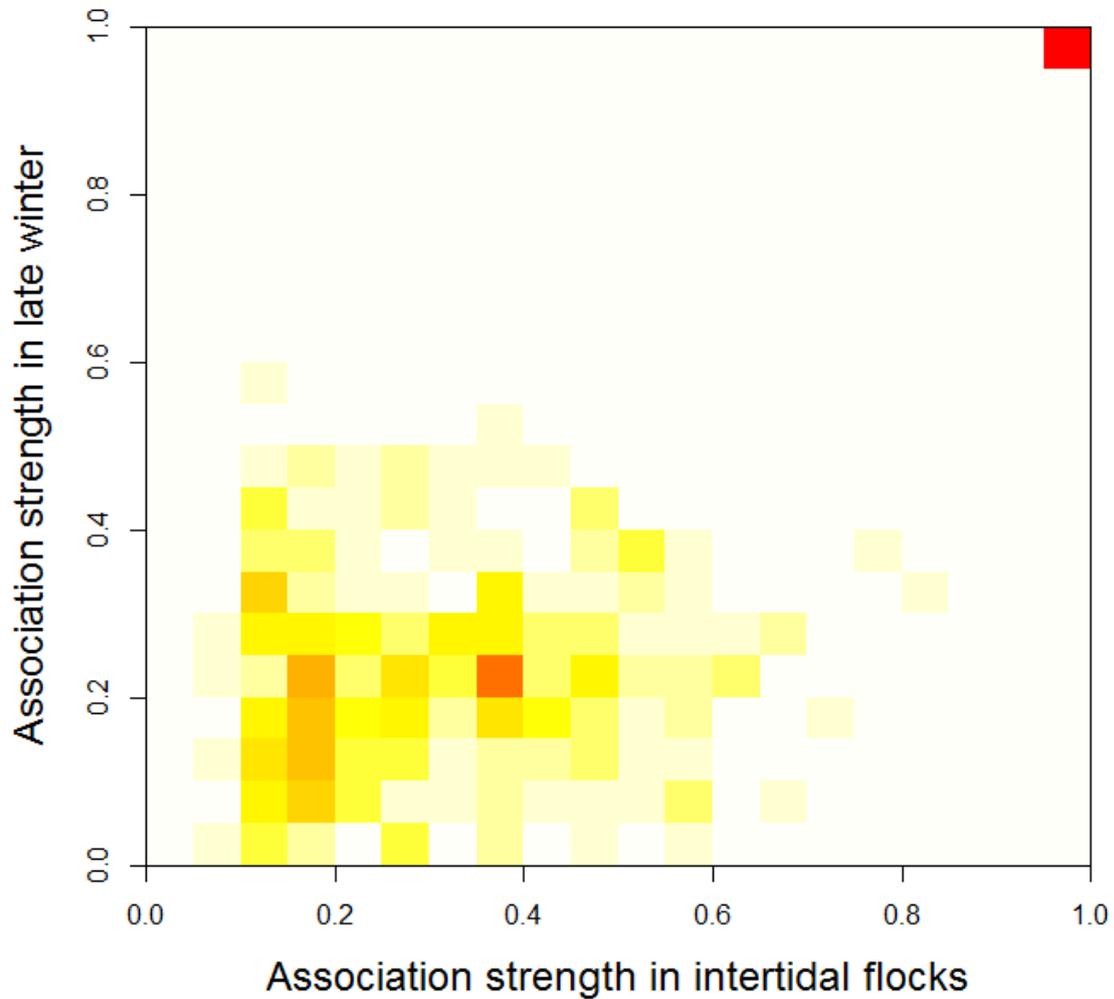


Figure 5.3. The relationship between association strength in intertidal and terrestrial networks during winter staging

A 3-D histogram showing the correlation between association strength when foraging intertidally and association strength in terrestrial foraging flocks later in the winter for Dublin in winter 2012/2013. Darker colours represent a higher frequency of dyads possessing associations of that strength in each network.

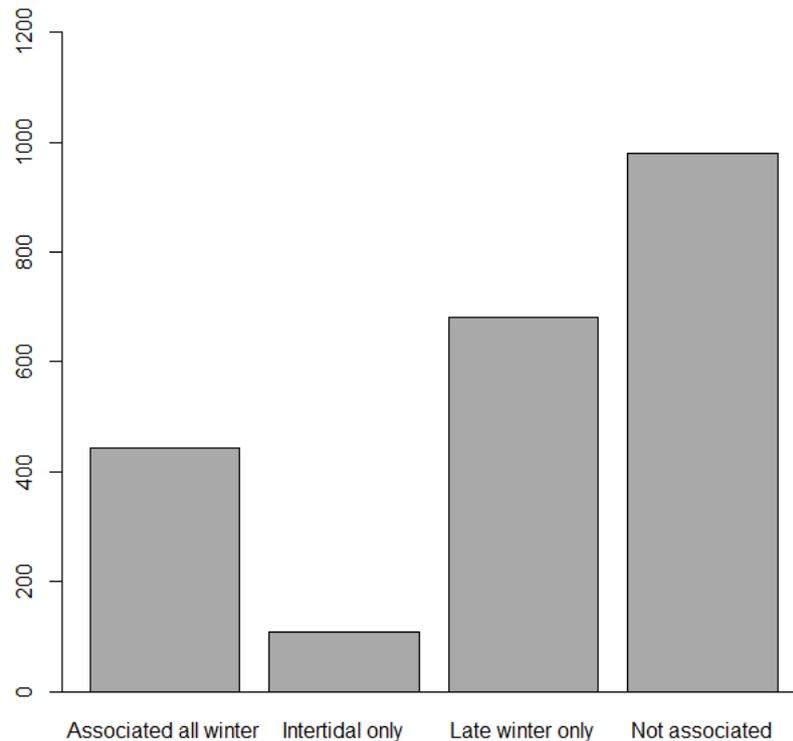


Figure 5.4. Changes in associations between intertidal and late winter networks

The frequency of different changes in social associations between all individuals resighted regularly in both EW and LW networks in Dublin Bay in 2012/2013. The height of the bars represents the number of dyads for each type of change.

3. Dynamics of social networks between staging periods

Structure in social networks is broadly similar between different staging periods, despite differences in habitat and local topology (Table 5.4). Figure 5.2 shows the mean network metric values for LW (Dublin) and S (Iceland) 2012 (in proportion to the maximum observed value of that metric in the network) and additionally their coefficients of variation. It can be seen that for all metrics the values in these networks are very similar (Fig. 5.2, Table 5.4). Individuals

typically form a very similar number of connections of similar strength in both LW and S staging periods relative to the maximum that occurs. In Iceland the mean coefficient of variation tends to be higher relative to the maximum value, suggestive of individuals having a more restricted set of social associations during this period. This pattern is more pronounced in intertidal networks, in which mean eigenvector centrality was lower and mean association strengths higher, suggesting that this network was much more structured. Variation in all key network metrics were similar in all staging periods investigated.

However, there is no evidence from these study populations that social relationships persist in light-bellied brent geese outside pair or family bonds. Despite Dublin Bay and Álfanes being important staging population containing several hundred marked individuals only 46 individuals from 39 family units were observed five or more times at each study site in 2012, and 42 individuals from 36 family units were observed on five occasions or more at each study site in 2013. Once only one member of each family unit was included in analyses there was no correlation between association strength during winter staging and spring staging in either year (2012: $r = -0.011$, $n=39$, $p=0.583$; 2013: $r=0.010$, $n=36$, $p=0.366$; Fig. 5.5). For example, in 2012 most dyads observed in both staging seasons were weakly related in each staging season, some were relatively strongly associated in Dublin but lost these associations in Iceland and only four non-pair dyads were relatively strongly associated in each (Fig. 5.5).

Pop	Season	Year	Size of network	Metric	Network-level mean	Max value	Mean as a proportion of the maximum value
Dublin	EW intertidal	2012	239	Degree	20.7	76	0.272
Dublin	EW intertidal	2012	239	Mean association strength	0.331	1	0.331
Dublin	EW intertidal	2012	239	Coefficient of variation	5.54	15.5	0.357
Dublin	EW intertidal	2012	239	Eigenvector centrality	0.177	1	0.177
Dublin	EW intertidal	2012	239	Betweenness	257	4761	0.054
Dublin	LW	2012	449	Degree	114	283	0.403
Dublin	LW	2012	449	Mean association strength	0.186	0.500	0.372
Dublin	LW	2012	449	Coefficient of variation	2.90	21.2	0.137
Dublin	LW	2012	449	Eigenvector centrality	0.297	1	0.297
Dublin	LW	2012	449	Betweenness	347	3736	0.093
Dublin	LW	2013	429	Degree	110	226	0.487
Dublin	LW	2013	429	Mean association strength	0.199	0.479	0.415
Dublin	LW	2013	429	Coefficient of variation	2.61	12.1	0.215
Dublin	LW	2013	429	Eigenvector centrality	0.259	1	0.259
Dublin	LW	2013	429	Betweenness	358	4907	0.073
Iceland	S	2012	373	Degree	67.5	165	0.409
Iceland	S	2012	373	Mean association strength	0.144	0.291	0.495
Iceland	S	2012	373	Coefficient of variation	3.18	15.1	0.211
Iceland	S	2012	373	Eigenvector centrality	0.229	1	0.229
Iceland	S	2012	373	Betweenness	349	4187	0.083
Iceland	S	2013	339	Degree	61.1	154	0.397
Iceland	S	2013	339	Mean association strength	0.138	0.297	0.465
Iceland	S	2013	339	Coefficient of variation	3.38	13.2	0.256
Iceland	S	2013	339	Eigenvector centrality	0.229	1	0.229
Iceland	S	2013	339	Betweenness	326	3767	0.087

Table 5.4. Descriptive network-level statistics for five of the networks investigated (one example of an intertidal network and networks for LW and S periods for both years). The size of the network is the number of individuals resighted two or more times in that study population during that period.

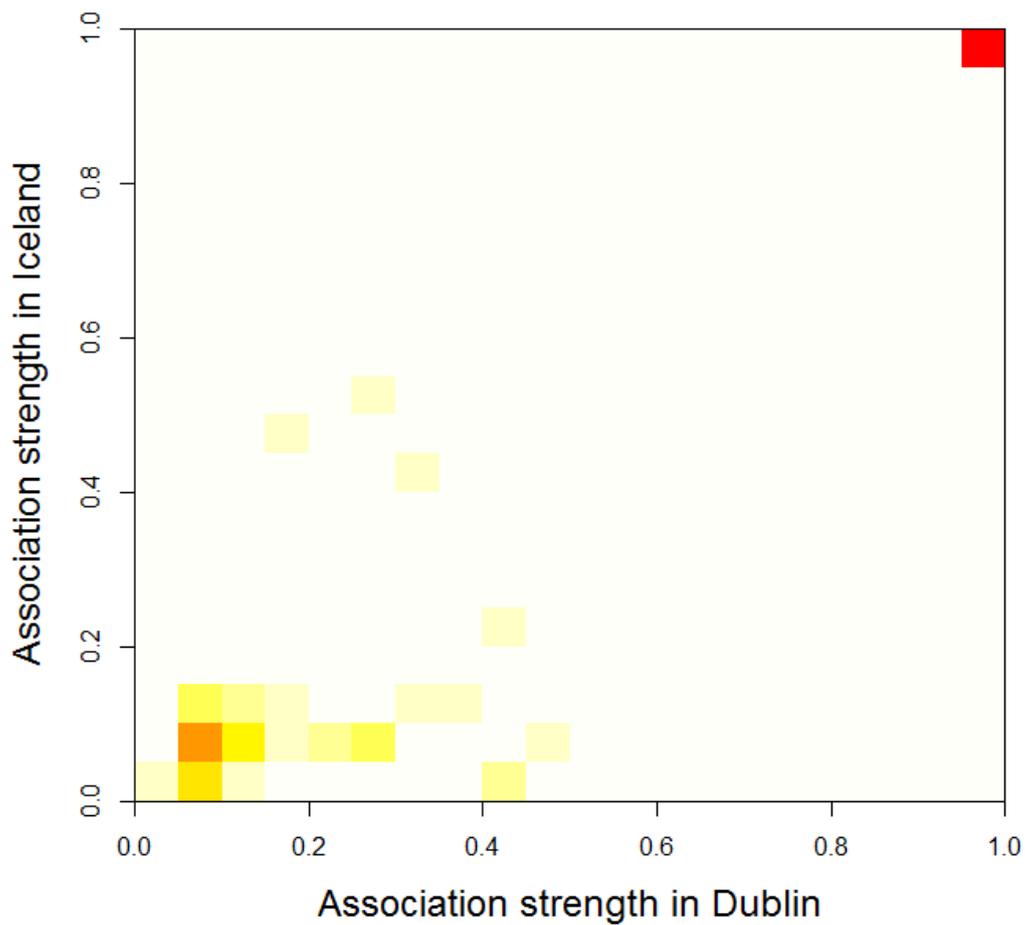


Figure 5.5. The relationship between association strength during late winter and spring networks for individuals recorded in both study areas in 2012

A 3-D histogram showing the correlation between association strength amongst individuals that were resighted five or more times in LW 2012 in Dublin and S 2012 in Iceland. Darker colours represent a higher frequency of dyads possessing associations of that strength in each network.

4. Inter-annual stability in network structure

Dyads in observed networks tended to be found in the same and different communities in different frequencies than would be predicted using entirely randomised null networks (Fig. 5.6). During winter staging dyads tended to be found in the same community in both years more often ($Z= 22.9$, $p<0.001$), and be found in different communities less often ($Z=11.8$, $p<0.001$) than would be predicted if networks were entirely random. During spring staging dyads were found in the same communities in both years more than would be predicted if networks were random ($Z= 9.56$, $p<0.001$), and fewer dyads were found in the same community in only one year ($Z=3.70$, $p<0.001$), but there was no significant difference in the number of dyads found in different communities in both years ($Z=-0.63$, $p=0.53$). In both staging seasons randomised networks that accounted for spatial constraints were a much better match for the inter-annual variability of shared community membership (Fig. 5.6). During winter staging observed networks fitted well within the distribution predicted by these spatially-constrained null networks. During spring staging in Iceland, the frequency of dyads found in the same communities in both years was the same as in spatially-constrained null networks ($Z=1.40$, $p=0.16$), however more dyads were found in the same community in neither year than would be predicted by these spatially-constrained null models ($Z=3.71$, $p<0.001$). This latter result indicates some role for previous social relationships in generating non-random patterns of social associations in addition to spatial factors.

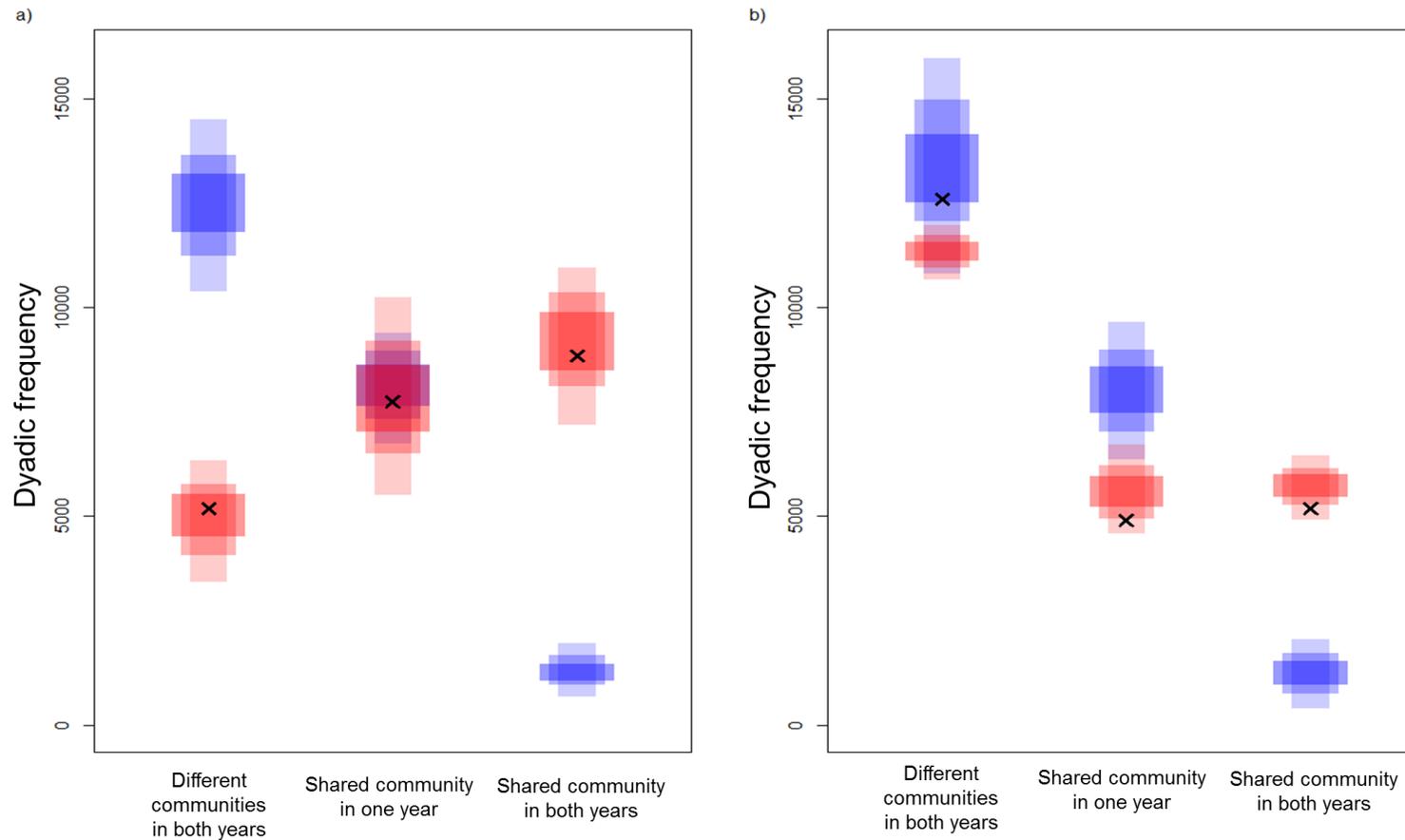


Figure 5.6. Inter-annual social community dynamics in observed and randomised networks

The frequency of dyads of individuals that occurred in the same community in neither, one of or both years (2012 and 2013) during a) late winter staging in Dublin and b) spring staging in Iceland. Crosses represent the frequencies in observed networks, red shaded polygons a normal distribution obtained from 100 pairs of spatially constrained null networks and blue distributions a normal distribution obtained from 100 pairs of randomised null networks. Box widths represent quantiles containing 95%, 75% and 50% of the normal distribution.

5.5 Discussion

We utilised social network analysis at multiple points in the annual cycle of a migratory population for the first time to explore the factors important in social structure and dynamics in these populations. We reveal that non-random social structures are linked to spatial constraints, but with additional non-randomness that can't be explained by spatial factors and is likely to be linked directly to social factors. However, despite the importance of social factors in structuring non-random patterns of interactions, stable associations outside family groups persist between staging areas only infrequently. Therefore, by using social network approaches at different stages of the annual cycle, we have demonstrated the dynamic nature of social associations over the course of the annual cycle as individuals change foraging preferences and move between different staging sites. This study highlights the importance of disentangling the relative importance of social and spatial explanations in explaining both social structure within a staging period and social dynamics throughout the year. This has important implications for our understanding of disease dynamics and patterns of social foraging behaviour in migratory populations.

Social networks in this study system display a predominantly spatial structure. Networks show strong spatial structuring at a population-level but social interactions are relatively fluid at smaller spatial scales. A similar pattern has been found in other avian taxa (Conklin & Colwell 2008; Aplin *et al.* 2012; Farine, Garroway & Sheldon 2012; Shizuka *et al.* 2014), and spatial structure in social networks is widespread across many taxa (Mourier, Vercelloni & Planes 2012; Carter *et al.* 2013; Garroway, Bowman & Wilson 2013). The importance

of limited space use in the development of highly geographically structured social networks, and the role this has in influencing the social interactions of individuals might be strongly linked to the evolution of dispersal and home ranges. Traditionally, limited dispersal is explained by the advantages of interacting with kin (Bowler & Benton 2005; Hatchwell 2010), benefits accrued from familiarity with a landscape (Greenwood & Harvey 1982) or as a variance stabilising strategy due to the high risks associated with dispersal (Bowler & Benton 2005; Ronce 2007). In light-bellied brent geese, for example, juveniles remain with their parents for their entire first winter and learn migration routes and staging sites from them. This results in birds recruiting into or close to parental sites (Harrison *et al.* 2010), despite the potential for detrimental effects of inbreeding (Harrison *et al.* 2011). However, limited natal and adult dispersal coupled with high levels of site fidelity will be important mechanisms in driving geographical patterns of non-random social interactions. If individuals accrue benefits by forming non-random social associations in this way then the development of geographically constrained population social structure provides another explanation for these patterns of dispersal and site use that has rarely been considered. It may be that familiarity with the social environment is as important or even more important as familiarity with the ecological environment in the evolution of site fidelity in group foragers.

In particular, remaining highly site faithful and interacting with only a subset of the population will have a considerable influence on social behaviour. Interacting repeatedly with only a subset of individuals in the population will increase an individual's familiarity with other group members and facilitate the formation of dominance hierarchies (Goessmann, Hemelrijk & Huber 2000; Hsu, Earley & Wolf 2006). Stable dominance hierarchies reduce aggression levels in

foraging groups (Hsu, Earley & Wolf 2006), especially as levels of familiarity increase (Goessmann, Hemelrijk & Huber 2000; Utne-Palm & Hart 2000), and will thus have a beneficial effect on individual time budgets (Hsu, Earley & Wolf 2006; Marshall *et al.* 2012). Whilst these benefits will accrue even when repeated social interactions occur solely as a result of shared patterns of space use, there would additional benefits obtained by individuals if social mechanisms develop to drive additional non-random variation in the social associations formed.

Individual social strategies in a dynamic fission-fusion social system

In this system, whilst spatial constraints clearly represent the most important single factor explaining patterns of social associations in these populations, there was additional variation in patterns of social associations that could not be explained by these constraints. Null models that imposed spatial constraints fitted the observed data considerably better than null models without these constraints, but values obtained from the observed networks were still rather different for a number of key metrics (Fig. 5.2). Individuals tended to form fewer and stronger social associations than predicted by both randomised and spatially constrained networks. There also tended to be more variation in mean individual association strength (in all networks from completely randomised networks) and eigenvector centrality (in most networks from both sets of null networks) than predicted by these spatially constrained randomised networks, indicating that individuals varied more in their social strategies than would be predicted by chance.

Variation in eigenvector centrality had previously been shown to be an important predictor of the speed at which individuals can acquire social

information in a similarly structured fluid fission-fusion social system of mixed-species passerine flocks (Aplin *et al.* 2012), and in the acquisition of tool use in bottlenose dolphins *Tursiops aduncus* (Mann *et al.* 2012). The Dublin wintering population of light-bellied brent geese frequently forage on agricultural land, golf courses and sports pitches making a better understanding of the spread of information in this population valuable in tackling potential human-wildlife conflicts.

Variation in mean association strength represents variation in the number of repeated interactions between individuals. Varying familiarity among group members represents an important aspect of an individual's social environment and is likely to mediate levels of aggression (Johnsson 1997; Utne-Palm & Hart 2000; Griffiths *et al.* 2004) and vigilance (Carter *et al.* 2009; MacIntosh & Sicotte 2009; Gaynor & Cords 2012) with potential implications for foraging efficiency (Griffiths *et al.* 2004, Chapter 6). The benefits obtained by individuals from occupying social network positions, and the differences in these strategies generated by individual differences (Aplin *et al.* 2013; Wilson *et al.* 2013), are another important explanation for the existence of non-random patterns of social associations that can't be explained purely by spatial factors. Variation among individuals in association strengths in this system is clearly linked to space use, differing from entirely random null networks but not those containing spatial constraints. This indicates an important role of space use in determining individual patterns of social associations, and thus influencing social foraging behaviour.

The consequences of fission-fusion sociality in the context of migration

It is also clear that despite the potential benefits obtained by forming stable social associations, social interactions are dynamic across the annual cycle in this species (Fig. 5.4, Fig. 5.5). Even within staging periods, changes in foraging behaviour alter the nature of the population social structure and therefore patterns of social interactions. Whilst social interactions formed while foraging on intertidal resources during early winter clearly explain some of the variation in social association strength later in the winter, the altered nature of social dynamics later in the winter result in individuals forming many new associations (Fig. 5.4). It is also clear there is limited connectivity between the winter and spring staging populations studied beyond family relationships, and that the vast majority of social associations formed during spring staging are with a different set of individuals (Fig. 5.5). Whilst this is the first study to look at the social networks of individuals of a migratory species in multiple staging areas, our findings are supported by work that found no evidence of stable associations persisting across during migration in colour-ringed snow geese (Desnoyers, Gauthier & Lefebvre 2012) or humpback whales (Valsecchi *et al.* 2002). These migratory social dynamics will have important consequences on epidemiological processes in particular. The formation of a largely new set of associations in each staging period will present pathogens with the opportunity of spreading between different subpopulations that wouldn't exist if connectivity between staging sites were stronger, and stable social associations persisted during migration. Given that waterfowl are important vectors of avian influenza, this is likely to have important implications for our understanding of disease dynamics in these populations (Hoye *et al.* 2011; Hill *et al.* 2012; Dijk *et al.*

2014), and therefore how they are likely to contribute to the global spread of these potentially zoonotic pathogens (Ellis *et al.* 2004; Chen *et al.* 2005).

For individuals, the fact that stable associations (outside of family groups) only rarely persist across an annual cycle is likely to influence social and foraging and behaviour throughout a staging period. After arriving in a new staging area, there are likely to be more aggressive interactions and reduced foraging while individuals are less familiar with each other and dominance hierarchies are still to be formed. This effect may be mediated somewhat by the high inter-annual stability in social network structure and space use, especially the establishment of dominance hierarchies. Although dominance in geese is somewhat determined by family group size (Black & Owen 1989; Mulder, Williams & Cooke 1995; Poisbleau *et al.* 2006), and therefore will vary between years to some extent, differences in individual quality are likely to mean dominance is relatively fixed over longer time-scales. Therefore, in cases where dominance hierarchies are key mediators of social behaviour, the continuation of familiarity with the social environment may be just as important as familiarity with the ecological environment in influencing limited dispersal and site fidelity in migratory populations.

Conclusions

This is the first study to investigate social network dynamics across multiple stages of the annual cycle of a migratory species. We found that patterns of social associations within staging periods and between years are highly stable. This is largely, but not exclusively, driven by high levels of site fidelity in these populations. We have highlighted the relationship between space use, non-random social interaction and the evolution of limited dispersal

and high site fidelity. These processes will be closely interlinked, and a better theoretical understanding of how they might evolve together would be very beneficial. We have also supported the growing evidence that even in fluid fission-fusion social systems such as this one, individuals will vary in the social strategies that they follow. Finally, we have stressed the importance of following social interactions across multiple stages of an annual cycle to fully understand their impact on social behaviour and population level processes.

6. Familiarity breeds content: the importance of social context in explaining group foraging behaviour



6.1 Abstract

Social foraging is widespread in animals, and often occurs in the context of highly dynamic fission-fusion social groups. This is likely to generate substantial variation in the social environment of foraging groups that would be predicted to have major implications for social behaviour and individual time-budgets. In addition there are often non-random structures that persist within these fission-fusion populations, as sub-sets of individuals form stable long term associations with one another. However, our understanding of the role of the social environment in explaining individual behaviour in fission-fusion social groups remains limited, and few studies have investigated the potential foraging benefits of forming long-term associations in this type of system. Here we use social network analysis in a population of socially foraging light-bellied brent geese to quantify the social environment in groups and enable us to explore how the composition of social groups can influence aggression and vigilance. We show that familiarity, at a flock level and individual level, alongside more conventional explanations for social behaviour is vital in explaining variation in individual time budgets and foraging success. Individuals tend to spend less time involved in aggressive interactions and vigilance when feeding in more familiar flocks, with an additional effect of an individual's familiarity with the rest of the flock able to mediate this effect in less familiar flocks. Furthermore, increased aggression leads directly to increases in vigilance highlighting how small differences in social context can scale-up to having large effects. This is a rare demonstration of the benefits of forming non-random social associations in fission-fusion social systems for foraging success, with implications for the evolution of individual strategies and population-level patterns of social associations in these dynamic societies.

6.2 Introduction

Many animals forage in groups, and the benefits and costs of group foraging have been the subject of considerable ecological research (Krause & Ruxton 2002). From this it is clear that understanding social behaviour and time budgets of animals that forage in groups is in turn fundamental to understanding the evolutionary dynamics of those systems. One of the most important trade-offs in group foraging is that between the anti-predation benefits of being in a group (Elgar 1989; Lima 1995; Parrish & Edelman-Keshet 1999), and the increased competition for resources with conspecifics (Janson 1988; Focardi & Pecchioli 2005). This results in individuals having to balance time spent foraging with time spent vigilant and involved in aggressive interactions. Their ability to manage this trade-off is highly likely to have direct consequences for their survival and fitness (Inger *et al.* 2006a; Watson, Aebischer & Cresswell 2007; Cresswell & Whitfield 2008). It will therefore have considerable implications for the evolution of how individuals manage behavioural trade-offs as distinct behavioural strategies or personalities (Carter, Pays & Goldizen 2009; Sansom, Lind & Cresswell 2009; Couchoux & Cresswell 2012), and even social systems themselves (Carter *et al.* 2009; Silk *et al.* 2014). This is especially true when these interactions occur in dynamic fission-fusion social systems (Aureli *et al.* 2008; Couzin & Laidre 2009), as group membership, and therefore the social context of behaviour, is more dynamic than in more stable social groups. Despite this there has been little exploration on social behaviour in group foragers in a fission-fusion context.

More generally, individual time-budgets in group foragers have received considerable empirical attention (Elgar 1989; Beauchamp 1998; Krause & Ruxton 2002; Marshall *et al.* 2012), particularly the role of anti-predator

vigilance as an explanation for social foraging (Elgar 1989; Lima 1995; Beauchamp 2008; Beauchamp 2013). However, it is likely that vigilance behaviour could be beneficial when used to monitor any potential threat, not specifically predators. In social foragers it is probable that the most frequent threats to an individual are aggressive conspecifics. This would mean that a significant component of vigilance behaviour in these systems could well be social (MacIntosh & Sicotte 2009; Favreau, Goldizen & Pays 2010; Gaynor & Cords 2012), rather than anti-predatory vigilance. Thus, incorporating social vigilance into our view of group foraging has the potential to substantially alter our understanding of the trade-offs involved in group foraging. It is likely to considerably increase the costs of increases in aggression due to the positive feedback this will have on vigilance behaviour (McDonough & Loughry 1995; Pannozzo *et al.* 2007), as well as masking, or increasing variation in, the group size effect on anti-predator vigilance (Beauchamp 2013). The social environment in fission-fusion social groups will be highly variable and thus have an important influence on social vigilance behaviour. However, there is still a limited understanding of the role of the social environment on aggression and social vigilance in fission-fusion social groups.

In fission-fusion systems the role of the social environment on social behaviour within foraging groups is likely to be much more complex than the outcome of well-studied processes such as stable dominance hierarchies (Hsu, Earley & Wolf 2006) and group size effects (Elgar 1989; Beauchamp 1998; Beauchamp 2008). In these systems, where group membership is spatio-temporally dynamic (Couzin & Laidre 2009; Sueur *et al.* 2011b), familiarity with other group members will be a particularly important mechanism in influencing social behaviour (Sueur *et al.* 2011b; Silk *et al.* 2014) that operates alongside,

and in addition to, the formation of dominance hierarchies. Familiarity in dynamic social systems will be fundamental in the development of social hierarchies. For example, dominance hierarchies in juvenile European crayfish have been demonstrated to become more stable with reduced aggression as individuals become more familiar with each other (Goessmann, Hemelrijk & Huber 2000). However, familiarity with other individuals will also alter how individuals use social information (Swaney *et al.* 2001; Kavaliers, Colwell & Choleris 2005), with potential implications for how vigilance is used in a social context. In eastern grey kangaroos *Macropus giganteus* vigilance is more synchronised than would be expected as a result of independent scanning (Pays *et al.* 2007b; Pays *et al.* 2009), and experiments presenting a predator to a single focal female have demonstrated that individuals increase their own vigilance in response to other individuals detecting a threat without being able to detect it themselves (Pays *et al.* 2013). In this species stronger previous social associations reduce levels of vigilance in foraging groups, with it being speculated that this was due to a reduction in this vigilance copying behaviour (Carter *et al.* 2009).

In order to understand the role of familiarity and the social environment in influencing individual time budgets it is necessary to be able to quantify patterns of social associations at a population level. The recent development of social network analysis (SNA) as a tool in animal behaviour research (Croft, James & Krause 2008; Wey *et al.* 2008; Pinter-Wollman *et al.* 2013) provides a methodology by which we can now improve our knowledge of the social environment in animal groups, and therefore start understanding the social context of these behaviours more comprehensively. SNA provides an opportunity to describe the social relationships of all the individuals in a

population, and as such can provide metrics that describe the closeness with which any two individuals in a population have previously associated. Using these metrics should provide a novel perspective on the social composition of animal groups, and is thus likely to prove very important in furthering our understanding of how variation in the social environment influences patterns of behaviour and consequently individual time budgets.

Here we test predictions relating to the key factors that influence vigilance and aggressive behaviour in a social forager, the light-bellied brent goose (*Branta bernicla hrota*). This species forms a dynamic fission-fusion social system, generating considerable variation in the social environment in foraging groups. We combine a suite of covariates shown to be important in other studies of social behaviour with complementary social network information from the same population. This provides a unique opportunity to explore the importance of the social and ecological environment in explaining patterns of social behaviour in groups of this species. Our key predictions are that i) increasing levels of familiarity (as measured by social association strengths in a social network) in foraging flocks, both at a flock level and an individual level, will reduce the probability of aggression occurring and the amount of time individuals spend involved in agonistic interactions, ii) both reduced aggression levels and increased familiarity will decrease vigilance behaviour so that iii) individuals can spend more time foraging in flocks with higher levels of familiarity.

6.3 Methods

Study system

The research was conducted on a long-term study population of East Canadian High Arctic (ECHA) light-bellied brent geese (Inger *et al.* 2006a; Inger *et al.* 2008; Harrison *et al.* 2010; Inger *et al.* 2010; Harrison *et al.* 2011). Birds in this population are caught with cannon nets and fitted with coloured Darvic leg rings with alphanumeric combinations to make individuals uniquely identifiable. When caught wing length, head-bill length and mass are measured (Inger *et al.* 2006b; Harrison *et al.* 2010; Inger *et al.* 2010) and some individuals are sexed either by cloacal examination or using molecular methods at a later date (Inger *et al.* 2006b; Harrison *et al.* 2010). Data were collected in the Dublin Bay and Baldoyle Bay winter-staging areas between November 2012 and March 2013. Colour-ringed individuals made up approximately 10% of this staging population during this period.

Social network analysis

Social networks were constructed based on resightings of colour-ringed individuals during the periods November 1st – December 31st 2012 and January 16th – March 16th 2013. Networks based on the whole winter period were used for all observations to ensure greater reliability in association measures. All resightings available in the Irish Brent Goose Research Group (IBGRG) database were used provided records included a site, date and flock size. Any duplicated records of flocks were removed from the analysis. Social networks were constructed using the gambit of the group assumption (Whitehead & Dufault 1999; Croft, James & Krause 2008) using all individuals resighted two or

more times in either study period. Only multiply resighted individuals were used to reduce error associated with misidentification of individuals. This resulted in a social network containing 467 unique individuals. Edges were weighted using the half weight index (HWI) to account for the fact that two individuals were more likely to be recorded when they co-occurred in a group (Whitehead 2008). No group size correction was applied (Chapter 4), as individuals are highly mobile within terrestrially foraging flocks of this species and we were interested in group-level patterns of social behaviour. Measures of binary degree (Bonacich 1972), strength (Barrat *et al.* 2004), betweenness (Freeman 1977), mean association strength (strength divided by degree) and eigenvector centrality (Bonacich 1987; Bonacich 1991) were calculated for all individuals in this network.

The values of all network metrics with the exception of betweenness depended on the number of times and individual was resighted during network construction. To correct for this effect and collapse the network metrics used into a single measure of social position, a principal components analysis (PCA) was used. PC1 was closely correlated with resighting frequency ($r=0.77$, $n=134$, $p<0.001$) and therefore accounted for the relationship between most of the network metrics and resighting frequency (loadings: degree = 0.433, strength = 0.588, mean association strength = 0.364, betweenness = -0.003, eigenvector centrality = 0.578). PC2 was then selected as a measure of individual social position as it was uncorrelated with resighting frequency ($r=0.09$, $n=134$, $p=0.31$) and described differences in sociality between individuals which were of interest. High values of PC2 represented individuals that had high mean association strength (loading = 0.602) and low degree (loading = -0.549) and betweenness (loading = -0.570), but explained little variation in strength

(loading = -0.052) and eigenvector centrality (loading =0.083). Thus a high PC2 score represents an “associative” social strategy, in which individuals tended to interact repeatedly with a smaller number of individuals. This measure of “associativeness” was categorised into high or low for use as an explanatory variable in statistical models based on whether individuals had positive or negative values for PC2.

Behavioural Data Collection

302 focal observations of behaviour were conducted on 134 uniquely identifiable colour-ringed individuals. Regularly resighted individuals were selected opportunistically for focal behavioural sampling. Observations were conducted for a minimum time period of three minutes and a target time period of five minutes, which provided a sufficient length of observation to record differences in the behaviours of interest. For each observation, the site of the observation (one of 21 urban green spaces in Dublin), date, time, group size and the identity of all other colour-ringed birds in the group were also recorded. Archived weather data for Dublin airport was also collected online for use in analyses.

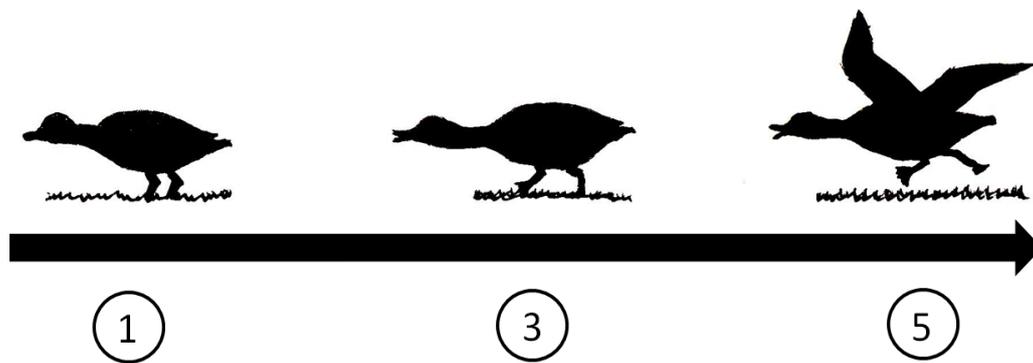


Figure 6.1. An illustration of scores of aggression intensity in light-bellied geese. Aggressive interactions are scored on a scale from 1-5 with three examples given here. A score of 1 indicates a bird pointing its head towards another individual. A score of 3 would indicate a bird extending its head and neck towards another individual and advancing several steps. A score of 5 would be given if a bird advances rapidly towards another individual and physical contact occurs. For further detail see Inger *et al.* (2006).

For the duration of each focal observation birds were recorded as either head up or head down. At the same time all agonistic interactions that involved the focal individual were recorded and scored for aggression intensity using the methods of Inger *et al.* (2006a), as illustrated in figure 6.1. A distinction was made between interactions in which the focal individual was the aggressor and those in which it received aggression from other individuals. Throughout all focal observations periods preening, scratching or stretching were recorded as comfort behaviour (a distinct classification from vigilant or aggressive behaviour) and excluded from the analysis if they exceeded 30 seconds in length. Additionally, head up periods that contained walking behaviour (three or more steps in a single direction) or high local vigilance behaviour (exceptional levels of synchronised vigilance behaviour in all neighbouring individuals) were recorded. Both of these behaviours recorded simultaneously were a proxy for

disturbance, and so head up periods including both of these behaviours were excluded from the analysis.

Statistical Analysis

A proportion of time that an individual spent aggressive (head ups that included one or more aggressive interactions) and vigilant (head ups that did not include any aggression or comfort behaviour) were calculated by dividing the time each individual spent performing these activities by the total focal time. It was assumed that for the remaining time an individual was foraging (periods of comfort behaviour were sufficiently unusual to have a negligible impact). These proportions were then logit transformed to ensure the data had a gaussian error distribution (Warton & Hui 2011).

HWI values from the association matrix were used to calculate the mean association strength of all ringed individuals in a flock, and that of each focal individual to all other ringed individuals in a flock. Mean individual association strengths were within group centred by subtracting the mean flock association from their value (van de Pol & Wright 2009). This prevented them from being correlated with flock mean association strengths and enabled us to detect how the advantage of association strength at an individual level depended on the mean familiarity of the flock.

Linear mixed models and generalised linear mixed models were used to determine how vigilance and aggressive behaviour were related to a number of social and ecological variables (Table 6.1). “Ecological” fixed effects were used as blocking variables for factors known to influence individual time budgets. All two-way interactions between “social” fixed effects and individual social position were included in the full model. Group sizes were logged as the effect of group

size on vigilance is expected to be non-linear (Beauchamp 2003). Sex was not used as an explanatory variable in the models as insufficient individuals in this study population had been sexed on capture. Models containing a complete set of candidate variables and the interactions outlined above were constructed in R3.1.1 (R development Core Team 2014) using lme4 (Bates *et al.* 2014) for i) the occurrence of aggressive interactions (logistic model; binomial error), ii) the proportion of time an individual spent in aggressive head ups (head up periods that included one or more aggressive interactions, n=230 focal observations; logit-transformed, normal error), iii) the proportion of time spent vigilant (logit transformed, normal error) and iv) proportion of time spent feeding (logit transformed, normal error). Measures of group size, time of day, total aggression initiated, total aggression received and mean aggression intensity were grand mean centred in all models to make model estimates for the intercept more biologically relevant (Schielzeth 2010).

Candidate models from each full model were then ranked by AICc values using the package MuMIn (Bartoń 2013) and models within 2 AICc units of the top model were retained. The estimates discussed in the results section and used to plot figures are from the top model in each candidate model set (Table 6.2). However, the aggregate weights of the models in which each parameter in the top model set appears are represented in Table 6.2 to demonstrate that these variables were included in all, or the majority, of the most parsimonious models. Intra-class correlation coefficients (ICCs) were calculated for model i) to find the proportion of variation explained by flock and individual traits, and site differences. ICCs were calculated according to the methods of Nakagawa and Schielzeth (2010), with $\frac{\pi^2}{3}$ used as the residual variance.

Variable	Variable type	Effect type	Hypothesis
Season (early vs. late winter)	Ecological	Fixed 2-level factor	Lower vigilance in late winter Less aggression in late winter
Time of day	Ecological	Fixed covariate	Vigilance increases as birds reach daily energy intake requirement
Minimum night time temperature	Ecological	Fixed 2-level factor (above/below zero) in vigilance and foraging model	Vigilance is reduced when the night time temperature dropped below zero due to reduced feeding efficiency
Group size	Ecological	Fixed covariate	Reduced vigilance in larger groups Increased aggression in larger groups
Site	Ecological	Random	Differences between sites due to variation in risk and habitat structure
Mean flock association	Social	Fixed covariate	Less vigilance and aggression in flocks with higher mean association strength
Mean individual association	Social	Fixed covariate (within group centred)	Reduced vigilance and aggression as mean individual association strength increases
Total aggression initiated	Social	Fixed covariate in vigilance models	Increased vigilance as aggression increases if social vigilance is important
Total aggression received	Social	Fixed covariate in vigilance models	Increased vigilance as aggression received increases if social vigilance is important
Mean aggression intensity	Social	Fixed covariate in aggression models	Increased rate of aggression and time spent aggressive as intensity increases
Flock	Social	Random	Unexplained differences between flocks
Social position*	Individual	Fixed 2-level factor	Reduced vigilance and aggression in "associative" geese
Individual	Individual	Random	Individual differences driven by personality traits and differences in status

*Social position is PC2 of a PCA of the five network metrics used in this study. "Associative" birds had lower degree, lower betweenness, and higher mean association strength.

Table 6.1. Explanatory variables used in mixed models in Chapter 6, how they were used in the models and the reasons for their inclusion

6.4 Results

What makes aggression more likely?

No aspect of the ecological or social environment outlined in Table 6.1 was found to have a significant effect on the probability that aggression occurred. The null model was within two AICc units of the top model. However, a considerable amount of the total variation was explained by differences between flocks ($R=0.23$), suggesting that the probability of aggressive interactions may be explained by other factors operating at a flock-level. This may be driven by recent events such as disturbance or time since arrival at a site, differences in the density of individuals (although densities of foraging flocks in Dublin tend not to be particularly variable), or positive feedback between agonistic interactions generating differences between flocks by making aggressive interactions more likely throughout a flock once some aggression has occurred.

What influences the amount of time individuals spending in aggressive interactions?

The top model for the proportion of time an individual spent aggressive involved the mean flock-level association strength, an additional effect of mean individual-level association strength, aggression intensity and social position (Table 6.2). These variables were also well supported by the rest of the top model set (Table 6.2). The strongest effect in this model was an interaction between aggression intensity and mean flock-level association strength. An increase in mean aggression intensity had a stronger effect in flocks with higher mean association strength (Fig. 6.2). This resulted in individuals spending less

time aggressive in these more familiar flocks when mean aggression intensities were average (flock-level association strength intercept = -2.22 ± 1.21) or below average, but more time aggressive when mean aggression intensity was high. While the top model did include additional effects of individual-level mean association strength and social position, the confidence intervals for these effects and their interactions crossed zero indicating that they had limited effect on the time each individual was spending aggressive.

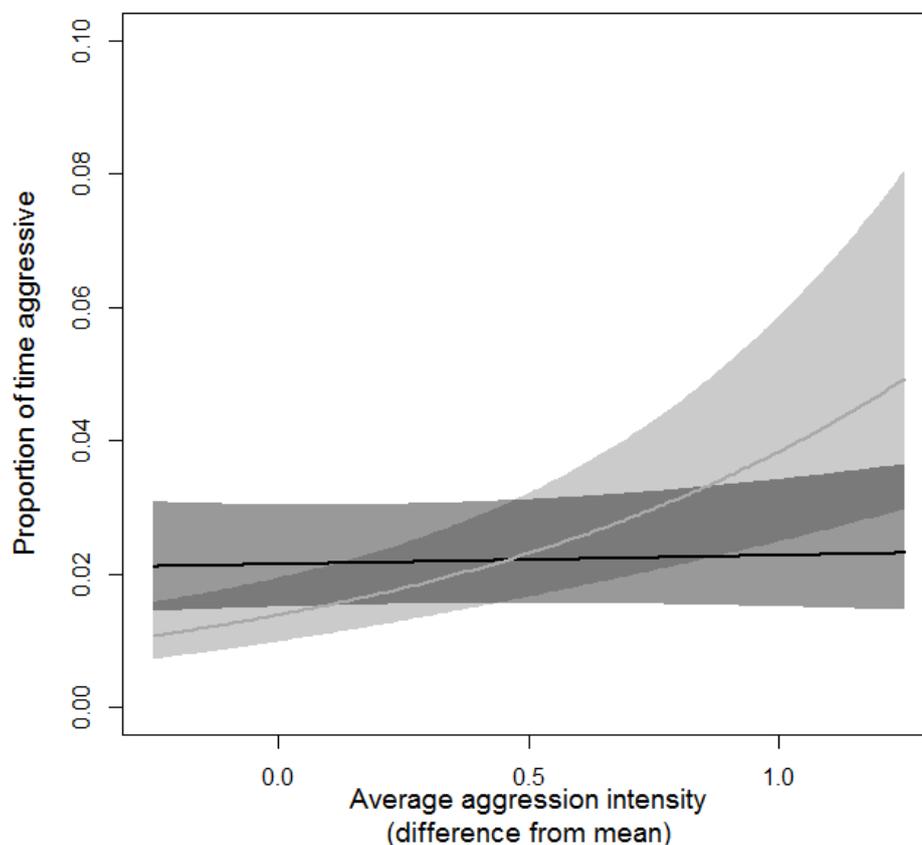


Figure 6.2. The relationship between mean aggression intensity and the proportion of time spent in agonistic interactions in foraging light-bellied brent geese

These results are for individuals in flocks of two different mean association strengths: mean association strength = 0.13 (black) and mean association strength = 0.33 (grey). Lines are model predictions for unassociative individuals in flocks with a mean individual-level association strength to the rest of the flock. Shaded areas are 95% confidence intervals around these predictions.

Response Variable	Variables in top model set	Importance	Estimate in top model
Probability of aggression occurring	<i>Null model in top model set</i>	NA	NA
	Mean flock association	1	-2.22±1.21
	Mean individual association	1	1.29±2.26
	Mean aggression intensity	1	0.55±0.12
	Social position	0.96	0.32±0.16
	Season	0.42	NA
	Group size	0.23	NA
Time spent in agonistic interactions	Mean flock association*Mean aggression intensity	1	4.91±1.49
	Mean flock association*Mean individual association	1	11.71±13.47
	Mean flock association*Social position	0.68	0.32±1.99
	Mean individual association*Mean aggression intensity	0.9	0.62±2.49
	Mean individual association*Social position	0.92	-0.30±3.22
	Mean aggression intensity*Social position	0.32	NA
	Mean flock association	1	-2.36±0.81
	Mean individual association	1	-0.99±1.27
	Total aggression received	1	0.04±0.01
	Social position	0.75	0.02±0.10
Time spent vigilant	Group size	1	-0.43±0.15
	Season	1	-0.33±0.10
	Mean flock association*Mean individual association	1	10.49±8.35
	Mean flock association*Social position	0.75	2.41±1.23
	Mean individual association*Social position	0.75	-1.24±1.95
	Mean flock association	1	1.54±0.74
	Mean individual association	1	1.59±0.86
Time spent feeding	Mean aggression intensity	1	-0.31±0.05
	Social position	0.48	NA
	Season	1	0.38±0.10
	Group size	1	0.43±0.16
	Mean flock association*Mean individual association	1	12.38±7.54
	Mean flock association*Mean aggression intensity	0.64	-0.87±0.65
	Mean individual association*Mean aggression intensity	0.74	-1.29±0.98
	Mean flock association*Social position	0.48	NA
	Mean individual association*Social position	0.39	NA

Table 6.2. Explanatory variables present in the top model set for the four behavioural models constructed in Chapter 6, the importance of the models they are contained in and the estimate ± standard error in the top model

Variables in bold are present in the top model.

What influences the proportion of time individuals spend vigilant?

A number of social and ecological variables were found to be important in influencing the proportion of time an individual spent vigilant. The variables included in the top model and the weighted importance of models containing each variable in the top model set is shown in Table 6.2. The proportion of time an individual spent vigilant increased as the total aggression it received increased (Fig. 6.3), whilst there was no evidence for any effect of aggression initiated in the top model set (Table 6.2). This is strongly suggestive of social vigilance being important in monitoring conspecific threats. Flock-level mean association strengths, individual-level mean association strengths, social position and their interactions were also all present in the top model. Individuals tended to be less vigilant in flocks with higher mean association strengths (Fig. 6.4, Fig. 6.5), but this effect was also influenced by their relationship to other individuals in the group (Fig. 6.4) and the social position of an individual (Fig. 6.5). Stronger individual relationships tended to reduce vigilance in weakly associated flocks, but not in more closely associated flocks, resulting in individuals only being more vigilant in flocks with low mean association strength when they had average or below average mean individual-level association strength (Fig. 6.4). Individuals in different social network positions responded to changes in mean flock-level association strength differently, with there being no effect of increasing mean flock-level association strength in individuals with an “unassociative” social position and reduced vigilance in “associative” individuals as flock-level association strengths became higher (Fig. 6.5). As would be expected individuals also spent less time vigilant as group size increased (estimate = -0.43 ± 0.15) and later in the winter closer to migration (-0.33 ± 0.10).

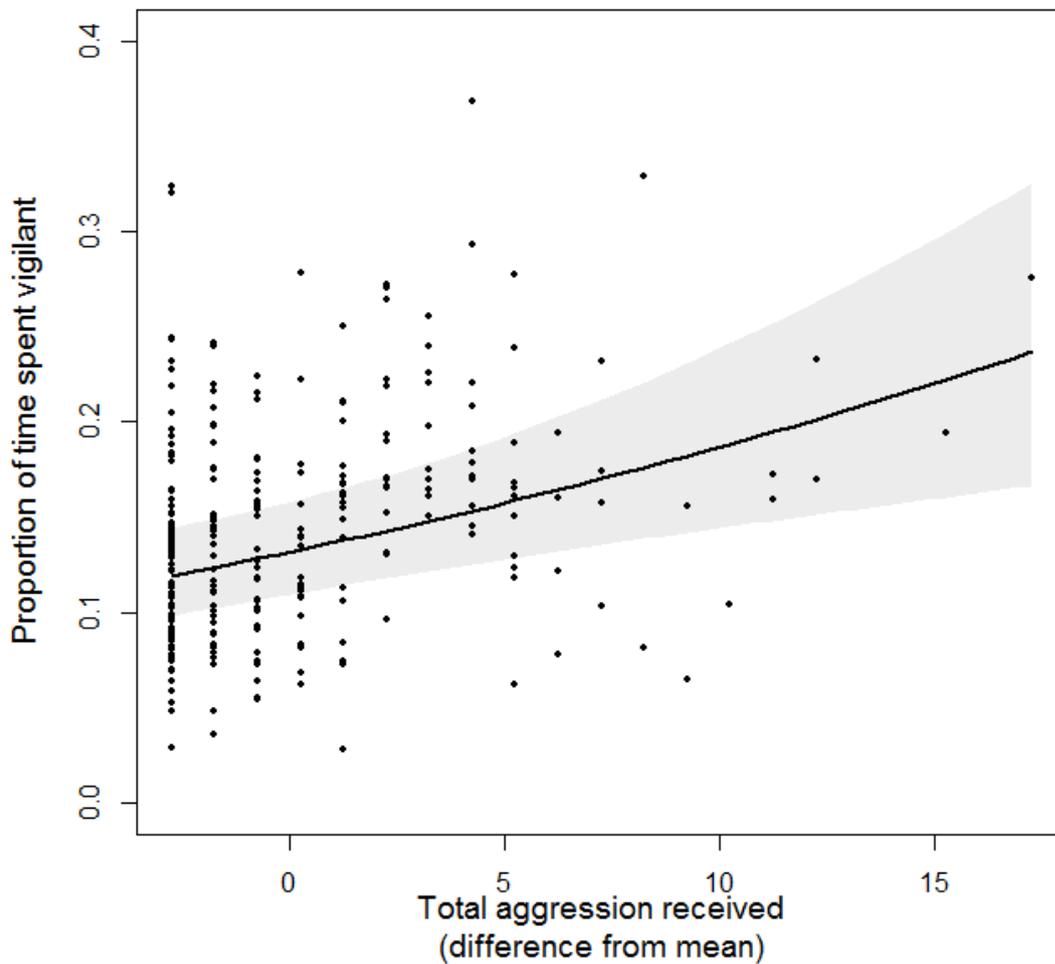


Figure 6.3. The relationship between the proportion of time an individual spends vigilant and the amount of aggression it receives in light-bellied brent geese

The line shows the prediction of the top model for an unassociative individual in an early winter flock with the flock size, mean flock-level association and mean individual-level association set to mean values. The grey shaded area represents the 95% confidence intervals around this prediction. Points are the residuals from the model fit.

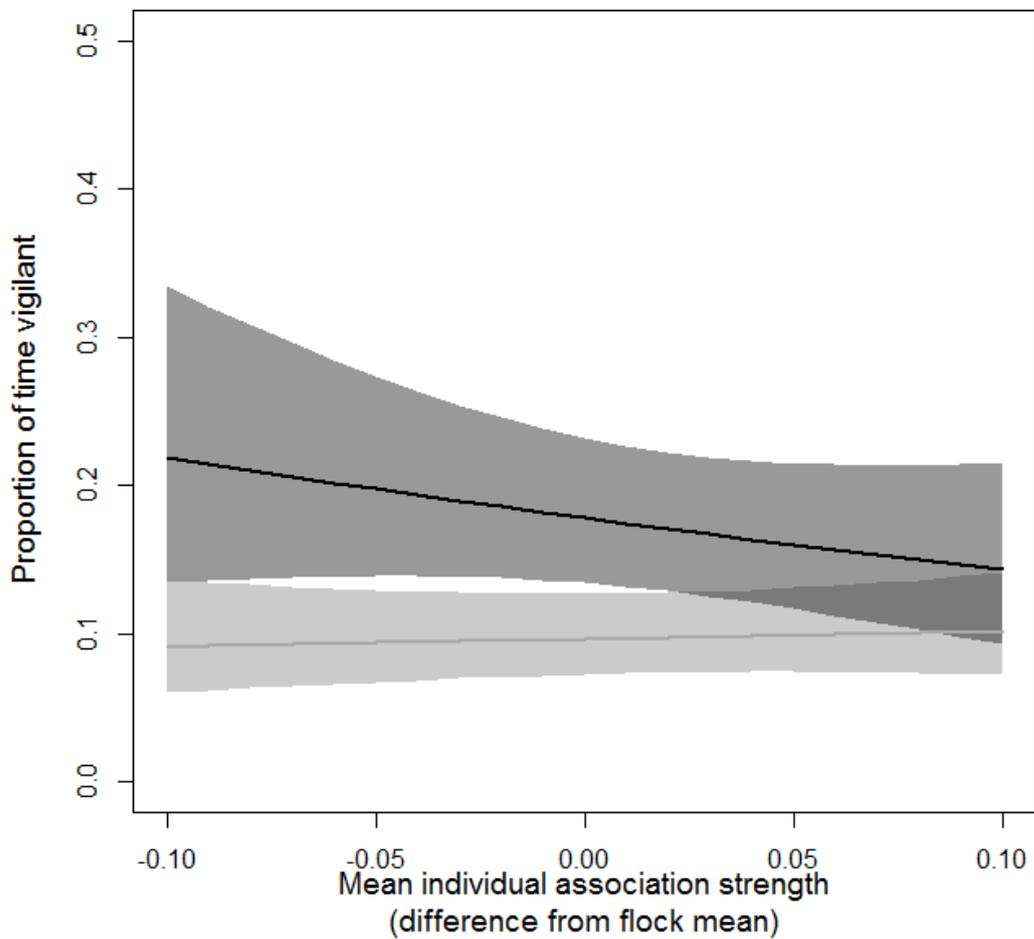


Figure 6.4. The relationship between vigilance rate and the mean individual-level association strength in flocks of light-bellied brent geese varying in mean flock-level association strength

The lines are model predictions for individuals foraging in flocks with low mean flock-level association strength (mean = 0.08; black line) and high mean flock-level association strength (mean = 0.38; grey line) for unassociative individuals in early winter flocks with aggression received and group size set to their mean values. Shaded areas are 95% confidence intervals around these predictions.

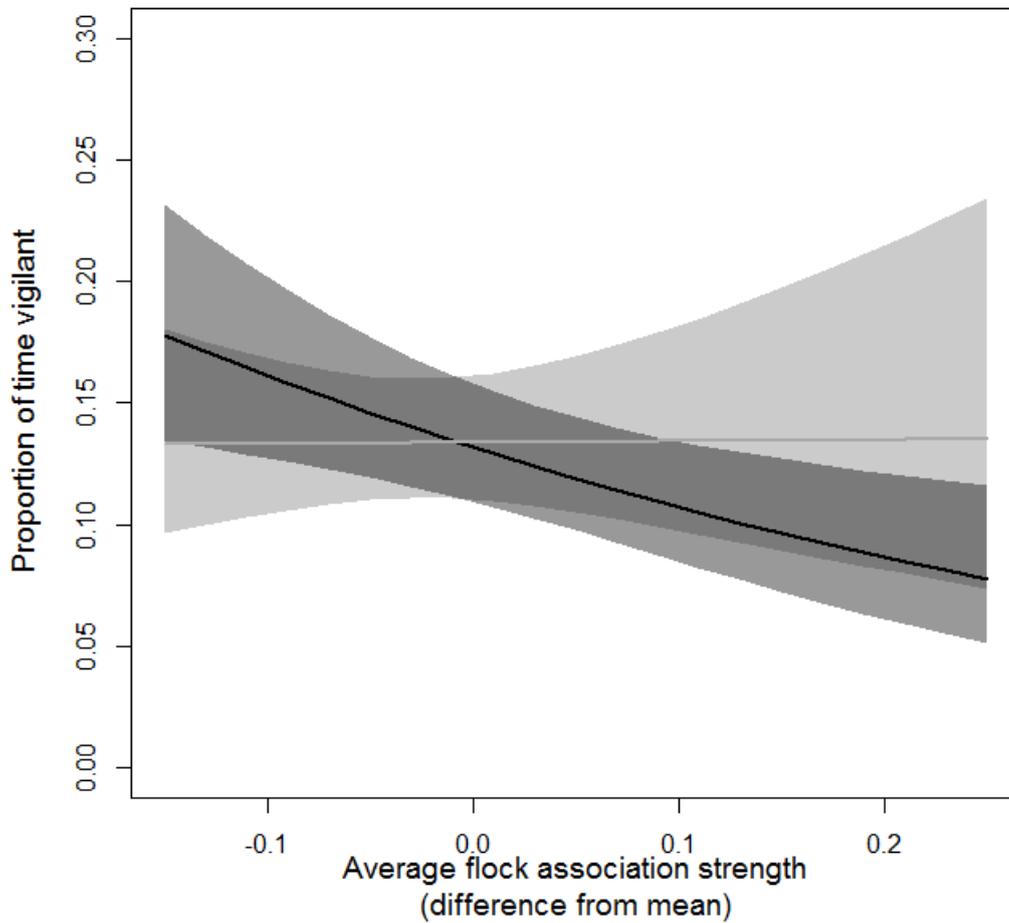


Figure 6.5. The relationship between mean flock-level association strength and the proportion of time an individual spends vigilant for light-bellied brent geese varying in social strategy

The lines are for associative (black line) and unassociative (grey line) individuals. They are model predictions for early winter flocks with group size, aggression received and mean individual-level association strengths set to their mean values. Shaded areas are 95% confidence intervals around these predictions.

Does this have knock-on implications for foraging success?

As would be predicted from their effects on the time spent aggressive and vigilant, flock-level mean association strength, an additional effect of individual-level association strength, aggression intensity, group size and season were all found to be important in explaining the amount of time an individual could spend foraging (Table 6.2). Individual social position was also present in the top model set, but only in models that were relatively weakly supported (Table 6.2). There was an interaction between flock-level mean association strength and the additional effect of individual-level mean association strength. Individuals in groups with lower mean flock-level association strengths obtained a benefit from being more closely associated with other members of the group on average, but there was no benefit in more familiar groups (Fig. 6.6). Increasing mean aggression intensity reduced the amount of time an individual spent foraging (estimate = -0.31 ± 0.05), with weak evidence that this effect was stronger as flock-level mean association strength (estimate = -0.87 ± 0.65) and the additional effect of individual-level association strength (-1.29 ± 0.98) increased. The weakness of this effect suggests that while this has an important influence on the time spent in aggressive interactions (Fig. 6.2), it has no additional effects on vigilance. Individuals also spent more time feeding in larger groups (estimate = 0.43 ± 0.16) and later in the winter (0.38 ± 0.10), as would be predicted from the results of the vigilance model.

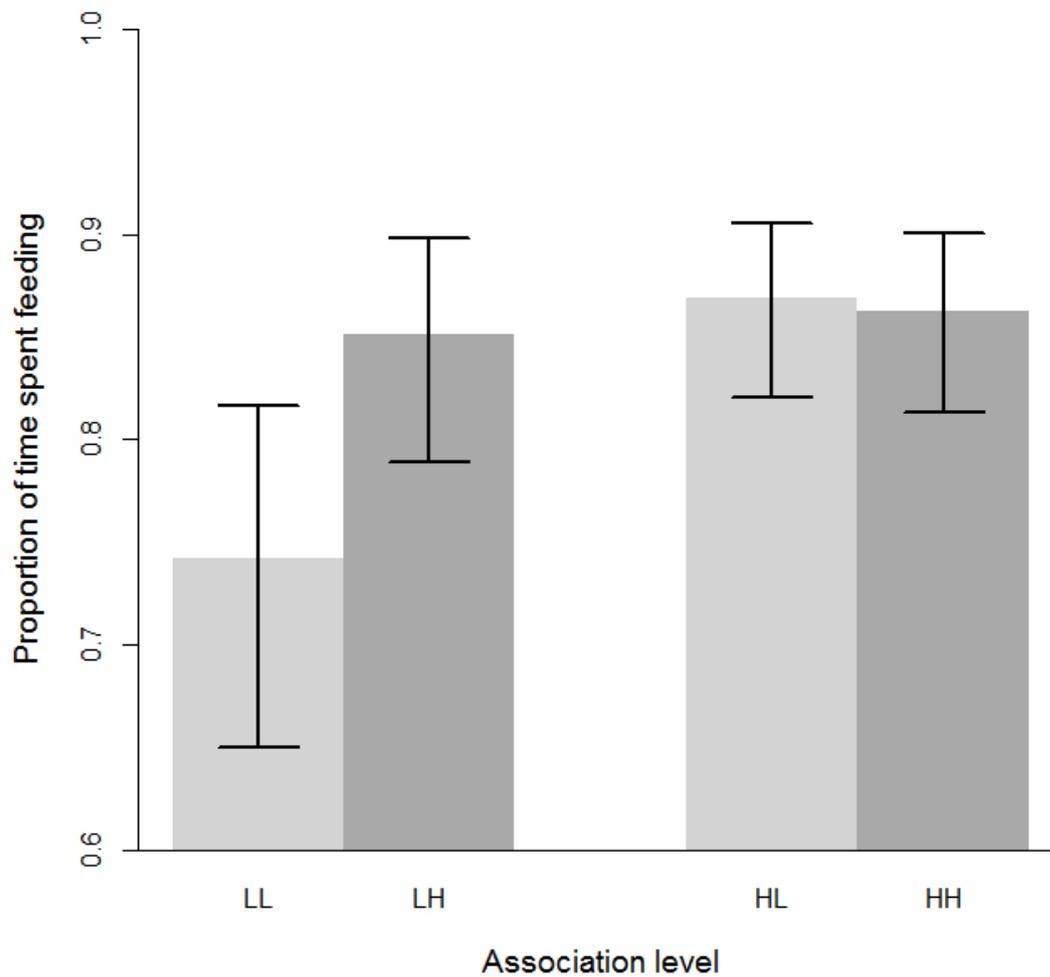


Figure 6.6. The relationship between within flock association strengths and time spent foraging in light-bellied brent geese

Bars represent different combinations of flock-level mean association strength (first letter) and mean individual-level association strength (second letter). H is high and L is low. The graph shows the predictions of the top model when group size and mean aggression are set to their mean values in an early winter flock. Error bars represent 95% confidence intervals of the model predictions.

6.5 Discussion

The benefits obtained by interacting with more familiar individuals provide an argument often used to explain non-random social structures in fission-fusion populations (Sueur *et al.* 2011b; Silk *et al.* 2014). However, empirical evidence for the benefits of foraging in familiar groups in fission-fusion social systems is very limited. We clearly demonstrate that increased levels of familiarity, both at a flock-level and an individual-level are important mediators of aggressive interactions and vigilance behaviour in socially foraging light-bellied brent geese alongside other more frequently investigated factors such as group size, seasonal differences and site differences. We then show that these effects result in individuals being able to spend more time foraging in more familiar groups. This provides important evidence that how an individual interacts with its social environment will be an important mediator of fitness in a dynamic social system, with implications for our understanding of individual social strategies and population-level patterns of social associations.

Stable social associations, dominance hierarchies and reduced aggression

Increased familiarity has previously been shown to influence the intensity of aggressive interactions in laboratory experiments on fish (Johnsson 1997; Utne-Palm & Hart 2000; Griffiths *et al.* 2004; Edenbrow & Croft 2012), amphibians (Jaeger, Peterson & Montgomery 2002) and rodents (delBarco-Trillo, McPhee & Johnston 2009). For example, Utne-Palm and Hart (2000) showed that the frequency and intensity of aggressive interactions between three-spined sticklebacks (*Gasterosteus aculeatus*) reduced as individuals

became more familiar with each other. However, the only evidence from natural systems are cases of reduced aggression directed towards individuals from the same rather than different social groups (e.g. Andino *et al.* 2011). This reduction in aggression is likely to be closely linked to the establishment and stabilisation of dominance hierarchies (Goessmann, Hemelrijk & Huber 2000; Hsu, Earley & Wolf 2006). Repeated interactions between individuals are required for the positions of individuals in a hierarchy to be determined (Goessmann, Hemelrijk & Huber 2000), and will additionally stabilise social status through winner and loser effects (Dugatkin 1997; Dugatkin & Druen 2004; Dugatkin & Earley 2004; Hsu, Earley & Wolf 2006). In our study, the intensity of agonistic interactions was directly linked to the amount of time an individual spent performing agonistic behaviours (Fig. 6.2), but the strength of this relationship depended on the familiarity of individuals in flocks. In more familiar flocks increased interaction intensity had more of an effect on the time an individual spent involved in aggressive interactions. This perhaps suggests that interactions of higher intensity are less expected in these more familiar groups, and thus have a bigger effect on individual social behaviour than they would otherwise. Understanding this interaction between aggression and familiarity is vital in establishing the full extent of its implications for individual time budgets, as it would be predicted to have a considerable additional effect on individual vigilance levels

Aggression and social monitoring

If vigilance is important in monitoring conspecific threats, as well as an anti-predator behaviour, then aggression and vigilance would be expected to be positively correlated. Without this link then the expectation would be for a

negative relationship due to the mutually exclusive nature of the activities. We found a clear link between aggression and vigilance in this study (Fig. 6.3), suggesting that social monitoring is an important explanation for vigilance in this species, something that remains relatively poorly documented (but see McDonough & Loughry 1995; Pannoizzo *et al.* 2007). Using multiple observations in each social group allows us to rule out an alternative explanation that increased predation risk increases both anti-predator vigilance and aggression (due to decreased inter-individual distances) at a flock-level. We also found that increased vigilance was closely linked to aggression received rather than aggression initiated. This supports evidence from brown capuchins (*Cebus apella*) that vigilance behaviour was directed towards group members that were more aggressive (Pannoizzo *et al.* 2007), highlighting that social monitoring is most likely as the threat posed by a conspecific becomes greater. There are two likely explanations for this result (which are not mutually exclusive by any means), both closely linked to the idea that social monitoring is linked to threat posed by other group members. Most simply, it may be that individuals that receive the most aggression are subordinate individuals that gain more from social monitoring behaviour. Links between vigilance levels and social status have been described in a number of primates (e.g. Pannoizzo *et al.* 2007; Gaynor & Cords 2012), but rarely in other species (but see Cameron & du Toit 2005) despite the fact it is probably a widespread occurrence. The other likely explanation is a more direct link between receiving aggression and being vigilant. Individuals would be expected to respond to receiving aggression on a short-term basis by increasing vigilance to monitor other neighbouring individuals or monitor aggressive group members more closely, as observed by Pannoizzo *et al.* (2007).

Social associations and reduced social vigilance

There is considerably more evidence for a role of familiarity in explaining patterns of vigilance behaviour. Familiarity has been found to affect vigilance in a range of mammal species (European rabbits *Oryctolagus cuniculus*: Roberts 1988, eastern grey kangaroos *Macropus giganteus*: Carter *et al.* 2009), especially primates (common chimpanzees *Pan troglodytes*: Kutsukake 2006, blue monkeys *Ceropitheicus mitis*: Gaynor & Cords 2012, ursine colobus monkeys *Colobus vellerosus*: MacIntosh & Sicotte 2009, Teichroeb & Sicotte 2012). However, many of these studies have taken place in primate social systems with highly structured patterns of interactions rather than the more fluid social interactions, constrained by space use, that are typical of many animals (e.g. Conklin & Colwell 2008; Mourier, Vercelloni & Planes 2012; Garroway, Bowman & Wilson 2013). Furthermore, none of these studies have considered the relative role of familiarity at an individual level and group level.

Familiarity, both at a group level and individual level, is likely to influence aggression levels, the requirement to scan agonistic interactions to provide information about the current social environment, and the use of social information more generally. For example, MacIntosh and Sicotte (2009) attributed reduced vigilance in the presence of familiar neighbours to a reduced need for social monitoring, whilst in eastern grey kangaroos a reduction in allelomimetic vigilance - the copying of a neighbour's vigilance behaviour (Pays *et al.* 2007c) - was suggested as an explanation (Carter *et al.* 2009). Given that we have demonstrated the familiarity has a direct effect on the time spent in agonistic interactions in light-bellied brent geese it seems likely that this forms at least part of the explanation for reduced vigilance in this study system.

However, allelomimetic vigilance cascades (Beauchamp 2011; Hare, Campbell & Senkiw 2014) do occur in this population (Rutter, Silk and Bearhop unpublished data) indicating that social information is also important. Furthermore, vigilance can often result from individuals responding to agonistic interactions between neighbouring individuals (Rutter, Silk and Bearhop unpublished data), which raises the possibility that social monitoring and allelomimetism interact closely in influencing group-level patterns of vigilance. It is these latter mechanisms that make considering the familiarity of all group members, rather than just the social relationships of a focal individual key in this species, and in fission-fusion social groups more generally.

The social environment, individual time-budgets and fitness

It is clear that previous and current social interactions in a group are key in determining agonistic interactions and vigilance behaviour in light-bellied brent geese, despite the importance of environmental variables (Fig. 6.2, Fig. 6.4, Fig. 6.5). We have gone on to demonstrate that this directly influences how much time an individual can spend foraging, therefore having a substantial impact on individual time budgets (Fig. 6.6). This is despite light-bellied brent geese forming highly dynamic fission-fusion social systems in which group membership is highly variable and many social associations relatively weak. It demonstrates how even small changes in the social context could have substantial implications for an individual's foraging success as a result of its combined effect on aggression and vigilance. This may be of particularly important in highly-constrained migrants, in which small differences in foraging success will have an important effect on phenology and reproductive success. For example, in light-bellied brent geese carry-over effects from winter and

spring foraging are important in mediating reproductive success (Inger *et al.* 2010), making it probable that these patterns of social behaviour could have substantial fitness implications.

One key aspect of this process that has received relatively little attention is how feedback mechanisms operating between and within different social behaviours could result in relatively small differences in the social environment having major implications on individual time budgets and foraging. Allelomimetic vigilance (Gautrais *et al.* 2007; Pays *et al.* 2007c), and the vigilance cascades that result (Beauchamp 2011), provide an example of how positive feedback can result in changes in individual behaviour having a major influence on collective behaviour, which in turn will further affect the individuals involved. However, as we have shown, aggression and vigilance are also explicitly linked by changes to social monitoring behaviour. Our finding that flock differences explain a large proportion of variance in the probability of aggression occurring perhaps also hint that positive feedback mechanisms operate within agonistic interactions as well. It therefore seems plausible that aggression can result in further aggression, agonistic interactions trigger increased vigilance through an increased requirement for social monitoring and changes in vigilance patterns are able to propagate through allelomimetism. These processes provide a key mechanism by which small changes in the social environment can have considerable implications for collective social behaviour. Clearly this will have a major impact on the time budgets and foraging of all individuals in a group with numerous important consequences, especially on the modification of the trade-offs that exist between foraging and anti-predator behaviour, and the acquisition of resources.

Conclusions

We have demonstrated that social context is important in explaining aggressive interactions and vigilance behaviour in a long-term study population of light-bellied brent geese. Importantly, there was evidence for an interaction between agonistic behaviour and vigilance that has received little empirical attention in other species. This highlights that relatively small changes in social context or environmental conditions can have major implications for individual time budgets. Given the potential importance of changes in individual time budgets for fitness in dynamic social systems, further empirical and theoretical work exploring the impact of repeated interactions on group foraging in fission-fusion systems will be fundamental to improving our understanding of why these widespread social systems are structured the way they are.

7. Social network position and body condition in a highly dynamic fission-fusion social system



7.1 Abstract

Dynamic social systems are widespread in animals. In these systems, individual social network position will be correlated with phenotypic differences and social status. Some studies have also been able to link individual social network position with fitness differences among individuals. However, a correlation between fitness and social position may be generated by differences in individual quality generating variation in social strategy, or by differences in the success of different social strategies. The relative importance of these processes has yet to be resolved. We investigate the relationship between social status, social network position and body condition in a time-constrained staging population of long distance migrant bird. We found that social network position is closely linked to social status in this highly fluid fission-fusion social system. However, even once differences in social status had been accounted for, social network position was related to the ability of individuals to accrue energy resources and migrate to breeding grounds in better condition. The most beneficial social network position varied between dominants and subordinates and closely matched the social network position that they were likely to occupy. This demonstrates that social interaction rules in fission-fusion social systems can be adjusted according to the relative benefits obtained by following different social strategies. Differences in fitness related to variation in social position will be central in driving evolutionary processes in dynamic social systems, and this study highlights the importance of accounting for other differences between individuals when understanding the consequences of variation in social network position.

7.2 Introduction

Fission-fusion dynamics, in which group membership is spatio-temporally dynamic (Couzin & Laidre 2009; Sueur *et al.* 2011b), are widespread in animal social systems (Croft *et al.* 2003; Kerth, Ebert & Schmidtke 2006; Lehmann, Korstjens & Dunbar 2007; Kerth 2008; Fortin *et al.* 2009; Aplin *et al.* 2012). These dynamics generate considerable variation in the social environments experienced by individuals in groups, which will have implications for social behaviour (Carter *et al.* 2009; Farine *et al.* 2014) and fitness (McDonald 2007; Oh & Badyaev 2010; Marshall *et al.* 2012). This in turn will be important in the evolution of non-random social structure in these dynamic social systems (e.g. Croft *et al.* 2005; Mourier, Vercelloni & Planes 2012; Shizuka *et al.* 2014), and generate variation among individuals in the social strategies they use as a function of both fixed (phenotypic differences: Croft *et al.* 2003, sex: Wolf *et al.* 2007, personalities: Croft *et al.* 2009; Aplin *et al.* 2013) and conditional (age: Ramos-Fernández *et al.* 2009, body condition: Farine, Garroway & Sheldon 2012, disease status: Weber *et al.* 2013) traits. As a result, it is often unclear to what extent links between social network position and fitness in fission-fusion social systems are cause or consequence.

Fission-fusion dynamics evolve when there is temporal or spatial heterogeneity in the environment (Sueur *et al.* 2011b). The recent application of social network analysis in animals (Croft, James & Krause 2008; Wey *et al.* 2008; Pinter-Wollman *et al.* 2013) has resulted in the quantification of population social structure, and individual social network position, in an increasing number of fission-fusion social systems. It is clear that patterns of social associations are frequently highly non-random, with spatial constraints on interactions (Mourier, Vercelloni & Planes 2012; Carter *et al.* 2013; Garroway,

Bowman & Wilson 2013), and other factors such as kinship (Wolf & Trillmich 2008; Carter *et al.* 2013), phenotypic similarities (Croft *et al.* 2005; Croft *et al.* 2009) and social preferences (Mourier, Vercelloni & Planes 2012; Carter *et al.* 2013; Shizuka *et al.* 2014) key to driving these patterns. Within these broader population social structures individuals have often been demonstrated to occupy different positions in a social network as a result of phenotypic differences (Farine, Garroway & Sheldon 2012; Aplin *et al.* 2013). For example, Aplin *et al.* (2013) showed that social network position and personality traits were closely linked in a population of great tits *Parus major*. However, the relationship between social dominance, individual status (e.g. body condition) and social network position remains poorly understood (but see Farine, Garroway & Sheldon 2012) for an example involving dominance in a mixed-species study system). Social dominance in particular would be expected to be closely linked to patterns of social interactions in a group (Rands *et al.* 2006; Marshall *et al.* 2012) and space use (Whiteman & Côté 2004; Murray, Mane & Pusey 2007), and thus be an important consideration when exploring the links between social network position and fitness. However, very few studies have linked dominance and differences in social network position (but see Farine, Garroway & Sheldon 2012), and this has meant the relative importance of differences in individual status in explaining links between social network position and fitness remain unknown. Unravelling this relationship will be crucial to improving our understanding of social evolution within fission-fusion social systems.

An important part of this process is to understand how variation in social strategies may affect different individuals in different ways. Non-random social associations would be expected to have a substantial influence on individual

behaviour in group foragers. In particular, familiarity with individuals is known to modulate aggression (Johnsson 1997; Utne-Palm & Hart 2000), vigilance (Carter *et al.* 2009; MacIntosh & Sicotte 2009; Gaynor & Cords 2012) and social learning (Swaney *et al.* 2001; Kavaliers, Colwell & Choleris 2005), with implications for foraging success (Griffiths *et al.* 2004). Likewise, interacting with similar phenotypes facilitates activity synchrony (Conradt & Roper 2000) and reduces consensus costs (Conradt & Roper 2000; Conradt & Roper 2003; Conradt & Roper 2005), increasing the likelihood of social cohesion with individuals with similar phenotypes. As such it may be predicted that individuals that form fewer but stronger social associations in a dynamic social system would be more successful. However, this may depend on differences among individuals, with variation in phenotypic or conditional traits, such as personality, influencing the way in which individuals benefit from different social strategies in dynamic social systems (e.g. see Aplin *et al.* 2013). For example, when dominance hierarchies are important in influencing social behaviour within groups, the benefits obtained from social foraging are accrued asymmetrically (Rands *et al.* 2006). It may therefore be expected that social dominance status and social network position covary, creating the mechanism by which conditional traits may be important in generating as well as being a consequence of any links between social network position and fitness.

Here we combine social network analysis and a novel randomisation-based mixed-modelling approach to explore the link between social dominance, social strategy and body condition in a long-distance migrant, the light-bellied brent goose *Branta bernicla hrota* (Robinson *et al.* 2004). Social network analysis was used to determine variation in social position between individually identifiable colour-ringed light-bellied brent geese. Light-bellied brent geese

forage in large groups (Inger *et al.* 2006a), and form highly dynamic fission-fusion social systems with patterns of social associations that are strongly spatially structured, but with social factors additionally important (Chapter 5). Furthermore, the familiarity of individuals in foraging flocks has been demonstrated to have an impact on individual time budgets and foraging success, with the extent of this effect influenced by individual social network position (Chapter 6). During spring staging in particular, this population is highly time-constrained and individuals must quickly accumulate energy reserves for migration and breeding, with these energy reserves being predictive of reproductive success (Inger *et al.* 2010). This makes this period an ideal time to investigate the extent to which social network position can influence proxies of fitness.

Firstly we explore what generates variation in individual social position, linking differences in association strength and network centrality to social status and home range areas. We then go on to investigate whether differences in an individual's social position influence changes in body condition over the course of spring staging once the effects of sex and social status have been accounted for. We test the predictions that: i) an individual's social network position is closely linked to its use of space, with individuals using larger areas forming more and weaker social associations and being more important in connecting different parts of the network; ii) that individuals lower in social status tend to be these individuals that utilise larger areas and occupy these "transient" positions in the population social structure (more but weaker associations and higher betweenness). However, we predict that iii) more associative social network positions (in particular the formation of stronger social associations) will tend to improve the ability of individuals to end spring staging in better condition even

once social status has been accounted for; but that iv) variation in social dominance status will alter how social network position is related to body condition, with the ability of subordinate individuals to gain body condition being more affected by differences in social network position due to more constrained foraging opportunities. In order to incorporate non-independent network data in a suitable modelling framework to test these hypotheses, we compare the results from linear mixed-effects models run in observed networks to results obtained from models run in randomised networks that account for resightings effects and group structure.

7.3 Methods

Study system

Data were collected during spring staging (29th April - 29th May) populations of east Canadian high arctic (ECHA) light-bellied brent geese in 2012 and 2013. The study population was centred on Alftanes, Iceland (64.1N - 22.0W). In this population ~10% of geese are marked with individual alphanumeric-coded colour leg-rings enabling social and spatial information about these ringed individuals to be gathered. This site is one of the most important spring staging sites for this population. Spring staging is a key period in which individuals rapidly accumulate energy resources for migration and breeding (Inger *et al.* 2008; Inger *et al.* 2010).

Data collection

During each study period the date, time, location and flock size of all observed foraging flocks that contained ringed birds were recorded. The principal observer and team conducted observations in a structured manner. Observations were conducted on a fixed route three times on each day that observers were present. This ensured all sites were visited regularly and that observations of social associations were conducted over a timeframe which made them independent observations. For each flock the identity of each ringed individual was recorded, and additional observations of family relationships (presence or absence of partner and number of offspring) and body condition were made where possible. Individuals were classified as being adults in family groups (with a count of juveniles), paired adults, unpaired adults, juveniles in family groups or unassociated juveniles. Assignment to families required individuals to be found in close proximity and exhibit spatially and temporally coordinated movements (Inger *et al.* 2006a). Assignment of families in this way has been demonstrated to be highly accurate in this population (Harrison *et al.* 2010; Inger *et al.* 2010). The identity of family relationships in any families containing multiple colour-ringed individuals was also recorded. Body condition was measured using abdominal profile indices (APIs; Clausen, Green & Alerstam 2003; Inger *et al.* 2008). In this study these were measured on a 13 point scale (1-7 with 0.5 increments) by experienced and inter-calibrated observers only. In previous studies of geese APIs have been demonstrated to be related to body mass and total energy reserves (e.g. Madsen & Klaassen 2006).

Social network analysis

Social networks were constructed for 373 uniquely colour-ringed individuals in 2012 and 339 individuals in 2013. Social networks were constructed using the gambit of the group (GoG) assumption (Whitehead & Dufault 1999; Croft, James & Krause 2008). Two individuals were deemed to have associated when they co-occurred in a foraging group. Distinct foraging groups were defined using a chain rule (Croft, James & Krause 2008) that classified individuals as being in distinct groups if there was a separation of 50 metres or more, or were split by an artificial barrier that they would not cross while feeding (e.g. a road or fence-line). For each year networks were created using half weight association indices (HWI), as HWI measures better account for their being a higher probability of encountering two individuals when they are found together in a group (Whitehead 2008). From these networks measures of degree (the number of connections), mean association strength (the mean weight of each of these connections), eigenvector centrality (the importance of an individual within the network; a measure that takes into account second order connections) and betweenness (the importance of an individual in connecting different parts of the network) were calculated.

Construction of null networks

Null models for social network structure were constructed by randomly redistributing individuals between groups whilst maintaining the number and size of groups from the observed data. The order of individuals and groups were randomised before each re-assignment. Individuals could also only be assigned to a group once. If individuals remained at the end of the re-

assignment process that couldn't be assigned to any of the remaining groups they were added to a randomly selected group that they were not already present in. On the rare occasions that this was required, the process led to some groups being incompletely filled and thus slightly smaller, with other groups correspondingly slightly larger, than those in the observed data set. However, this made negligible difference to the group size distribution. The fact that observed groups also contain a variable number of unidentifiable individuals further reduces the impact of these slight changes to the group size distribution. For each spring staging season 1000 random sets of social information were generated and used to construct null networks to be compared to the observed network for each study period. The methods of network construction were the same as in the observed dataset, and the same metrics were calculated to describe the social network position of individuals.

Spatial analysis

Home ranges of individuals were calculated using the spatial information provided by resightings data. Home ranges were only generated for individuals which had been resighted 10 or more times to reduce the impact of the number of relocations on the area calculated. Home ranges were calculated using bivariate normal kernels in the package `adehabitatHR` (Calenge 2006) in R 3.1.1 (R development Core Team 2014) for all of these individuals that were observed at more than one distinct location ($n=218$ for 2012, $n=195$ for 2013). Home range areas were calculated using 95% contours of usage probability.

Statistical analysis

1. Space use, social status and social position

Home range areas were modelled as a function of the number of times an individual was resighted, social status and sex, using linear mixed models in the package lme4 (Bates *et al.* 2014) in R 3.1.1 (R development Core Team 2014) with year and individual as random effects. Home range area was log transformed to satisfy assumptions of normality. Social status in many goose species, including this study population, is linked to family group size (Black & Owen 1989; Mulder, Williams & Cooke 1995; Poisbleau *et al.* 2006; Inger *et al.* 2010). Therefore, we used family relationship data to classify social status, with only adults included in the analysis. Individuals were categorised as a) a member of a family group, b) a member of a reproductive pair or c) unpaired for this analysis. Individuals are sexed on capture, either by molecular methods or by cloacal examination (Inger *et al.* 2010). Only individuals for which sex and social status were available were included in the model. Model selection using the package MuMIn (Bartoń 2013) was used to identify the most parsimonious model by minimising AICc values.

The correlation between four key network metrics (degree, mean association strength, eigenvector centrality and betweenness) and home range area for 2012 data was then calculated in UCINET 6.380 (Borgatti, Everett & Freeman 2002), with the number of resightings also included as an explanatory variable. This approach uses permutation methods to test the significance of the model by randomly permuting values of network metrics between individuals 10,000 times and calculating the corresponding multiple regressions. Values for degree, mean association strength and betweenness were transformed to be normally distributed for this analysis.

We then used a novel mixed-modelling approach to explain variation in social network position. This approach involved comparing the effect sizes calculated in the observed social network with equivalent values generated by running the same model in 1000 randomised networks. This approach accounts for the non-independence of network data and the data structure imposed by gambit of the group sampling, enabling us to use linear mixed-effects models on this association-based data. The values of degree, mean association strength, eigenvector centrality and betweenness were related to the number of times an individual was resighted, social status and sex using this approach. Values for degree, mean association strength and betweenness were transformed to satisfy assumptions of normality. The effect size of each explanatory variable in the model for the observed dataset was then compared to the distribution of effect sizes from models run in the null networks for each explanatory variable in turn. Observed effect sizes that lay outside the 95% confidence interval of the mean effect size in randomised networks was treated as significantly different from that expected by random chance.

2. Social position and body condition during staging

Linear mixed effects models were also used to investigate changes in body condition during spring staging for 5316 API measurements from 328 unique individuals in the 2012 and 2013 study periods. Year and individual were fitted as random intercepts, and a random slope for day within year was included to account for the potential of environmental factors generating differences in the rate of energy gain between the two years of the study. Explanatory variables were day, sex, social status, degree, mean association strength and eigenvector centrality. The values of the three metrics were

standardised within each year to be mean centered and have unit variance in the model, as raw values were of different orders of magnitude otherwise. Interactions between day, sex and each network metric, and day, social status and each network metric were fitted in the model. Models were fitted with a normal error distribution as API scores were approximately normally distributed and model plots further indicated the suitability of using this error distribution. The model was then run in the observed dataset and also in all the randomised datasets using the approach described previously. The effect size of fixed effects including network metrics were considered significant when the estimate from the observed network lay outside the 95% confidence intervals of the mean effect size calculated from the randomised networks.

7.4 Results

1. What explains variation in individual social position?

Only social status was present in the top model to explain home range areas of individuals. Individuals that were unassociated, and therefore of low social status, typically used larger areas than family groups (estimate = 0.91 ± 0.51 ; Fig. 7.1) or pairs (estimate = 1.15 ± 0.48 ; Fig. 7.1). Individual social network position was also closely linked to social status and not to sex. Unassociated individuals formed more, but weaker associations than those in pairs or family groups, and these values were outside the 5% confidence interval obtained from running identical models in the null networks (Table 7.1). These individuals also had considerably higher betweenness than individuals either in pairs or family groups (Table 7.1, Fig. 7.2). Individuals in pairs and family groups also seemed to show some differences in social network position

with the former having stronger associations and higher values of eigenvector centrality (Table 7.1). Finally, all network metrics were affected by resighting frequency, but the extent of this effect was reduced in the observed network relative to randomised networks (Table 7.1). This highlights that individual social network positions in these populations are different to those that would be expected if patterns of social interactions were truly random.

Differences in social network position are partially driven by differences among the utilisation distributions of individuals at a population level. Both degree ($r=0.166$, $n=168$, $p=0.003$) and betweenness ($r=0.265$, $n=168$, $p<0.001$) are weakly and positively correlated with home range size. There was no relationship, however, with mean association strength ($r=0.021$, $n=168$, $p=0.318$). Taken together these relationships indicate that differences in home range are of some importance in explaining the differences in social associations among individuals of different social statuses, but that additional explanations are also required.

Metric	Contrast	Model estimate	Null estimate 2.5% quantile	Null estimate 97.5% quantile	p value
Degree	Male cf. Female	-0.06±0.13	-0.11	0.12	0.27
Degree	Pair cf. Family	-0.00±0.12	-0.19	0.13	0.66
Degree	Unassociated cf. Family	0.53±0.41	-0.40	0.26	<0.001
Degree	Resightings	0.05±0.01	0.11	0.12	<0.001
MAS	Male cf. Female	0.02±0.04	-0.01	0.01	0.006
MAS	Pair cf. Family	0.08±0.04	-0.02	0.02	<0.001
MAS	Unassociated cf. Family	-0.24±0.12	-0.04	0.05	<0.001
MAS	Resightings	-0.01±0.00	-0.01	-0.01	<0.001
EC	Male cf. Female	0.06±0.13	-0.17	0.17	0.51
EC	Pair cf. Family	0.28±0.10	-0.27	0.20	0.007
EC	Unassociated cf. Family	-0.26±0.41	-0.59	0.47	0.22
EC	Resightings	-0.01±0.01	0.07	0.09	<0.001
Betweenness	Male cf. Female	0.12±0.16	-0.16	0.17	0.16
Betweenness	Pair cf. Family	0.18±0.22	-0.23	0.22	0.10
Betweenness	Unassociated cf. Family	1.68±0.59	-0.53	0.44	<0.001
Betweenness	Resightings	-0.01±0.01	-0.04	-0.019	0.003

Table 7.1. The effect size of sex, social status and number of resightings on social network position in observed and randomised networks

Models for degree, mean association strength (MAS), eigenvector centrality (EC) and betweenness are presented. Contrasts for which p values for the comparison between observed and null networks are significant once a Bonferroni correction for multiple testing has been applied are in bold.

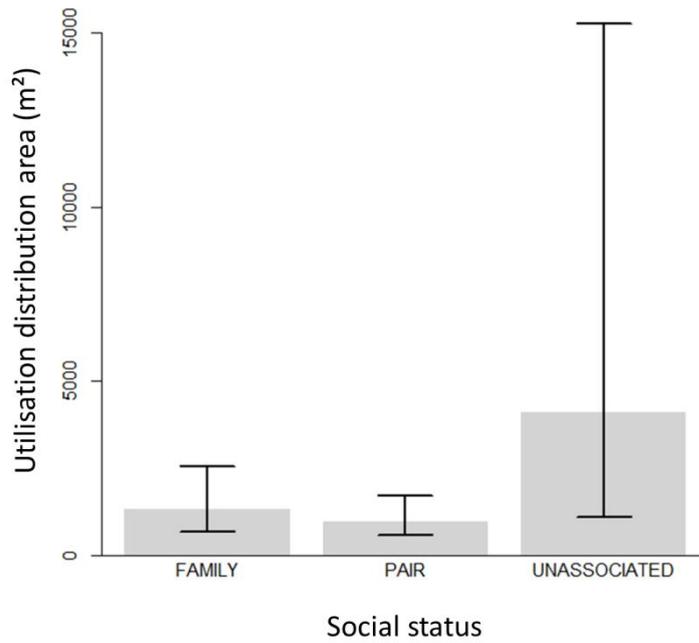


Figure 7.1. The relationship between social status and utilisation distribution area

The graph shows predictions from a linear mixed effects model. Error bars represent the 95% confidence intervals around model predictions.

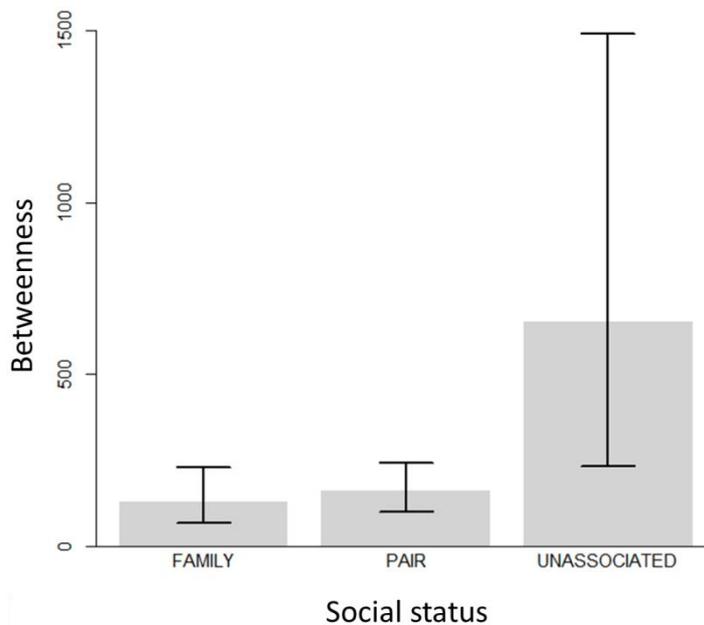


Figure 7.2. The relationship between social status and betweenness

The graph shows predictions from a linear mixed effects model for males resighted 20 times. Error bars represent the 95% confidence intervals around model predictions.

2. How are social network position and changes in body condition related during spring staging?

Change in API during spring staging was found to be affected by sex and social status (Table 7.2, Fig. 7.3, Fig. 7.4). Unassociated individuals gained body condition at a slower rate had lower fat scores at the end of spring staging than individuals in pairs (estimate = -1.00 ± 0.175 API units; Fig. 7.3) or family groups (estimate = -0.93 ± 0.18 API units; Fig. 7.3). Males also tended to gain body condition at a lower rate (estimate = -0.020 ± 0.002 API units) and depart spring staging in poorer condition than females (estimate = -0.60 ± 0.06 API units; Fig. 7.4). Several terms in the model containing measures of social network position also had confidence intervals that would not cross zero (see standard errors in Table 7.3 and Table 7.4). However, when the estimates from the model run in the observed network were compared to equivalent estimates from randomised networks only mean association strength was found to have a significant effect on changes in API scores (Table 7.3 and Table 7.4). Unassociated individuals differed from individuals in pairs and family groups. Increases in mean association strength had a negative effect on their ability to gain body condition, with some weak support that this meant they departed spring staging in worse body condition (Fig. 7.5). This results in unassociated individuals doing considerably worse relative to individuals of higher social status when following these “associative” social strategies, but faring relatively less badly when values of mean association strength are lower.

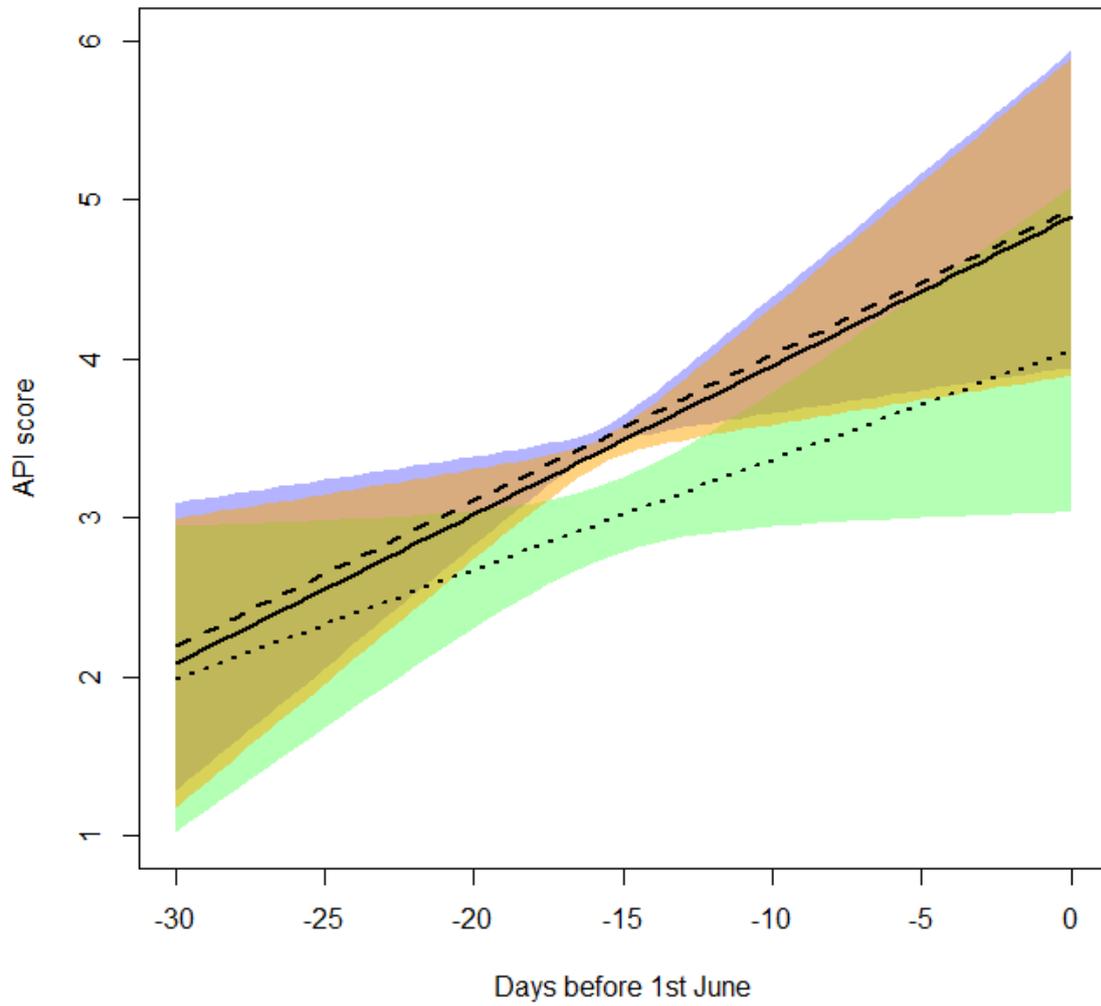


Figure 7.3. The effect of social status on API scores in spring staging light-bellied brent geese

The increase in body condition during spring staging in light-bellied brent geese for females in pairs (dashed line), females in family groups (solid line) and unassociated females (dotted line). The lines are predictions from linear mixed effects models. Shaded areas represent the 95% confidence intervals around model predictions.

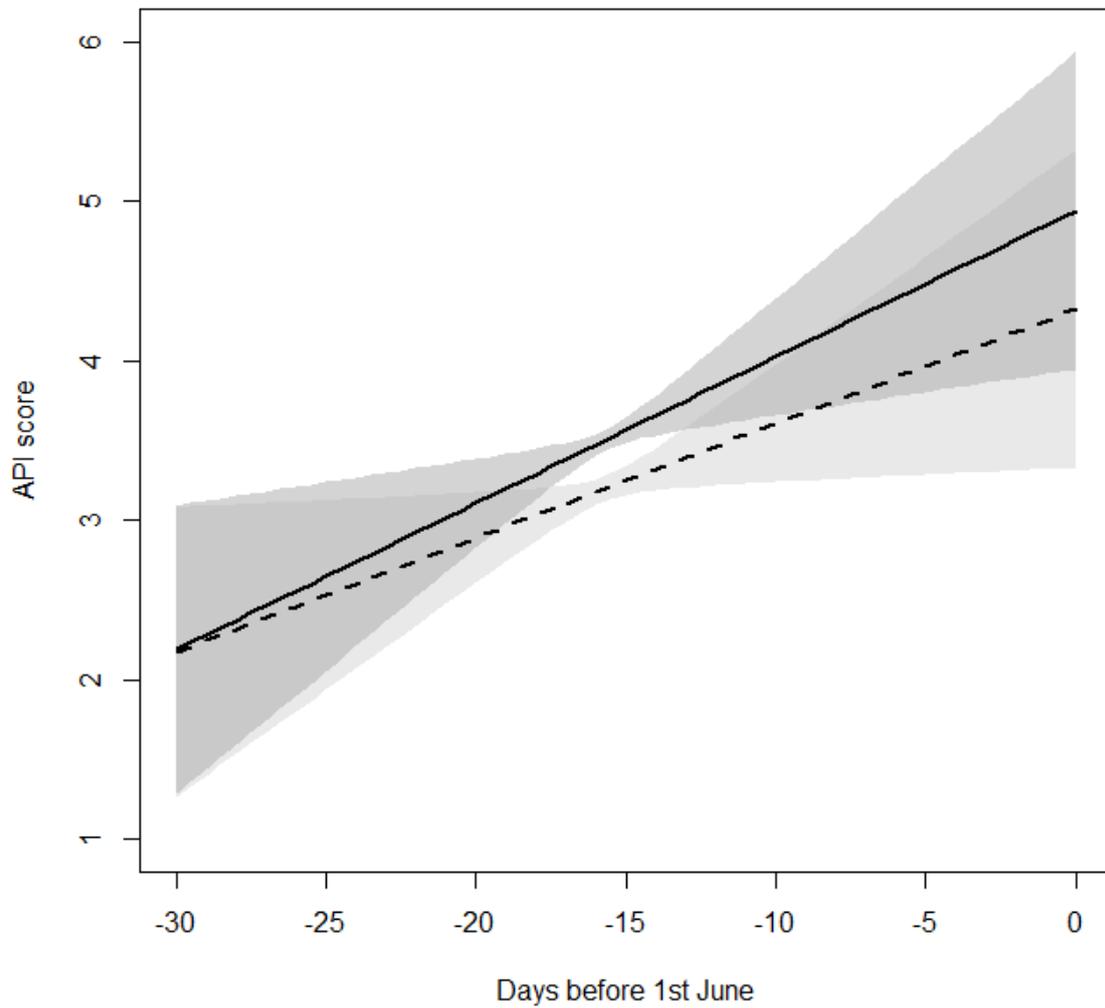


Figure 7.4. The effect of sex on API scores in spring staging light-bellied brent geese

The increase in body condition during spring staging for male (dashed line) and female (solid line) light-bellied brent geese. The lines are predictions from linear mixed effects models for individuals in reproductive pairs. Shaded areas represent the 95% confidence intervals around model predictions.

Contrast	Model estimate	Standard error
Daily change: Female in pair	0.091	0.032
Daily change: Male in pair	0.072	0.032
Daily change: Female in family	0.093	0.032
Daily change: Male in family	0.074	0.032
Daily change: Unassociated female	0.062	0.034
Daily change: Unassociated male	0.043	0.034
Departure condition: Female in pair	4.93	0.50
Departure condition: Male in pair	4.33	0.50
Departure condition: Female in family	4.87	0.50
Departure condition: Male in family	4.27	0.50
Departure condition: Unassociated female	3.93	0.53
Departure condition: Unassociated male	3.33	0.53

Table 7.2. The model estimates and associated standard errors for terms not containing social network information in a linear mixed-effects model for API scores

All estimates are in API units. Estimates for each level of a factor in this model have been obtained by re-levelling factors to change the model intercept.

Contrast	Model estimate	Null estimates 2.5% quantile	Null estimates 97.5% quantile	p value
MAS	0.04±0.07	-0.29	0.41	0.91
Degree	0.20±0.06	-0.45	1.04	0.84
EC	-0.08±0.07	-0.84	0.44	0.73
MAS*Sex	-0.07±0.06	-0.28	0.18	0.80
Degree*Sex	-0.15±0.05	-0.67	0.29	0.94
EC*Sex	0.00±0.07	-0.30	0.59	0.59
MAS*Pair	0.02±0.06	-0.39	0.33	0.83
MAS*Unassociated	-1.00±0.37	-1.12	0.80	0.11
Degree*Pair	-0.06±0.06	-0.83	0.68	1.00
Degree*Unassociated	-0.74±0.33	-2.84	1.91	0.87
EC*Pair	-0.03±0.07	-0.30	0.59	0.85
EC*Unassociated	0.91±0.35	-1.90	2.57	0.66

Table 7.3. Summary of model estimates for the effect of network metrics and interactions containing network metrics on departure body condition in the observed network and randomised networks

Units of estimates and quantile values are API scores. Model estimates from the observed networks are provided with standard errors. MAS is mean association strength, EC is eigenvector centrality.

Contrast	Model estimate	Null estimates 2.5% quantile	Null estimates 97.5% quantile	p value
MAS	0.001±0.003	-0.015	0.017	0.98
Degree	0.005±0.003	-0.028	0.041	0.91
EC	0.001±0.003	-0.034	0.027	0.73
MAS*Sex	0.002±0.003	-0.013	0.020	0.69
Degree*Sex	-0.001±0.002	-0.025	0.027	0.79
EC*Sex	-0.003±0.003	-0.025	0.024	0.85
MAS*Pair	0.001±0.003	-0.014	0.020	0.88
MAS*Unassociated	-0.063±0.025	-0.038	0.065	0.006
Degree*Pair	-0.003±0.003	-0.031	0.040	0.77
Degree*Unassociated	-0.041±0.015	-0.100	0.143	0.32
EC*Pair	-0.003±0.004	-0.036	0.026	0.99
EC*Unassociated	0.051±0.025	-0.133	0.090	0.20

Table 7.4. Summary of model estimates for the effect of network metrics and interactions containing network metrics on daily rate of change in body condition in the observed network and randomised networks

Units of estimates and quantile values are API scores. Model estimates from the observed networks are provided with standard errors. MAS is mean association strength, EC is eigenvector centrality.

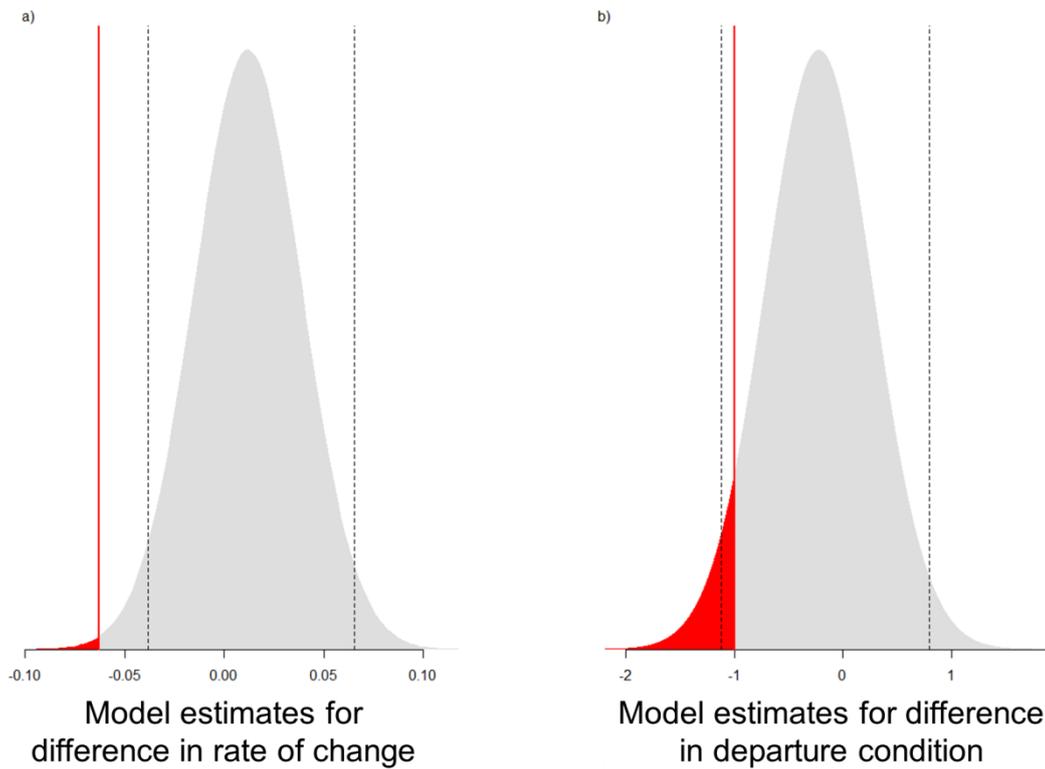


Figure 7.5. A comparison of the effect of mean association strength on body condition during spring staging in the observed and randomised networks

The model estimates for the difference between unassociated adults and adults in family groups in a) the effect of mean association strength on the daily rate of change in body condition and b) the effect of mean association strength on departure condition. The grey distribution is a normal distribution based on the distribution of model estimates in 1000 randomised networks. The dashed lines represent the 2.5% and 97.5% quantiles of this distribution. The red line represents the model estimate of the observed network, and the red shaded area the extent of the normal distribution with more extreme values than this.

7.5 Discussion

Using social network analysis we have demonstrated that individual status is likely to be both a cause (through the effect of social dominance status) and a consequence (through effects on body condition) of differences in social network position between individuals in a fission-fusion population for the first time. Whilst an increasing number of studies have linked social network metrics with fitness (McDonald 2007; Barocas *et al.* 2011; Formica *et al.* 2012; Wey *et al.* 2013), they have failed to account for the fact that differences in social network position maybe caused by differences among individuals in phenotype or social status, as well as having an impact on individual differences themselves. We clearly show that individuals differing in their social dominance occupy different positions in a social network, in part due to possessing larger utilisation distributions. However, we also show that differences in network position have implications for the ability for individuals to gain body condition during spring staging, with tentative evidence to suggest that this means they may leave staging areas in better condition (which can be directly linked to fitness: Inger *et al.* 2010; Harrison *et al.* 2013) even once these differences had been accounted for. Importantly, individuals of different social status typically did best in the social network positions that they were most likely to occupy.

As predicted, individuals that had larger utilisation distributions in this population had higher values of degree and betweenness. Unassociated individuals, that were lower in social hierarchies, were more likely to use larger areas (Fig. 7.2) and also formed more, but weaker social associations (Fig. 7.2) than individuals in pairs or family groups. It seems highly likely that space use explains some but not all of these differences in social network position

between individuals of different social dominance status. The ability to improve body condition during spring staging was related to social network position, although this effect was limited to subordinate individuals (Table 3, Table 4). Finally, there was a difference between individuals of different social status in the relationship between social network position and body condition. Unassociated individuals did worse relative to individuals in pairs or family groups when they formed stronger social associations than if they used a more “transient” social strategy. Therefore, it seems that individuals tend to occupy positions in the social network that are of most benefit to them in terms of foraging success. Potential explanations for subordinate individuals being more successful when not forming stable non-random associations, and for the fact that the effects of social network position were only apparent in these individuals, and not in more socially dominant individuals, are discussed in more detail in the following sections.

Social status and social network position

Correlations between social network position and success have now been found in a wide-range of taxa (McDonald 2007; Barocas *et al.* 2011; Formica *et al.* 2012; Wey & Blumstein 2012; Wiszniewski *et al.* 2012; Wey *et al.* 2013), but whilst several of these studies used multifactorial models, they did not fully account for differences in individual quality in influencing social network position. We clearly demonstrate that differences in social status among individuals is closely linked to variation in their social network position (Fig. 7.2), and that this is at least partly linked to differences in their utilisation distributions (Fig. 7.1).

The fact that subordinate individuals occupy different home range areas than more dominant individuals raises the question as to whether they are being coerced into following these strategies. For example, in sponge-dwelling cleaning gobies *Elacatinus prochilos*, dominants are able to monopolise exclusive territories, forcing subordinates to occupy larger home ranges (Whiteman & Côté 2004). In fission-fusion social systems, if dominant individuals regularly attack subordinates and force them from groups (e.g. Murray, Mane & Pusey 2007), then they may end up in a “transient” social network position that is sub-optimal for them as a consequence of this coercion. However, we found that relative to more dominant individuals subordinates did better in these “transient” social network positions. Unassociated individuals gained condition at a much slower rate relative to individuals in pairs or family groups when comparisons were made for individuals that had high mean association strengths (Fig. 7.5). For more “transient” social strategies, in which social associations tended to be weaker, these differences between individuals of different social status were much less pronounced. This suggests that these individuals are more likely to be occupying positions in the social network with higher degree and betweenness (Fig. 7.2) at least in part because they do better in these social network positions, rather than purely as a result of coercion. This is likely to be a result of asymmetries in benefits obtained from the formation of dominance hierarchies (Hsu, Earley & Wolf 2006) resulting in these individuals being transient and moving more regularly between smaller social groups.

The benefits obtained from interacting repeatedly with other individuals and forming dominance hierarchies include reduced aggression (Goessmann, Hemelrijk & Huber 2000; Hsu, Earley & Wolf 2006), and in fission-fusion social

systems this is likely to increase the stability of larger social groups. However, these benefits are likely to be reduced for individuals at the bottom of these hierarchies if they still receive aggression and have to monitor the behaviour of other flock members to avoid aggressive encounters (Pannoizzo *et al.* 2007; MacIntosh & Sicotte 2009; Favreau, Goldizen & Pays 2010; Gaynor & Cords 2012). Additionally, subordinate individuals may be more successful in smaller flocks. There are increased individual contributions to anti-predator vigilance in smaller groups (Elgar 1989; Beauchamp 2008), and increased need for social monitoring in large groups (Favreau, Goldizen & Pays 2010). This results in reduced asymmetry in the requirement for vigilant behaviour between individuals at the top and bottom of dominance hierarchies in smaller groups due to changes in the predominant explanation for vigilance behaviour. This might result in subordinate individuals moving more frequently between different social groups in response to changes in group sizes. This will result in them occupying different social network positions, and following a more “transient” social strategy due to differences in the optimal size and composition of social groups, supporting the idea that direct coercion is unlikely to be important in this system.

Social network position and foraging success

For individuals higher in social hierarchies there was no strong effect of different social strategies on body condition (Table 7.3 and Table 7.4). Familiarity within foraging flocks has been demonstrated to influence foraging success during winter staging in this population (Chapter 6). Furthermore, there is empirical evidence for similar effects of familiarity on social behaviour (Utne-Palm & Hart 2000; Carter *et al.* 2009; Gaynor & Cords 2012) and foraging

efficiency (Griffiths *et al.* 2004) in a range of other taxa. Therefore, this result is somewhat surprising given the scale of energy resource acquisition during spring staging in this population (Inger *et al.* 2008), and the impact of social network position on individuals of lower social status.

This may suggest that spring staging is not sufficiently time-constrained for the differences in foraging success generated by variation in the social environment to be important in these more dominant individuals. In similar barnacle geese, for example, it has been shown that individuals arriving in worse condition can compensate to some extent and increase API scores slightly faster during the staging period (Prop, Black & Shimmings 2003). It was suggested by the authors that this may be achieved by individuals increasing the amount of time they were foraging for. Alternatively, the importance of accumulating energy reserves during this period may reduce aggression and vigilance in foraging flocks, reducing the importance of forming strong social associations. For example, in turnstones *Arenaria interpres* individuals spent more time foraging and less time vigilant closer to migration periods (Metcalf & Furness 1984), and a similar effect in this system would reduce the impact of being familiar with other group members. However, it is also possible that there are hidden costs of reduced foraging success, such as the intake of specific nutrients or poor anti-oxidant balance, that are not apparent from observing the quantity of fat reserves an individual has accumulated.

The costs of variation in social network position outlined above will be accrued on other aspects of an individual's physiology or behaviour, and so are not apparent in terms of changes to APIs. Inefficient or sub-optimal accumulation of energy reserves may carry hidden physiological costs (McWilliams *et al.* 2004). It has been demonstrated in some migrant bird

species that the fatty acid composition of adipose tissue can be important (McWilliams *et al.* 2004; Pierce & McWilliams 2005). For example, the peak metabolic rate of migratory red-eyed vireos *Vireo olivaceus* can depend on the fatty acid composition of their diet (Pierce *et al.* 2005), and there is evidence that they adjusted their diets accordingly (Pierce *et al.* 2004). Similarly, transport of fatty acids to flight muscles requires a substantial up-regulation of fatty acid transporter proteins (Guglielmo, Haunerland & Williams 1998; Guglielmo 2010), and this together with the requirement to increase lean body mass (e.g. Piersma, Gudmundsson & Lilliendahl 1999) will require increased uptake of nitrogen rich resources. Therefore, it is highly likely that the quality of resource intake, as well as the quantity, will be important. Additionally, the balance of reactive oxygen metabolites and anti-oxidants may be an important mediator of the costs of migration (Costantini 2008; Jenni-Eiermann *et al.* 2014). It has been shown that migrant passerines in poor condition during staging periods have been found to have a poorer balance between reactive oxygen metabolites and plasma anti-oxidant capacity (Costantini, Cardinale & Carere 2007), and it may be that individuals that are having to compensate for less efficient feeding may also pay similar costs.

Statistical approaches to network analysis

We used a permutation-based method to enable us to use linear mixed-effects models for the multifactorial analysis of association-based social networks. By running our model in the observed network and 1000 randomised networks generated from the original data, we were able to account for the non-independence of individuals in the network and, importantly, the group structure of the original dataset in our analyses. The value of using this approach in

avoiding potentially erroneous conclusions is clearly highlighted by the fact that several terms that appeared important in the observed model, especially the effect of degree on departure condition (Table 7.3), were found to have an effect no different to that observed in the randomised networks. Therefore our use of this method indicates the importance of the continued development of network-based modelling approaches (e.g. Croft *et al.* 2011; Krivitsky 2012; Pinter-Wollman *et al.* 2013).

Conclusions

This work highlights the importance of teasing apart individual status and quality when investigating the consequences of individual social strategies. By doing this we were able to show that much of the variation in condition attributable to variation in social network position was driven by differences in social status. Differences in social network position, however, still remained important once social dominance status had been accounted for. Our findings also indicate that work linking social network position and social dominance to physiological differences may bring important new insights, as it may be possible for individuals, especially more dominant individuals, to compensate for the relatively small differences to behaviour and foraging that occur as a result of variation in individual social strategies.

8. General Discussion



8.1 Overview

I have used social network analysis and behavioural observations to explore the causes and consequences of fission-fusion social dynamics in a migratory bird species over multiple stages of its annual cycle for the first time. This work demonstrated that light-bellied brent geese form highly spatially structured social systems, akin to many other animals (Mourier, Vercelloni & Planes 2012; Carter *et al.* 2013; Garroway, Bowman & Wilson 2013; Shizuka *et al.* 2014). Furthermore, social associations within these social structures are highly stable within staging periods and among years. Behavioural observations of individuals foraging within flocks taught us that social behaviour was strongly influenced by the presence of familiar individuals, with implications for foraging success. Variation in social strategy among individuals during spring staging was closely linked to their social dominance status and utilisation distribution, and links between social status and social strategy were associated with success. Subordinate individuals did less well relative to dominants when following an “associative” social strategy, compared to when following more “transient” social strategies. This provides evidence that individuals in these fission-fusion populations tend to occupy social network positions that are optimal for them.

8.2 Using association-based social networks in natural systems

Initially I explored the validity of using the co-occurrence of uniquely colour-ringed individuals in social groups to build social networks in this population. I was concerned that conclusions drawn from network analysis may

be influenced by the fact that it was only possible to identify approximately 10% of individuals in our study populations. Additionally, I was keen to test how strongly the assumption that co-occurrence in a social group would constitute a meaningful social interaction. Brent geese form social groups that vary considerably in size from a handful of individuals to well over a thousand. It seems possible that depending on how individuals behave and interact within groups, this might affect how likely or strong an interaction could be considered to be.

Despite a large body of work elsewhere in the social networks literature focussing on the effects of sampling from networks on the accuracy of network metrics at a network or population level (e.g. Borgatti, Carley & Krackhardt 2006; Lee, Kim & Jeong 2006), there was little research on the ability to use a sampled “partial network” to make inferences about individuals (although see Stumpf & Thorne 2006 for an example from neurological networks). I found that for individual-level metrics in a simulated population with highly fluid fission-fusion dynamics it was appropriate to make inferences about the social position or strategy from small partial networks, although care should be taken in interpreting the value of some metrics. I highlight that, based on work demonstrating the susceptibility of network-level properties to changes in network topology (Frantz, Cataldo & Carley 2009), work extending this to a wide range of animal study systems, especially those with highly structured patterns of interactions (e.g. Connor, Heithaus & Barre 2001; Wittemyer, Douglas-Hamilton & Getz 2005; Lehmann, Korstjens & Dunbar 2007; Wiszniewski, Brown & Möller 2012) would be greatly beneficial. However, in the meantime these results suggest the application of social networks in long-term marking, tagging or biologging projects (e.g. Hamede *et al.* 2009; Aplin *et al.* 2013;

Farine & Milburn 2013; Weber *et al.* 2013), in which not all individuals in a population are identifiable is still likely to provide a reliable indication of the real social strategy of individuals.

The use of association-based methods of network construction in natural systems is also going to be influenced by the second issue outlined at the start of this section. By modelling within-group behaviour, I showed that relationship between the likelihood of meaningful social interactions occurring and group size would be highly dependent on the nature of the interaction, the ephemerality of social groups, the movement of individuals within them, and how group density depended on group size. Understanding within-group dynamics and deploying the appropriate correction for this effect is likely to be of great importance, as I demonstrated that the use of different corrections can have considerable qualitative and quantitative effects on network- and individual-level metrics. Brent geese are highly mobile within their social groups and group density often increases with the size of the groups. Furthermore, I was interested in group-level effects on social behaviour. As a result I chose to persist with using traditional association indices. However, this approach may not be suitable in all studies using association-based methods of network construction, and I would advocate a careful consideration of how individuals behave within groups and the types of interaction of interest before deciding whether association indices should be corrected for group size effects. It is certainly clear that the use of association indices in the current literature is too prescriptive given the extent of the qualitative effect that using different measures of association can have.

Collectively, these simulation-modelling chapters highlight that social network analysis in natural study systems will continue to be very useful in

providing a framework to improve our understanding of fission-fusion dynamics, and the variation in individual strategies within them. However, there has very been little effort made to validate the use of network analysis in many of the systems it is now used in, and further modelling work exploring the role of missing individuals and interactions on the conclusions made (both at an individual and network level) should be considered a priority. Integrating ideas from elsewhere in the networks literature into the approaches we use to study animal sociality is likely to be an especially useful approach to this problem.

8.3 Fission-fusion dynamics in a migratory species

Migration is likely to be an important process in driving changes in social associations across larger temporal scales, affecting both overall social dynamics and individual associations. Migration is likely to lead to changes in social dynamics if the habitats used or distribution of resources changes at different points across the migratory cycle. For example, Cortes-Avizanda *et al.* (2011) found social dynamics in black kites *Milvus migrans* and Egyptian vultures *Neophron percnopterus* social dynamics differed between breeding and non-breeding areas due to changes in resource distribution. However, my research is the first to use social network analysis across multiple stages of a migratory cycle, and I found that social structure was relatively similar between my two core study sites. I did find overall changes in social structure, however, when individuals moved from foraging on intertidal to terrestrial resources early in winter staging, supporting the importance of resource distribution in driving variation in social dynamics in migrants. The broad similarity between population-level patterns of social interactions during winter and spring staging

suggests that birds are using similar social foraging strategies for terrestrial areas during both staging periods, despite differences in habitats. Further research, relating population social structures to changes in habitat, diet or resource distribution across multiple points of a migratory cycle could provide some useful insights into the flexibility of social dynamics in fission-fusion systems. It might be predicted that there will be some plasticity in social dynamics, but there may be constraints on the extent of the changes that can occur in any one population.

The persistence and stability of individual social associations across the annual cycle will be central to some key population-level processes, especially disease dynamics. Previous work in wildfowl has suggested that non-family associations do not persist across the migratory cycle (Desnoyers, Gauthier & Lefebvre 2012). Our results in chapter 5 indicate that this is also likely to be the case in this population, albeit with the caveat that I was only working with one pair of staging sites and a relatively low number of marked individuals. Migration routes are culturally inherited in wildfowl with juveniles learning staging sites from their parents during their first winter (Åkesson & Hedenström 2007; Harrison *et al.* 2010; Inger *et al.* 2010; Jonker *et al.* 2011). Thus, there is no expectation for social associations to be the key process in driving migratory connectivity. However, the limited natal dispersal observed in this species (Harrison *et al.* 2010), may result in a cryptic kin structure (Hatchwell 2010) that persists across multiple stages of the annual cycle and explain some low-level persistence of social associations between winter and spring staging in our study populations. This can be illustrated very clearly with the example of a family group caught in south Dublin in February 2012 that continued to be seen

at the same winter and spring staging sites, and often in the same flocks, throughout the 2012/2013 winter and 2013 spring (Silk M. pers. obs.).

Understanding the influence of migration on the temporal dynamics of fission-fusion social systems has clear implications for understanding how information and disease might spread through an entire population. For example, changes in social dynamics, and in particular any changes in individual social associations, will have major implications for the transmission of infections between sub-populations. Therefore, not only does using social network analysis provide us information on the fine-scale social structure in different periods, but also an insight into the level of mixing between different staging sub-populations. Given the importance of migratory populations in transferring disease between geographically widely separated areas, better understanding the epidemiology of these populations is of great consequence (Hoye *et al.* 2011). This is nowhere more true than in wildfowl, which are important vectors of avian influenza (Chen *et al.* 2005; Hoye *et al.* 2011; Dijk *et al.* 2014). Migratory wildfowl populations are therefore often feared to have the potential to be major players in any global pandemic of this zoonotic infection (Chen *et al.* 2005).

8.4 Space use, repeated interactions and stable social hierarchies

In chapter 5 I discussed the difficulties of distinguishing between stable social associations and space use at the finest spatial scales. For networks such as ours that are based on the spatio-temporal co-occurrence of two individuals (albeit in a pre-defined social group), it can be very hard to separate

these two processes. As a result, our spatially constrained randomised networks did not account for differences in the probabilities of site use within the home range of an individual as it was felt that this would potentially incorporate social effects into the randomised data. Our results made it clear that incorporating space in this way was insufficient to explain the network structures that I observed in our populations. Thus I concluded that it was highly likely that social factors were involved to some extent in the social structures found in light-bellied brent goose staging populations. Whilst, I can't entirely rule out differences in space use at incredibly fine-scales, it seems unlikely that this is a sufficient explanation given that birds will travel together to these foraging areas from communal roosts.

It is also clear that shared use of space and social interactions will be closely linked processes in the evolutionary ecology of social systems such as this regardless. The benefits obtained from interacting with familiar individuals will be present even in the case that individuals make grouping decisions entirely independently of the social environment, as long as shared patterns of site use result in individuals interacting repeatedly. Thus the evolution of limited (adult) dispersal and high levels of site fidelity might be closely related to the advantages of developing structured patterns of social interactions. This might be predicted to be particularly important or frequent in species with social hierarchies, as familiarity will result in a better-established hierarchy and reduced aggression (Goessmann, Hemelrijk & Huber 2000). The link between high levels of site fidelity, social interactions and the stability of dominance hierarchies may add a new level to our understanding of why social animals use limited home ranges. In these species it may be that familiarity with the social environment is just as important as familiarity with the ecological environment.

Furthermore, these benefits of familiarity with the social environment will additionally be influenced by the development of cryptic kin structure (Hatchwell 2010) if natal dispersal is also limited, as is the case in this population (Harrison *et al.* 2010).

The importance of the social environment in explaining social behaviour in group foragers is borne out by the growing empirical evidence for a role of social monitoring in explaining vigilance behaviour (Cameron & du Toit 2005; Pannozzo *et al.* 2007; Favreau, Goldizen & Pays 2010; Gaynor & Cords 2012). I was able to demonstrate in chapter 6 that light-bellied brent geese that received aggression were more vigilant, and that flocks that were more familiar with each other tended to be less vigilant. These results are strongly indicative of social monitoring being a key process in helping to explain individual time budgets in this population. It would be of great interest to extend our understanding of social behaviour in this species to directly link aggressive behaviour and vigilance at shorter temporal scales and explore how individual or dyadic behaviour scales up to collective group-level phenomena. This is an exciting area of animal behaviour research that is closely linked to growing interest in dynamic social systems. Placing this sort of behavioural research in the context of repeated interactions and familiarity would provide fascinating insights into the co-evolution of space use and social structure in these social systems.

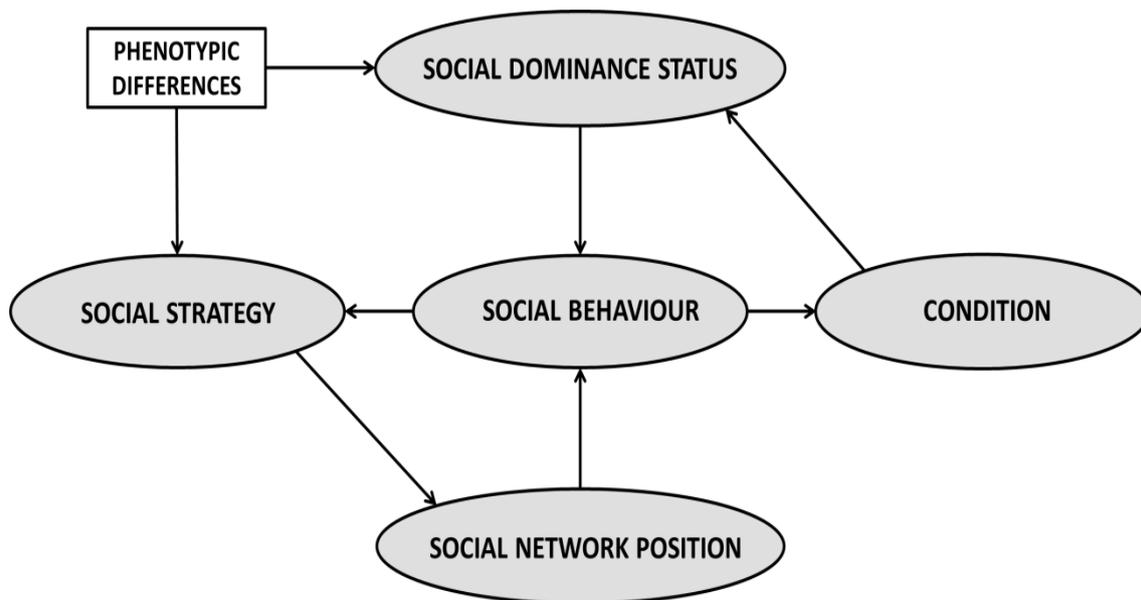


Figure 8.1. A framework for a better understanding of the relationship between conditional traits and social network position for individuals in a fission-fusion social system

8.5 The individual in a complex social world

Interaction rules and social decision-making will be highly dependent on these patterns of behaviour and interactions within groups, as they will be important in determining the costs and benefits associated with different individual social strategies (Fig. 8.1). There is a great deal of complexity in the dynamics of individual time budgets, which I explored to some extent in chapter 6. Feedback mechanisms operating within and between social behaviours can have a massive influence on individual time budgets. For example I showed how increased aggression could lead to increased vigilance. Furthermore, the social context of these interactions will also be important in determining group-level collective patterns of behaviour (Marshall *et al.* 2012), as the use of social information often results in cascades of behaviours within groups (Beauchamp 2011; Beauchamp, Alexander & Jovani 2012; Hare, Campbell & Senkiw 2014).

A better understanding of how these feedback mechanisms influence individual time budgets will be fundamental in determining how familiarity, dominance and personality alter foraging success in different groups (Fig. 8.1). Clearly this forms a necessary part in understanding of the evolution of interaction rules, the decisions of individuals in fission-fusion social systems, and thus the development and evolution of individual social strategies in these dynamic systems.

The dynamic nature of fission-fusion systems results in greater complexity in the social environment, and this creates a different set of problems for individuals in these social systems than in species with more stable social groups. In fission-fusion social systems an individual's social strategy will be flexible and depend on the interaction between its condition, the ecological environment and social environment. Plasticity in social strategies would be expected to result in individuals occupying social positions (or niches; Bergmüller & Taborsky 2010) that are optimal for them at that given time, a concept supported by the results of chapter 7. This will make individual social position an incredibly dynamic concept, with knock-on implications for population-level social structures. Thus, in order to fully understand how social behaviour and interaction rules combine to determine flexible strategies in these dynamic social systems a vital step will be to further develop temporally dynamic network approaches (Pinter-Wollman *et al.* 2013). A key approach here is likely to be to i) develop agent-based models of fission-fusion social systems that can be used to better understand how variation in interaction rules leads to the development of distinct social strategies that can vary over time; and ii) develop models to better understand the formation or breaking of social associations according to a range of fixed and time-dependent individual

attributes. These approaches would help us understand how independent social decisions or a set of state-dependent interaction rules can combine to build social strategies, and how this may relate to phenotypic differences between individuals.

8.6 Concluding remarks

This research demonstrates the potential of applying social network methods in long-term study populations where individuals can be identified at repeated time points. I used simulation-modelling approaches to test the robustness of network approaches under the sort of conditions likely to arise in natural systems, before applying network-based methods to study the causes and consequences of variation in social structure and individual social strategy in a migratory population. I was able to show the key processes important in generating non-random patterns of social associations in this species, and how they drive social dynamics across the annual cycle. I was also able to demonstrate the importance of these non-random social associations in influencing individual time budgets in foraging groups. I then showed that variation between individuals in social network position could influence body condition, over and above the confounding effects of social status. Intriguingly, this effect was most apparent in subordinate individuals, suggesting that its influence on foraging success is higher in individuals whose foraging opportunities are more restricted by the social environment. These individuals tended to do relatively better using a transient social strategy that was typical of individuals of their social status, highlighting how the interaction between individual differences and social strategy may well be adaptive. Additional

empirical research focussed on linking behaviour within groups to variation in individual social position and space use using individually-marked animals would be of great benefit in unravelling these processes further.

References

- Åkesson, S. & Hedenström, A. (2007) How migrants get there: migratory performance and orientation. *BioScience*, **57**, 123-133.
- Alba, R.D. (1982) Taking stock of network analysis: A decade's results. *Research in the Sociology of Organizations*, **1**, 39-74.
- Amano, T., Ushiyama, K., Fujita, G. & Higuchi, H. (2006) Costs and benefits of flocking in foraging white-fronted geese (*Anser albifrons*): effects of resource depletion. *Journal of Zoology*, **269**, 111-115.
- Andino, N., Reus, L., Cappa, F.M., Campos, V.E. & Giannoni, S.M. (2011) Social environment and agonistic interactions: Strategies in a small social mammal. *Ethology*, **117**, 992-1002.
- Aplin, L., Farine, D., Morand-Ferron, J. & Sheldon, B. (2012) Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4199-4205.
- Aplin, L., Farine, D., Morand-Ferron, J., Cole, E., Cockburn, A. & Sheldon, B. (2013) Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters*, **16**, 1365-1372.
- Aplin, L.M., Sheldon, B.C. & Morand-Ferron, J. (2013) Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, **85**, 1225-1232.
- Archie, E.A., Moss, C.J. & Alberts, S.C. (2006) The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 513-522.
- Asensio, N., Korstjens, A.H. & Aureli, F. (2009) Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology*, **63**, 649-659.
- Atton, N., Galef, B., Hoppitt, W., Webster, M. & Laland, K. (2014) Familiarity affects social network structure and discovery of prey patch locations in foraging stickleback shoals. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20140579.

- Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fiore, A., Dunbar, R.I. & Henzi, S.P. (2008) Fission-fusion dynamics. *Current Anthropology*, **49**, 627-654.
- Aureli, F., Schaffner, C.M., Asensio, N. & Lusseau, D. (2012) What is a subgroup? How socioecological factors influence interindividual distance. *Behavioral Ecology*, **23**, 1308-1315.
- Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A. & Viale, M. (2008) Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. *Animal Behaviour*, **76**, 201-215.
- Barocas, A., Ilany, A., Koren, L., Kam, M. & Geffen, E. (2011) Variance in Centrality within Rock Hyrax Social Networks Predicts Adult Longevity. *PloS one*, **6**, e22375.
- Barrat, A., Barthelemy, M., Pastor-Satorras, R. & Vespignani, A. (2004) The architecture of complex weighted networks. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 3747-3752.
- Bartoń, K. (2013) MuMIn: multi-model inference, R package version 1.9.13.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. <http://CRAN.R-project.org/package=lme4>.
- Beauchamp, G. (1998) The effect of group size on mean food intake rate in birds. *Biological Reviews*, **73**, 449-472.
- Beauchamp, G. (1999) The evolution of communal roosting in birds: origin and secondary losses. *Behavioral Ecology*, **10**, 675-687.
- Beauchamp, G. (2003) Group-size effects on vigilance: a search for mechanisms. *Behavioural Processes*, **63**, 111-121.
- Beauchamp, G. (2008) What is the magnitude of the group-size effect on vigilance? *Behavioral Ecology*, **19**, 1361-1368.
- Beauchamp, G. (2010) Relationship between distance to cover, vigilance and group size in staging flocks of semipalmated sandpipers. *Ethology*, **116**, 645-652.
- Beauchamp, G. (2011) Collective waves of sleep in gulls (*Larus* spp.). *Ethology*, **117**, 326-331.
- Beauchamp, G., Alexander, P. & Jovani, R. (2012) Consistent waves of collective vigilance in groups using public information about predation risk. *Behavioral Ecology*, **23**, 368-374.

- Beauchamp, G. (2013) Is the magnitude of the group-size effect on vigilance underestimated? *Animal Behaviour*, **85**, 281-285.
- Beeton, N. & McCallum, H. (2011) Models predict that culling is not a feasible strategy to prevent extinction of Tasmanian devils from facial tumour disease. *Journal of Applied Ecology*, **48**, 1315-1323.
- Beisner, B.A., Jackson, M.E., Cameron, A.N. & McCowan, B. (2011) Detecting instability in animal social networks: genetic fragmentation is associated with social instability in rhesus macaques. *PLoS ONE*, **6**, e16365.
- Bercovitch, F.B. & Berry, P.S. (2010) Ecological determinants of herd size in the Thornicroft's giraffe of Zambia. *African Journal of Ecology*, **48**, 962-971.
- Bergman, T.J., Beehner, J.C., Cheney, D.L. & Seyfarth, R.M. (2003) Hierarchical classification by rank and kinship in baboons. *Science*, **302**, 1234-1236.
- Bergmüller, R. & Taborsky, M. (2010) Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, **25**, 504-511.
- Black, J.M. & Owen, M. (1989) Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Animal Behaviour*, **37**, 199-209.
- Black, J.M., Carbone, C., Wells, R.L. & Owen, M. (1992) Foraging dynamics in goose flocks: the cost of living on the edge. *Animal Behaviour*, **44**, 41-50.
- Blakeslee, C., McRobert, S., Brown, A. & Clotfelter, E. (2009) The effect of body coloration and group size on social partner preferences in female fighting fish (*Betta splendens*). *Behavioural Processes*, **80**, 157-161.
- Blumstein, D.T., Wey, T.W. & Tang, K. (2009) A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3007-3012.
- Bode, N.W., Wood, A.J. & Franks, D.W. (2011) Social networks and models for collective motion in animals. *Behavioral Ecology and Sociobiology*, **65**, 117-130.
- Bonacich, P. (1972) Factoring and weighting approaches to status scores and clique identification. *Journal of Mathematical Sociology*, **2**, 113-120.
- Bonacich, P. (1987) Power and Centrality: A Family of Measures. *American Journal of Sociology*, **92**, 1170-1182.

- Bonacich, P. (1991) Simultaneous group and individual centralities. *Social networks*, **13**, 155-168.
- Boogert, N.J., Nightingale, G.F., Hoppitt, W. & Laland, K.N. (2014) Perching but not foraging networks predict the spread of novel foraging skills in starlings. *Behavioural Processes*.
- Borgatti, S.P., Everett, M.G. & Freeman, L.C. (2002) UCINET 6 For Windows: Software for Social Network Analysis.
- Borgatti, S.P., Carley, K.M. & Krackhardt, D. (2006) On the robustness of centrality measures under conditions of imperfect data. *Social networks*, **28**, 124-136.
- Bos, D., Van De Koppel, J. & Weissing, F.J. (2004) Dark-bellied Brent geese aggregate to cope with increased levels of primary production. *Oikos*, **107**, 485-496.
- Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, **80**, 205-225.
- Braun, A. & Bugnyar, T. (2012) Social bonds and rank acquisition in raven nonbreeder aggregations. *Animal Behaviour*, **84**, 1507-1515.
- Brent, L., Semple, S., Dubuc, C., Heistermann, M. & MacLarnon, A. (2011) Social capital and physiological stress levels in free-ranging adult female rhesus macaques. *Physiology & Behavior*, **102**, 76-83.
- Brown, C.R. & Brown, M.B. (1986) Ectoparasitism as a Cost of Coloniality in Cliff Swallows (*Hirundo Pyrrhonota*). *Ecology*, **67**, 1206-1218.
- Brown, C.R. (1988) Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. *Animal Behaviour*, **36**, 780-792.
- Brown, J.L. (1982) Optimal group size in territorial animals. *Journal of Theoretical Biology*, **95**, 793-810.
- Browning, L., Patrick, S., Rollins, L., Griffith, S. & Russell, A. (2012) Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 3861-3869.
- Buchanan, J.B., Lyons, J.E., Salzer, L.J., Carmona, R., Arce, N., Wiles, G.J., Brady, K., Hayes, G.E., Desimone, S.M. & Schirato, G. (2012) Among-year site fidelity of Red Knots during migration in Washington. *Journal of Field Ornithology*, **83**, 282-289.
- Bull, C., Godfrey, S. & Gordon, D. (2012) Social networks and the spread of *Salmonella* in a sleepy lizard population. *Molecular Ecology*, **21**, 4386-4392.

- Butts, C.T. (2008) Social network analysis with sna. *J. Stat. Softw*, **24**, 1-51.
- Butts, C.T. (2014) sna: Tools for Social Network Analysis. R package version 2.3-2. <http://CRAN.R-project.org/package=sna>.
- Calenge, C. (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516-519.
- Calhim, S., Shi, J. & Dunbar, R. (2006) Sexual segregation among feral goats: testing between alternative hypotheses. *Animal Behaviour*, **72**, 31-41.
- Camazine, S. (2003) *Self-organization in biological systems*. Princeton University Press.
- Cameron, E.Z. & du Toit, J.T. (2005) Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. *Animal Behaviour*, **69**, 1337-1344.
- Cantor, M., Wedekin, L.L., Guimarães, P.R., Daura-Jorge, F.G., Rossi-Santos, M.R. & Simões-Lopes, P.C. (2012) Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society. *Animal Behaviour*, **84**, 641-651.
- Carere, C., Montanino, S., Moreschini, F., Zoratto, F., Chiarotti, F., Santucci, D. & Alleva, E. (2009) Aerial flocking patterns of wintering starlings, *Sturnus vulgaris*, under different predation risk. *Animal Behaviour*, **77**, 101-107.
- Carter, A.J., Macdonald, S.L., Thomson, V.A. & Goldizen, A.W. (2009) Structured association patterns and their energetic benefits in female eastern grey kangaroos, *Macropus giganteus*. *Animal Behaviour*, **77**, 839-846.
- Carter, A.J., Pays, O. & Goldizen, A.W. (2009) Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. *Behavioral ecology and sociobiology*, **64**, 237-245.
- Carter, K.D., Seddon, J.M., Frère, C.H., Carter, J.K. & Goldizen, A.W. (2013) Fission–fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. *Animal Behaviour*, **85**, 385-394.
- Carter, S.P., Delahay, R.J., Smith, G.C., Macdonald, D.W., Riordan, P., Etherington, T.R., Pimley, E.R., Walker, N.J. & Cheeseman, C.L. (2007) Culling-induced social perturbation in Eurasian badgers *Meles meles* and the management of TB in cattle: an analysis of a critical problem in applied ecology. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2769-2777.

- Cavagna, A., Cimarelli, A., Giardina, I., Parisi, G., Santagati, R., Stefanini, F. & Tavarone, R. (2010) From empirical data to inter-individual interactions: Unveiling the rules of collective animal behavior. *Mathematical Models and Methods in Applied Sciences*, **20**, 1491-1510.
- Chapman, C.A., Chapman, L.J. & Wrangham, R. (1995) Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, **36**, 59-70.
- Chen, H., Smith, G., Zhang, S., Qin, K., Wang, J., Li, K., Webster, R., Peiris, J. & Guan, Y. (2005) Avian flu: H5N1 virus outbreak in migratory waterfowl. *Nature*, **436**, 191-192.
- Claidiere, N., Messer, E.J., Hoppitt, W. & Whiten, A. (2013) Diffusion Dynamics of Socially Learned Foraging Techniques in Squirrel Monkeys. *Current Biology*, **23**, 1251-1255.
- Clausen, P., Green, M. & Alerstam, T. (2003) Energy limitations for spring migration and breeding: the case of brent geese *Branta bernicla* tracked by satellite telemetry to Svalbard and Greenland. *Oikos*, **103**, 426-445.
- Clutton-Brock, T. (2009) Cooperation between non-kin in animal societies. *Nature*, **462**, 51-57.
- Colwell, M.A. (2010) *Shorebird ecology, conservation, and management*. Univ. of California Press.
- Conklin, J.R. & Colwell, M.A. (2008) Individual associations in a wintering shorebird population: do Dunlin have friends? *Journal of Field Ornithology*, **79**, 32-40.
- Connor, R.C., Mann, J., Tyack, P.L. & Whitehead, H. (1998) Social evolution in toothed whales. *Trends in Ecology & Evolution*, **13**, 228-232.
- Connor, R.C., Heithaus, M.R. & Barre, L.M. (2001) Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 263-267.
- Connor, R. & Whitehead, H. (2005) Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission–fusion societies. *Animal Behaviour*, **69**, 127-132.
- Connor, R.C. (2007) Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 587-602.

- Conradt, L. (1998) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **265**, 1359-1368.
- Conradt, L., Clutton-Brock, T.H. & Guinness, F.E. (2000) Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behaviour*, **59**, 1049-1060.
- Conradt, L. & Roper, T. (2000) Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **267**, 2213-2218.
- Conradt, L., Gordon, I., Clutton-Brock, T., Thomson, D. & Guinness, F. (2001) Could the indirect competition hypothesis explain inter-sexual site segregation in red deer (*Cervus elaphus* L.)? *Journal of Zoology*, **254**, 185-193.
- Conradt, L. & Roper, T.J. (2003) Group decision-making in animals. *Nature*, **421**, 155-158.
- Conradt, L. & Roper, T.J. (2005) Consensus decision making in animals. *Trends in Ecology & Evolution*, **20**, 449-456.
- Cortes-Avizanda, A., Almaraz, P., Carrete, M., Sanchez-Zapata, J.A., Delgado, A., Hiraldo, F. & Donazar, J.A. (2011) Spatial heterogeneity in resource distribution promotes facultative sociality in two trans-Saharan migratory birds. *PLoS ONE*, **6**, e21016.
- Costantini, D. (2008) Oxidative stress in ecology and evolution: lessons from avian studies. *Ecology Letters*, **11**, 1238-1251.
- Costantini, D., Cardinale, M. & Carere, C. (2007) Oxidative damage and anti-oxidant capacity in two migratory bird species at a stop-over site. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, **144**, 363-371.
- Couchoux, C. & Cresswell, W. (2012) Personality constraints versus flexible antipredation behaviors: how important is boldness in risk management of redshanks (*Tringa totanus*) foraging in a natural system? *Behavioral Ecology*, **23**, 290-301.
- Couzin, I.D., Krause, J., James, R., Ruxton, G.D. & Franks, N.R. (2002) Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology*, **218**, 1-11.
- Couzin, I.D. & Krause, J. (2003) Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior*, **32**.

- Couzin, I.D. (2006) Behavioral ecology: social organization in fission–fusion societies. *Current Biology*, **16**, R169-R171.
- Couzin, I.D. & Laidre, M.E. (2009) Fission–fusion populations. *Current Biology*, **19**, R633-R635.
- Craft, M.E., Volz, E., Packer, C. & Meyers, L.A. (2011) Disease transmission in territorial populations: the small-world network of Serengeti lions. *Journal of the Royal Society Interface*, **8**, 776-786.
- Creel, S. & Winnie Jr, J.A. (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, **69**, 1181-1189.
- Cresswell, W. (1994) Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour*, **47**, 433-442.
- Cresswell, W. (1998) Variation in the strength of interference competition with resource density in blackbirds, *Turdus merula*. *Oikos*, 152-160.
- Cresswell, W. & Whitfield, D.P. (2008) How starvation risk in Redshanks *Tringa totanus* results in predation mortality from Sparrowhawks *Accipiter nisus*. *Ibis*, **150**, 209-218.
- Cristol, D.A. (1995) The coat-tail effect in merged flocks of dark-eyed juncos: social status depends on familiarity. *Animal Behaviour*, **50**, 151-159.
- Croft, D., Arrowsmith, B., Bielby, J., Skinner, K., White, E., Couzin, I., Magurran, A., Ramnarine, I. & Krause, J. (2003) Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos*, **100**, 429-438.
- Croft, D., James, R., Ward, A., Botham, M., Mawdsley, D. & Krause, J. (2005) Assortative interactions and social networks in fish. *Oecologia*, **143**, 211-219.
- Croft, D.P., James, R., Thomas, P.O.R., Hathaway, C., Mawdsley, D., Laland, K.N. & Krause, J. (2006) Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, **59**, 644-650.
- Croft, D.P., James, R. & Krause, J. (2008) *Exploring animal social networks*. Princeton University Press.
- Croft, D.P., Krause, J., Darden, S.K., Ramnarine, I.W., Faria, J.J. & James, R. (2009) Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, **63**, 1495-1503.
- Croft, D.P., Madden, J.R., Franks, D.W. & James, R. (2011) Hypothesis testing in animal social networks. *Trends in Ecology & Evolution*, **26**, 502-507.

- Cross, P., Creech, T., Ebinger, M., Heisey, D., Irvine, K. & Creel, S. (2012a) Wildlife contact analysis: emerging methods, questions, and challenges. *Behavioral Ecology and Sociobiology*, **66**, 1437-1447.
- Cross, P.C., Creech, T.G., Ebinger, M.R., Heisey, D.M., Irvine, K.M. & Creel, S. (2012b) Wildlife contact analysis: emerging methods, questions, and challenges. *Behavioral Ecology and Sociobiology*, **66**, 1437-1447.
- Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695.
- Danon, L., Ford, A.P., House, T., Jewell, C.P., Keeling, M.J., Roberts, G.O., Ross, J.V. & Vernon, M.C. (2011) Networks and the epidemiology of infectious disease. *Interdisciplinary perspectives on infectious diseases*, **2011**.
- Darden, S.K., James, R., Ramnarine, I.W. & Croft, D.P. (2009) Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2651-2656.
- De Silva, S. & Wittemyer, G. (2012) A comparison of social organization in Asian elephants and African savannah elephants. *International Journal of Primatology*, **33**, 1125-1141.
- Dekker, D., Krackhardt, D. & Snijders, T.A. (2007) Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika*, **72**, 563-581.
- delBarco-Trillo, J., McPhee, M.E. & Johnston, R.E. (2009) Nonagonistic familiarity decreases aggression in male Turkish hamsters, *Mesocricetus brandti*. *Animal Behaviour*, **77**, 389-393.
- Desnoyers, M., Gauthier, G. & Lefebvre, J. (2012) Stable Associations within Flocks of Greater Snow Geese (*Chen caerulescens atlantica*): Do They Exist Beyond Family Bonds? *The Auk*, **129**, 611-622.
- Dey, C.J., Reddon, A.R., O'Connor, C.M. & Balshine, S. (2013) Network structure is related to social conflict in a cooperatively breeding fish. *Animal Behaviour*, **85**, 395-402.
- Dijk, J.G., Hoyer, B.J., Verhagen, J.H., Nolet, B.A., Fouchier, R.A. & Klaassen, M. (2014) Juveniles and migrants as drivers for seasonal epizootics of avian influenza virus. *Journal of Animal Ecology*, **83**, 266-275.

- Donaldson, R., Finn, H., Bejder, L., Lusseau, D. & Calver, M. (2012) The social side of human–wildlife interaction: wildlife can learn harmful behaviours from each other. *Animal Conservation*, **15**, 427-435.
- Donnelly, C.A., Woodroffe, R., Cox, D., Bourne, F.J., Cheeseman, C., Clifton-Hadley, R.S., Wei, G., Gettinby, G., Gilks, P. & Jenkins, H. (2005) Positive and negative effects of widespread badger culling on tuberculosis in cattle. *Nature*, **439**, 843-846.
- Drent, R. & Swierstra, P. (1977) Goose flocks and food finding: field experiments with barnacle geese in winter. *Wildfowl*, **28**, 6.
- Drewe, J., Madden, J. & Pearce, G. (2009) The social network structure of a wild meerkat population: 1. Inter-group interactions. *Behavioral Ecology and Sociobiology*, **63**, 1295-1306.
- Dugatkin, L.A. (1997) Winner and loser effects and the structure of dominance hierarchies. *Behavioral Ecology*, **8**, 583-587.
- Dugatkin, L.A. & Druen, M. (2004) The social implications of winner and loser effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, S488-S489.
- Dugatkin, L.A. & Earley, R.L. (2004) Individual recognition, dominance hierarchies and winner and loser effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 1537-1540.
- Edenbrow, M., Darden, S., Ramnarine, I., Evans, J., James, R. & Croft, D. (2011) Environmental effects on social interaction networks and male reproductive behaviour in guppies, *Poecilia reticulata*. *Animal Behaviour*, **81**, 551-558.
- Edenbrow, M. & Croft, D.P. (2012) Kin and familiarity influence association preferences and aggression in the mangrove killifish *Kryptolebias marmoratus*. *Journal of Fish Biology*, **80**, 503-518.
- Elgar, M.A. (1986) House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour*, **34**, 169-174.
- Elgar, M.A. (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews*, **64**, 13-33.
- Ellis, T.M., Barry Bousfield, R., Bissett, L.A., Dyrting, K.C., Luk, G.S., Tsim, S., Sturm-Ramirez, K., Webster, R.G., Guan, Y. & Peiris, J.M. (2004) Investigation of outbreaks of highly

- pathogenic H5N1 avian influenza in waterfowl and wild birds in Hong Kong in late 2002. *Avian Pathology*, **33**, 492-505.
- Engeszer, R.E., Ryan, M.J. & Parichy, D.M. (2004) Learned social preference in zebrafish. *Current Biology*, **14**, 881-884.
- Farine, D.R., Garroway, C.J. & Sheldon, B.C. (2012) Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Animal Behaviour*, **84**, 1271-1277.
- Farine, D.R. & Milburn, P.J. (2013) Social organisation of thornbill-dominated mixed-species flocks using social network analysis. *Behavioral Ecology and Sociobiology*, **67**, 321-330.
- Farine, D.R. (2014) Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. *Animal Behaviour*, **89**, 141-153.
- Farine, D.R., Aplin, L.M., Garroway, C.J., Mann, R.P. & Sheldon, B.C. (2014) Collective decision making and social interaction rules in mixed-species flocks of songbirds. *Animal Behaviour*, **95**, 173-182.
- Favreau, F.-R., Goldizen, A.W. & Pays, O. (2010) Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2089-2095.
- Fieberg, J. & Kochanny, C.O. (2005) Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management*, **69**, 1346-1359.
- Fleischer, R.C. (1983) Relationships between tidal oscillations and Ruddy Turnstone flocking, foraging, and vigilance behavior. *Condor*, **85**, 22-29.
- Flynn, R.E. & Giraldeau, L.A. (2001) Producer–scrounger games in a spatially explicit world: tactic use influences flock geometry of spice finches. *Ethology*, **107**, 249-257.
- Focardi, S. & Pecchioli, E. (2005) Social cohesion and foraging decrease with group size in fallow deer (*Dama dama*). *Behavioral Ecology and Sociobiology*, **59**, 84-91.
- Formica, V., Wood, C., Larsen, W., Butterfield, R., Augat, M., Hougen, H. & Brodie, E. (2012) Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*). *Journal of Evolutionary Biology*, **25**, 130-137.
- Fortin, D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009) Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology*, **90**, 2480-2490.

- Fox, A. & Salmon, D. (1994) Breeding and moulting shelduck (*Tadorna tadorna*) of the Severn Estuary. *Biological Journal of the Linnean Society*, **51**, 237-245.
- Frank, L.G. (1986) Social organization of the spotted hyaena *Crocuta crocuta*. II. Dominance and reproduction. *Animal Behaviour*, **34**, 1510-1527.
- Franks, D.W., Ruxton, G.D. & James, R. (2010) Sampling animal association networks with the gambit of the group. *Behavioral Ecology and Sociobiology*, **64**, 493-503.
- Frantz, T.L., Cataldo, M. & Carley, K.M. (2009) Robustness of centrality measures under uncertainty: Examining the role of network topology. *Computational and Mathematical Organization Theory*, **15**, 303-328.
- Franz, M. & Nunn, C.L. (2009) Network-based diffusion analysis: a new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1829-1836.
- Fraser, O.N. & Bugnyar, T. (2012) Reciprocity of agonistic support in ravens. *Animal Behaviour*, **83**, 171-177.
- Freeman, L.C. (1977) A Set of Measures of Centrality Based on Betweenness. *Sociometry*, **40**, 35-41.
- Freeman, L.C., Borgatti, S.P. & White, D.R. (1991) Centrality in valued graphs: A measure of betweenness based on network flow. *Social networks*, **13**, 141-154.
- Frigerio, D., Weiss, B. & Kotrschal, K. (2001) Spatial proximity among adult siblings in greylag geese (*Anser anser*): evidence for female bonding? *Acta Ethologica*, **3**, 121-125.
- Frommen J.G. and Bakker T.C.M. 2004. Adult Three-Spined Sticklebacks Prefer to Shoal with Familiar Kin. *Behaviour*, **141**, 1401-1409.
- Gaidet, N., Caron, A., Cappelle, J., Cumming, G., Balanço, G., Hammoumi, S., Cattoli, G., Abolnik, C., de Almeida, R.S. & Gil, P. (2012) Understanding the ecological drivers of avian influenza virus infection in wildfowl: a continental-scale study across Africa. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1131-1141.
- Garroway, C.J., Bowman, J. & Wilson, P.J. (2013) Complex social structure of southern flying squirrels is related to spatial proximity but not kinship. *Behavioral Ecology and Sociobiology*, **67**, 113-122.
- Gautrais, J., Michelena, P., Sibbald, A., Bon, R. & Deneubourg, J.-L. (2007) Allelomimetic synchronization in Merino sheep. *Animal Behaviour*, **74**, 1443-1454.

- Gaynor, K.M. & Cords, M. (2012) Antipredator and social monitoring functions of vigilance behaviour in blue monkeys. *Animal Behaviour*, **84**, 531-537.
- Geldenhuys, J. (1981) Moults and moult localities of the South African Shelduck. *Ostrich*, **52**, 129-134.
- Gilby, I.C. & Wrangham, R.W. (2008) Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, **62**, 1831-1842.
- Gill, J.A., Sutherland, W.J. & Norris, K. (2001) Depletion models can predict shorebird distribution at different spatial scales. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 369-376.
- Girvan, M. & Newman, M.E. (2002) Community structure in social and biological networks. *Proceedings of the National Academy of Sciences*, **99**, 7821-7826.
- Godde, S., Humbert, L., Côté, S.D., Réale, D. & Whitehead, H. (2013) Correcting for the impact of gregariousness in social network analyses. *Animal Behaviour*, **85**, 553-558.
- Godfrey, S.S., Bull, C.M., James, R. & Murray, K. (2009) Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. *Behavioral Ecology and Sociobiology*, **63**, 1045-1056.
- Goessmann, C., Hemelrijk, C. & Huber, R. (2000) The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. *Behavioral Ecology and Sociobiology*, **48**, 418-428.
- Goldenberg, S.Z., de Silva, S., Rasmussen, H.B., Douglas-Hamilton, I. & Wittemyer, G. (2014) Controlling for behavioural state reveals social dynamics among male African elephants, *Loxodonta africana*. *Animal Behaviour*, **95**, 111-119.
- Gompper, M.E., Gittleman, J.L. & Wayne, R.K. (1997) Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. *Animal Behaviour*, **53**, 781-797.
- Grabowska-Zhang, A.M., Sheldon, B.C. & Hinde, C.A. (2012) Long-term familiarity promotes joining in neighbour nest defence. *Biology Letters*, **8**, 544-546.
- Grabowska-Zhang, A.M., Wilkin, T.A. & Sheldon, B.C. (2012) Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*). *Behavioral Ecology*, **23**, 322-333.
- Greenwood, P.J. & Harvey, P.H. (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, 1-21.

- Griesser, M., Barnaby, J., Schneider, N.A., Figenschau, N., Wright, J., Griffith, S.C., Kazem, A. & Russell, A.F. (2009) Influence of winter ranging behaviour on the social organization of a cooperatively breeding bird species, the apostlebird. *Ethology*, **115**, 888-896.
- Griffiths, S., Brockmark, S., Hojesjo, J. & Johnsson, J. (2004) Coping with divided attention: the advantage of familiarity. *Proceedings of the Royal Society of London-B*, **271**, 695-700.
- Guglielmo, C.G. (2010) Move that fatty acid: fuel selection and transport in migratory birds and bats. *Integrative and Comparative Biology*, **50**, 336-345.
- Guglielmo, C.G., Hauerland, N.H. & Williams, T.D. (1998) Fatty acid binding protein, a major protein in the flight muscle of migrating western sandpipers. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, **119**, 549-555.
- Guillemain, M., Fritz, H. & Blais, S. (2000) Foraging methods can affect patch choice: an experimental study in Mallard (*Anas platyrhynchos*). *Behavioural Processes*, **50**, 123-129.
- Hamede, R.K., Bashford, J., McCallum, H. & Jones, M. (2009) Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecology Letters*, **12**, 1147-1157.
- Hancock, P.A., Milner-Gulland, E. & Keeling, M.J. (2006) Modelling the many-wrongs principle: the navigational advantages of aggregation in nomadic foragers. *Journal of Theoretical Biology*, **240**, 302-310.
- Haney, J.C., Fristrup, K.M. & Lee, D.S. (1992) Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scandinavica*, 49-62.
- Hanneman, R.A. & Riddle, M. (2005) Introduction to social network methods. University of California Riverside.
- Hansson, B., Bensch, S., Hasselquist, D. & Nielsen, B. (2002) Restricted dispersal in a long-distance migrant bird with patchy distribution, the great reed warbler. *Oecologia*, **130**, 536-542.
- Hare, J.F., Campbell, K.L. & Senkiw, R.W. (2014) Catch the wave: prairie dogs assess neighbours' awareness using contagious displays. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132153.

- Harrison, F., Sciberras, J. & James, R. (2011) Strength of Social Tie Predicts Cooperative Investment in a Human Social Network. *PLoS ONE*, **6**, e18338.
- Harrison, X.A., Tregenza, T., Inger, R., Colhoun, K., Dawson, D.A., Gudmundsson, G.A., Hodgson, D.J., Horsburgh, G.J., McElwaine, G. & Bearhop, S. (2010) Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. *Molecular Ecology*, **19**, 5484-5496.
- Harrison, X.A., Bearhop, S., Inger, R., Colhoun, K., Gudmundsson, G.A., Hodgson, D., McElwaine, G. & Tregenza, T. (2011) Heterozygosity–fitness correlations in a migratory bird: an analysis of inbreeding and single-locus effects. *Molecular Ecology*, **20**, 4786-4795.
- Harrison, X.A., Hodgson, D.J., Inger, R., Colhoun, K., Gudmundsson, G.A., McElwaine, G., Tregenza, T. & Bearhop, S. (2013) Environmental conditions during breeding modify the strength of mass-dependent carry-over effects in a migratory bird. *PLoS one*, **8**, e77783.
- Hatchwell, B.J. (2010) Cryptic Kin Selection: Kin Structure in Vertebrate Populations and Opportunities for Kin-Directed Cooperation. *Ethology*, **116**, 203-216.
- Helm, B., Piersma, T. & Van der Jeugd, H. (2006) Sociable schedules: interplay between avian seasonal and social behaviour. *Animal Behaviour*, **72**, 245-262.
- Henzi, S., Lusseau, D., Weingrill, T., Van Schaik, C. & Barrett, L. (2009) Cyclicity in the structure of female baboon social networks. *Behavioral Ecology and Sociobiology*, **63**, 1015-1021.
- Heyes, C.M. (1994) Social learning in animals: categories and mechanisms. *Biological Reviews*, **69**, 207-231.
- Hill, N.J., Takekawa, J.Y., Ackerman, J.T., Hobson, K.A., Herring, G., Cardona, C.J., Runstadler, J.A. & Boyce, W.M. (2012) Migration strategy affects avian influenza dynamics in mallards (*Anas platyrhynchos*). *Molecular Ecology*, **21**, 5986-5999.
- Hoare, D., Couzin, I., Godin, J.-G. & Krause, J. (2004) Context-dependent group size choice in fish. *Animal Behaviour*, **67**, 155-164.
- Hoye, B.J., Munster, V.J., Nishiura, H., Fouchier, R.A., Madsen, J. & Klaassen, M. (2011) Reconstructing an annual cycle of interaction: natural infection and antibody dynamics to avian influenza along a migratory flyway. *Oikos*, **120**, 748-755.

- Hsu, Y., Earley, R.L. & Wolf, L.L. (2006) Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biological Reviews*, **81**, 33-74.
- Inger, R., Bearhop, S., Robinson, J.A. & Ruxton, G. (2006a) Prey choice affects the trade-off balance between predation and starvation in an avian herbivore. *Animal Behaviour*, **71**, 1335-1341.
- Inger, R., Ruxton, G.D., Newton, J., Colhoun, K., Robinson, J.A., Jackson, A.L. & Bearhop, S. (2006b) Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. *Journal of Animal Ecology*, **75**, 1190-1200.
- Inger, R., Gudmundsson, G.A., Ruxton, G.D., Newton, J., Colhoun, K., Auhage, S. & Bearhop, S. (2008) Habitat utilisation during staging affects body condition in a long distance migrant, *Branta bernicla hrota*: potential impacts on fitness? *Journal of Avian Biology*, **39**, 704-708.
- Inger, R., Harrison, X.A., Ruxton, G.D., Newton, J., Colhoun, K., Gudmundsson, G.A., McElwaine, G., Pickford, M., Hodgson, D. & Bearhop, S. (2010) Carry-over effects reveal reproductive costs in a long-distance migrant. *Journal of Animal Ecology*, **79**, 974-982.
- Ioannou, C., Guttal, V. & Couzin, I. (2012) Predatory fish select for coordinated collective motion in virtual prey. *Science*, **337**, 1212-1215.
- Jacobs, A. (2010) Group cohesiveness during collective movements: Travelling apart together. *Behavioural Processes*, **84**, 678-680.
- Jacobs, A., Sueur, C., Deneubourg, J.L. & Petit, O. (2011) Social network influences decision making during collective movements in brown lemurs (*Eulemur fulvus fulvus*). *International Journal of Primatology*, **32**, 721-736.
- Jaeger, R.G., Peterson, M.G. & Montgomery, W. (2002) Familiarity affects agonistic interactions between female red-backed salamanders. *Copeia*, **2002**, 865-869.
- James, R., Croft, D.P. & Krause, J. (2009) Potential banana skins in animal social network analysis. *Behavioral Ecology and Sociobiology*, **63**, 989-997.
- Janson, C.H. (1988) Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour*, 53-76.
- Jenni-Eiermann, S., Jenni, L., Smith, S. & Costantini, D. (2014) Oxidative Stress in Endurance Flight: An Unconsidered Factor in Bird Migration. *PLoS ONE*, **9**, e97650.

- Johnsson, J.I. (1997) Individual recognition affects aggression and dominance relations in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, **103**, 267-282.
- Jonker, R.M., Kuiper, M.W., Snijders, L., Van Wieren, S.E., Ydenberg, R.C. & Prins, H.H. (2011) Divergence in timing of parental care and migration in barnacle geese. *Behavioral Ecology*, **22**, 326-331.
- Kavaliers, M., Colwell, D.D. & Choleris, E. (2005) Kinship, familiarity and social status modulate social learning about "micropredators"(biting flies) in deer mice. *Behavioral Ecology and Sociobiology*, **58**, 60-71.
- Kerth, G., Ebert, C. & Schmidtke, C. (2006) Group decision making in fission–fusion societies: evidence from two-field experiments in Bechstein's bats. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2785-2790.
- Kerth, G. (2008) Causes and consequences of sociality in bats. *Bioscience*, **58**, 737-746.
- Kerth, G. (2010) Group decision-making in fission–fusion societies. *Behavioural Processes*, **84**, 662-663.
- Kerth, G., Perony, N. & Schweitzer, F. (2011) Bats are able to maintain long-term social relationships despite the high fission–fusion dynamics of their groups. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2761-2767.
- Kohn, G.M., King, A.P., Dohme, R., Meredith, G.R. & West, M.J. (2013) Robust autumn social attributes predict spring courtship skills in juvenile female brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour*, **85**, 727-732.
- Krause, J., James, R. & Croft, D. (2010) Personality in the context of social networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 4099-4106.
- Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S. & Rutz, C. (2013) Reality mining of animal social systems. *Trends in Ecology & Evolution*, **28**, 541-551.
- Krause, J., Lusseau, D. & James, R. (2009) Animal social networks: an introduction. *Behavioral Ecology and Sociobiology*, **63**, 967-973.
- Krause, J. & Ruxton, G.D. (2002) *Living in groups*. OUP Oxford.
- Krivitsky, P.N. (2012) Exponential-family random graph models for valued networks. *Electronic Journal of Statistics*, **6**, 1100-1128.

- Kubota, H. & Nakamura, M. (2000) Effects of supplemental food on intra-and inter-specific behaviour of the Varied Tit *Parus varius*. *Ibis*, **142**, 312-319.
- Kurvers, R.H.J.M., Eijkelenkamp, B., van Oers, K., van Lith, B., van Wieren, S.E., Ydenberg, R.C. & Prins, H.H.T. (2009) Personality differences explain leadership in barnacle geese. *Animal Behaviour*, **78**, 447-453.
- Kurvers, R.H., Prins, H.H., van Wieren, S.E., van Oers, K., Nolet, B.A. & Ydenberg, R.C. (2010) The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 601-608.
- Kurvers, R.H., Adamczyk, V.M., Kraus, R.H., Hoffman, J.I., van Wieren, S.E., van der Jeugd, H.P., Amos, W., Prins, H.H. & Jonker, R.M. (2013) Contrasting context dependence of familiarity and kinship in animal social networks. *Animal Behaviour*, **86**, 993-1001.
- Kutsukake, N. (2006) The context and quality of social relationships affect vigilance behaviour in wild chimpanzees. *Ethology*, **112**, 581-591.
- Lachlan, R.F., Crooks, L. & Laland, K.N. (1998) Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, **56**, 181-190.
- Lee, S.H., Kim, P.-J. & Jeong, H. (2006) Statistical properties of sampled networks. *Physical Review E*, **73**, 016102.
- Lee, T.M., Soh, M.C.K., Sodhi, N., Koh, L.P. & Lim, S.L.H. (2005) Effects of habitat disturbance on mixed species bird flocks in a tropical sub-montane rainforest. *Biological Conservation*, **122**, 193-204.
- Lehmann, J., Korstjens, A.H. & Dunbar, R. (2007) Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology*, **21**, 613-634.
- Lehmann, J. & Dunbar, R.I.M. (2009) Network cohesion, group size and neocortex size in female-bonded Old World primates. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 4417-4422.
- Lima, S.L. (1995) Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, **49**, 11-20.
- Lima, S.L. & Bednekoff, P.A. (1999) Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. *The American Naturalist*, **153**, 649-659.

- Lindström, Å. (1989) Finch flock size and risk of hawk predation at a migratory stopover site. *The Auk*, 225-232.
- List, C., Elsholtz, C. & Seeley, T.D. (2009) Independence and interdependence in collective decision making: an agent-based model of nest-site choice by honeybee swarms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 755-762.
- Livoreil, B. & Giraldeau, L.-A. (1997) Patch departure decisions by spice finches foraging singly or in groups. *Animal Behaviour*, **54**, 967-977.
- Lusseau, D. (2003) The emergent properties of a dolphin social network. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, S186-S188.
- Lusseau, D. (2007) Evidence for social role in a dolphin social network. *Evolutionary Ecology*, **21**, 357-366.
- MacIntosh, A.J. & Sicotte, P. (2009) Vigilance in ursine black and white colobus monkeys (*Colobus vellerosus*): an examination of the effects of conspecific threat and predation. *American journal of primatology*, **71**, 919-927.
- Madden, J.R., Drewe, J.A., Pearce, G.P. & Clutton-Brock, T.H. (2009) The social network structure of a wild meerkat population: 2. Intragroup interactions. *Behavioral Ecology and Sociobiology*, **64**, 81-95.
- Madden, J., Drewe, J., Pearce, G. & Clutton-Brock, T. (2011) The social network structure of a wild meerkat population: 3. Position of individuals within networks. *Behavioral Ecology and Sociobiology*, **65**, 1857-1871.
- Madsen, J., Cracknell, G. & Fox, T. (1999) *Goose populations of the Western Palearctic: a review of status and distribution*. National Environmental Research Institute Rønde.
- Madsen, J. & Klaassen, M. (2006) Assessing body condition and energy budget components by scoring abdominal profiles in free-ranging pink-footed geese *Anser brachyrhynchus*. *Journal of Avian Biology*, **37**, 283-287.
- Mann, J., Stanton, M.A., Patterson, E.M., Bienenstock, E.J. & Singh, L.O. (2012) Social networks reveal cultural behaviour in tool-using dolphins. *Nature communications*, **3**, 980.
- Marshall, H.H., Carter, A.J., Rowcliffe, J.M. & Cowlshaw, G. (2012) Linking social foraging behaviour with individual time budgets and emergent group-level phenomena. *Animal Behaviour*, **84**, 1295-1305.

- McCallum, H., Jones, M., Hawkins, C., Hamede, R., Lachish, S., Sinn, D.L., Beeton, N. & Lazenby, B. (2009) Transmission dynamics of Tasmanian devil facial tumor disease may lead to disease-induced extinction. *Ecology*, **90**, 3379-3392.
- McDonald, D.B. (2007) Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences*, **104**, 10910-10914.
- McDonald, D.B. (2009) Young-boy networks without kin clusters in a lek-mating manakin. *Behavioral Ecology and Sociobiology*, **63**, 1029-1034.
- McDonald, R.A., Delahay, R.J., Carter, S.P., Smith, G.C. & Cheeseman, C.L. (2008) Perturbing implications of wildlife ecology for disease control. *Trends in Ecology & Evolution*, **23**, 53-56.
- McDonough, C.M. & Loughry, W. (1995) Influences on Vigilance in Nine-banded Armadillos. *Ethology*, **100**, 50-60.
- McGowan, A., Fowlie, M.K., Ross, D.J. & Hatchwell, B.J. (2007) Social organization of co-operatively breeding Long-tailed Tits *Aegithalos caudatus*: flock composition and kinship. *Ibis*, **149**, 170-174.
- McGowan, A., Sharp, S.P., Simeoni, M. & Hatchwell, B.J. (2006) Competing for position in the communal roosts of long-tailed tits. *Animal Behaviour*, **72**, 1035-1043.
- McKinnon, L., Gilchrist, H.G. & Scribner, K.T. (2006) Genetic evidence for kin-based female social structure in common eiders (*Somateria mollissima*). *Behavioral Ecology*, **17**, 614-621.
- McWilliams, S.R., Guglielmo, C., Pierce, B. & Klaassen, M. (2004) Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology*, **35**, 377-393.
- Metcalfe, N. & Furness, R. (1984) Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. *Behavioral Ecology and Sociobiology*, **15**, 203-206.
- Michelena, P., Noël, S., Gautrais, J., Gerard, J.-F., Deneubourg, J.-L. & Bon, R. (2006) Sexual dimorphism, activity budget and synchrony in groups of sheep. *Oecologia*, **148**, 170-180.

- Michelena, P., Jeanson, R., Deneubourg, J.-L. & Sibbald, A.M. (2010) Personality and collective decision-making in foraging herbivores. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1093-1099.
- Micheletta, J., Waller, B.M., Panggur, M.R., Neumann, C., Duboscq, J., Agil, M. & Engelhardt, A. (2012) Social bonds affect anti-predator behaviour in a tolerant species of macaque, *Macaca nigra*. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4042-4050.
- Miller, N., Garnier, S., Hartnett, A.T. & Couzin, I.D. (2013) Both information and social cohesion determine collective decisions in animal groups. *Proceedings of the National Academy of Sciences*, **110**, 5263-5268.
- Morse, D.H. (1970) Ecological Aspects of Some Mixed-Species Foraging Flocks of Birds. *Ecological Monographs*, **40**, 119-168.
- Mourier, J., Vercelloni, J. & Planes, S. (2012) Evidence of social communities in a spatially structured network of a free-ranging shark species. *Animal Behaviour*, **83**, 389-401.
- Mulder, R., Williams, T. & Cooke, F. (1995) Dominance, brood size and foraging behavior during brood-rearing in the lesser snow goose: an experimental study. *Condor*, 99-106.
- Murray, C.M., Mane, S.V. & Pusey, A.E. (2007) Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. *Animal Behaviour*, **74**, 1795-1804.
- Myers, J. (1983) Space, time and the pattern of individual associations in a group-living species: sanderlings have no friends. *Behavioral Ecology and Sociobiology*, **12**, 129-134.
- Nakagawa, S. & Schielzeth, H. (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, **85**, 935-956.
- Newman, M.E. (2001) Clustering and preferential attachment in growing networks. *Physical Review E*, **64**, 025102.
- Newman, M.E. (2002) Assortative mixing in networks. *Physical review letters*, **89**, 208701.
- Newman, M.E. & Girvan, M. (2004) Finding and evaluating community structure in networks. *Physical Review E*, **69**, 026113.
- Oh, K.P. & Badyaev, A.V. (2010) Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *The American Naturalist*, **176**, E80-E89.

- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) vegan: Community Ecology Package. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>.
- Opsahl, T. (2009) *Structure and Evolution of Weighted Networks*. University of London (Queen Mary College), London, UK.
- Painter, J., Crozier, R., Poiani, A., Robertson, R. & Clarke, M. (2000) Complex social organization reflects genetic structure and relatedness in the cooperatively breeding bell miner, *Manorina melanophrys*. *Molecular Ecology*, **9**, 1339-1347.
- Pannozzo, P.L., Phillips, K.A., Haas, M.E. & Mintz, E.M. (2007) Social monitoring reflects dominance relationships in a small captive group of brown capuchin monkeys (*Cebus apella*). *Ethology*, **113**, 881-888.
- Parrish, J.K. & Edelstein-Keshet, L. (1999) Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*, **284**, 99-101.
- Patriquin, K.J., Leonard, M.L., Broders, H.G. & Garroway, C.J. (2010) Do social networks of female northern long-eared bats vary with reproductive period and age? *Behavioral Ecology and Sociobiology*, **64**, 899-913.
- Pays O., Benhamou S., Helder R. & Gerard J.-F. (2007a) The dynamics of group formation in large mammalian herbivores: an analysis in the European roe deer. *Animal Behaviour*, **74**, 1429-1441
- Pays, O., Jarman, P.J., Loisel, P. & Gerard, J.-F. (2007b) Coordination, independence or synchronization of individual vigilance in the eastern grey kangaroo? *Animal Behaviour*, **73**, 595-604.
- Pays, O., Renaud, P.-C., Loisel, P., Petit, M., Gerard, J.-F. & Jarman, P.J. (2007c) Prey synchronize their vigilant behaviour with other group members. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1287-1291.
- Pays, O., Goulard, M., Blomberg, S.P., Goldizen, A.W., Sirot, E. & Jarman, P.J. (2009) The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*. *Behavioral Ecology*, **20**, 469-477.
- Pays, O., Beauchamp, G., Carter, A.J. & Goldizen, A.W. (2013) Foraging in groups allows collective predator detection in a mammal species without alarm calls. *Behavioral Ecology*, **24**, 1229-1236.

- Pierce, B.J., McWilliams, S.R., Place, A.R. & Huguenin, M.A. (2004) Diet preferences for specific fatty acids and their effect on composition of fat reserves in migratory Red-eyed Vireos (*Vireo olivaceus*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **138**, 503-514.
- Pierce, B.J. & McWilliams, S.R. (2005) Seasonal changes in composition of lipid stores in migratory birds: causes and consequences. *The Condor*, **107**, 269-279.
- Pierce, B.J., McWilliams, S.R., O'Connor, T.P., Place, A.R. & Guglielmo, C.G. (2005) Effect of dietary fatty acid composition on depot fat and exercise performance in a migrating songbird, the red-eyed vireo. *The Journal of experimental biology*, **208**, 1277-1285.
- Piersma, T., Gudmundsson, G.A. & Lilliendahl, K. (1999) Rapid Changes in the Size of Different Functional Organ and Muscle Groups during Refueling in a Long-Distance Migrating Shorebird. *Physiological and Biochemical Zoology*, **72**, 405-415.
- Pike, T.W., Samanta, M., Lindström, J. & Royle, N.J. (2008) Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2515-2520.
- Pinter-Wollman, N., Hobson, E.A., Smith, J.E., Edelman, A.J., Shizuka, D., de Silva, S., Waters, J.S., Prager, S.D., Sasaki, T. & Wittemyer, G. (2013) The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behavioral Ecology*, art047.
- Poisbleau, M., Fritz, H., Valeix, M., Perroi, P.-Y., Dalloyau, S. & Lambrechts, M.M. (2006) Social dominance correlates and family status in wintering dark-bellied brent geese, *Branta bernicla bernicla*. *Animal Behaviour*, **71**, 1351-1358.
- Popa-Lisseanu, A.G., Bontadina, F., Mora, O. & Ibáñez, C. (2008) Highly structured fission–fusion societies in an aerial-hawking, carnivorous bat. *Animal Behaviour*, **75**, 471-482.
- Prop, J., Black, J.M. & Shimmings, P. (2003) Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos*, **103**, 403-414.
- Pulliam, H.R. & Caraco, T. (1984) Living in groups: is there an optimal group size. *Behavioural ecology: an evolutionary approach*, **2**, 122-147.
- R development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- Ramos-Fernández, G., Boyer, D., Aureli, F. & Vick, L.G. (2009) Association networks in spider monkeys (*Ateles geoffroyi*). *Behavioral ecology and sociobiology*, **63**, 999-1013.
- Ramos-Fernández, G., Boyer, D. & Gómez, V.P. (2006) A complex social structure with fission–fusion properties can emerge from a simple foraging model. *Behavioral Ecology and Sociobiology*, **60**, 536-549.
- Rands, S.A., Pettifor, R.A., Rowcliffe, J.M. & Cowlshaw, G. (2006) Social foraging and dominance relationships: the effects of socially mediated interference. *Behavioral ecology and sociobiology*, **60**, 572-581.
- Rasa, O.A.E. (1989) The costs and effectiveness of vigilance behaviour in the dwarf mongoose: implications for fitness and optimal group size. *Ethology Ecology & Evolution*, **1**, 265-282.
- Ratchford, S.G. & Eggleston, D.B. (2000) Temporal shift in the presence of a chemical cue contributes to a diel shift in sociality. *Animal Behaviour*, **59**, 793-799.
- Roberts, S. (1988) Social influences on vigilance in rabbits. *Animal Behaviour*, **36**, 905-913.
- Robinson, J., Colhoun, K., Gudmundsson, G., Boertmann, D., Merne, O., O'Brian, M., Portig, A., Mackie, K. & Boyd, H. (2004) *Light-bellied Brent Goose Branta bernicla hrota [East Canadian High Arctic population] in Canada, Ireland, Iceland, France, Greenland, Scotland, Wales, England, the Channel Islands and Spain: 1960/61-1999/2000*. The Wildfowl and Wetlands Trust/Joint Nature Conservation Committee, Slimbridge.
- Rodgers, G.M., Kelley, J.L. & Morrell, L.J. (2010) Colour change and assortment in the western rainbowfish. *Animal Behaviour*, **79**, 1025-1030.
- Rolland, C., Danchin, E. & Fraipont, M.d. (1998) The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. *The American Naturalist*, **151**, 514-529.
- Ronce, O. (2007) How Does It Feel to Be like a Rolling Stone? Ten Questions about Dispersal Evolution. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 231-253.
- Ryder, T.B., Blake, J.G., Parker, P.G. & Loiselle, B.A. (2011) The composition, stability, and kinship of reproductive coalitions in a lekking bird. *Behavioral Ecology*, **22**, 282-290.
- Salomon, M. (2009) Social Environment and Feeding State Influence Movement Decisions in a Web-building Spider. *Ethology*, **115**, 916-927.

- Sansom, A., Lind, J. & Cresswell, W. (2009) Individual behavior and survival: the roles of predator avoidance, foraging success, and vigilance. *Behavioral Ecology*, ar110.
- Schieggel, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, **1**, 103-113.
- Schülke, O., Wenzel, S. & Ostner, J. (2013) Paternal relatedness predicts the strength of social bonds among female rhesus macaques. *PLoS ONE*, **8**, e59789.
- Shizuka, D., Chaine, A.S., Anderson, J., Johnson, O., Laursen, I.M. & Lyon, B.E. (2014) Across-year social stability shapes network structure in wintering migrant sparrows. *Ecology Letters*, **17**, 998-1007.
- Sih, A., Hanser, S.F. & McHugh, K.A. (2009) Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, **63**, 975-988.
- Sih, A., Ziemba, R. & Harding, K.C. (2000) New insights on how temporal variation in predation risk shapes prey behavior. *Trends in Ecology & Evolution*, **15**, 3-4.
- Silk, M.J., Croft, D.P., Tregenza, T. & Bearhop, S. (2014) The importance of fission–fusion social group dynamics in birds. *Ibis*, **156**, 701-715.
- Stanley, C.R. & Dunbar, R. (2013) Consistent social structure and optimal clique size revealed by social network analysis of feral goats, *Capra hircus*. *Animal Behaviour*, **85**, 771-779.
- Stumpf, M. & Thorne, T. (2006) Multi-model inference of network properties from incomplete data. *J. Integr. Bioinformatics*, **3**, 32.
- Sueur, C. & Petit, O. (2008) Organization of group members at departure is driven by social structure in Macaca. *International Journal of Primatology*, **29**, 1085-1098.
- Sueur, C., Petit, O. & Deneubourg, J.-L. (2010) Short-term group fission processes in macaques: a social networking approach. *The Journal of experimental biology*, **213**, 1338-1346.
- Sueur, C., Deneubourg, J.-L. & Petit, O. (2011) From the first intention movement to the last joiner: macaques combine mimetic rules to optimize their collective decisions. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1697-1704.
- Sueur, C., Jacobs, A., Amblard, F., Petit, O. & King, A.J. (2011a) How can social network analysis improve the study of primate behavior? *American Journal of Primatology*, **73**, 703-719.

- Sueur, C., King, A.J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C.M., Williams, L., Zinner, D. & Aureli, F. (2011b) Collective decision-making and fission–fusion dynamics: a conceptual framework. *Oikos*, **120**, 1608-1617.
- Sundaresan, S.R., Fischhoff, I.R., Dushoff, J. & Rubenstein, D.I. (2007) Network metrics reveal differences in social organization between two fission–fusion species, Grevy’s zebra and onager. *Oecologia*, **151**, 140-149.
- Swaney, W., Kendal, J., Capon, H., Brown, C. & Laland, K.N. (2001) Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, **62**, 591-598.
- Teichroeb, J.A. & Sicotte, P. (2012) Cost-free vigilance during feeding in folivorous primates? Examining the effect of predation risk, scramble competition, and infanticide threat on vigilance in ursine colobus monkeys (*Colobus vellerosus*). *Behavioral ecology and sociobiology*, **66**, 453-466.
- Templeton, J.J. & Giraldeau, L.-A. (1996) Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. *Behavioral Ecology and Sociobiology*, **38**, 105-114.
- Tome, M.W. (1988) Optimal foraging: food patch depletion by ruddy ducks. *Oecologia*, **76**, 27-36.
- Tóth, Z., Bókonyi, V., Lendvai, Á.Z., Szabó, K., Péntes, Z. & Liker, A. (2009) Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. *Behavioural Processes*, **82**, 173-177.
- Tóth, Z., Baldan, D., Hoi, H. & Griggio, M. (2014) Food reduction has a limited effect on following relations in house sparrow flocks. *Animal Behaviour*, **90**, 91-100.
- Utne-Palm, A.C. & Hart, P.J. (2000) The effects of familiarity on competitive interactions between three-spined sticklebacks. *Oikos*, **91**, 225-232.
- Valsecchi, E., Hale, P., Corkeron, P. & Amos, W. (2002) Social structure in migrating humpback whales (*Megaptera novaeangliae*). *Molecular Ecology*, **11**, 507-518.
- van de Pol, M. & Wright, J. (2009) A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal Behaviour*, **77**, 753-758.
- van Doorn, G.S. & Taborsky, M. (2012) The evolution of generalized reciprocity on social interaction networks. *Evolution*, **66**, 651-664.

- van Veelen, M., García, J., Rand, D.G. & Nowak, M.A. (2012) Direct reciprocity in structured populations. *Proceedings of the National Academy of Sciences*, **109**, 9929-9934.
- Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilová, J. & Gregory, R.D. (2014) The decline of Afro-Palaeartic migrants and an assessment of potential causes. *Ibis*, **156**, 1-22.
- Vonhof, M.J., Whitehead, H. & Fenton, M.B. (2004) Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. *Animal Behaviour*, **68**, 507-521.
- Ward, A.J., Hart, P.J. & Krause, J. (2004) Assessment and assortment: how fishes use local and global cues to choose which school to go to. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, S328-S330.
- Warnock, N. (2010) Stopping vs. staging: the difference between a hop and a jump. *Journal of Avian Biology*, **41**, 621-626.
- Warton, D.I. & Hui, F.K. (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, **92**, 3-10.
- Watanuki, Y., Ishikawa, K., Takahashi, A. & Kato, A. (2004) Foraging behavior of a generalist marine top predator, Japanese cormorants (*Phalacrocorax filamentosus*), in years of demersal versus epipelagic prey. *Marine Biology*, **145**, 427-434.
- Watson, M., Aebischer, N.J. & Cresswell, W. (2007) Vigilance and fitness in grey partridges *Perdix perdix*: the effects of group size and foraging-vigilance trade-offs on predation mortality. *Journal of Animal Ecology*, **76**, 211-221.
- Watts, D.J. & Strogatz, S.H. (1998) Collective dynamics of 'small-world' networks. *Nature*, **393**, 440-442.
- Weber, N., Carter, S.P., Dall, S.R., Delahay, R.J., McDonald, J.L., Bearhop, S. & McDonald, R.A. (2013) Badger social networks correlate with tuberculosis infection. *Current Biology*, **23**, R915-R916.
- Webster, M.M., Atton, N., Hoppitt, W.J. & Laland, K.N. (2013) Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *The American Naturalist*, **181**, 235-244.
- Webster, M.M. & Ward, A.J. (2011) Personality and social context. *Biological Reviews*, **86**, 759-773.

- Wey, T., Blumstein, D.T., Shen, W. & Jordán, F. (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, **75**, 333-344.
- Wey, T.W. & Blumstein, D.T. (2010) Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour*, **79**, 1343-1352.
- Wey, T.W. & Blumstein, D.T. (2012) Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behavioral Ecology and Sociobiology*, **66**, 1075-1085.
- Wey, T.W., Burger, J.R., Ebensperger, L.A. & Hayes, L.D. (2013) Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Animal Behaviour*, **85**, 1407-1414.
- Whitehead, H. & Dufault, S. (1999) Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. *Adv. Study Behav.*, **28**, 33-74.
- Whitehead, H. (1997) Analysing animal social structure. *Animal Behaviour*, **53**, 1053-1067.
- Whitehead, H. (2008) *Analyzing animal societies: quantitative methods for vertebrate social analysis*. University of Chicago Press.
- Whiteman, E.A. & Côté, I.M. (2004) Dominance hierarchies in group-living cleaning gobies: causes and foraging consequences. *Animal Behaviour*, **67**, 239-247.
- Williams, C.K., Lutz, R.S. & Applegate, R.D. (2003) Optimal group size and northern bobwhite coveys. *Animal Behaviour*, **66**, 377-387.
- Willson, S.K. (2004) Obligate army-ant-following birds: a study of ecology, spatial movement patterns, and behavior in Amazonian Peru. *Ornithological Monographs*, 1-67.
- Wilson, A.D., Krause, S., Dingemanse, N.J. & Krause, J. (2013) Network position: a key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology*, **67**, 163-173.
- Winkler, D.W., Wrege, P.H., Allen, P.E., Kast, T.L., Senesac, P., Wasson, M.F., Llambías, P.E., Ferretti, V. & Sullivan, P.J. (2004) Breeding dispersal and philopatry in the tree swallow. *The Condor*, **106**, 768-776.
- Wiszniewski, J., Allen, S.J. & Möller, L.M. (2009) Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour*, **77**, 1449-1457.

- Wiszniewski, J., Brown, C. & Möller, L.M. (2012) Complex patterns of male alliance formation in a dolphin social network. *Journal of Mammalogy*, **93**, 239-250.
- Wiszniewski, J., Corrigan, S., Beheregaray, L.B. & Möller, L.M. (2012) Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Journal of Animal Ecology*, **81**, 423-431.
- Wittemyer, G., Douglas-Hamilton, I. & Getz, W.M. (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, **69**, 1357-1371.
- Wolf, J.B. & Trillmich, F. (2008) Kin in space: social viscosity in a spatially and genetically substructured network. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2063-2069.
- Wolf, J.B.W., Mawdsley, D., Trillmich, F. & James, R. (2007) Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Animal Behaviour*, **74**, 1293-1302.
- Wong, B. & Rosenthal, G.G. (2005) Shoal choice in swordtails when preferences conflict. *Ethology*, **111**, 179-186.
- Woodroffe, R., Donnelly, C.A., Jenkins, H.E., Johnston, W.T., Cox, D.R., Bourne, F.J., Cheeseman, C.L., Delahay, R.J., Clifton-Hadley, R.S. & Gettinby, G. (2006) Culling and cattle controls influence tuberculosis risk for badgers. *Proceedings of the National Academy of Sciences*, **103**, 14713-14717.

*If I could have it back
All the time that we wasted
I'd only waste it again
If I could have it back
You know I'd love to waste it again*

[Win Butler/Arcade Fire]