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Investigating social dynamics using automated radiotracking of winter flocks of Black-capped chickadees (Poecile atricapillus)

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Abstract

The major forces that govern social groups, namely fission-fusion dynamics, cohesion and maintenance, are nearly ubiquitous across animal groups. The field of animal collective behaviour has recently been married with automated radiotracking producing a ‘re-wilding’ of field research into sociality. The combination of this with Social Network Analysis has led to discoveries such as population wide information transfer and the flexibility of animal groups to change social connectivity based on environmental context. However, these networks are constructed, and do not include the dynamic environmental, spatio-temporal, and social contexts which directly affect sociality. I conducted the first automated radiotracking study I know of to track free-living flocks of black-capped chickadees, through the non-breeding season. My major objective was to combine existing radiotelemetry methods with advanced statistical techniques to create novel methodologies to track and quantify socially relevant movements and behaviours. Firstly, I used Linear Discriminant Analysis to match signal strength profiles of key individuals to all others as a new method of flock identification. Secondly, I examined onset of daily activity to test whether this was cohesive in flocks. Since unexpected spikes of early activity prior to onset were observed, I investigated the possibility that these restless events were related to environmental stressors. Finally, I used known activity thresholds to investigate the general activity patterns of ranks to address previous contradictions of rank and activity, and to test if field activity was consistent with theoretical predictions of optimal winter bird activity. Flocks were effectively tracked and identified with automated radiotelemetry alone and fusion-fission events could be tracked as well. Onset of activity was found to be cohesive within flocks, which was further supported by onset changes during fission-fusion events. Environmental pressure, temperature, windspeed and winter storm events were all related to sleep disturbances. Daily activity amount was higher in high ranks than low ranks and general activity patterns agreed with theoretical models. My findings contribute new methodologies to the field of collective animal movement and demonstrate the importance of automated radiotelemetery studies in providing important applications to social dynamics and beyond.

Summary for Lay Audience

Advancements in the field of radiotelemetry (e.g. smaller radiotags with longer battery life), have allowed small animals to be tracked for longer than ever before. By using a network of radiotower stations, the process of detecting pulses from tagged individuals is completely automated, meaning that multiple individuals can be tracked simultaneously and in real-time directly in the field.

The black-capped chickadee (*Poecile atricapillus*) is a small bird found in mostly wooded habitats from coast to coast in most of North America. In winter, chickadees form flocks of approximately 3-12 individuals which a range of roughly 9.5 hectares. Flocks are relatively stable, and flock-mates engage in most behaviours as a group through the winter, before ultimately breaking up into breeding pairs in the spring. Occasionally, individuals will 'flock-switch' and leave one flock and join another or become solitary. Flocks are organized via a dominance hierarchy in that the highest ranking bird, outcompetes lower ranks for resources and skews fitness in their favour. Because chickadees do not migrate in the winter, they provide an excellent model to explore how automated radiotelemetery can advance the study of social dynamics.

I erected four radiotelemetry stations in a 60 hectare forest in Elginfield, Ontario and caught and tagged chickadees with Avian Nanotags (0.35g) via a figure-8 harness. I ultimately tracked the movements of 12 flocks in the winter seasons of 2016 and 2017. I first used advanced statistical methods to discover a new method to separate and track both flocks and flock switchers. Next, I examined the wake-up times of flocks, and found these were synchronized in the group. During this analysis, unexpected early spikes of activity were observed, so I compared weather data from a local station to these events and found extreme weather (winter storms) likely caused sleep disturbances. Lastly, I used this dataset to examine rank-specific daily activity, and found high ranks are more active and that daily activity curves from all birds are consistent with theoretical predictions. Collectively, my thesis expanded on known methods of radiotelemetry and demonstrated the value of such a dataset to the animal collective movement field.

Keywords

Activity synchronization, Animal collective movement, Automated radiotelemetery, black-capped chickadee, Dominance hierarchy, Fission-Fusion dynamics, Linear Discriminant Analysis, Mixed Models, Rank activity, Sleep.

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dBm	Decibels per milliwatt
GPS	Global positioning system
PIT	Passive infrared transponder
RFID	Radio-frequency identification
SS	Signal strength
VHF	Very high frequency
Flocks	
CF	Central flock
EF	East flock
SCF	South central flock
SF	South flock
SSF	South south flock
WCF	West central flock
WF	West flock
Towers	
ET	East tower
CT	Central tower
ST	South tower
WT	West tower
Statistics	
GAM	Generalized Additive Model
GLMM	Generalized Linear Mixed Model
LDA	Linear Discriminant Analysis
LOESS	Locally Estimated Scatterplot Smoothing
LMM	Linear Mixed Model
SNA	Social Network Analysis

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Chapter 1

General Introduction

1.1 Social Dynamics

Social dynamics are the constantly changing interactions among individuals within a social group. These interactions are variable because they depend on temporal, spatial (Castles et al., 2014; Pinter-Wollman et al., 2014), social (Castles et al., 2014; Maldonado-Chaparro et al., 2018) and environmental contexts (Firth & Sheldon, 2015; Wilson et al., 2015). Since social interactions are known to have direct fitness consequences via social selection (Wolf et al. 1999), studying how, when, and why these occur in a natural environment is an important pursuit in the areas of social evolution, population dynamics, and conservation (Snijders et al., 2017).

Social groups also have their own dynamics, and almost all undergo the same major processes. Groups begin to form when the early and often aggressive interactions between conspecifics begin to change and stabilize. This often occurs in the form of a dominance hierarchy, which reduces aggressive interactions and is said to 'maintain' group functionality (Bourke, 2011). Once stable, the group is considered 'cohesive' – group members act in unison, and coordinate behaviour together as is evident in schools of fish and bird flocks. At this stage, the beneficial nature of social life is most apparent since group members have increased benefits in the form of predation reduction and increased foraging efficiency (Conradt & Roper, 2005; 2003). While it is generally beneficial to maintain group cohesion, in almost all social groups conditions which increase group conflict (e.g. the breeding season) are inevitable, and in these instances the group undergoes fission, only to start the entire process over when the benefits of group-living outweigh the costs once again (Silk et al., 2014). The processes of: Fusion, Maintenance, Cohesion and Fission are so ubiquitous in social organisms that they are referred to as 'the social principles' and are not only integral to group functionality, but also the process of social evolution itself (Bourke, 2011).

Understanding how these social principles work has been greatly aided by self-organization theory, which postulates that complex group phenomena are often the result of simple individual changes in behaviour communicated among group-members (Couzin & Krause, 2003). Studies using simulation modelling allow individual parameters such as: movement speed, direction, turning rate, and zone of orientation, to be manipulated in the context of behavioural rules that mimic natural group behaviour (e.g. group members prioritize minimizing individual to individual distance) to uncover the mechanisms of how groups statistically behave. This approach has been successfully applied to different aspects of social life including: activity synchronization, leadership, spatial positioning, consensus decisions and transitions to different group structures (Conradt et al., 2009; Conradt & Roper, 2000; 2005; Couzin et al., 2002; 2005). The major contributions of these models to social behaviour and evolution are threefold. Firstly, cohesive groups can form or self-organize, based on internal factors alone, namely, individual to individual reactions. Secondly, behavioural parameters can be isolated and tested, thereby tracing the mechanistic explanation of how individual behaviour translates to group action. Lastly, experimentation with simulation modelling can reveal novel group behavioural phenomena such as the existence of collective memory (Couzin et al., 2002). While these advances are certainly impactful in a theoretical social evolution context, they simultaneously provide specific mechanisms which are useful for guiding hypothesis testing in experimental and field studies in number of taxa including: insects, fish, birds and primates (Strandburg-peshkin et al., 2015; 2017; Sumpter et al., 2008a; 2008b).

Another method of modelling social behaviour is Social Network Analysis (SNA), a flexible tool which simplifies social behaviour of a group to individual elements, so the connectedness among all individuals of a group can be measured. To construct a social network, researchers first define a network's *Nodes* and *Edges*. *Nodes* are the discernable units of the network and most often represent individuals but can also be used to represent groups or group attributes, while *Edges* are the relationships between nodes that describe the degree of connectivity among the nodes, which are often represented as frequency of social contact (Croft et al., 2016; Farine & Whitehead, 2015). The resulting 'map' of nodes and edges can then be used to track the effect of any individual behaviors through the levels of group member interactions, and finally to the larger population (Aplin et al., 2012).

An example which illustrates the construction and interpretation of SNA is Johnson et al. (2012) study of bat roosting networks. In this experiment, three colonies of Rafinesque's bigeared bats (*Corynorhinus rafinesquii*) were radio-tracked to day-roosting locations over three summers to examine the connectivity of individuals in the bat network by measuring the frequency of bats sharing roosts together. The resulting networks revealed: bats changed roosts often, thereby revealing a high level of fission-fusion dynamics; females were more centralized and tended to roost with a higher number of individuals than males; colonies in areas of low roost availability had a less central network than those with high roosting opportunities. This work demonstrates the flexibility of SNA as a technique to simultaneously examine how individual characteristics (e.g. sex) affects group structure, as well as testing the social impact of external factors, such as habitat.

Not surprisingly, the applications of SNA are widespread and are of growing crucial importance for the fields of conservation, ecology (Snijders et al., 2017), and social dynamics (Wilson et al., 2015). In recent years, SNA has become a very common approach and can be used to examine many aspects of social dynamics in a wide range of taxa (Hillemann et al., 2019; Ilany & Akçay, 2016; Smith-Aguilar et al., 2019).

Both simulation and SNA modelling have helped to reveal the social principles in theoretical and practical applications. These have, for instance, illuminated the commonality of fusion-fission dynamics in nearly all social groups, with the impact that this term has been adapted from describing whether or not a group expresses them, to the *degree* they are expressed in the group (Aureli et al., 2008).

1.2 Sociality in birds

Like most animal groups, birds form flocks when the benefits of group-living outweigh the costs of living alone. These benefits often include: increased foraging time, predator protection, and survival (Hogstad, 2014; Smith, 1991). When flocks are cohesive, and conflict is low, being in a group also contributes to effectiveness in decision-making. An example of this is navigational accuracy in groups of migratory birds, which can increase with group size (Tamm, 1980). The mechanism in this case is that individuals tend to follow their neighbors, which across all members results in a majority preference for a direction. To maintain cohesion, it is also important for group-members to communicate when it is beneficial for the group state to change, as for instance, initiating a predator evasion response, or in the onset of foraging (Couzin et al., 2005). Birds are known to communicate and achieve activity synchronization by using pre-flight vocal and behavioural (e.g. head movements, wing extensions) signals to initiate departure flights (Abraham, 1974; Black, 1988; Nesbitt & Bradley, 1997; Raveling, 1969). Such democratic decisions in cooperative animal groups can directly contribute to fitness, and are therefore important in a deeper understanding of sociality in animals (Conradt & Roper, 2003; 2005).

Because being in a group is not always beneficial, especially when competition is high (e.g. the breeding season), animal groups change group composition on a spatial and temporal scale such that groups form when sociality is beneficial, and disband when it is not. This social flexibility, or Fusion-Fission dynamics, is typical in most animal groups and is a key component of social evolution (Conradt & Roper, 2003; 2005; Couzin & Krause, 2003). While unpredictable events such as sudden profitable resources do affect fusion-fission dynamics – as in the formation of aggregations of black-capped chickadee (*Parus atriciapillus*) flocks over a deer carcass in winter (Smith, 1991), or army-ant-following-birds forming foraging groups during ant swarms in the tropics (Wilson, 2004), they typically evolve in groups which experience spatial variation and temporal predictability (Sueur et al., 2011).

There are a few examples in birds of demonstrated social consequences of spatial variation. Lantz & Karubian (2017), examined the social connectivity of flocks of redbacked fairy-wrens (*Malurus melanocephalus*) before and after a natural forest fire and found that flocks had more associations with flock-mates after the fire, which was driven by the reduction of grassy areas. Firth & Sheldon, (2015) experimentally manipulated artificial feeder access to block certain members of mixed species tit flocks in a forested environment and observed the social effects using SNA. Individuals that were blocked from feeder sites during the non-breeding season had lower social connectivity to the flock during the nesting season. These studies together demonstrate that habitat changes directly impact the social connectivity of individuals of a group, and the later indicates these changes can be carried across different seasonal contexts.

Every year most temperate breeding birds undergo a series of major seasonal changes in behaviour which typically progresses in the order of: fall migration, overwintering, spring migration, breeding, and then moulting, which is then followed by fall migration once again.

Since each of these events are tied to survival and reproduction, and often occur at precise times (Helm et al., 2006), correct timing is critical, and has strongly influenced the evolution of timing in birds. While internal mechanisms such as the photoperiod system are instrumental in timing these behaviours (MacDougall-Shackleton et al., 2009), social cues also play an important role. For example, while melatonin cycles are linked to nocturnal migratory flights (Gwinner, 1996), birds will often communicate by pre-migratory flight behaviours which increase in frequency across group members just prior to migratory departure (Conradt & Roper, 2003). This means endogenous time programmes individually set seasonal behaviours, but social cues serve to fine-tune the timing of execution. This strong interplay between seasonal and social behaviour in birds results in a relatively predictable social pattern, in that most birds form flocks in the fall and remain in social groups until splitting up in the spring to breed (Helm et al., 2006). This is important for two reasons. Firstly, it demonstrates that birds are an excellent model for studying temporal predictability on social behaviours and secondly, that birds have a specific social season, making the non-breeding season the key to understanding sociality in birds (Boucherie et al., 2019). However, since this coincides with migration, it is difficult to obtain accurate and simultaneous records of individual and group movements of birds as they cover vast distances, thereby making it difficult to study social dynamics (Favreau et al., 2009). Not surprisingly, the wintering season is an under-researched area in many birds (Knudsen et al., 2011; Lemoine et al., 2007), making field studies focussing on long-term individual and group behaviour during the full winter season an important step in understanding sociality in birds.

1.3 Sociality of the *Paridae* family

Birds of the family *Paridae* (chickadees, tits and titmice) are typically non-migratory and highly philopatric birds that form social flocks in the winter, break into pairs in the breeding season and re-form flocks in the fall all within the same area (Ratcliffe et. al., 2007; Smith, 1991). This provides an excellent model to study avian social dynamics in real time as *all* key social events— fusion, cohesion, maintenance and fission are all occurring in a relatively small area.

For an animal group to be truly cohesive and be able make important communal decisions, such as when to change activity, and what direction to travel, the group needs to be maintained in a state of low conflict (Conradt & Roper, 2005). In the case of parids, this maintenance is in the form of the linear hierarchy, an organized group of varying rank positions, in which the alpha is dominant over all individuals of the group, the beta is dominant over all except the alpha and so on (Chase & Seit, 2011). High-ranking individuals are often older, larger, and more aggressive than lower ranks and maintain their position by actively excluding subordinates from higher-quality resources and access to mates, resulting in survival and reproductive fitness skewed in their favour (Ratcliffe et al., 2007). Although it seems counterinitiative that this unequal sharing of resources reduces conflict, lower ranked birds still share group advantages such as anti-predator and foraging benefits (Olson et al., 2015), and increased winter survival (Hogstad, 1989). In addition, lower ranks typically increase rank over years and therefore, increased survival and reproductive success (Schubert et al., 2008, 2007). These factors have contributed to the evolution of stable winter hierarchies in the parid family (S. M. Smith, 1991), which act as a mechanism of conflict resolution and help ensure group cohesion.

While the major fusion (fall) and fission (spring) events in parids are predictably seasonal, there are notable instances of smaller fusion-fission events which occur during the winter in which individuals leave one flock, join another, or become solitary. These flock ‘switchers’ or ‘floaters’ have been observed in flocks of willow tits (*Poecile montanus*), mountain chickadees (*Poecile gambeli*) and black-capped chickadees and have been observed to switch between as many as 5 different flocks in a season (Hogstad, 2014; Lahti et al., 1997; Smith, 1991). These flexibly social individuals present two potential insights into sociality. Firstly, the benefits of group-living can be compared directly, since these birds experience both solitary and social environments within a short time. Secondly, ‘floater’ parids allow the flock to be examined from an individual perspective. Since animal groups consist of individuals of unequal biological or behavioural states (e.g. sex, age, hunger) which has an impact on ultimate group decisions and therefore cohesion (Conradt et al., 2009; Conradt & Roper, 2000), understanding why birds leave a flock could be just as revealing to why they join in the first place. While field records suggest that the typically younger and lower ranking birds, switch to flocks opportunistically to replace higher ranking birds that have died in other flocks (Hogstad, 2014; Smith, 1991), it may also represent an individual disagreement in a consensus decision.

While maintenance via the dominance hierarchy is well understood in parids and explains a number of important correlates of fitness and behaviour (Desrochers, 1989; Mennill et al., 2004; Ramsay & Ratcliffe, 2003; Ratcliffe et al., 2007; Schubert et al., 2007; Smith, 1991), other key aspects of social activity like cohesion, activity synchronization and fission-fusion dynamics have received less attention (Silk et al., 2014). Because of the pivotal role that movement plays in social dynamics besides maintenance (Couzin et al., 2002; 2005; Strandburg-peshkin et al., 2015; Sumpter, et al., 2008), being able to accurately record both individual and group movements of multiple flocks of known dominance ranks of parids has the potential to simultaneously examine all major seasonal social events, including smaller fusion-fission events and would be instrumental in shedding light on the mechanisms of social dynamics in birds in real time.

1.3 Tracking technologies

While radio-tracking technology has been around since the 1960s (Craighead & Craighead, 1965) recent advances include lightweight transmitters (Hansbauer et al., 2008) and automated detection arrays (Řeřucha et al., 2015). These methods allow for accurate and continuous movement data to be automatically recorded for multiple animals as small as passerines in a field setting. While tracking studies are typically concerned with large-scale movement patterns involving home ranges, migration and habitat preferences (Habib, et. al., 2014), individual behaviours such as sleeping, roosting (Greives et al., 2015a) and extra-pair matings (Mennill et. al., 2004) can also be assessed. Tracking techniques that can assess both regional and individual movements in a natural setting would be especially useful to both model and understand the complexity of social interactions in nature, which will improve with more rich datasets of individual and social behaviours in the field (Croft et al., 2016).

The Motus Wildlife Tracking System (Motus) is an automated animal tracking system (Taylor et al., 2017) which currently consists of a network of over 1000 radiotelemetry receivers located across 30 countries and 4 continents. It is unique in being the only collaborative automated animal tracking network, and includes hundreds of independent research projects and has tracked over 200 species of birds, bats and insects to date. Since all tags are digitally coded, all towers on the network listen to the same frequency and can therefore simultaneously provide any tagged individual’s position from any active tower within range. While the shared aspect of the network make it ideal to track long distance migration and direction of migration, the Motus system has also been recently applied to individual behaviour on a more regional scale as well (Brown & Taylor, 2017; Holberton et al., 2019; Morbey et al., 2018; Wright et al., 2018). Automated radio-tracking provides an exciting opportunity to study social groups in a natural context and will greatly contribute to the fields of ecology and conservation in the future (King, Fehlmann, Biro, Ward, & Fürtbauer, 2018).

1.4 Collective movement ecology

Due to the complexity of incorporating the natural contexts that affect social dynamics, advanced tracking studies which can monitor real-time individual movement using electronic tags directly in the field (e.g. VHF radiotags, RFID tags) have become increasingly popular to investigate questions of social dynamics and behaviour (Aplin et al., 2013, 2012; Farine et al., 2015; Mennill et al., 2004). Combining advanced tracking data with social network analysis has revolutionized how social dynamics can be examined (Snijders et al., 2017; Wilson et al., 2015), and has in part led to the emergent field of 'collective movement ecology' (Westley et al., 2018) which recognizes the importance of animal movement in a social context, allowing the ultimate function of collective movement to be examined in a much deeper way.

A good example of research in collective movement ecology is Aplin et. al., (2012)'s study of social information transfer in wild birds. In this experiment, blue tits (*Cyanistes caeruleus*), marsh tits (*Poecile palustrius),* and great tits (*Parus major*) were captured and marked with RFID tags and were released in two natural forest locations in Wytham Woods, Oxfordshire, England. After the birds were marked, the experimenters introduced novel food patches with RFID antennae that automatically recorded positional information as the birds foraged. In order to determine if social information played a role in a bird's ability to locate the foraging patches, a SNA was conducted between each individual forager (nodes) and the number of associations between foragers at food patches (edges). The resulting SNA demonstrated that individuals with more social associations appeared at more novel foraging patches than those that had less, therefore suggesting that social information is used to increase the chances of foraging success in wild birds. Aplin et. al. (2012)'s study demonstrates some of the major strengths of SNA. Firstly, that the impact of individual behavior can be measured at the level of the population, Secondly, that the pathway of flow of social information through the network can be traced and, thirdly, that SNA can be used in conjunction with advanced tracking methods to test specific questions about social behaviour in a natural environment.

Subsequent experiments conducted on the mixed population of tits in Wytham Woods have revealed that information about novel foraging patches is transmitted at higher rates among conspecifics than heterospecifics, and some species are more likely than others to initially discover the novel foraging patches (Farine et al., 2015). When food patches were experimentally manipulated to either be profitable (with food) or unprofitable (no food), there was no difference in the visiting rates of individual with more associations than those with less, suggesting that patch quality is not transmitted in the social network of foraging tits (Hillemann et al., 2019). SNA analysis of the flocks themselves revealed that group members tend to associate according to similar age and similar dispersal status – with flocks being comprised of mostly either local birds or recent immigrants (Farine, et al., 2015). When certain individual flock members were experimentally excluded from feeding stations, flock-mates did not associate with them at nesting sites, but after the experimental segregation ceased however, the flocks re-formed to the pre-experiment condition (Firth & Sheldon, 2015). These findings suggest that environmentally caused social segregation can influence behaviour in multiple ecological contexts, but also points to the flexibility of flocks to re-form and provides an excellent case of fission-fusion dynamics in real time.

By using a combination of automated tracking (PIT and RFID tags) at foraging stations with SNA analysis, the studies of tits at Wytham Woods have provided a large and rich dataset a novel way of studying social dynamics at scales ranging from individual social associations, flock composition and stability, to how information can be transmitted within and between flocks on a population level in real-time. To date, this is the most impressive real-time social dataset to date on wild birds.

1.5 Next steps in collective movement ecology

While the potential for SNA to address specific ecological hypotheses is clear, a number of major issues need to be addressed before large scale ecological studies can be attempted (King et al., 2018; Snijders et al., 2017). Chief among these is the consideration that SNA is most often used as an analytical technique that uses representations of social behaviours (number of interactions, proximity) as a proxy for social behaviours and is thus a *constructed* network (Farine & Whitehead, 2015). A *true* social network by comparison, includes direct associations such as: dominance, competitive and mating interactions. This means that SNA as a technique hinges on how the researcher defines the nodes and edges of a social system and as such is subject to failing to reflect a true social network. This problem is exemplified in Castles et al. (2014) study which compared constructed networks based on both nearest neighbor distances (proximity), and non-aggressive social interactions and grooming (interactions) in wild baboons. Because the resulting networks were substantially different, the authors concluded that commonly used SNA techniques may not be reflective of real social relationships. This makes sense because there are a number of reasons that animals may group together which do not relate to a continued social relationship. Examples of this include animals grouping as a antipredator defense as in starling murmurations (Goodenough et al., 2017), and the tendency for multiple flocks to forage on a high reward food such as a deer carcasses in black-capped chickadees (Smith, 1991). This is potentially problematic in recent studies that examine social information transfer of wild birds based on groups defined by individual proximity of neighbors at artificial food sites alone (Aplin et al., 2013, 2012; Farine et al., 2015a; Firth & Sheldon, 2015; Hillemann et al., 2019). Considering that groups of Great Tits defined by the above methodology were found to be unstable after 10 mins (Farine, et al., 2015), it is likely that the definition of an animal group in these cases has been oversimplified and the resulting network may not be reflective of the social group that exists in nature (Castles et al., 2014; Pinter-Wollman et al., 2014).

Another problem in the current use of SNA techniques in ecological settings is the dynamic nature of the group itself. It is well known that the cohesion of animal groups in nature is greatly dependent on temporal, spatial (Castles et al., 2014; Pinter-Wollman et al., 2014), social (Castles et al., 2014; Maldonado-Chaparro et al., 2018) and environmental contexts (Firth & Sheldon, 2015; Wilson et al., 2015). However, these factors are often ignored in SNA networks, which provide a static snapshot of sociality. Currently this problem is being tackled by multilayer social network analysis which allows for multiple context-dependent social behaviours to be introduced into the SNA and makes the resulting models more dynamic friendly (Finn, et. al., 2019; Silk, et al., 2018). While a promising method for use in large-scale ecological applications, the problem remains that SNA is highly reflective of the quality of data that is used in its network construction. Because current social-tracking studies of wild birds rely on a single context (e.g. proximity at a feeder between individuals) to define groups on which social patterns are analyzed (Aplin et al., 2013, 2012; Farine et al., 2015a; Hillemann et al., 2019), there is a need for advanced tracking techniques to supply a highly precise, and accurate dataset that encompasses multiple natural contexts and can simultaneously differentiate between individual and social group movements, which are all necessary components to truly understand social dynamics of animals (Silk et al., 2014). There is momentum in tracking techniques to both simplify and continue to revolutionize the field of ecology (Croft, et. al., 2016; King et al., 2018). Such datasets would provide a novel way to explore social patterns in the field, provide new analysis techniques for tracking regional movements of birds in the field, and provide a much richer and more precise dataset from which techniques like SNA would greatly benefit.

1.6 Dissertation Structure

To satisfy the relevant environment, seasonal and social contexts on which social dynamics depend (Couzin & Krause, 2003; King et al., 2018; Westley et al., 2018), I conducted the first automated radiotracking study of free-living flocks of birds through the entire non-breeding season, the key to understanding bird social behaviour (Boucherie et al., 2019). The major objective was to use a radiotelemetry dataset to address social dynamics– specifically in developing methods and techniques to study elements of each of the social principles (Fusion, Cohesion, Maintenance and Fission). I organized the following chapters around this central framework.

In *Chapter 2: Developing social radiotracking*, I developed methods to identify flocks based on signal strength from multiple radiotowers, to apply this to examine seasonal flock and individual patterns of social interest. While flocks can be identified using the raw radioprofiles alone, I found that by using towers as predictor variables, a Linear Discriminant Analysis (LDA) approach was also successful in separating flocks in statistical space using signal strengths of flock-faithful birds over the full winter season. Using these two approaches together, both individual and seasonal flock movements can be identified as well as individuals of interest such as seasonal movements of flock-switchers and pairs.

In *Chapter 3: Do Birds of a feather wake up together?: Radiotracking onset of activity in flocks of black-capped chickadees*, I applied known techniques (Adelman et al., 2010; Greives et al., 2015) to identify timing of individual morning onset of activity and explore whether or not this is a cohesive flock behaviour. I use known fission and fusion examples to compare how activity onset changes when these individuals were in a flock or not and discuss the possibility that onset of activity is a communal decision.

While studying the onset of activity of flocks in the previous chapter, I discovered that there were occasional early morning spikes of activity in individual and flocks, well before sunrise over both seasons. To test whether these early morning wake-ups might have environmental causes, I conducted an investigation of early morning restlessness in *Chapter 4: Environmental impacts on early morning restlessness,* to determine whether conditions like wind, pressure, and inclement weather affect bird sleep before onset of activity.

Finally, I examine the dominance hierarchy in *Chapter 5: Rank activity and seasonal rank patterns* and examine how this dataset can address some of the existing contradictions that exist regarding dominant and subordinate behaviour in winter flocks.

Throughout each of the chapters, I indicate how the techniques I developed can be applied to studying fission-fusion dynamics in general using an automated regional telemetry array.

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Chapter 2

Developing social radiotracking

2.1 Introduction

While the social group has adapted to maintain cohesion, eventually, internal competition arises to the point of group fission until environmental or seasonal conditions favour groups to fuse once again. These fission-fusion dynamics occur in nearly all social taxa and are an adaptive response to maximize individual survival and reproduction on a spatial and temporal scale (Silk et al., 2014). This is evident in the flocking behaviour of many birds that remain cohesive during the migratory season, and then break up in the breeding season (Helm et al., 2006). While the group benefits of navigation (Nagy et al., 2018), and predator protection (Beauchamp, 2013), help migrating birds survive to reach the breeding grounds to reproduce, once there, flocks immediately break-up when individual competition rises as birds set up and aggressively defend pair mating territories from their previous flock-mates. Once the breeding season has concluded, flocks then re-fuse and migrate to the wintering grounds. This is typical of many birds and demonstrates the strong seasonal component in bird sociality (Helm et al., 2006). Fission-fusion dynamics can also occur as an response to resource uncertainty (Ramos-Fernandez et al., 2018). In groups of spider monkeys for example, subgroups are larger when food availability is high, but break into smaller subgroups when food availability is scarce (Asensio et al., 2009). Taken together, these examples provide evidence that flexibility of social groups is selected for in accordance with changing environmental contexts.

Individual choices of group members also play a role in fission-fusion dynamics especially considering that not all decisions are unanimous in nature – as in a choice between two equidistant high quality patches to a group of foragers. Miller et al. (2013) ran an experiment with golden shiners (*Notemigonus crysoleucas*), in which groups of fish were conditioned to associate either a striped wall (A) or coloured floor (B) with a food reward. Groups were then tested in a 3-arm choice apparatus which had both conditioned visual stimuli in separate arms, and a third ‘consensus’ arm containing both stimuli. Group behaviour was found to be based on first choices made by leaders at the front of the group. These fish tended to follow their preference, whereas individuals at the back tended to choose cohesively -- If early followers move with the leaders, then the group moves together, but when conflicts of conditioned preference were introduced, early followers choose differently from the leaders causing the later followers to choose their own preference and ultimately cohesion was lost. It is suggested that such ‘democratic decisions’ (Conradt & Roper, 2003; 2005) are adaptive in the sense that they serve to both reduce uncertainty and maintain cohesion. Since multiple group members contribute to the ultimate decision, this avoids less extreme decisions that would be made if only one individual chose for the group. The leader-follower hierarchical relationship has been demonstrated in the wild, and has been successful in explaining how bird flocks can navigate mid-flight (Nagy et al., 2010) and synchronize behaviour during migratory flights (Nagy et al., 2018).

Winter flocks of birds of the family *Paridae* provide an excellent example of the constant balancing act between the costs and benefits of living in a group and how this can affect fission-fusion rates. While flocking in winter results in individual fitness benefits such as reduced time required for predator vigilance (Hogstad, 1986), increased efficiency of food patch discovery (Aplin et al., 2012), and increased winter survival (Hogstad, 1989), flocks are maintained by a linear dominance hierarchy—and therein lies the clear cost to flock membership. In parids, high ranking birds are typically older, larger and more aggressively displace lower ranking birds so that ultimately resources are skewed in their favour (Smith, 1991). Dominants displace subordinates from safe foraging patches (Desrochers, 1989; Ficken et al.,1990), exploit them by scrounging their newly found food sources (Hegner, 1984; Stahl et al., 2001), and spend less time than subordinates on predator vigilance (Hogstad, 1986), all of which places subordinates at higher risk of predation and starvation. This means that the throughout the winter the motivations of different ranks of flock-members are likely often in conflict, which ultimately likely impacts group cohesion (Couzin et al., 2002).

It is not surprising then that in addition to the major seasonal fission event at the end of the winter, smaller fission events of individual flock-mates suddenly leaving a flock and re-joining others throughout the winter have been observed in willow tits, mountain chickadees and black-capped chickadees (Hogstad, 2014; Lahti et al., 1997; Smith, 1991). While the majority of birds are sedentary to their territory, 20% have inter-territorial movements and these ‘switchers’ can in some cases can move between as many as 5 different flocks or more in a single winter

(Hogstad, 2014; Smith, 1991). While the majority of these birds move immediately to another flock, Smith, (1991) has also described other types of birds of unusually wide range, including 'dominant wanderers' which have expanded territories that overlap with multiple flock territories and 'migrants' that move between neighbouring populations of chickadees, joining flocks seldomly but remaining mostly solitary (Smith, 1991).

All of these wanderers are interesting since they experience multiple fusion-fission events, and therefore exist both socially and solitarily in a single winter which provides a valuable opportunity to examine and compare the benefits of group-living. Despite the potential for this, flock-switchers have received little attention with few exceptions (Hogstad, 1990, 2002, 2014; Smith, 1991). What is known is that 'switchers' tend to be the lowest ranking and younger birds in the flock, spend significantly more time scanning for predators and less time foraging than residents, and therefore have poorer nutritional status than residents (Hogstad, 2002, 2014). While these transient birds still remain much of a mystery, cases where floaters have successfully replaced birds of higher rank of neighbouring flocks and survived to breed in the previous dominant's territory supports the contention that these are socially opportunistic birds (Smith, 1991).

At least part of the reason wandering birds are understudied is due to the varying opinions of how a flock is defined (Smith & Buskirk, 1988; Smith, 1991; Desrochers et al., 1988), which influences the degree to which wanderers can be identified. Some researchers contend that flocks are birds that forage together throughout the winter (Aplin et al., 2012; Desrochers et al., 1988; Farine, 2015). This is likely an oversimplification, considering that foraging birds often wander, and high reward food bounties (e.g. feeders) often draw multiple flocks to the same area (Smith, 1991), thereby making flock separation by this method alone difficult. When flocks are defined this way, they have been observed to become unstable in as little as 10 mins (Farine, et al., 2015). Considering that flocking is argued to be an adaptation to help survive the winter (Hogstad 1989; 2014), and theoretically all winter behaviours occur in a social context, flocks are more accurately groups of birds that show constant and stable membership throughout the winter in multiple behavioural contexts (e.g. foraging, roosting, flying) (Smith, 1991). Using the most conservative definition of a social group possible is of critical importance since all forms of social dynamics and the social principles of fusion-fission, cohesion and maintenance are all dependent on how the social group is identified (Bourke, 2011; Couzin & Krause, 2003; Couzin et al., 2005). Cases in which social groups are defined on a single factor (e.g. proximity) have been shown to not be robust in modelling studies and do not accurately reflect social associations found in nature (Castles et al., 2014).

Because of the pivotal role that movement (Couzin et al., 2002; 2005; Strandburg-peshkin et al., 2015; Sumpter, et al., 2008), environmental, and social cues play in social dynamics (He et al., 2019; Helm et al., 2006; King et al., 2018; Silk et al., 2014), being able to accurately track both individual and group movements of multiple flocks of parids in the field has the potential to identify fission-fusion dynamics in real time. While previously this was done by directly observing one flock at a time (Hogstad, 2014; Smith, 1991), automated radiotracking provides the means of simultaneously tracking undisturbed flocks consistently over the full winter season, providing valuable socially relevant movement data with up to the minute accuracy. Considering the ever-growing size of radiotracking studies such as the Motus project (P. D. Taylor et al., 2017), this research provides a novel method of assessing collective animal movement which could be applied to a number of avian species. Being able to effectively radiotrack social dynamics in environments where they evolved will foster a deep understanding of the evolution, ecology and conservation of social animals (He et al., 2019; Helm et al., 2006; King et al., 2018; Silk et al., 2014).

At the simplest level, social dynamics are the interactions among individuals. These interactions are dynamic, and depend on environmental, temporal, spatial, and behavioural contexts. Current studies often fail to incorporate these interacting contexts, and therefore create a limited snapshot of sociality based on limited approximations of flocks. I demonstrate here the value of collecting a long-term and large-scale radiotracking dataset of multiple flocks of wild birds through the non-breeding season. This social radio-tracking dataset provides a novel method of defining a social group, and the ability to separate and track both individual and group movements on a local level. Because of the limitations of past studies which observed one flock at a time, I hypothesized that flock-switching occurs in chickadee flocks at a higher rate than previously recorded, and that this occurs regardless of rank. I furthermore predicted that other factors such as time of the season, and differences between flocks in rates of switching may help to explain why flock-switching occurs.

2.2 Methods

2.2.1 Radio-telemetry array

Four radio-towers were erected in a 60 hectare mixed forest next to the Elginfield Observatory, in Elginfield, ON (43.1925082,-81.3151531). Towers were constructed using the guidelines from the Motus project (https://motus.org/). Each station consisted of two horizontally oriented J-pole omni-directional antennas at 90° to one another (one due North, one due East), a SensorGnome© telemetry receiver, two 100 watt solar panels and four 12v 32AGM batteries to provide power. Due to the need to consistently charge the solar panels to keep the tower active, towers were placed in natural clearings to maximize sun exposure (Figure 2.1).

While the radius of reception for a single omni-directional antenna oriented vertically is 360° and extends to roughly 500m (Taylor et al., 2017), it has been found that a forested environment interferes with vertically oriented omni antennas and reduces the reception area. Therefore, I used two omni-directional antennae oriented horizontally modelled after the Blackpoll warbler (*Setophaga striata*) Motus tracking network in Bon Portage, Nova Scotia. This antenna setup uses a combination of each antenna's toroid (doughnut-shaped) area of reception and is thought to better penetrate forests to improve detection area (Morgan Brown, Personal communication).

2.2.2 Capture and tagging

Birds were captured by baited Potter traps at 4 field locations in the Elginfield field site from October-November of 2015 and 2016. This was done before chickadees are thought to form stable flocks which typically occurs in January (Smith, 1991). Immediately after capture, birds were fit with a radiotag (Lotek Avian Nanotag NTQB-2) attached via a 'figure 8' harness which was made by super-gluing (LePage© Gel Control) a 6cm length of elastic thread (Unique creativ©) into two loops on the tag (Rapole & Tipton, 1991). When attaching, the loops were placed over each leg and rested on each hip joint resulting in the tag ultimately resting on the dorsal side of the bird. The tags weighed 0.35 g (less than 5% of the chickadee's body weight) and were specifically designed for use with small songbirds (Brown & Taylor, 2017; Holberton et al., 2019; Wright et al., 2018). Birds were given a unique combination of coloured legs bands, and then released at the site of capture. The complete procedure, from capture to release, took about 3 min.

The radio tags were set at a pulse rate of 40 seconds, and were on a 12hr on-off cycle (4:00 AM – 4:00 PM) in order to conserve power so that birds could be tracked for the full winter season. Throughout the winter, radio-pulses from each tagged bird were continually received by the antennas of any of the 4 towers within range, and the signal strength (dBm) and timestamp of each pulse was automatically recorded by the SensorGnomes. Since all tags were digitally coded and on the Motus frequency of 166.380 MHz (P. D. Taylor et al., 2017), all towers were able to simultaneously track all tagged individuals within range for the full time that the tags were active (12 hrs) a day for the full duration of the 2015-2016 and 2016-2017 winter seasons. Seventy-nine chickadees were captured, marked and tracked over both seasons in total – with 50 being tracked in 2016 Winter season and 29 being tracked in the 2017 Winter season.

2.2.3 Rank assessment

Ranks of chickadees were determined by video recording dyad interactions on dominance boards on which shelled sunflower seeds were provided. Interactions were filmed at each of the 4 tower sites, using a GoPro Hero© camera mounted on a tripod, which filmed continuously, from the hours of 10am to 5pm. Video-recording commenced after January of the 2016 and 2017 Winter seasons, at which time flocks are typically stable, and ceased in March when flock-fission typically occurs (Ratcliffe, et al., 2007; Smith, 1991). Videos were taken on a rotating schedule so that each of the four sites was filmed at least once a week. In total there were 2,683 interactions filmed over both seasons.

Dominance interactions were scored based on the result of competitive interactions which comprised of: supplants, chases, resisting a supplant, and waiting for an opponent to eat before collecting a seed (Otter et al., 1998). Frequencies of wins and losses per interaction were put into a win/loss matrix (Appendix A), and the resulting win proportions and loss proportions (and win/loss proportions weighted by win/loss values of its interactants) were used to calculate David's scores (DS) for each individual (De Vries, 2006). The use of weighted win/loss proportions in the DS calculation ensures that beating a high-ranking individual reflects a higher dominance score than if rank was ignored in the interaction. DS is considered a superior method of rank assessment since it appropriately addresses the win/loss asymmetry characteristic of linear hierarchies, opposed to other methods which do not (Gammell et al., 2003).

The nominal ranks of ‘high’, ‘middle’ and ‘low’ were assigned by dividing each flock into thirds, similar to Mennill et al. (2004), and assigning individuals to the three group categories according to their DS scores. In this way, flocks of varying sizes could be standardized for comparison. When flocks were not divisible into equal thirds, (e.g. a flock of four) after the rank of high, middle and low were assigned, the remaining bird(s) rank was decided by the DS of smallest difference between this bird and the high, middle or low rank bird of that flock.

2.2.4 Statistical Methods

To track individual movements through the winter season, I used the seasonal positions of the highest ranking (alpha) individuals of flocks and compared these to all other birds to obtain positions for every individual. This was possible for two reasons. First, flocks of chickadees hold distinct seasonal territories through the winter (Smith, 1991), which is reflected in the radiotelemetry patterns of flocks (Figure 2.2), meaning that flocks can be partly isolated by visual separation of their radiodetection profiles. Second, individuals of the highest rank (alpha) tend to move between territories less often than lower ranks (Smith, 1991), making their relative position a logical proxy to flock territories. I used Linear Discriminant Analysis (LDA) to first find the best separation of relative alpha position based on the signal strength from all four towers. This alpha separation dataset was then used to predict all other individuals’ relative position each day, since LDA classified birds that had a similar separation to the corresponding alpha position as being in that alpha’s territory. LDA is suitable in this case, since it uses a combination of predictor values and projects these onto axes which achieve the highest possible linear separation of groups (Bet, 2017).

To achieve the seasonal positional separation of flock alphas, tag hits were filtered for the highest signal strength (SS) value per minute for all towers. Since all four towers did not consistently register a hit at each timestamp, I used a manual imputation value of -80 dBm in cases when tags were too far away from a tower to register a hit. The -80 dBm value was used because it was the lowest observed SS in the study and thus consistent with the dataset. LDA was then run for each day for both seasons, and the day resulting in the highest separation of alphas was used as the training set. To maximize accuracy, a combination of alphas that could not be separated with at least 80% accuracy were removed. This resulted in four alphas being used in Winter 2016 (SCF,SF,WCF,WF; Figure 2.3) and three being used in Winter 2017 (EF,SCF,WF; Figure 2.4)**.** These training datasets were then used to compare all other birds' daily detections, with LDA being ultimately used to predict each individual's daily flock assignment corresponding to the closest alpha's territory for every day from the period of January to March. In this manner, the separation of each alpha in LDA statistical space was used as a proxy for the centre of each alpha's territory**.** Since LDA classifications were done every day for every bird, flock-switches were assumed in the event that a bird from one flock was classified as being closer to an alpha of another flock and were defined in his way.

It is important to note that since these data are based on the axes computed by the LDA, they reflect the difference in statistical space between individuals rather than physical space (Figures 2.3, 2.4). Once flock separation was achieved, the raw detections of flocks could be used to provide an approximation of the relative positions of flocks in physical space. For example, in Figure 2.2 the four birds in the flock on the left (Southflock, SF) were much closer to the South Tower (ST) than any of the other towers, and the four birds on the right (Southcentral Flock – SCF) were closest to the East Tower (ET), relatively close to the (ST) tower, and closer to the Central Tower (CT) than the SF flock. Using these relative comparisons, approximate flock positions were assigned (Figure 2.1).

All statistics were analyzed using R version 4.0.4 (2021-02-15) -- 'Lost Library Book'. LDA scatterplots and predication-accuracy tables were created using the flipMultivariates package, and class prediction of daily proximity to alphas was done using the MASS package.

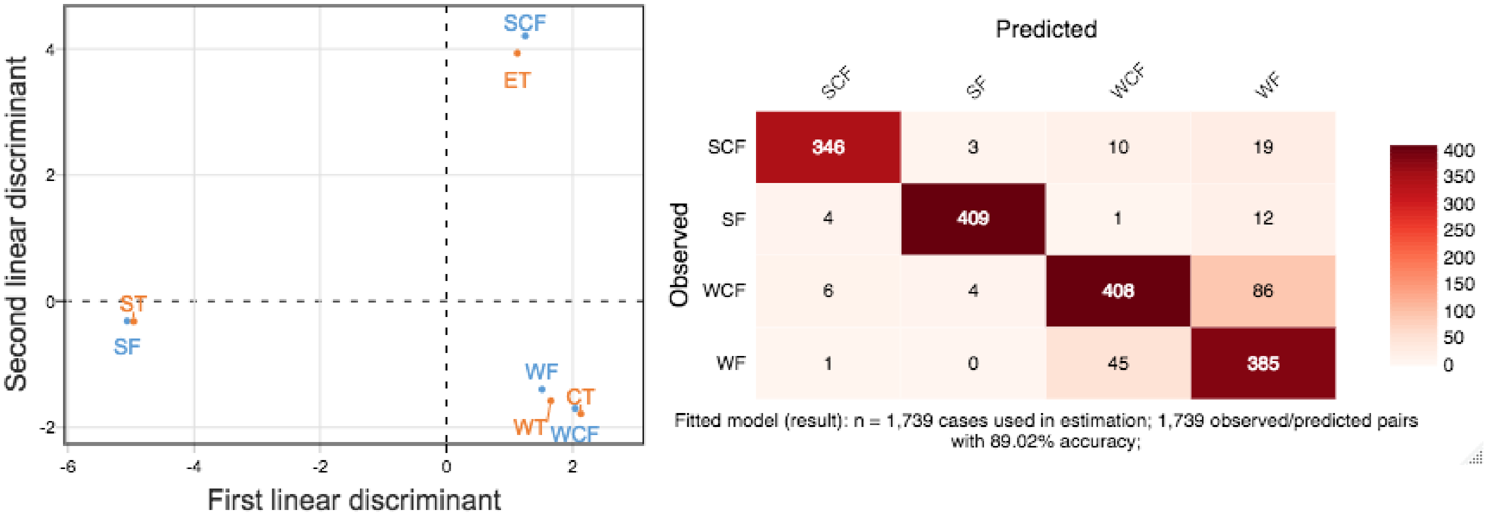
2.3 Results

All individuals LDA classifications per minute were filtered according to the highest number of alpha territory classifications per day, resulting in a representation of individual daily flock assignments with respect to alphas territories (Figure 2.5). Birds showing the same seasonal movement patterns were considered flockmates and were grouped into flocks based on visual similarity. In this way, seven flocks were identified in Winter 2016: Centralflock (CF, n=2), Eastflock (EF, n=6), Southcentralflock (SCF, n=5), Southflock (SF, n=9), Southsouthflock (SSF, n=3), Westcentralflock (WCF, n=3), and Westflock, (WF, n=4) and five flocks were identified in Winter 2017: Eastflock (EF, n=4), Southflock (SF, n=5), Southsouthflock (SSF, n=2), Westcentralflock (WCF, n=2), Westflock (WF, n=4). Some of these flocks were typically associated with the alphas used in the training set (primary flocks), and others could be identified that did not directly associate with the alphas (secondary flocks). There were cases of tagged birds that do not belong to a flock, and rarely if ever were observed to be close to any alpha's territory (Figure 2.5). In Winter 2016, these accounted for 20% of birds, and 38% in Winter 2017.

In the 2016 and 2017 Winter seasons, flock-switching occurred on 21% and 24% of total bird-days respectively. Individuals switched flocks an average of 13 (min 0 – max 40) times in Winter 2016 and 16 (min 0 – max 43) times in Winter 2017 (Figure 2.6). The number of switches per day decreased linearly from January to March in both Winters (Figure 2.7). There was no effect of rank as high, mid and low ranks had no difference in total seasonal switches ($F_{(2,36)} = 0.62$, $p = 0.544$). Flocks however did differ significantly in total seasonal switches in Winter 2016 and 2017 (Figure 2.8) and demonstrated that seasonal paths of movements were flock specific (Figure 2.9 and 2.10). In both years, when a switch occurred, it often included more than one flock-mate, and furthermore often occurred in the same direction (Figure 2.11).

Figure 2. 1 Map of study site showing tower locations (white dots), and approximate positions of flocks for both years. Primary flocks are shown as circles and secondary flocks as squares. Flocks that were primary in one year and secondary in another are shown as diamonds.

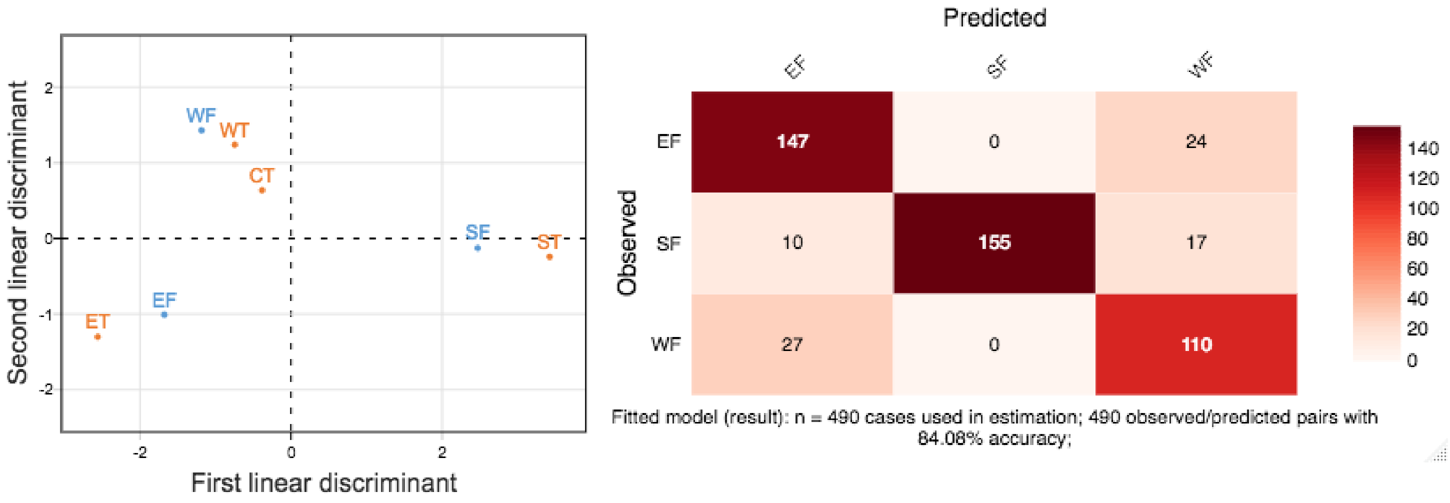
Figure 2. 2 Example of raw radiodetections from two different flocks in the 2016 Winter season. Colours represent birds. The four birds on the left are from flock SF, and the four on the right are from flock SCF. mfgID – bird ID, CT – Central tower, ET – East tower, ST – South tower, WT – West tower.



Observed \ Predicted	SCF	SF	WCF	WF
SCF	346	3	10	19
SF	4	409	1	12
WCF	6	4	408	86
WF	1	0	45	385

Fitted model (result): n = 1,739 cases used in estimation; 1,739 observed/predicted pairs with 89.02% accuracy;

Figure 2. 3 LDA scatterplot (left) showing separation of flock alpha means (blue) and tower projected correlations (orange). Prediction-accuracy table of the LDA model (right) showing the number of occurrences each alpha was classified correctly (89%) for the 2016 Winter season. Darker red colour indicates higher accuracy.



	EF	SF	WF
EF	147	0	24
SF	10	155	17
WF	27	0	110

Fitted model (result): n = 490 cases used in estimation; 490 observed/predicted pairs with 84.08% accuracy;

Figure 2. 4 LDA scatterplot (left) showing separation of flock alpha means (blue) and tower projected correlations (orange) and Prediction-accuracy table of the LDA model (right) showing the number of occurrences each alpha was classified correctly (84%) for the 2017 Winter season. Increasingly darker red colour indicates higher accuracy.

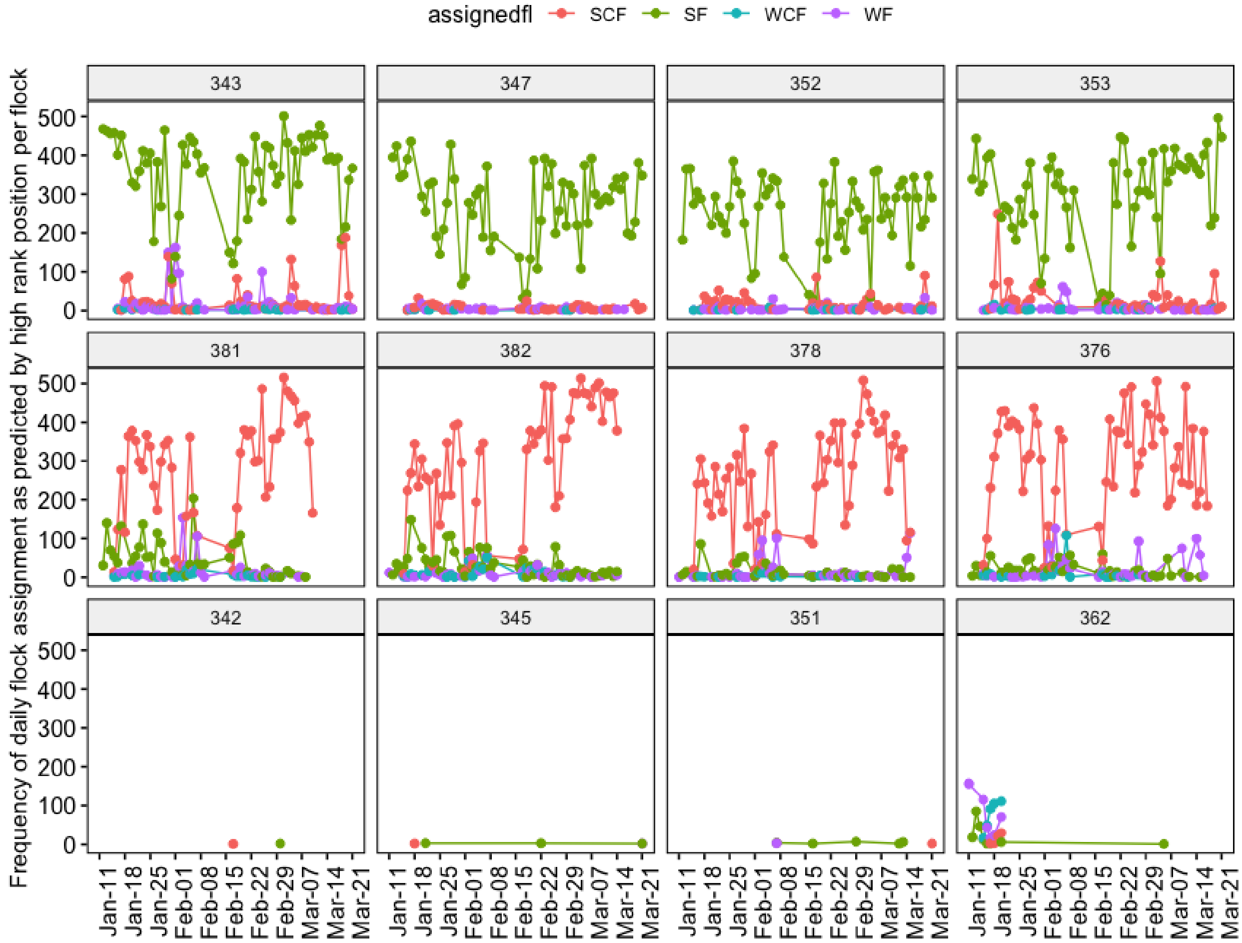


Figure 2. 5 Examples of daily flock assignments by LDA classification according to similarity to flock alphas in Winter 2016. The top and middle rows are two different flocks, and the bottom row are migrants. Numbered panels are individual birds, colours are the flock they were assigned to (assignedfl).

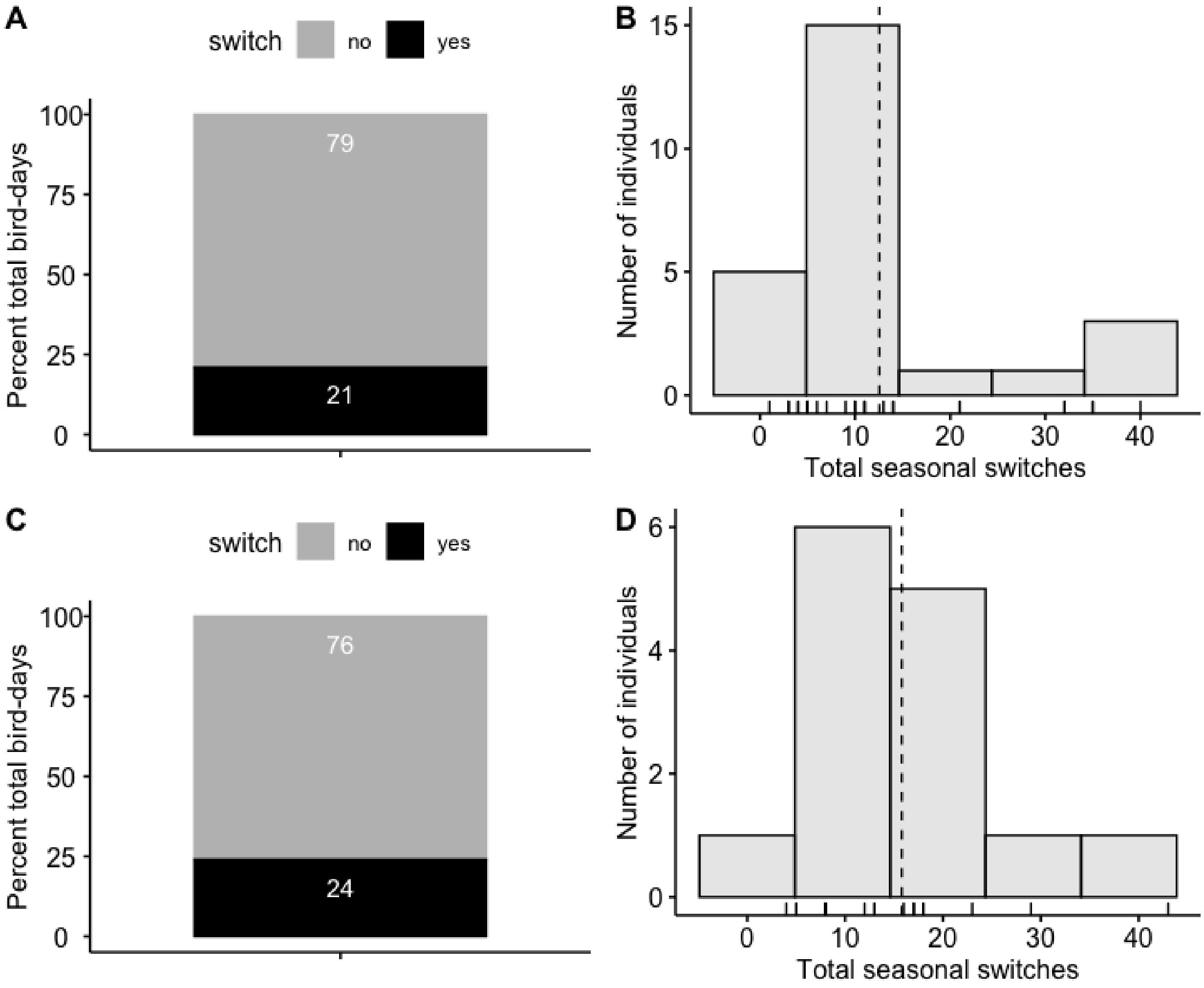


Figure 2. 6 Percent of all bird-days in which switches occurred or not, and histogram of the total seasonal number of switches per individual for the 2016 (A-B) and 2017 (C-D) Winter seasons.

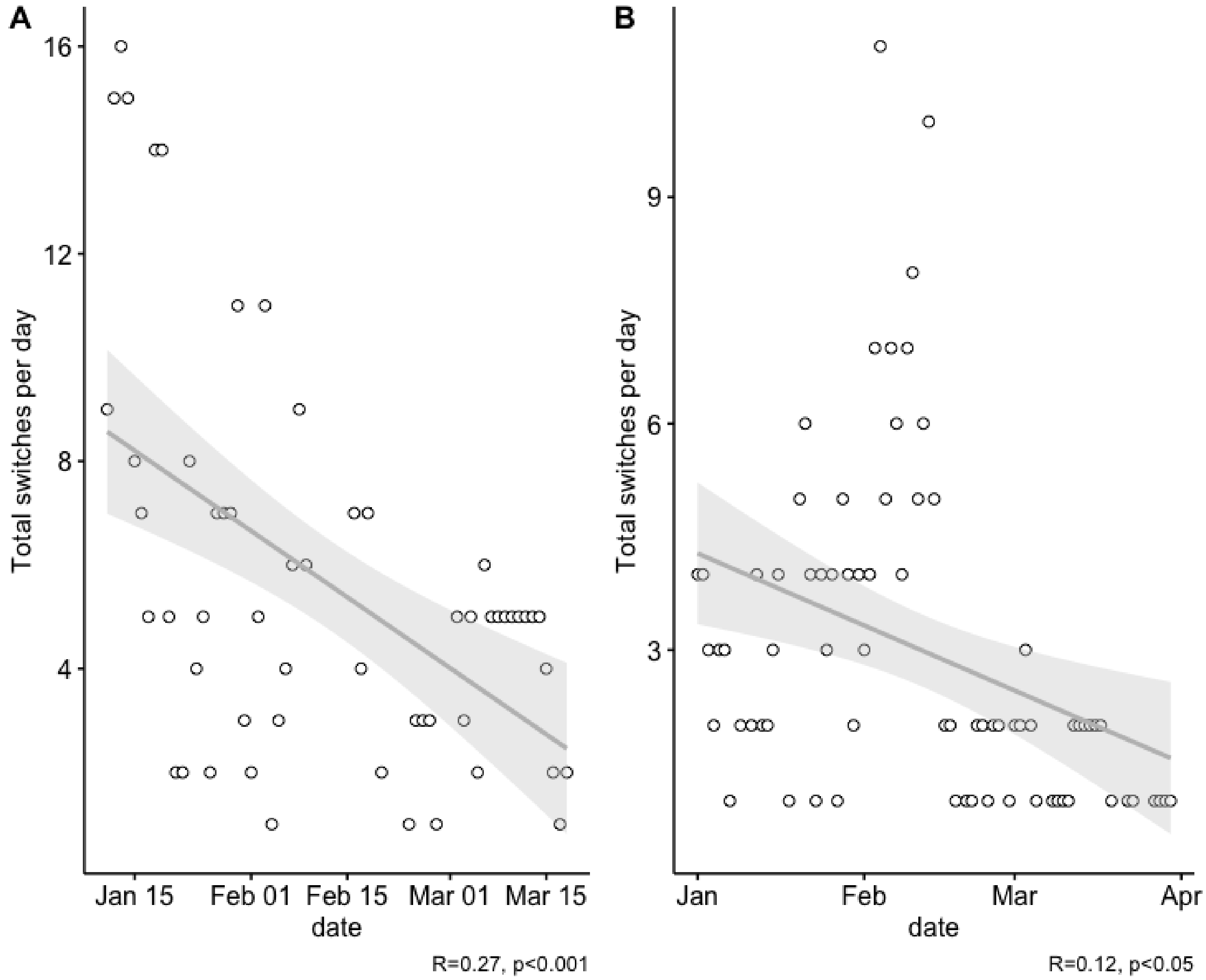


Figure 2. 7 Linear relation between total switches per day and date for the 2016 (A) and 2017 (B) Winter seasons.

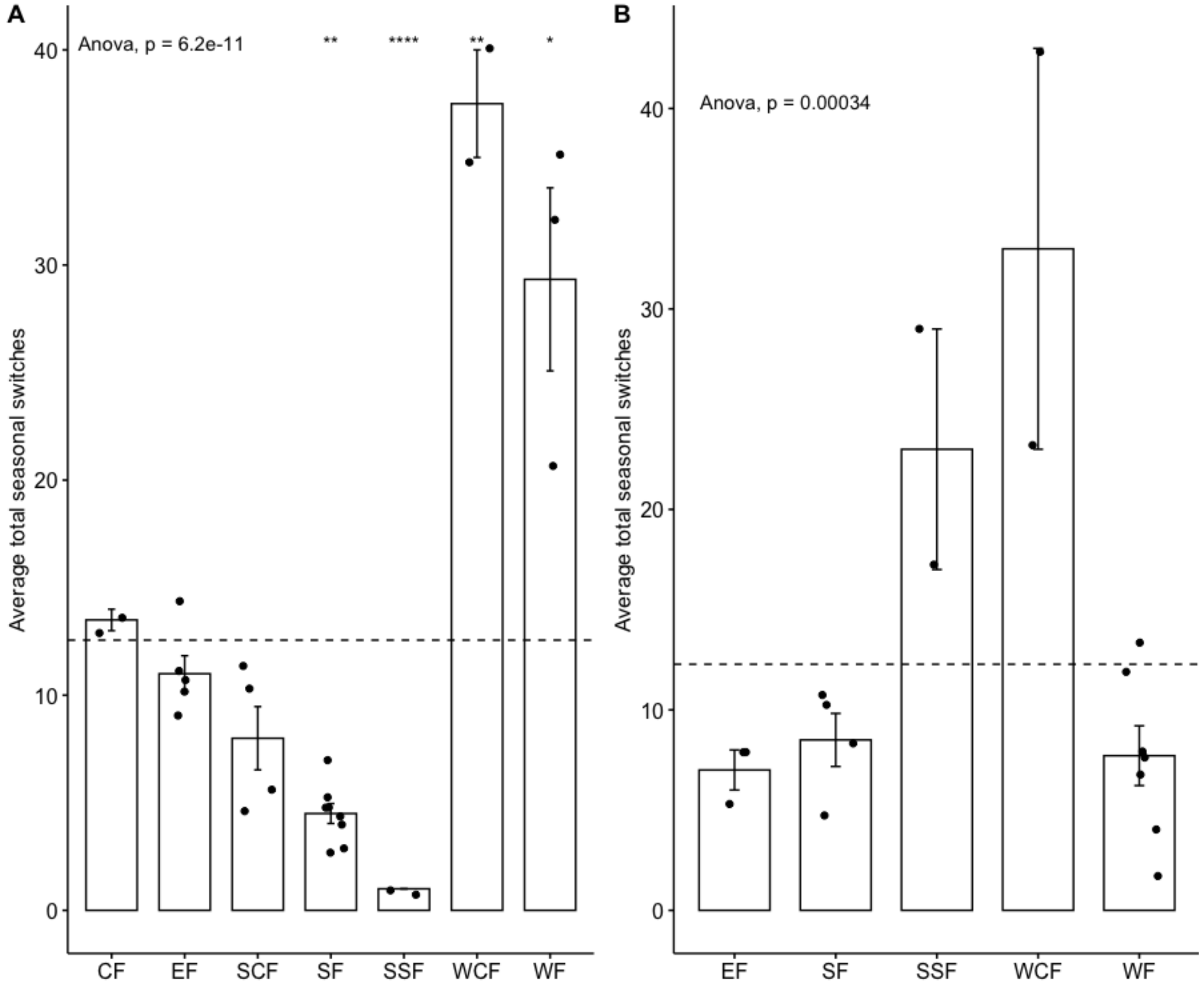


Figure 2. 8 Average switches per flock for the 2016 (A) and 2017 (B) Winter seasons.

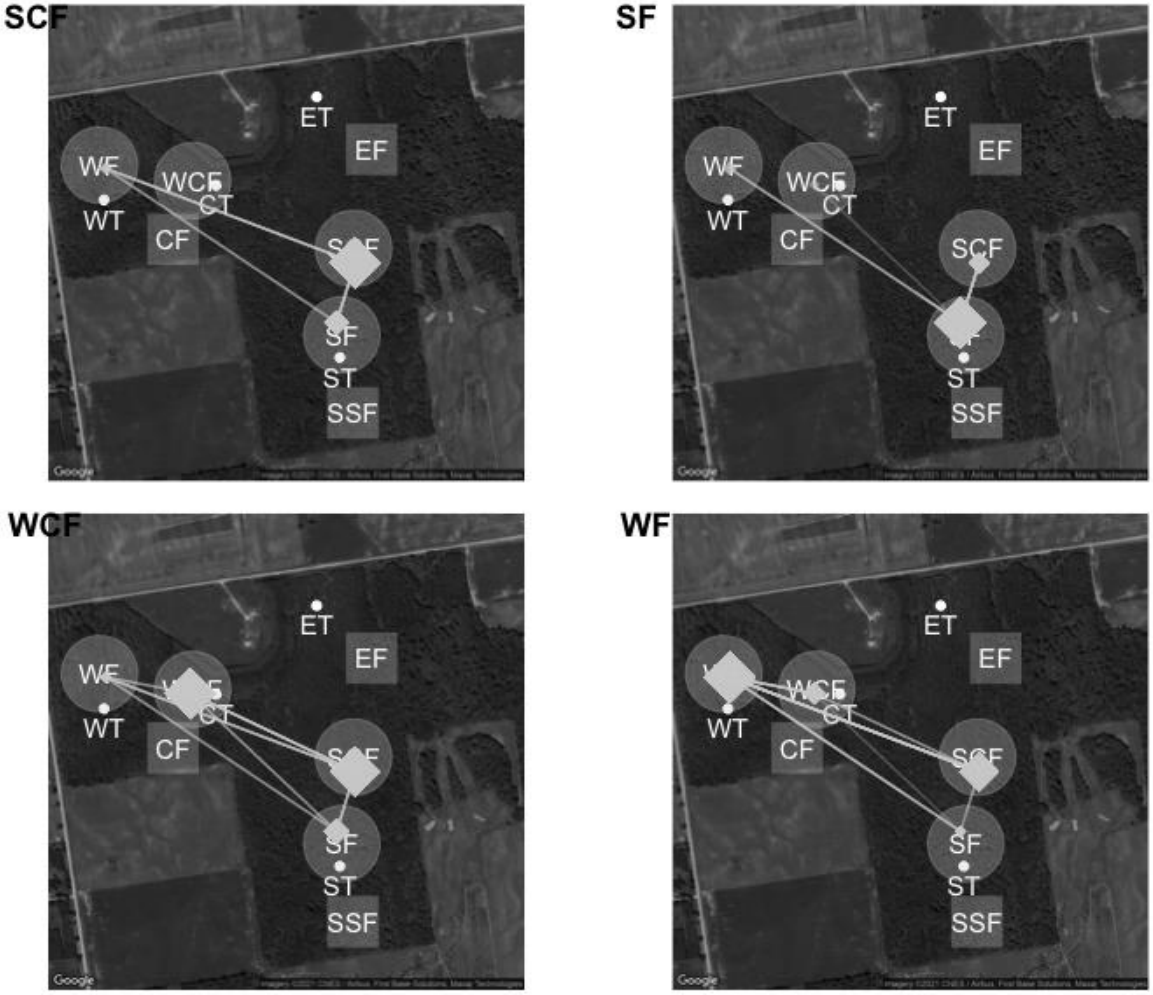


Figure 2. 9 Individual movement pathways for the four primary flocks of the 2016 Winter season. More flock assignments to alphas are represented by size of the diamonds, and more commonly travelled pathways are indicated by increasing line weight.

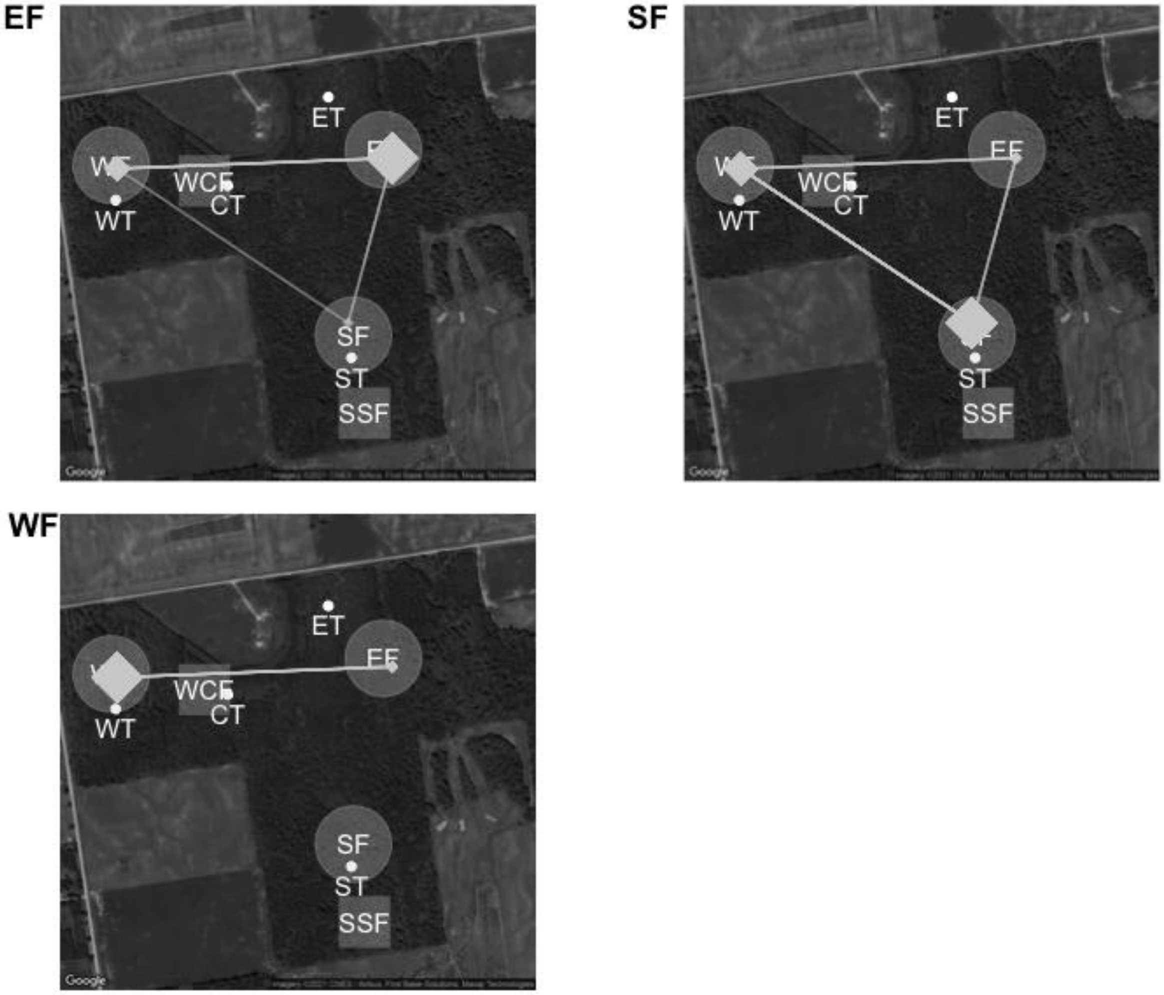


Figure 2. 10 Flock movement pathways for the three primary flocks in the 2017 Winter season. More flock associations are represented by size of the diamonds, and more commonly travelled pathways are indicated by increasing line weight.

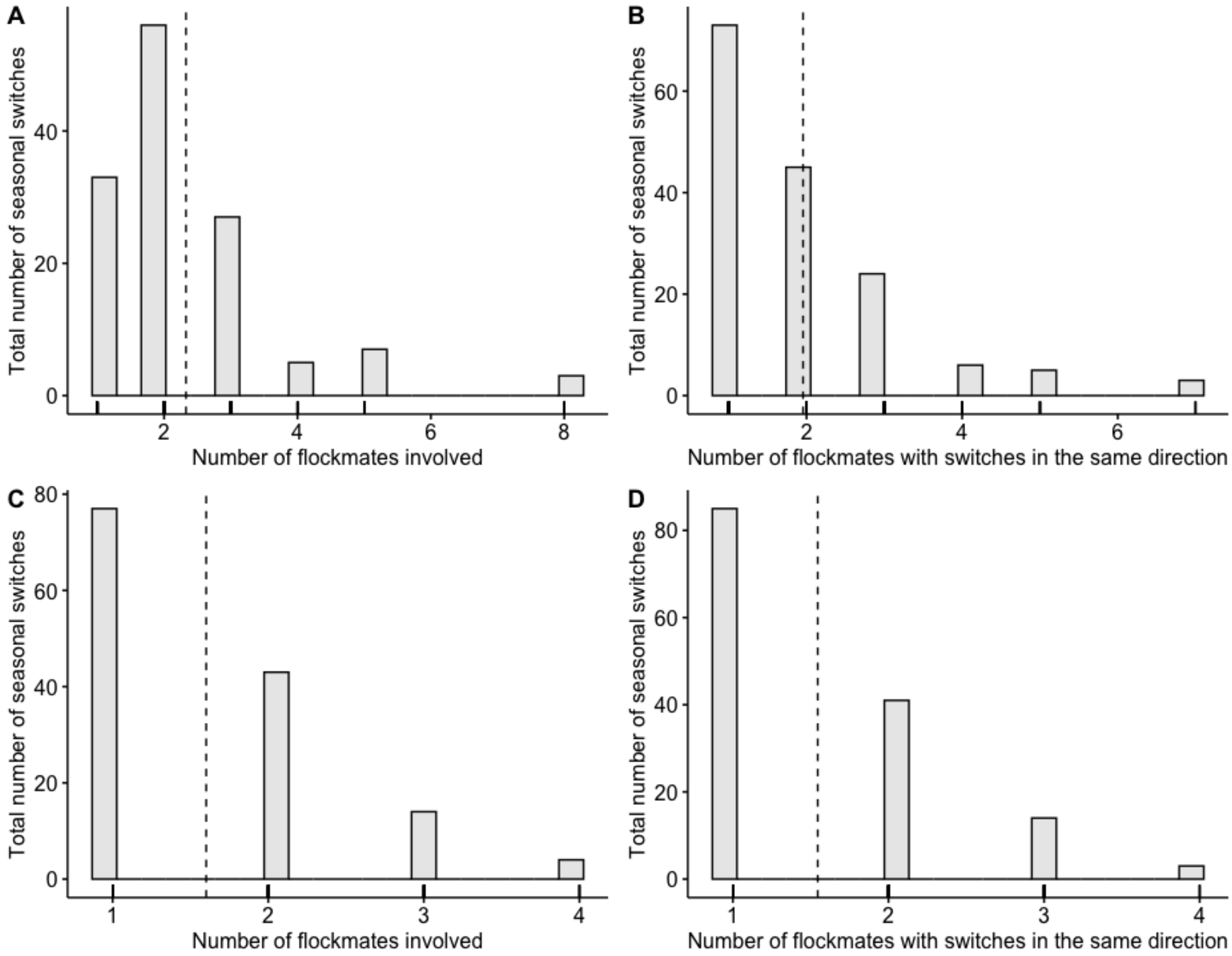


Figure 2. 11 Number of flockmates switching on the same day (A,C) and of these the number of flockmates switching to the same location (B,D) for the 2016 (A,B) and 2017 (C,D) Winter seasons.

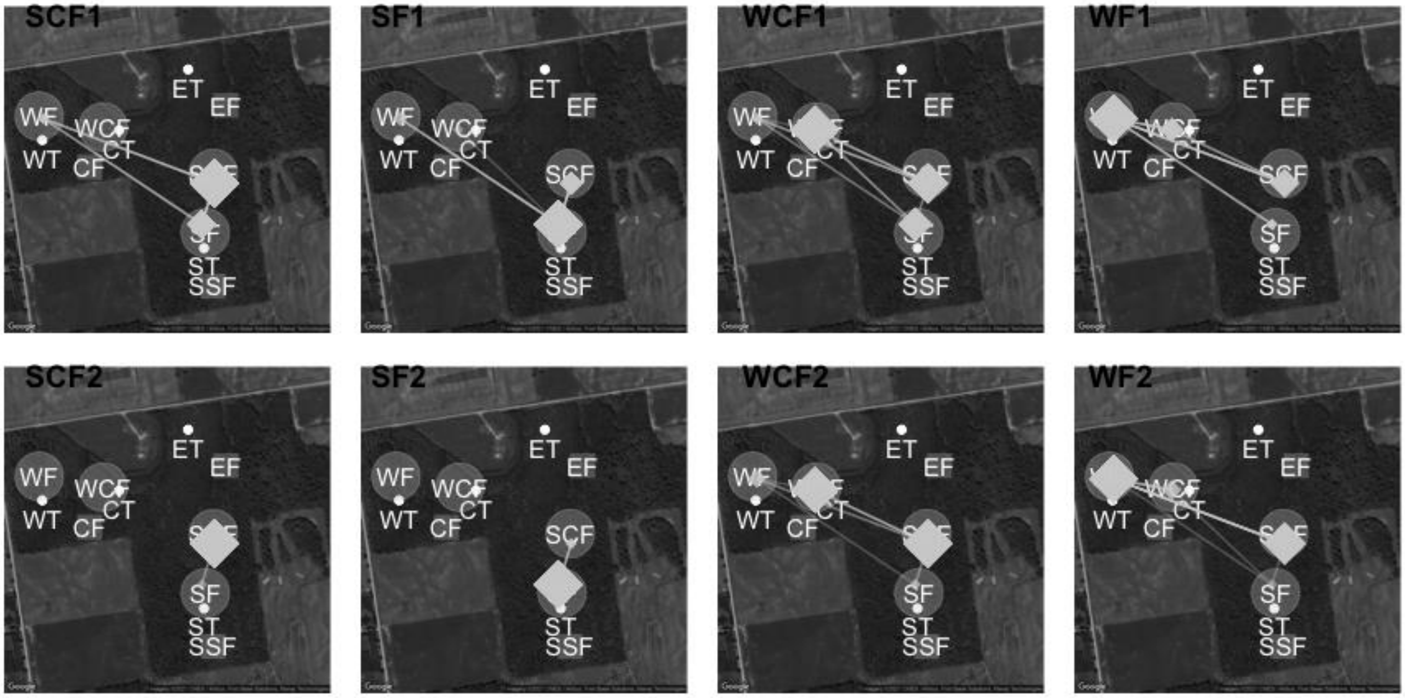


Figure 2. 12 Flock movement pathways of the four primary flocks in Winter 2016. The top row displays movements of the first half of the Winter season, and the bottom row represents the second half.

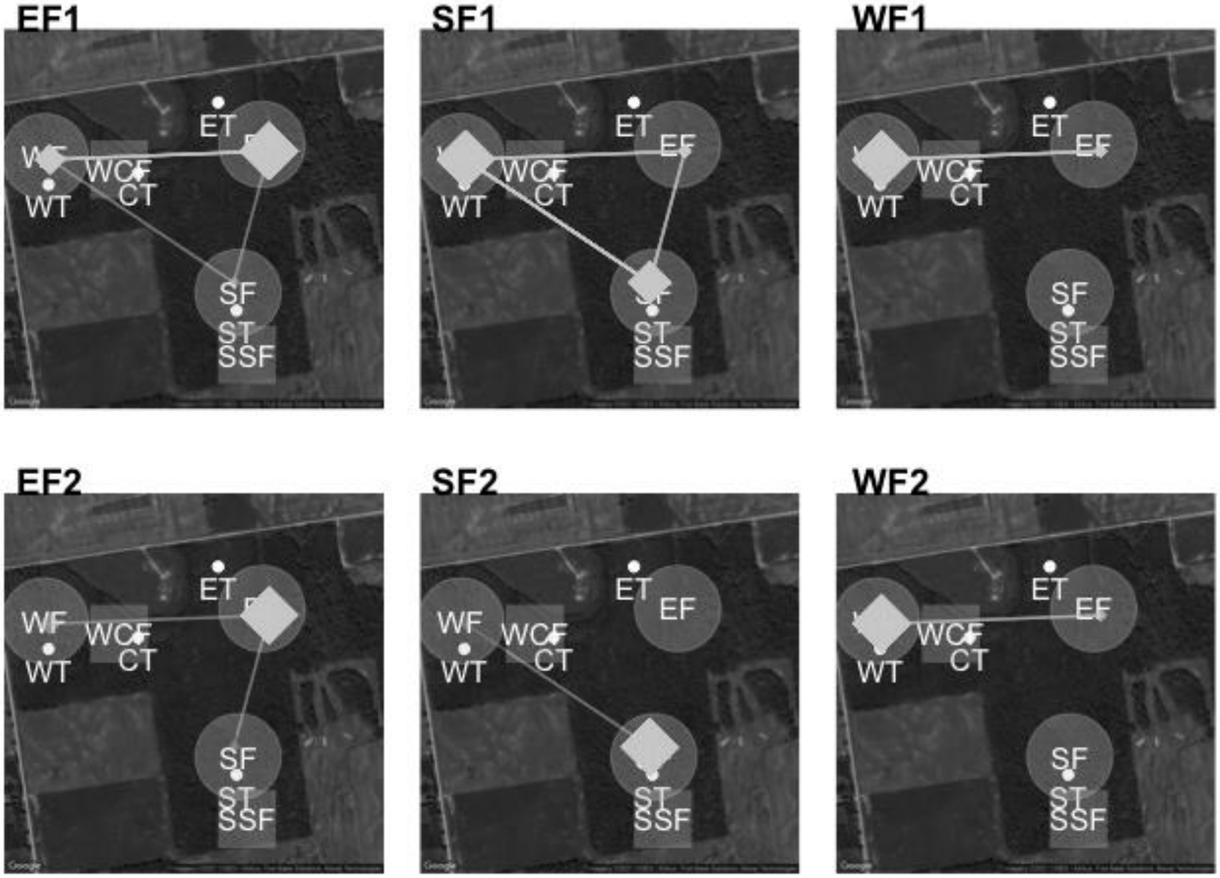


Figure 2. 13 Flock movement pathways of the three primary flocks of Winter 2017. The top row displays movements of the first half of the Winter season, and the bottom row represents the second half.

2.4 Discussion

I present the first large-scale, automated radiotelemetry dataset with a focus on identifying and tracking social groups in a wild population of birds. By using 4 automated radiotowers, detections from all tagged individuals from multiple flocks were continuously collected for two full winter seasons in real time in the important ecological, temporal and seasonal contexts known to influence social dynamics (Helm, 2006; M. Silk et al., 2014). I used LDA to provide a separation of alpha seasonal positions using tower signal strengths, and used this as a training set to identify the daily positions of all other birds for two winter seasons. I argue this can be used as a novel method to define a flock, and to track individual and flock seasonal movements. To my knowledge, this is the first automated tracking study to use real-time radiotelemetry data to both define flocks of birds in the field and to study socially relevant movements.

2.4.1 Defining a flock using radiotelemetry

While automated tracking methods can offer more precise ways to study large scale social phenomenon such as fusion-fission dynamics in the field (Farine, et al., 2015), it logically follows that an equally precise method is needed to define what constitutes a social group in the field. If the animal group is defined too liberally, it can lead to problems in social analysis, and may not be reflective of a true animal group in nature (Castles et al., 2014; Farine, 2015). This is especially important in groups which have a high rate of fission-fusion, as in birds of the family *Paridae* (Hogstad, 2014; Smith, 1991). Flocks of black-capped chickadees have been defined in many different ways and not surprisingly, this produced different descriptions of flocks, ranging from flocks with very restricted territories containing sedentary residents with no range overlap (Glase, 1973) to a completely flockless structure (Smith & Buskirk, 1988), and finally, some combination of these (Smith, 1991).

As an alternate method of defining a flock, I used LDA to find the relative position of selected alphas (four in Winter 2016 and three in Winter 2017), and then applied this training set to identify all other birds' daily positions. In this manner, alpha separation was used as a proxy for the flock territory centre point and was successful in both achieving separation of the alphas of both years (Figures 2.3,2.4) and identifying separate 'primary' flocks (Figure 2.5), which were flocks that included the alpha individual used in the original LDA training set. Interestingly, this method was also successful in identifying ‘secondary’ flocks, which were those that could be visually separated by examining the seasonal alpha classification plots, but that did not include an alpha in the original training set. This was possible in both seasons and resulted in an additional three flocks in Winter 2016 (CF, EF, SSF) and two flocks in Winter 2017 (WCF & SSF). In this way, more flocks could be identified based on a smaller set of relative alpha positions and demonstrates the potential of this technique of flock identification.

Defining flocks in this way offers two major advantages. Firstly, it is precise, in the sense that birds were assigned to flocks for every minute of every day, and in some cases had over 400 flock assignments per day. Secondly, data was collected on all birds simultaneously, which avoids the observer bias of watching only one flock at a time and missing relevant information about other flocks. This technique additionally uses the full winter movement data in defining flocks, which is necessary in defining flocks (Smith, 1991). Such constant assessment of flocks is particularly valuable in groups of high social flexibility, not only to more effectively pinpoint groups in the field, but also for the potential to track individual movements across groups.

2.4.3 Individual seasonal movements and fission-fusion dynamics

All social animals display some degree of fission-fusion dynamics (Silk, 2014). In the case of chickadees, like other birds, this occurs in the form of a major fusion event in Fall, and a major fission event in Spring (Helm et al., 2006). Aside from this, chickadees also display a wide range of social flexibilities which include: residents that never leave their flock’s territory, switchers which join and leave multiple flocks, and migrants that join flocks seldom but likely move between populations (Glase, 1973; Smith, 1991). While flocking during the winter is beneficial (Hogstad, 1989; Smith, 1991), the reasons underlying flock-switching or movements between territories are more of a mystery.

The LDA flock assignment results were not only useful for flock identification, but also for identifying the types of social flexibility. While the majority of tagged chickadees had a full tracking record for the winter, there were a number that after being tagged had very few detections and were never found to be close to any of the alphas. These are likely the ‘migrants’ described by Smith (1991) – birds that once are banded either leave the immediate area entirely or remain largely solitary and do not associate with other flocks. In my population, I found 20% migrants in Winter 2016, and 38% in Winter 2017. This is somewhat comparable to an 18% average migrants per year in Smith's (1991) flocks, and not surprising considering that some populations have been described as entirely consisting of migrants (Smith & Buskirk, 1988).

Using the LDA daily assignments, I examined flock-switching by quantifying the number of occurrences when individuals were assigned to an alpha that it was not typically associated with for the majority of the season, indicating that a bird moved toward another flock's territory and away from its own. These events occurred relatively rarely, and similarly to Smith (1991), the majority of the time individuals remained in their flocks (Figure 2.6). In contrast to Smith (1991) however, rather than define individuals as switchers or not, I quantified the number of switches per individual per season. I was surprised to see that only 16% of individuals in Winter 2016 and 5% in 2017, never switched to another flock. Rather, the majority of birds in my study switched at least once per season and on average of 13 times in Winter 2016 and 16 times in 2017. This means that at least in my population, sedentary flock regulars are atypical, which is opposite to most findings in black-capped chickadees (Glase, 1973; Smith, 1991) and other parids (Hogstad, 2002, 2014). Although chickadee populations of non-standard structure have been observed (Smith & Buskirk, 1988), I do not think my population is atypical, but instead suspect that the frequency of flock-switching has been underestimated. This higher estimate of flock-switching is likely due to the ability of automated tracking to detect far more data on individual movement than is possible with observational studies.

Another important finding in my population was that rank was not related to flock-switching disagrees with findings that flock-switchers are usually birds of lower rank (Smith, 1991; Hogstad, 2014). Considering the fact that the majority of birds in my population did engage in flock-switching, it makes sense that there would be no effect of rank. Furthermore, Smith (1991) describes 'dominant wanderers' as high-ranking birds which move between flock territories readily which suggests that birds of varying ranks are capable of inter-territory movements. Although these made up a low percent of the population (Smith, 1991) it is nonetheless support for the idea that inter-territory movements are occurring regardless of rank.

If rank is not an effective explanation of flock-switching, what is? Numbers of seasonal switches differed significantly between flocks in both years (Figure 2.8), suggesting that individual of flocks have differing rates of flock-switching, which is also evident in the flock-specific movement pathways between territories (Figures 2.9, 2.10). Interestingly, when the total number of switches per flock was compared to the mean of all flocks per season, the highest number was found in a central flock (WCF), while the lowest were found in flocks closer to the edge of the forest (Figures 2.1, 2.8). This may indicate two things. One possibility is that members of more central flocks only appear to move more because they are closer to more flock alphas and thus harder to separate and identify. This is probably not the case because: 1) the LDA was able to separate the alphas from two centrals flocks (SCF, WCF) in Winter 2016; 2) individual movement pathways of flocks indicate cases where birds moved to flock alphas while bypassing others in relatively close proximity – as is the case with the SCF in 2016 switching to the WF flock without being detected in the WCF flock, and the SF flock of the same year switching to WF and WCF on separate occasions (Figure 2.9); 3) differences in numbers of switches of flocks were not always consistent between seasons. All of these points indicate that the flock-switching is more indictive of inter-territory movements than birds being incorrectly assigned to flocks based on proximity alone. A more exciting possibility is that individuals that switch more may be increasing their social connectivity with other flocks. Automated tracking studies in tit flocks have shown that individuals that associate with a higher number of conspecifics have increased foraging success through social information transfer (Aplin et al., 2012; Farine et al., 2015), which could indicate a potential benefit of moving to other flock territories even on a short term basis. If this were the case in my population, flocks like WF and WCF in winter 2016 had higher social connectivity than for example the SF flock, which is evident by the total switches per flock (Figure 2.8), but also by the increased movement pathways between territories (Figure 2.9).

2.4.4 Seasonal flock movements

Assuming that flocking and flock-switching are both beneficial in winter then it would be expected that individuals would balance these two, or put more simply, move between flock territories in groups. In winter 2016, the majority of switches co-occurred on the same day with that of another flock-mate, and furthermore, roughly half of these switches were in the same direction (i.e. were both classified as moving to the same alpha’s territory). In 2017, roughly half of switches co-occurred with another flock-mate and of these, half were in the same direction (Figure 2.11). This means that while individuals do switch territories independently, they often occur in tandem with other flock-mates which provides evidence that flock-switching may be additionally considered a social phenomenon. It is important to note however, that I did not directly observe a flock-switch as an individual joining another flock (e.g. flying and foraging with it). This means that what I am describing may be more accurately described as flock movements, but all evidence suggests these are inter-territorial movements and therefore satisfy what is considered a flock-switch, or specifically, a bird whose range encompasses more than one flock (Smith, 1991).

In addition to the effect that flocks had on seasonal flock-switches, flock-switching was also dependent on the time of season, and in both years was negatively related to seasonal progression with less switches occurring at the end of winter (Figure 2.7). In both seasons, the switches dropped after mid-February and decreased into March. This is interesting considering an automated tracking study by Pitera et al. (2018), which demonstrated significant changes in foraging routines of mountain chickadees (*Poecile gambeli*) depending on seasonal conditions. Specifically, higher rates of foraging were associated in the Winter as compared to Spring and were attributed to a greater risk of starvation in the Winter. It is therefore possible that the flock-switches I observed could also be a reflection of increased foraging effort in different flocks' territories which would also indicate a higher degree of social connectivity between flocks during this time. Further evidence of this comes from the flock inter-territory movements compared between the first and second halves of the Winter season (before and after February 15th of both seasons). In most cases flocks were moving to a fewer number of neighboring territories and/or completing fewer pathways during the second half of the season (Figures 2.12, 2.13).

I present data which demonstrates that using LDA to classify daily movement of birds to a training set of relative seasonal position of flock alphas – is a sufficient and simple way to identify flocks using radiotelemetry data alone. I argue that this novel method is a superior way to identify and track flocks because it is based on a very large dataset of real-time relative positional data (over 100,000 pulses per individual) which is continually collected over the entire winter season. This means that seasonal, temporal and environmental dynamics are incorporated in not only the tracking of flocks and individuals, but also in the definition of the flocks themselves. I demonstrate that using these methods allows for a simple way to track seasonal patterns of individual flock-switchers and tracking seasonal movements of flocks.

In addition to this, flock structure can be investigated at any point in time, making it an excellent tool to study fusion-fission dynamics in real time and in a suitable ecological context. The applications of these findings include but are not limited to, field experiments in social behaviour, habitat use, and group fusion/fission dynamics, and can be used with any automated regional radiotracking study (such as Motus) concerned with measuring relative individual/group positional information.

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Chapter 3

Do birds of a feather wake up together? Radio-tracking onset of activity in flocks of black-capped chickadees

3.1 Introduction

Animal groups often must make communal decisions to maintain group cohesion. A foraging group of bees, a school of fish evading a predator, or a migrating flock of birds, all describe situations in which individuals must match their behaviours with other group-members so that they 'agree' on the onset, the direction, and the duration of the activity (Conradt & Roper, 2005). Often, consensus can be reached quickly and effectively through communication of simple social cues. An interesting example of this can be seen groups of Schneider's leaf-nosed bats (*Hipposideros speoris*) which synchronize the onset of foraging behaviour to exactly sunset every night, even though they dwell in caves with no reliable environmental cue of the time of day. Marimuthu et al., (1981) found that bats housed as a group had identifiable circadian rhythms, while those housed individually 'free-ran' thereby disrupting the onset of foraging behaviour. In this case, the acoustic stimuli and air displacement caused by conspecifics flying close to each-other served as social cues to maintain individual circadian rhythms and group cohesion. Other social cues such as body orientation to a certain direction (Conradt, & Roper, 2003), vocalizations at time of departure (Stewart & Harcourt, 1994) and pre-flight ritual behaviours (Black, 1988) have all been found to maintain group cohesion in the wild. When these social cues are expressed from multiple group members through a chain reaction, even large animal groups can achieve activity synchronization. Modelling techniques have been successful in showing how this simple mechanism can explain group, and even population level cohesion in many taxa (Couzin & Krause, 2003).

But what about cases in which there is a high conflict of interest in the group? Certainly not all decisions are unanimous in nature – like in a case of two equidistant high quality patches to a group of foragers. Miller et al. (2013) ran an experiment with golden shiners (*Notemigonus* *crysoleucas*), in which groups of fish were conditioned to associate either a striped wall (A) or coloured floor with a food reward (B). Groups were then tested in a 3-arm choice apparatus which had both conditioned visual stimuli in separate arms, and a third ‘consensus’ arm containing both stimuli. Group behaviour was found to be based on first choices made by leaders at the front of the group. These fish tended to follow their preference, whereas individuals at the back tended to choose cohesively -- If early followers move with the leaders, then the group moves together, but when conflicts of conditioned preference were introduced, early followers choose differently from the leaders causing the later followers to choose their preference and ultimately cohesion was lost. It is clear that such ‘democratic decisions’ (Conradt & Roper, 2003; 2005) are adaptive in the sense that they serve to both reduce uncertainty and maintain cohesion. Since multiple group members contribute to the ultimate decision, this avoids decisions that would be made if only one individual chose for the group.

While these studies have provided essential information of the mechanisms of social dynamics, considering the importance of external factors such as habitat on social dynamics (Firth & Sheldon, 2015; He et al., 2019; Lantz & Karubian, 2017) the importance of investigating the interaction of these dynamics in ecological contexts cannot be overstated. In order do this, however, individual behaviours have to be recorded simultaneously across group members (Favreau et al., 2009). In the case of birds, there is also the additional difficulty that flocks move quickly and are difficult to track in the entirety of their territories using observational methods. Electronic tags (e.g. GPS, radiotags, PIT, RFID, ‘encounternet’) placed directly on birds, transmit relative position to nearby receivers and can provide automated information such as: individual position, activity, and how frequently individuals come into contact with one another. Importantly, this information is recorded simultaneously across multiple group members (Farine et al., 2015a; Snijders et al., 2014). These advancements have been important in demonstrating the importance of leader-follower dynamics in collective behaviour in flight (Nagy et al., 2010; 2018).

The family *Paridae*, which includes the chickadees, tits, and titmice are an excellent candidate for automated social tracking, mostly because they typically do not migrate. In addition, the flock ranges are of limited sizes – roughly 8-25 ha (Hogstad, 2014; Siffczyk et al., 2003; Smith, 1991), thereby making it possible to use automated tracking techniques to track multiple flocks in the same forest in the non-breeding season. Studies using RFID tracking methods at feeders in conjunction with Social Network Analysis (SNA), have revealed a wealth of information including: social information transfer of food patch quality (Aplin et al. 2012), phenotypic selection in flock composition (Farine et al., 2015b), how behavioural tendencies can influence social network position (Snijders et al., 2014), the lasting effects of social segregation (Firth & Sheldon, 2015), and how flocks respond to the loss of flock-mates (Firth et al., 2017). While these findings provide direct evidence of how selection acts on individual behaviour, and how this is transmitted to associations within the population, they are exclusively based on foraging associations, and therefore do not examine social dynamics away from feeders. Because associations within and between flocks are affected by food patch quality (Smith, 1991), examining the social dynamics of flocks outside of a foraging context by means of automated telemetry is a worthy pursuit.

Most parids do not migrate and instead must endure the harsh conditions of winter which include: unpredictable food sources, shorter days for foraging, and long cold nights. This, combined with their higher metabolic demand because of their small size (Pravosudov et al., 2001), have led to a range of winter adaptations such as: facultative hypothermia (Brodin et al., 2017), caching and cache retrieval (McNamara et al., 1990; Sherry, 1984), and flexible foraging schedules (McNamara et al., 2016; Pitera et al., 2018), all of which have evolved as preventative measures to starvation. Because these behaviours occur in a social context, it is logical that social dynamics have also been selected to aid in group survival through the winter. For example, when dominant pairs are removed from winter flocks of willow tits, the survival rate of the flock decreases in comparison to flocks left intact (Hogstad, 1989), pointing to social dynamics being important for survival in such birds ‘living on the edge’ (Pitera et al., 2018) in harsh habitats.

The onset of foraging activity is a particularly important aspect of the diurnal routine in a winter parid since this coincides with the early morning – the point at which energy reserves are lowest, and risk of starvation is greatest (McNamara et al., 1994; Pitera et al., 2018). Since onset of activity occurs in a social context, it may be beneficial if flock-members cooperate and determine onset of activity as a consensus decision. This would be consistent with Conradt and Roper’s (2005) idea that cooperative decisions are a more likely when there is little conflict of interest – which in this case, all group members should benefit equally from more daily winter foraging time. Additionally, since winter flocks of birds likely huddle for warmth during the night (S. M. Smith, 1991), they are presumably in close quarters which would facilitate simple social cues to wakeup flock-mates to optimize early morning foraging.

Collective decisions, group cohesion, and activity synchronization are all inexorably linked to environmental cues, and studies which examine these dynamics in environments where they evolved are essential for a deep understanding of the evolution, ecology and conservation of social animals (He et al., 2019; Helm et al., 2006; King et al., 2018; Silk et al., 2014). The objective of this study was to use automated radiotracking methods to test whether or not the daily onset of activity is socially synchronized in winter flocks of black-capped chickadees. I predicted that onset of activity is flock synchronized, which was demonstrated by both the consistent flock onset of activity within flocks and that onset of activity is not equal across all flocks. Furthermore, I predicted that individual fission-fusion events would demonstrate a change in onset of activity, such that it was later in cases when individuals were flockless. These findings provide evidence that onset of activity is a collective decision in wild flocks of parids and may represent another adaptive social behaviour of winter survival.

3.2 Methods

3.2.1 Flock identification

Flocks were identified by similarity of daily radio-detections of each bird, relative to that of seasonal position of flock alphas as outlined in Chapter 2. In this way, seven flocks were identified in Winter 2016: Centralflock (CF, n=2), Eastflock (EF, n=6), Southcentralflock (SCF, n=5), Southflock (SF, n=9), Southsouthflock (SSF, n=3), Westcentralflock (WCF, n=3), and Westflock, (WF, n=4) and five flocks were identified in Winter 2017: Eastflock (EF, n=4), Southflock (SF, n=5), Southsouthflock (SSF, n=2), Westcentralflock (WCF, n=2), Westflock (WF, n=4). While flocks were identified and tracked from November to April for 2016-2017, I included data from (January 1 – March 15) for both seasons. Since flocks are typically not stable in the early winter months (Smith, 1991), and most tags became inactive in late March, data before January and after mid-March were excluded from this analysis. Rank in each flock was determined by the methods outlined in Chapter 2.

3.2.2 Determining onset of activity

Onset of activity was determined by first examining the daily activity of radioprofiles of one representative from five flocks for all recorded days in January and February in the 2015-2016 season. Since an inactive (or sleeping) bird shows radio-pulses of consistent signal strengths (SS), it is possible to visually pinpoint the time of onset of activity which is evident as a spike of change in SS. I calculated the SS differences at this point for each recorded day (n=109 total) and found a threshold difference to be an average of 4.0 dBm for activity onset. This also agreed with the 4.0 dBm cut-off of used to estimate bird activity in other radiotracking studies (Adelman et al., 2010; Greives et al., 2015), meaning onset of activity or 'wake-up' was defined as the first time of the day at which the signal strength difference reached > 4.0 dBm.

Individuals were then grouped according to flock, and the dataset was filtered to the tower and antenna per day which had the highest number of per flock observations, which allowed for activity measures between flock-mates to be measured from a common source. Daily individual onset of activity times per flock were then filtered to the nearest minute for all days from the January-March period for both winter seasons. For comparison of flock wake-up times to sunrise, sunrise times were obtained from historical weather records on the Environment Canada website (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html).

3.2.3 Statistical Methods

Onset of activity of each flock for both seasons were compared to sunrise using Welch's T tests and rounded to the nearest minute. Welch's T test was also used in comparing the difference of onset of activity to sunrise before and after individual switched into/out of a flock. This was done in both of these cases as there was unequal variance.

A one-way ANOVA with Tukey's post hoc test was used to compare the onset of activity between flocks for both Winter seasons.

All statistics were analyzed using R version 4.0.4 (2021-02-15) -- 'Lost Library Book'. Data was determined to be normal through confirmation of QQ plots.

3.3 Results

3.3.1 Flock onset of activity compared to sunrise

Welch's t-tests comparing each flock onset of activity times to sunrise determined that the EF flock were first active significantly earlier than sunrise, The CF and SSF flocks were significantly later, while the SCF, SF and WCF flock onset of activity was not different from sunrise in the Winter 2016 season. In Winter 2017, season the EF and WCF flock onset of activity was not significantly different than sunrise, and the SF, SSF and WF flocks were significantly later than sunrise (Table 3.1, Figure 3.1).

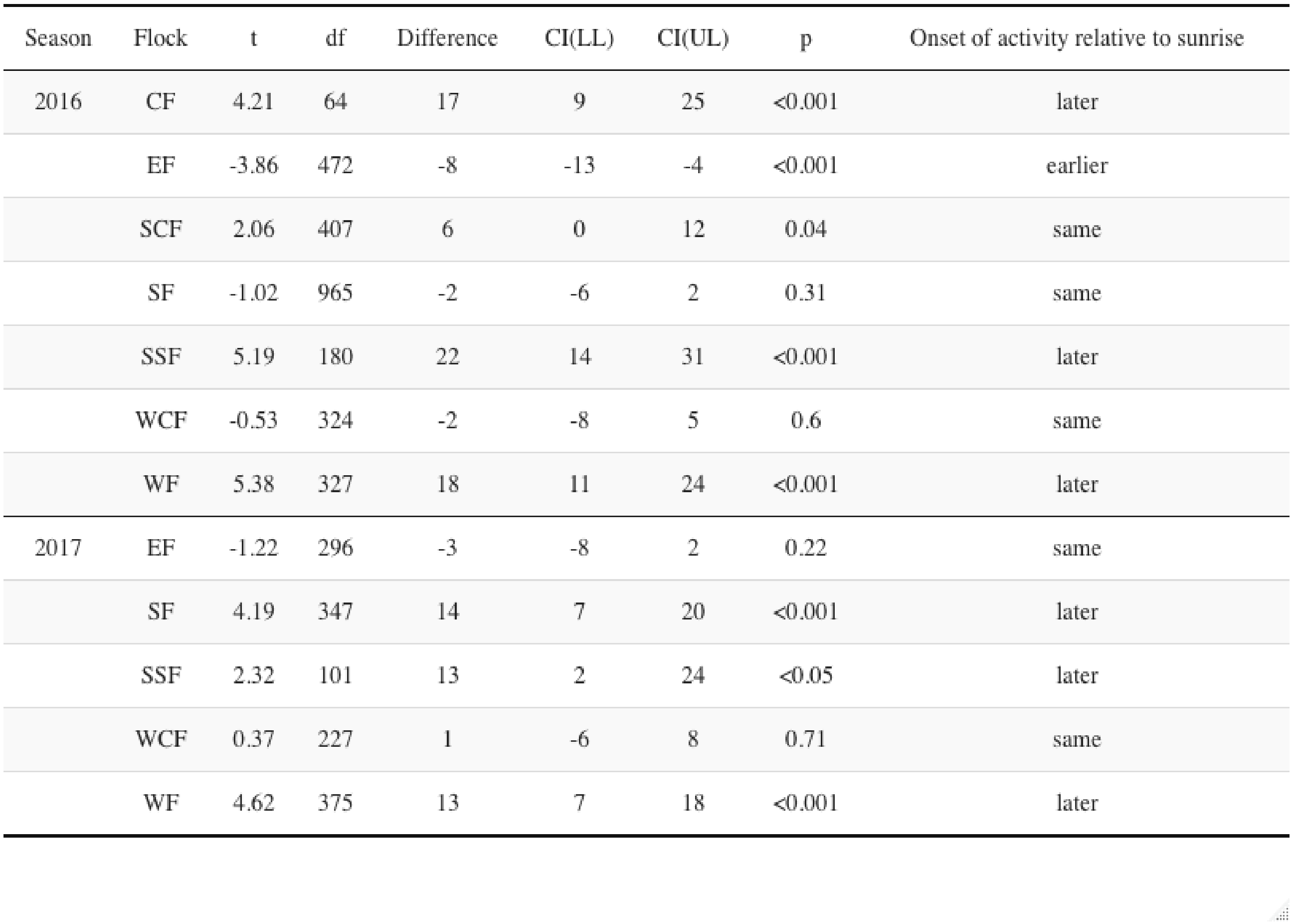
3.3.2 Onset of activity between flocks

A one-way ANOVA demonstrated that onset of activity was significantly different between flocks for the 2016 ($F_{(6,1540)} = 39.34$, $p < 0.001$) and 2017 ($F_{(4,817)} = 19.25$, $p<0.001$) Winter seasons. Tukey's post hoc tests determined that the daily onset of activity was different between the majority of flock comparisons with the exceptions of: WCF-EF, WCF-SF, CF-SCF, WF-CF, SSF-CF and SSF-WF in Winter 2016. In Winter 2017, the majority of flock onset of activity also differed between flocks with the exceptions of: WCF-EF, WF-SSF, SF-SSF, and SF-WF (Table 3.2). It was also determined that rank did not affect onset of activity ($F_{(2,2109)}= 1122$, $p=0.19$)

3.3.3 Onset of activity and flock fission-fusion events

In both seasons, I tracked four fission-fusion events in which birds either left a flock and moved into a new area, or switched into another flock's territory. These events were determined by a sudden and consistent change in an individual's raw radioprofile (Figure 3.2) and provided an interesting opportunity to examine fission-fusion events on flock onset of activity. Birds that left a flock had a significantly later onset of activity (compared to sunrise) after the fission events, and in the fusion event, had an earlier onset of activity (compared to sunrise) after the fusion event than before fusion (Table 3.3). The birds that left flock SF did not differ in onset of activity before leaving ($F_{(1,69)} = 0.14$ $p=0.77$) but were different from SF after leaving ($F_{(1,633)} = 55.62$, $p<0.001$). These three birds after leaving SF formed a new flock SSF, but did not have similar onset of activity within this flock ($F_{(2,100)} = 7.78$, $p<0.001$; Figure 3.3). The bird (442) that fused with flock EF, had a similar onset of activity with EF both before ($F_{(3,106)} =0.59$, $p=0.63$) and after fusion ($F_{(3,155)} = 2.44$, $p=0.07$); Figure 3.4).

Table 3. 1 Onset of activity in minutes relative to sunrise of all flocks of the 2016 and 2017 Winter seasons.

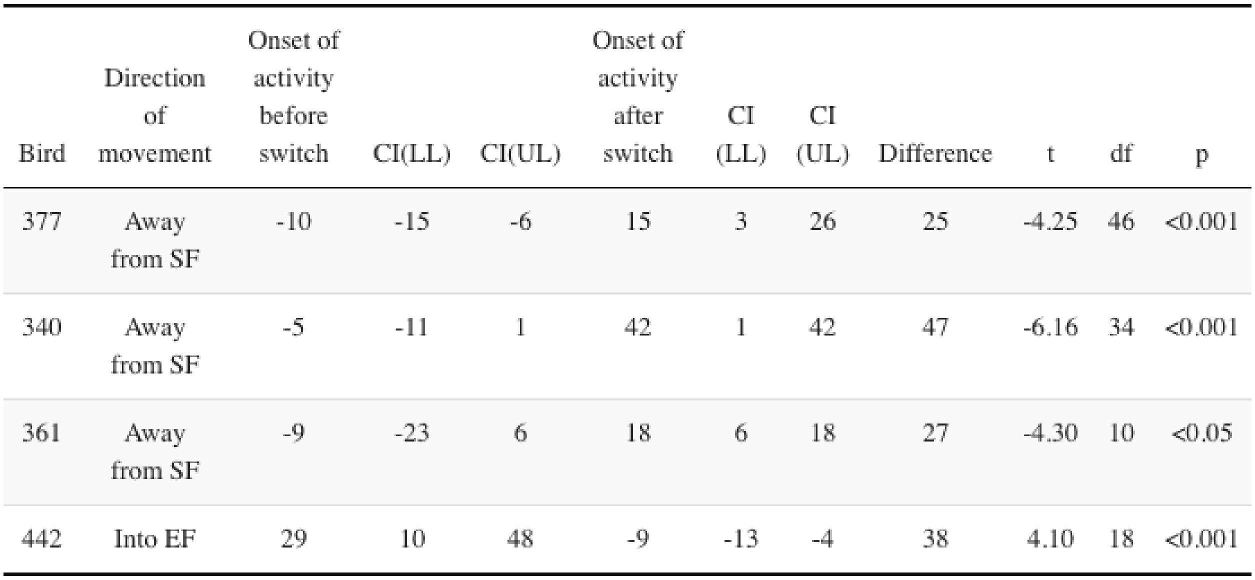


Season	Flock	t	df	Difference	CI(LL)	CI(UL)	p	Onset of activity relative to sunrise
2016	CF	4.21	64	17	9	25	<0.001	later
	EF	-3.86	472	-8	-13	-4	<0.001	earlier
	SCF	2.06	407	6	0	12	0.04	same
	SF	-1.02	965	-2	-6	2	0.31	same
	SSF	5.19	180	22	14	31	<0.001	later
	WCF	-0.53	324	-2	-8	5	0.6	same
	WF	5.38	327	18	11	24	<0.001	later
2017	EF	-1.22	296	-3	-8	2	0.22	same
	SF	4.19	347	14	7	20	<0.001	later
	SSF	2.32	101	13	2	24	<0.05	later
	WCF	0.37	227	1	-6	8	0.71	same
	WF	4.62	375	13	7	18	<0.001	later

Table 3. 2 Post-hoc comparison of onset of activity between flocks in minutes for the 2016 and 2017 Winter seasons. Degree of differences are indicated by grayscale with darker shades representing a larger difference.

Season	Comparison	Difference	CI(LL)	CI(UL)	p
2016	SF-EF	6	1	12	<0.05
	WCF-EF	7	-1	14	0.1
	SCF-EF	15	8	21	<0.001
	CF-EF	26	14	37	<0.001
	WF-EF	26	19	33	<0.001
	SSF-EF	31	23	39	<0.001
	WCF-SF	0	-6	7	1
	SCF-SF	8	3	14	<0.001
	CF-SF	19	8	30	<0.001
	WF-SF	19	13	26	<0.001
	SSF-SF	25	17	32	<0.001
	SCF-WCF	8	1	15	<0.05
	CF-WCF	19	7	31	<0.001
	WF-WCF	19	12	27	<0.001
	SSF-WCF	24	16	33	<0.001
	CF-SCF	11	0	22	0.06
	WF-SCF	11	4	18	<0.001
	SSF-SCF	16	8	25	<0.001
	WF-CF	0	-11	12	1
	SSF-CF	5	-7	18	0.85
	SSF-WF	5	-4	14	0.58
2017	WCF-EF	6	-3	14	0.32
	SSF-EF	17	7	27	<0.001
	WF-EF	17	10	24	<0.001
	SF-EF	19	12	26	<0.001
	SSF-WCF	11	1	22	<0.05
	WF-WCF	12	4	19	<0.001
	SF-WCF	13	6	21	<0.001
	WF-SSF	0	-9	10	1
	SF-SSF	2	-8	12	0.98
	SF-WF	2	-5	8	0.95

Table 3. 3 Onset of activity in minutes relative to sunrise before and after individual fission-fusion events



Bird	Direction of movement	Onset of activity before switch	CI(LL)	CI(UL)	Onset of activity after switch	CI (LL)	CI (UL)	Difference	t	df	p
377	Away from SF	-10	-15	-6	15	3	26	25	-4.25	46	<0.001
340	Away from SF	-5	-11	1	42	1	42	47	-6.16	34	<0.001
361	Away from SF	-9	-23	6	18	6	18	27	-4.30	10	<0.05
442	Into EF	29	10	48	-9	-13	-4	38	4.10	18	<0.001

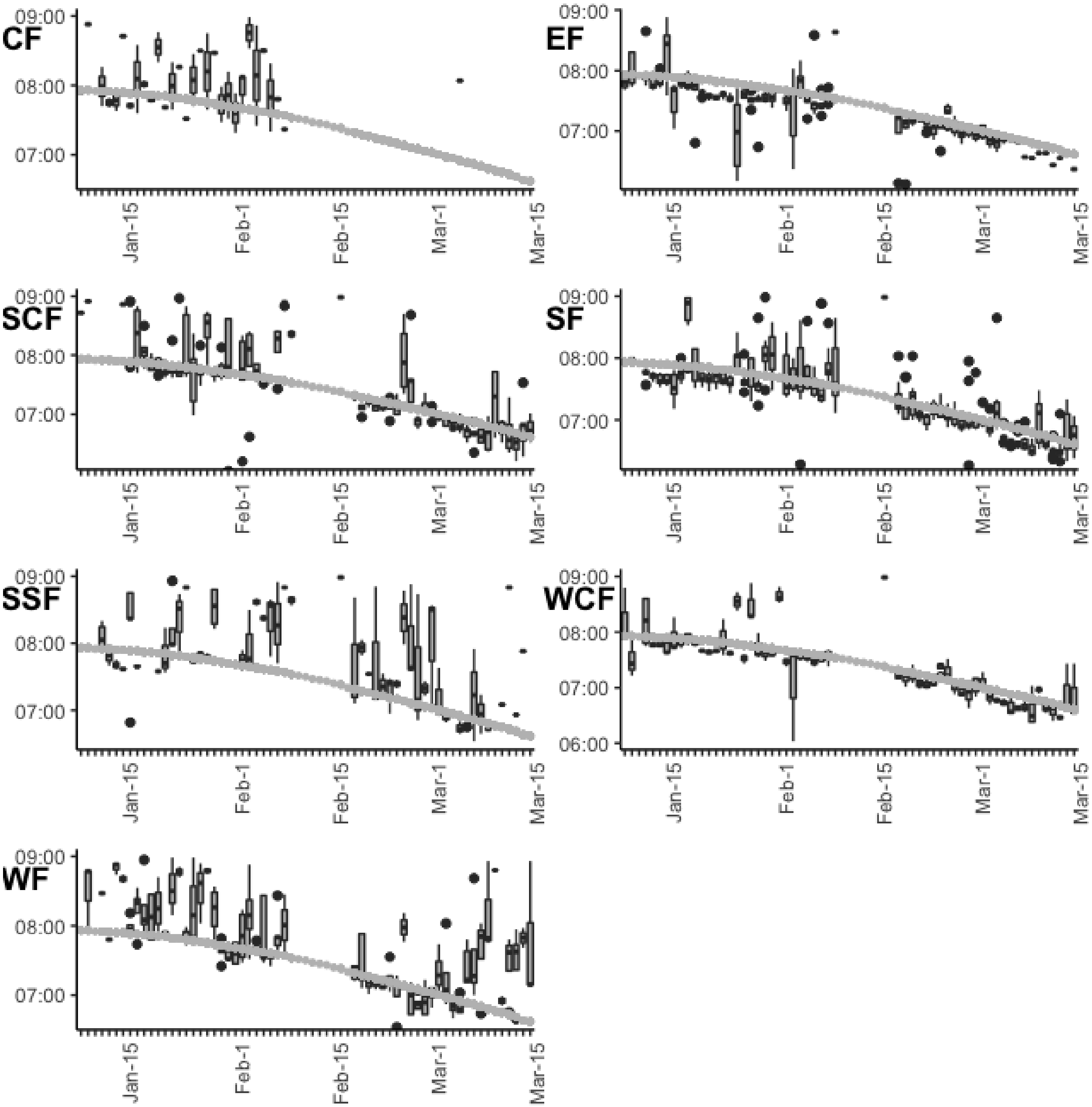


Figure 3. 1 Daily onset of activity per flock for the 2016 Winter season. Sunrise is represented as the gray dotted line.

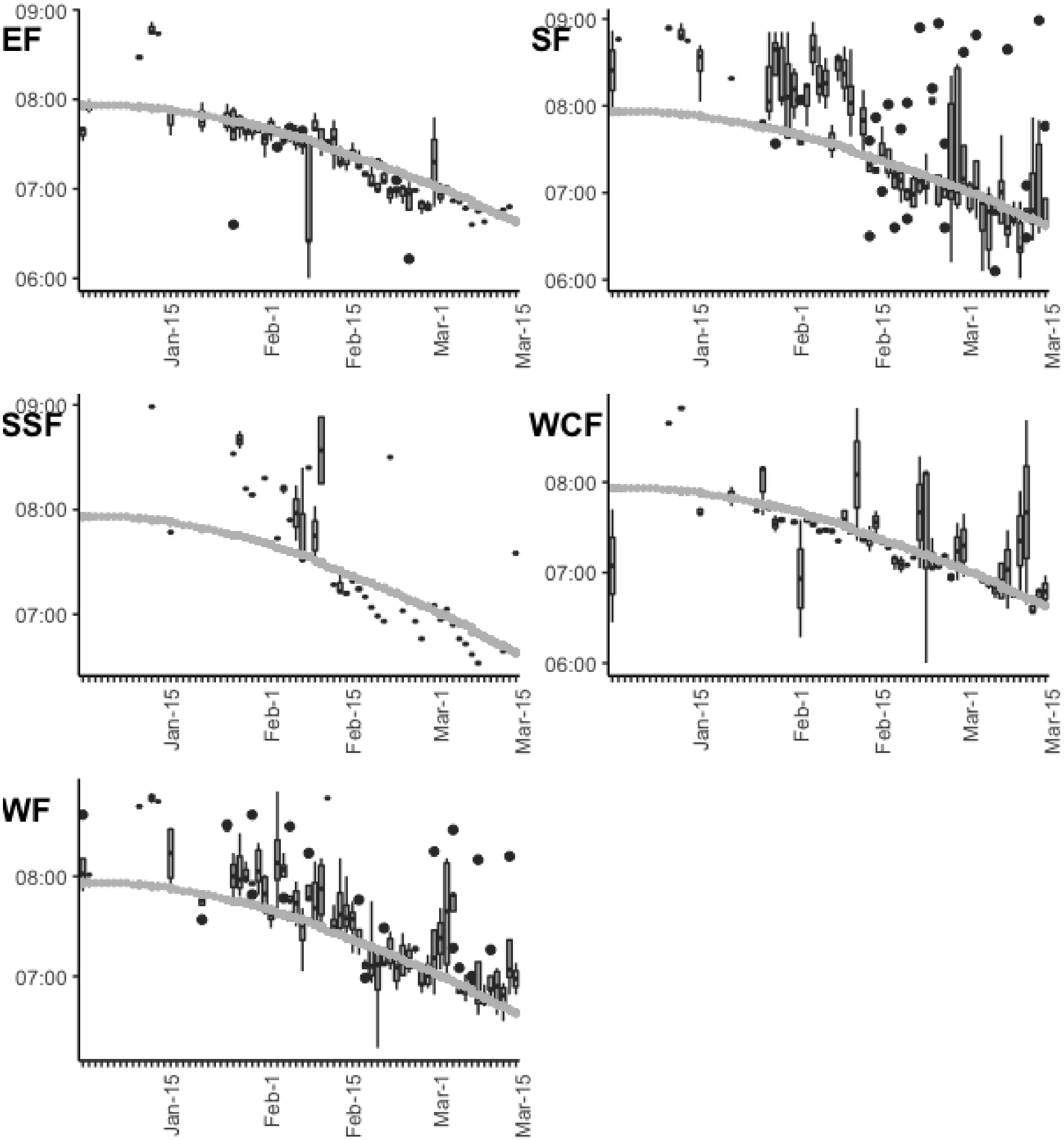


Figure 3. 2 Daily onset of activity per flock for the 2017 Winter season. Sunrise is represented as the gray dotted line.

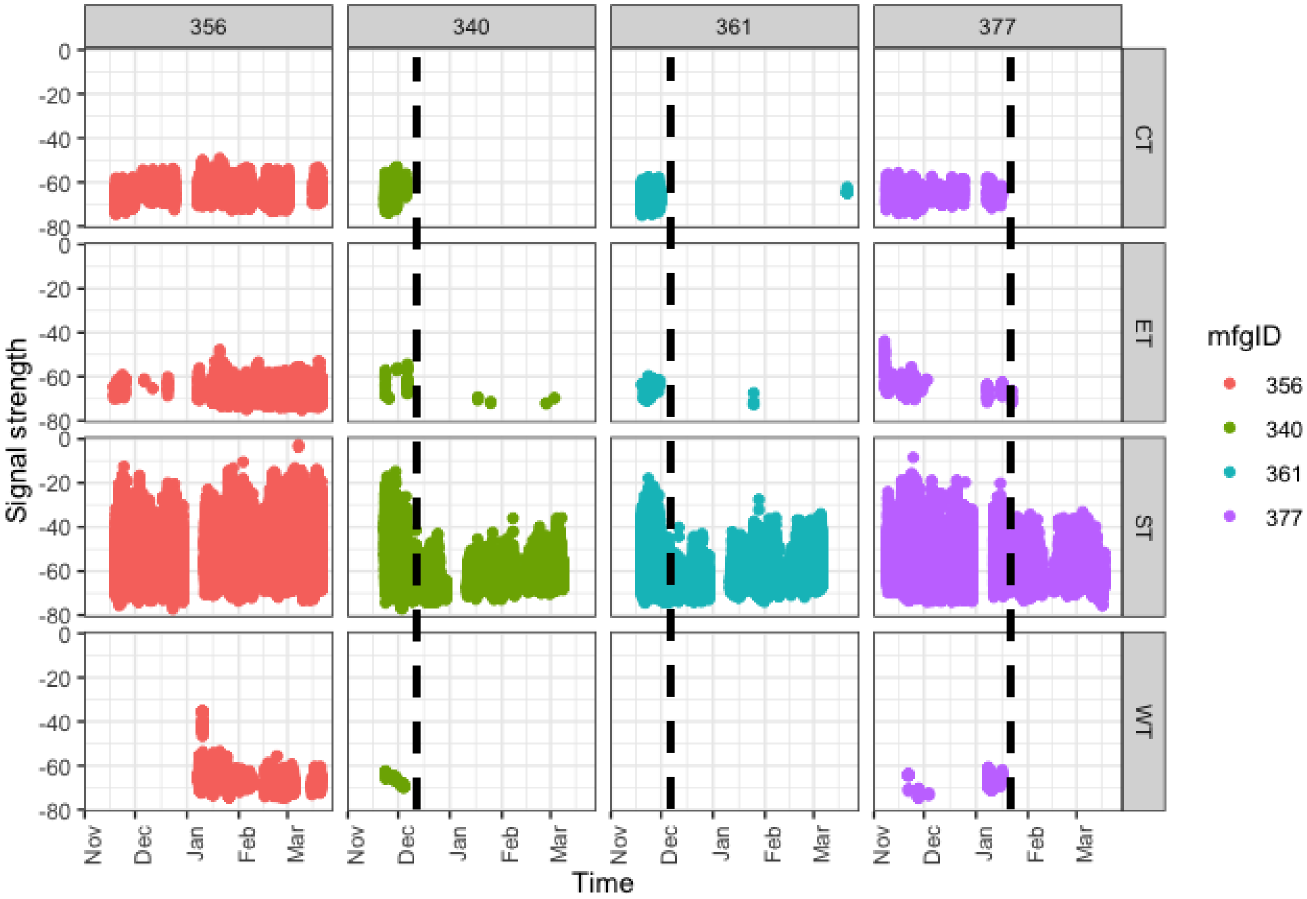


Figure 3. 3 Raw radioprofiles of a flock demonstrating three fission events. Bird 356 is a representative of flock SF, and 340, 361 and 377 are individuals that switched out of SF. The black dotted line indicates the time of switch per individual. mfgID – Bird ID.

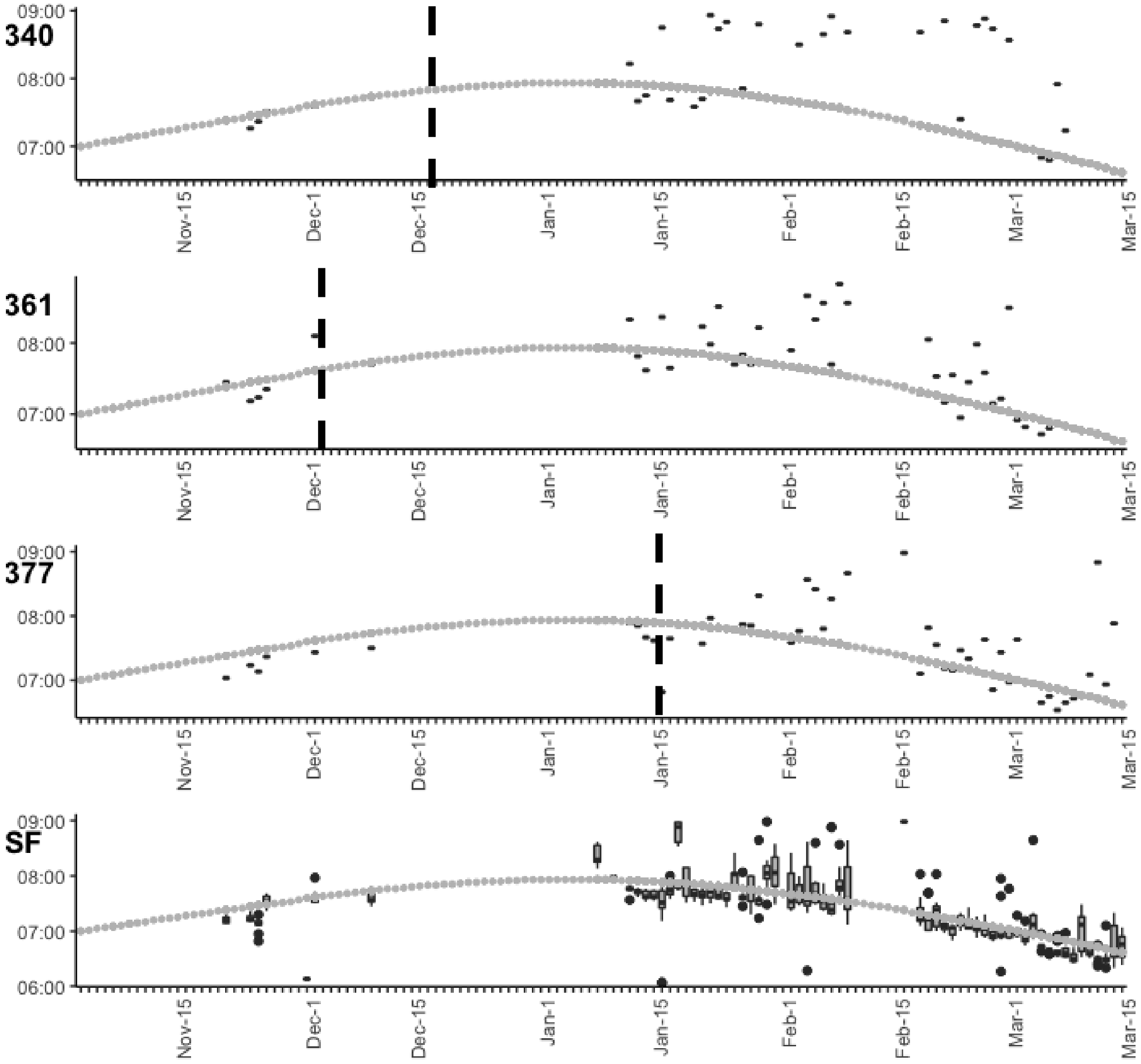


Figure 3. 4 Onset of activity of three flock-switchers out of flock SF in Winter 2016. Black dotted lines represent when flock-switch occurred. Flock onset of SF is shown for comparison, and sunrise is represented by gray dotted lines.

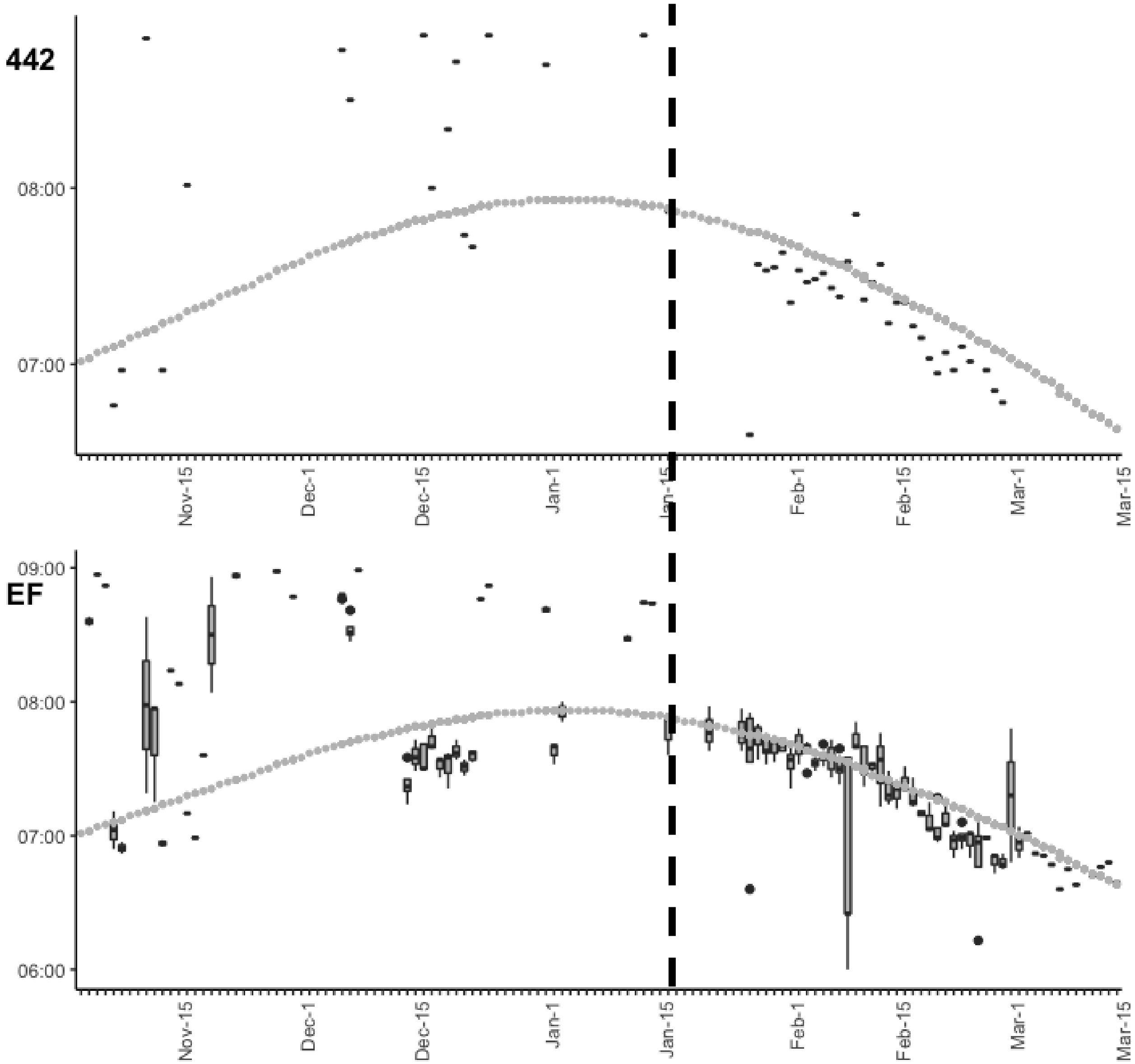


Figure 3. 5 Onset of activity of a flock-switcher into EF in Winter 2017. Flock onset of activity shown of EF for comparison, and black dotted line represents time of switch. Sunrise is represented by gray dotted lines.

3.4 Discussion

When flock wake-up times were compared to sunrise over the course of two winters from January to March, there were flocks in which onset of activity was before, on, or after sunrise. Out of the 12 flocks tracked, 5 had mean seasonal wake-up times at sunrise, 5 were significantly later, and 1 was significantly earlier. In total, flocks encompassed a total mean range of 8 minutes before sunrise to 22 minutes after. As predicted, the majority of comparisons among flocks' onset of activities were significantly different with few exceptions. Since within-flock seasonal onset of activity is relatively consistent through the season with respect to sunrise and between flock wake-up times are more often than not distinct from eachother together suggest that onset of activity is a flock-specific phenomenon. This was furthermore likely since rank did not affect onset of activity.

If onset of activity is indeed determined by the flock, then individuals leaving (or joining) should show an expected change in activity onset. While leaving a social group during the winter would be expected to be costly, it does occur in flocks in a number of species including willow tits, mountain chickadees and black-capped chickadees (Hogstad, 2014; Lahti, Koivula, & Orell, 1997; Smith, 1991). Flock switchers are interesting in the sense that they can experience a number of fusion-fission events in a winter and therefore present an important opportunity to examine and compare the benefits and costs of group-living.

I was able to track four major fission-fusion events in both seasons, in which birds either left, or joined a flock and did not return for the duration of the winter, which were confirmed by examination of raw seasonal radioprofiles (Figure 3.3). Interestingly, in the three cases of birds leaving flock SF in Winter 2016, all had a later onset of activity with respect to sunrise compared to when they were a member of the flock. These individuals all moved away from flock SF to a new location and appeared to form a new flock (SSF). Interestingly, after the fission event, these 3 individuals had significantly different onset of activities within the flock and contained some of the latest individual onset of activity times observed in the study – in some cases over half an hour later than sunrise. These findings together indicate that the flock SSF was not able to synchronize after the fission event for the duration of the winter season and furthermore suggest a cost to onset of activity. Given what is known about the importance of winter foraging at first light to avoid starvation (McNamara et al., 1994; Pitera et al., 2018) my results suggest that certainly from an individual perspective there is a cost of later onset of activity. This is even more striking considering that important fitness consequences can found in birds that delay their onset of activity by as little as 10 minutes (Greives et al., 2015).

If birds leaving a flock incur a cost to onset of activity than it should be the opposite for birds that fuse with another. In Winter 2017, flockless individual 442 joined flock EF in mid-January. Before joining, bird 442 had a significantly later onset of activity, and after the fusion event was active earlier for the rest of the season. At this point, bird 442's onset of activity was not different from the rest of the flock, indicating that 442 synchronized with the flock.

Consensus decisions evolve in animal groups to reduce uncertainty in the environment and maintain cohesion (Miller et al., 2013). In the case of chickadees which overwinter in unpredictable and harsh conditions, they have evolved behaviours such as food caching and plasticity in foraging schedules that decrease resource unpredictability, and thereby increase survival. Because of the importance of foraging at first light to prevent starvation in winter foraging parids (McNamara et al., 1994), I argue that activity synchronization of foraging would be of adaptive significance for all individuals in the flock and thereby a situation which should result in a strong flock consensus. In this study, since chickadee winter flocks had: 1) flock-specific onset of activities in winter and 2) flock switchers had earlier onset of activities when in a synchronized flock and later onset of activities when not, this is evidence that onset of activity is both flock-determined, and a cohesive behaviour. Considering that chickadees likely roost together in close proximity in winter conditions (Smith 1991), it is logical that chickadees wake-up in close proximity. The mechanism of social consensus is likely simple social cues such as acoustic signaling – possibility as part of the dawn chorus, or close proximity flights which have been shown to initiate foraging in other social groups (Marimuthu et al., 1981).

This is the first study to my knowledge to radio-track and study onset of activity in multiple flocks of birds through the entirety of their wintering habitat in a natural setting.

While the observed fission-fusion cases were few, they nonetheless indicate that birds entering a different flock will adopt flock onset of activity while those that leave a flock abandon it. This, combined with the fact that these changes to onset of activity appeared to be immediate after the switch (Figures 3.4, 3.5), provide initial evidence birds onset of activity is synchronized in the group, and that they indeed ‘wake up together’. Automated tracking studies that track natural flocks of parids in the field like this one, provide novel insight into how to study cohesion of animal groups, and thereby contribute equally to the fields of social dynamics and evolution.

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Chapter 4

Environmental impacts on early morning restlessness and activity onset

4.1 Introduction

In addition to the strongly predicted warming average temperatures, and rising sea levels associated with climate change (Allen et al., 2018; Oppenheimer et al., 2019), there is an expected poleward shift of storm-track activity (Seneviratne et al., 2012; Tamarin-Brodsky & Kaspi, 2017), resulting in a predicted increase in the intensity and frequency of winter storms in the Northern Hemisphere (Ulbrich et al., 2008; Yin, 2005). Metcalfe et al., (2013) tested the responses of white-throated sparrows in wintering condition to simulated storm systems using a hypobaric climatic wind tunnel, and found the birds directly responded to low-pressure changes by increasing movement and feeding behaviour. This winter storm response was further investigated by Boyer et al. (2020), who used a similar experimental setup to measure body condition after being exposed to either 1 storm or 2 simulated storms a week. Birds exposed to 1 storm per week responded by increasing body stores, but while birds exposed to 2 storms per week responded with increased feeding, they had lower body stores. These studies provide evidence that birds detect winter storms by the decrease in pressure, and behaviourally and physiologically respond to storms by increasing feeding and fat stores as an adaptation. This has it limits however, as birds exposed to an increased frequency of storms were pushed to their limit and could not increase fat stores even with increased feeding behaviour. This also suggests that winter birds are suitable indicators of climate change in the winter, which is an under-researched area (Knudsen et al., 2011; Lemoine et al., 2007).

The family *Paridae* are a particularly useful for studying adaptations to the environment and have been successfully used to model ecological traits including: foraging efficiency and survival (McNamara et al., 1990) and behavioural responses to harsh environmental conditions (Brodin, et al., 2017; Pitera, et al., 2018). A major reason these birds are of such interest is that most do not migrate and therefore must endure the harsh conditions of winter, which means their survival is tied to ability to make the right behavioural decisions (i.e. when to forage, when to retrieve caches, when to enter facultative hypothermia) in the right environmental condition (Brodin et al., 2017; McNamara et al., 1990, 2016; Pitera et al., 2018). This heightened environmental sensitivity combined with their well-documented and relatively small winter ranges 8-25 ha (Hogstad, 2014; Siffczyk et al., 2003; Smith, 1991), makes these key adaptations much easier to observe and study. Not surprisingly, the ‘little bird in winter’ (Brodin, 2007) is a fitting potential climate change indicator, not only because they satisfy the environmental sensitivity and responsiveness benchmarks for being an effective indicator (Bibby, 1999; Furness & Greenwood, 1993), but that these environmental reactions occur on the wintering grounds – the least understood area in climate change research in birds (Knudsen et al., 2011; Lemoine et al., 2007). Furthermore, their size also contributes to their potential as climate change indicators, as there is evidence that smaller birds are more sensitive to climate change (Mason et al., 2019; Stevenson & Bryant, 2000).

Animals need sleep for a wide variety of reasons. Studies on sleep deprivation in animals have reported: impaired immune function (Bryant et al., 2004), decreased rates of neurogenesis (Fernandes et al., 2015) decreased vigilance (Alhola & Polo-Kantola, 2007), increased neural cell damage (Weil et al., 2009), adverse effects on learning and memory (Hairston et al., 2005) and even survival (Rechtschaffen & Bergmann, 2002). While most of what is known is drawn from mammalian models, recent work with birds has confirmed that like mammals, sleep consists of two distinct activity patterns: slow-wave sleep and rapid eye movement (Roth, Rattenborg, & Pravosudov, 2010). Though the amount of time birds spend in REM is lower than mammals (van Hasselt et al., 2020), this convergence of sleep behaviour suggests that sleep is just as vital for birds.

Because sleep can be markedly different between captivity and the wild (Rattenborg et al., 2008), studying the ecological relevance of sleep in the field is necessary to truly understand its fitness consequences. Automated radiotracking studies with birds have shown that using a signal strength variance of +/- 4dB (decibels) represents activity, while inactivity falls below this threshold. Using this, Adelman et al., (2010) was able to record rest behaviour after immunochallenging part of a population of free-living song sparrows (*Melospiza melodia*) via LPS injection, and found that immunocompromised individuals rest more than control individuals. Furthermore, Greives et al., (2015) used experimental melatonin treatments on great tits during the breeding season and found that higher rates of cuckoldry occurred when individuals were experimentally induced to ‘sleep in’ even by as little as 10 minutes in the morning. These findings are important because they show direct support to the proposed fitness consequences of sleep in an ecological context, while demonstrating the possibilities and advantages of radiotracking free-living birds as a model system to study the adaptive components of sleep.

But how does a free-living bird naturally sleep in the wild? And moreover, what impacts does the environment have on sleep? To answer these questions, the 'little bird in winter' is again a suitable model to study because of the relationship of energy conservation and sleep during the winter nights. Since low temperatures increase metabolic demands, birds need to burn their fat stores during the night to survive. To combat this problem, parids have two major adaptations. Firstly, they rely on cached food to increase their fat stores to survive the night (McNamara et al., 2016; Pravosudov et al., 2001), and secondly, they can enter a facultative hypothermic state which lowers their body temperature and therefore, their metabolic demands (Anders Brodin et al., 2017). The interesting trade-off comes from the fact that cache retrieval is dependent on memory (Sherry, 1984; Sherry & Vaccarino, 1989), which in turn depends on sleep (Vorster & Born, 2015). Since animals in an hypometabolic state run a sleep deficit, which impairs their memory (Palchykova & Tobler, 2006), this trade-off between sleep and energy conservation means birds essentially must choose the nighttime behavioural state that is most beneficial at the time, making these birds an ideal to model to study the adaptive mechanism of sleep (Roth et al., 2010). Studies in sleep cycles of free-living tits have found that natural sleep-wake rhythms are effected by temperature, nighttime length (Mueller, Steinmeyer, & Kempenaers, 2012), and light intensity (Raap et al., 2015), which highlights the relationship between environmental cues and the possible fitness consequences of sleep in wild birds. As climate change continues to cause environmental fluctuations, including an increase in the frequency and duration of winter storms, the effect this would have on sleep in wild birds could have important implications, but has yet to be investigated.

I hypothesized that winter storms disrupt sleep in free-living flocks of black-capped chickadees, and that similar to lab studies, birds will increase activity in response to temperature and/or pressure drops consistent with winter storms (Boyer & MacDougall-Shackleton, 2020; Metcalfe et al., 2013). I additionally hypothesized that pressure, temperature and other weather variables may affect onset of activity and early morning restless throughout the winter and lower temperatures and pressures should result in an increase in restlessness. Since wild flocks of parids are known to increase foraging activity earlier in harsher winter conditions (Pitera et al., 2018), I predicted pressure and temperature changes to result in earlier onset of activity and to increase early morning restlessness.

4.2 Methods

Methods describing flock identification and rank determination can be found in Chapter 2.

4.2.1 Determining winter early morning restlessness and onset of activity

Since the radiotags were on a 12 hour on/off setting, it was not possible to examine sleep behaviour through the night. In lieu of this, I examined early morning sleeping behaviour from the period of tag activation to an hour before the daily onset of activity of the birds (3:00 – 6:00 AM). This way any activity that was recorded was well before sunrise and therefore occurred in low light conditions. Birds that are tracked using automated radiotelemetry are considered to be fully active when the signal strength variation is above the +/- 4.0 dBm benchmark (Adelman et al., 2010; Greives et al., 2015b). Since I found on non-restless mornings individual birds typically show a signal strength pattern of approx. +/- 1dBm (Figure 4.1), anything outside a +/- 2.0 dBm range was considered to be a 'restless event' (RE). In this way I aimed to capture any behaviour that was between fully sleeping and active.

Onset of activity was defined as the first time of day each individual passed the +/-4.0 dBm benchmark. These methods are outlined in Chapter 3.

4.2.2 Weather data

Minimum temperature (°C), pressure (kPa), windspeed (km/h), Total snow (cm), and total precipitation (mm) data were obtained from the Environment Canada website (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). Average pressure (kPa) was calculated per day, and average windspeed (km/h) was calculated for the early morning period (3:00AM – 6:00AM) during which restlessness was recorded. Daily pressure (kPa) and temperature change (°C) were calculated by subtracting the minimum daily value from the maximum. Total snow was calculated by adding snowfall with snowcover. A 'winter storm' was considered to be an event that included: a pressure drop to 97 kPa, moderate winds (20 km/h), and precipitation, which is consistent with Canadian winter storm behaviour (Taylor et al., 1993). In addition to this, I only considered storms that occurred during the early morning period, which was verified using the Environmental Canada Historical Radar (https://climate.weather.gc.ca/radar/).

4.2.3 Statistical methods

To investigate the role of the pressure, temperature, windspeed and precipitation on early morning restlessness (RE) in birds a GLMM approach using a Poisson distribution and log-link function was used, which is recommended for ecological studies containing non-independent, non-normal count data (Harrison et al., 2018). Since individuals were repeatedly measured but were grouped by flock, flock/bird ID was included as a random nested effect. Rank and season were also run as random effects and the environmental variables of interest (minimum temperature, windspeed, pressure, temperature change, pressure change, total snow (snowfall + snowcover) and total precipitation) were run as fixed effects. To improve model performance I used predictor centering on our fixed effects (Harrison et al., 2018), and I included an observation level random effect (OLRE) as recommended by (Harrison, 2014) as a robust method to deal with overdispersion in non-normal count data. This model was run as:

REs ~ Min temp + Wind + Press + Tchange + Pchange + Snowfall + Tprecip +
(1|Flock/BirdID) + (1|Rank) + (1|Season) + (1|OLRE)

To assess the relationship of the above environmental variables on onset of activity I combined all data from the 2016 & 2017 winter seasons and ran a linear mixed model (LMM) using a gaussian distribution. This was appropriate since onset of activity was normally distributed which was verified using quantile-quantile plots. The model was similar to the restlessness model with the exception that rank was removed since it was determined to have no effect on onset of activity (Chapter 3). This model was run as:

OOA ~ *Min temp + Wind + Press + Tchange + Pchange + Snowfall + Tprecip +*
(1|Flock/BirdID) + (1|Season)

Prior to model fitting, I assessed collinearity between variables using the *ggpairs* function in R and did not find any cases of Pearson's correlation was significant and ($r >= 0.5$) so no removal of variables were neccessary. Minimum temperature per day was used since this logically corresponds to the lower temperatures during the night that would be closest to what birds would experience in the early morning when restlessness was measured.

To examine model fit and performance for the restlessness model I used the DHARMa residual diagnostics package in R. DHARMa uses a simulation-based approach to provide easily interpretable residuals, tests for overdispersion and normality of residuals that the model predicts, and is suitable for use with GLMM (Hartig, 2020). Model fit and performance for the Onset of activity model was assessed using homogeneity of variance (residual vs fitted) plots.

All statistics were analyzed using R version 4.0.4 -- 'Lost Library Book'. Mixed models were run using the *lme4* package, and residual diagnostics for the GLMM model were run using the *DHARMa* package.

4.3 Results

4.3.1 Radiotracking restlessness

Using a (+/- 2 dBm) signal strength cut-off was sensitive enough to indicate when birds are being restless, while distinguishing this from sleeping, and fully active behaviour (Figure 4.1). Using this method, it was possible to distinguish between mornings of high restlessness (> 10 RE per bird), from others in which birds had little restlessness (< 2 RE per bird; Figure 4.2). The majority of the mornings for both seasons had relatively low REs per bird (Figure 4.3).

4.3.2 Modelling environmental variables on restlessness and onset of activity

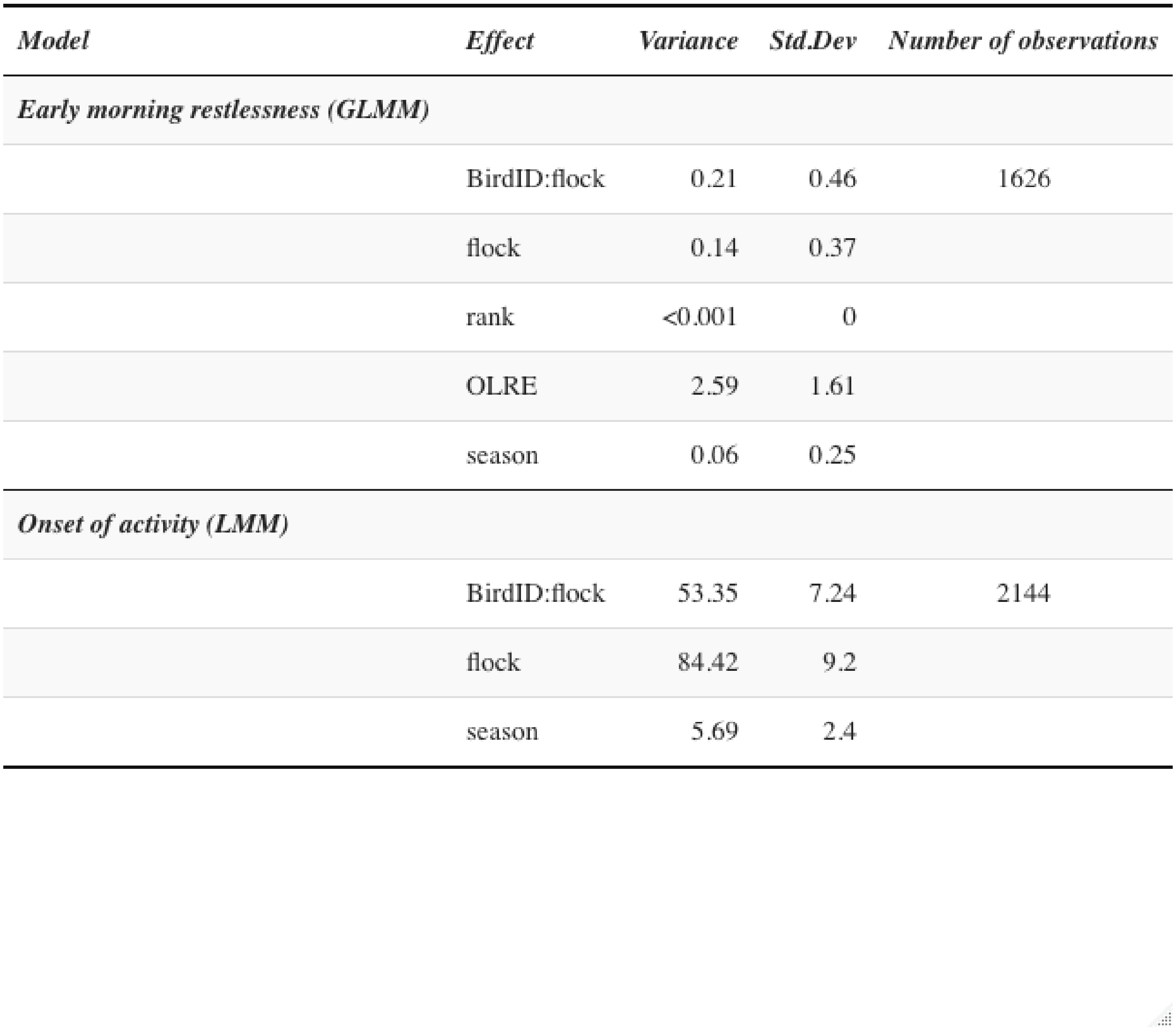
Minimum temperature, windspeed, and pressure change was significantly, and positively related to the number of restless events. Total snow and total precipitation were significant and negatively related to early morning restlessness. Average pressure and temperature change were significantly and negatively related to activity onset (Table 4.2; Figures 4.4-4.6). Flock had a significant effect on morning restlessness ($F_{(6,585)} = 4.69$, $p < 0.001$), but rank ($F_{(2,585)} = 0.71$, $p=0.49$), and season ($F_{(1,585)} = 1.88$, $p=0.17$) did not.

According to the DHARMa tests, our model was not overdispersed (Dispersion test, $p=0.72$) and did not have any outliers (Outlier test, $p=1.00$).

4.3.3 Winter storms

I observed 6 winter storms that occurred during the recorded early morning hours in 2016, and 5 in 2017. In each of these cases, these systems included a: pressure drop to 97 kPa, windspeeds approaching 20 km/h, and accompanied by precipitation which was overhead of the study site during the early morning period (3:00AM-6:00AM). Interestingly, the 6 mornings of highest restlessness (>10 RE per bird) were all associated with winter storms, and the remaining 5 storms showed a moderate response in restlessness (Figures 3.6 and 3.7). The remaining spikes of morning restlessness in both seasons that were not associated with the characteristic low pressure of a winter storm occurred in all cases with periods of moderate to high winds (>20 km/h).

Table 4. 1 Random effects of the Early morning restless (GLMM) and Onset of activity (LMM) models.



Model	*Effect*	*Variance*	*Std.Dev*	*Number of observations*
Early morning restlessness (GLMM)				
	BirdID:flock	0.21	0.46	1626
	flock	0.14	0.37	
	rank	<0.001	0	
	OLRE	2.59	1.61	
	season	0.06	0.25	
Onset of activity (LMM)				
	BirdID:flock	53.35	7.24	2144
	flock	84.42	9.2	
	season	5.69	2.4	

Table 4. 2 Environmental fixed effects of the Early morning restlessness and Onset of activity models.

Model	*Effects*	*Coefficent*	*Error*	*z value*	*Pr(<|z|)*
Early morning restlessness (GLMM)					
	Intercept	-1.62	0.28	-5.87	<0.001
	Minimum temperature	**0.07**	**0.02**	**4.88**	**<0.001**
	Windspeed	**0.1**	**0.01**	**9.99**	**<0.001**
	Pressure	0.01	0.02	0.13	0.90
	Temperature change	0.02	0.12	1.30	0.21
	Pressure change	**0.59**	**0.01**	**4.90**	**<0.001**
	Total snow	**-0.03**	**0.01**	**-2.12**	**<0.05**
	Total precipitation	**-0.04**	**0.01**	**-3.10**	**<0.05**
Onset of activity (LMM)				*t value*	*Pr(<|t|)*
	Intercept	8.23	4.12	2.00	0.10
	Minimum temperature	-0.07	0.14	-0.51	0.61
	Windspeed	0.03	0.09	0.38	0.70
	Pressure	**-2.21**	**0.82**	**-2.69**	**<0.05**
	Temperature change	**-0.82**	**0.16**	**-5.15**	**<0.001**
	Pressure change	0.33	1.13	0.30	0.77
	Total snow	-0.15	0.13	-1.10	0.28
	Total precipitation	-0.04	0.12	-0.34	0.73

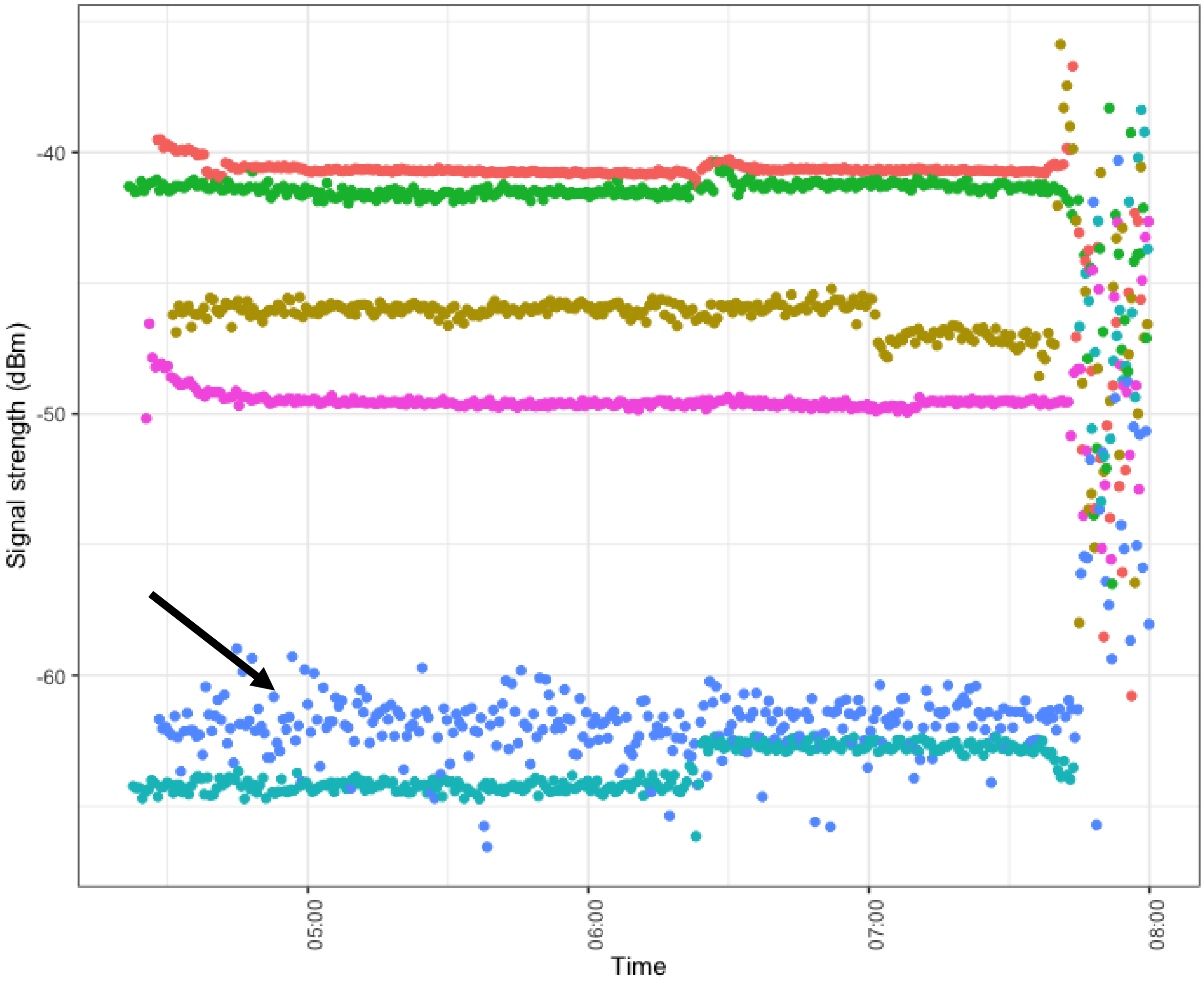


Figure 4. 1 Example of early morning activity of EF flock demonstrating the interpretation of different behaviours on Jan 19, 2016. Individuals are represented by colour. The restless individual is indicated by the black arrow. For behavioural comparison, onset of activity is included at occurs at approx. 7:45AM in this example.

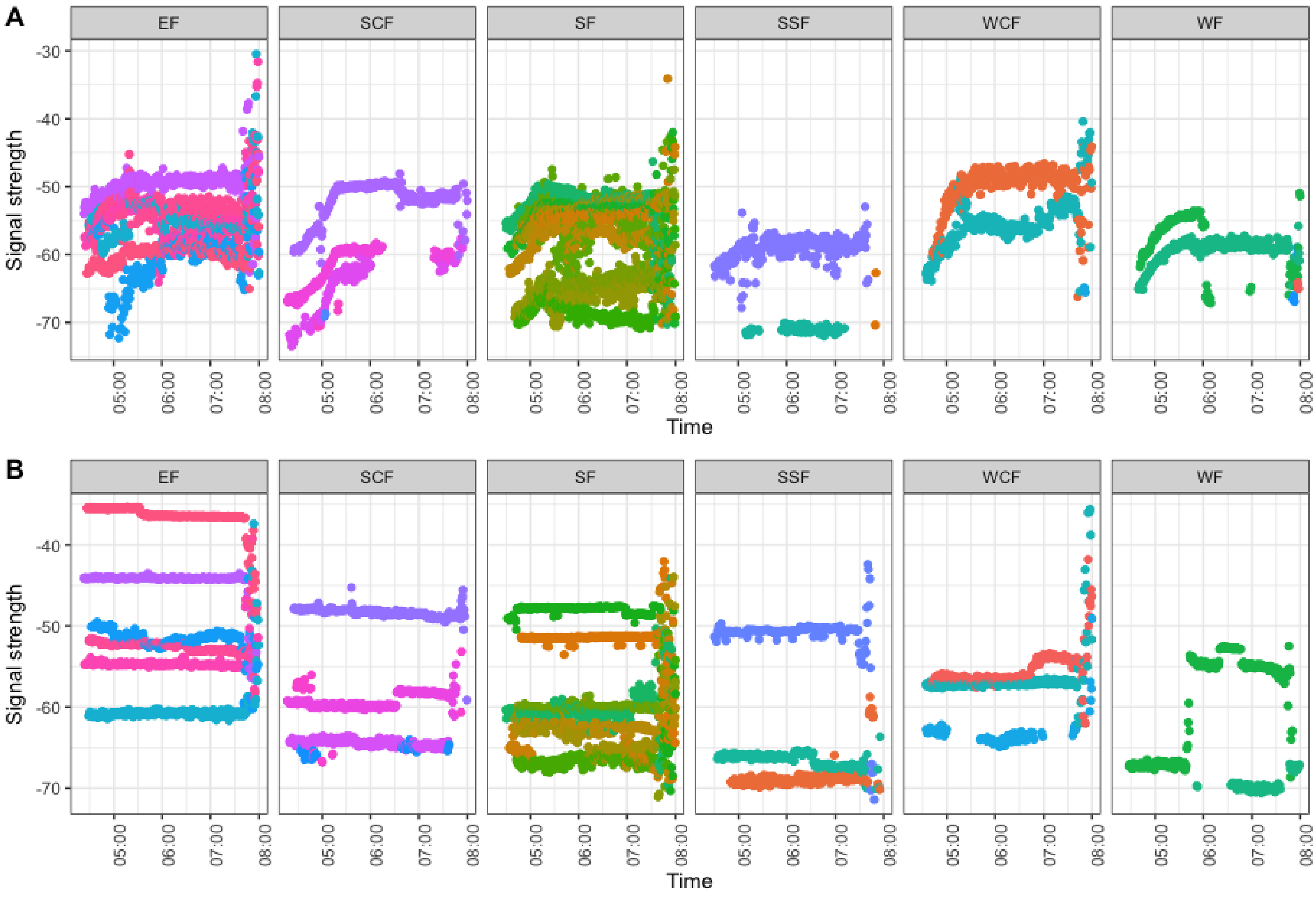


Figure 4. 2 Examples of early morning activity of six flocks from Winter 2016 demonstrating different levels of restlessness in signal strength (dBm) on two consecutive days: Jan 16 (**A**), and Jan 17 (**B**).

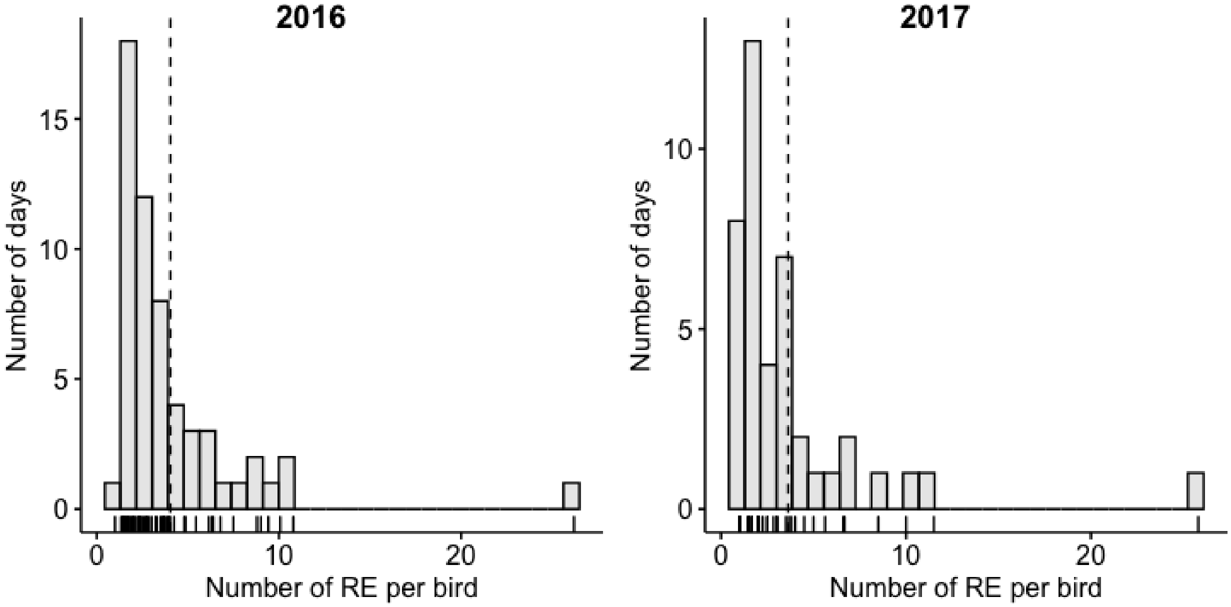


Figure 4. 3 Seasonal histograms for both winters of total number of days of restlessness events per bird

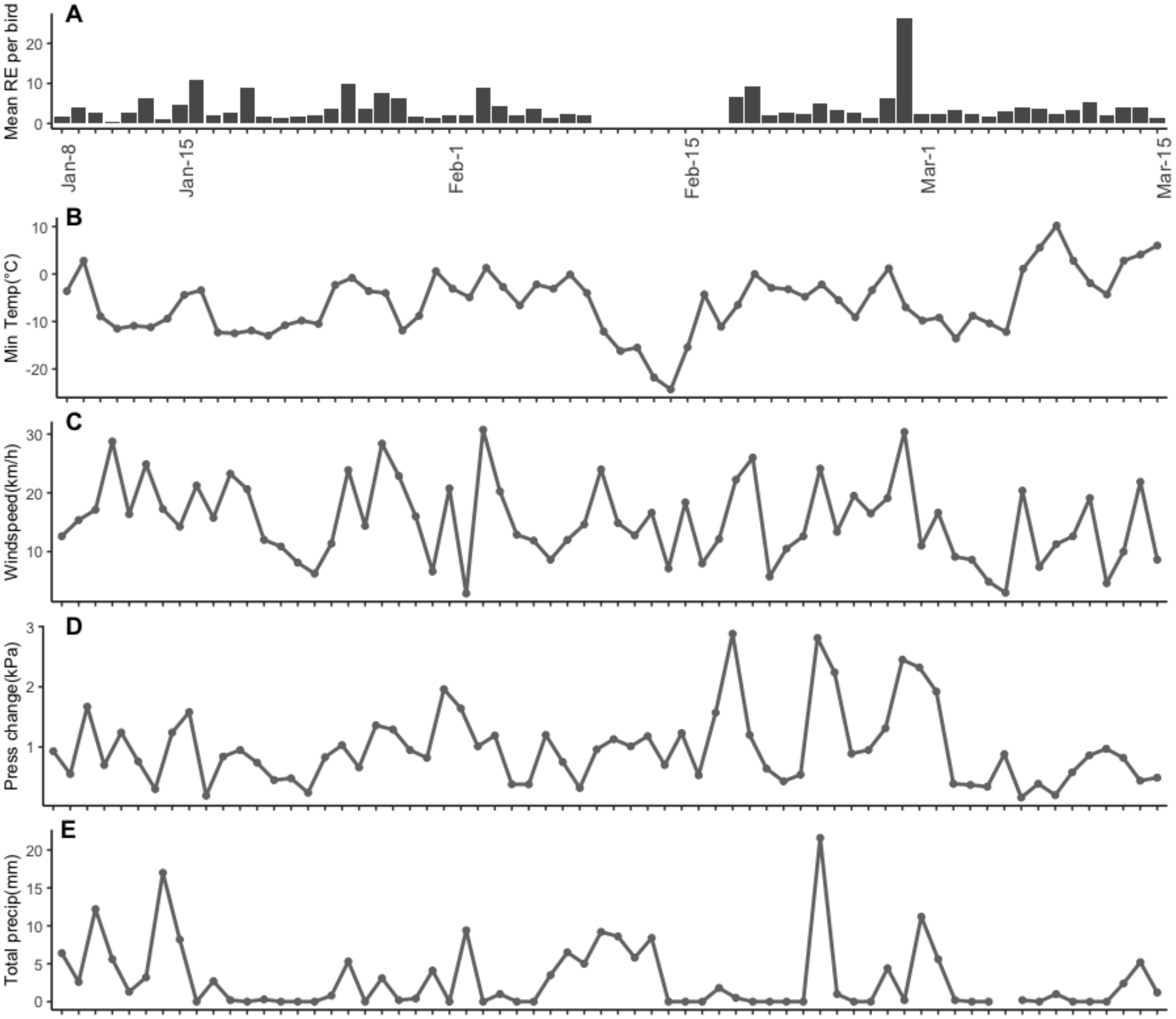


Figure 4. 4 Mean number of restless events (RE) per bird (**A**), Minimum temperature (**B**), Average early morning windspeed (**C**), Daily pressure change (**D**), and Total precipitation (**E**) for the 2016 Winter season.

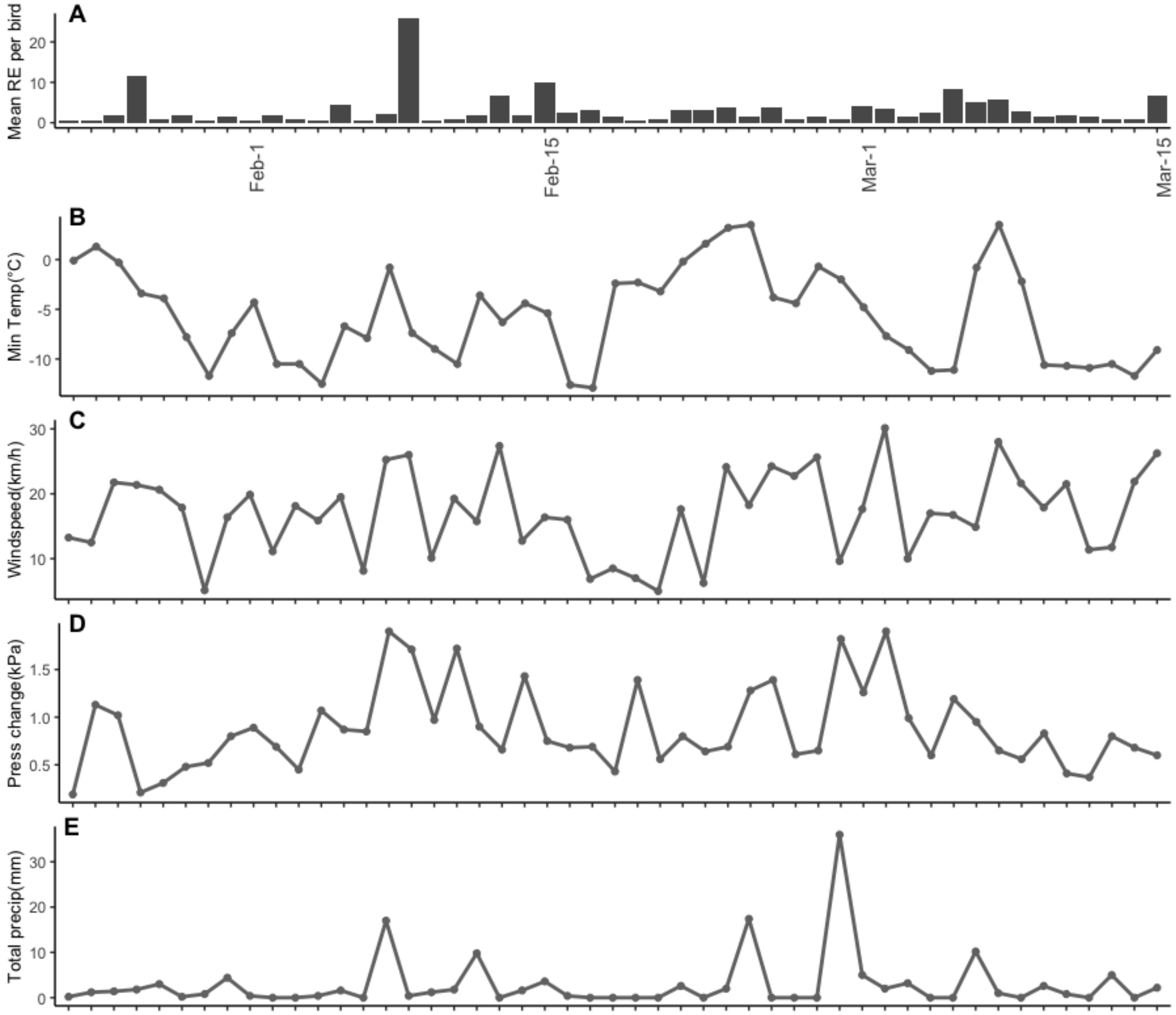


Figure 4. 5 Mean number of restless events (RE) per bird (**A**), Minimum temperature (**B**), Average early morning windspeed (**C**), Daily pressure change (**D**), and Total precipitation (**E**) for the 2017 Winter season.

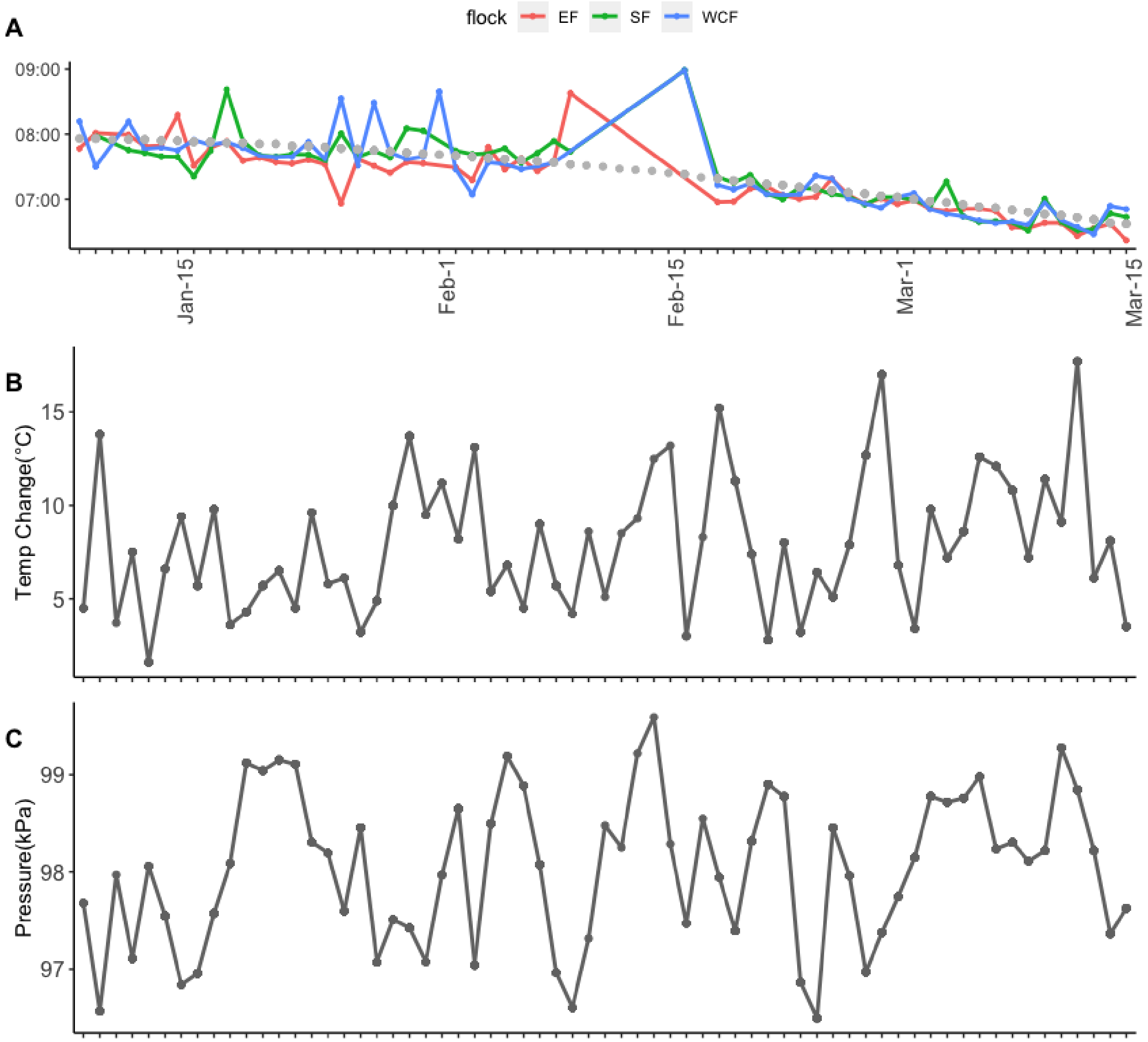


Figure 4. 6 Onset of activity for three representative flocks (**A**), Temperature change (**B**), and Average daily pressure (**C**), for the 2016 Winter season.

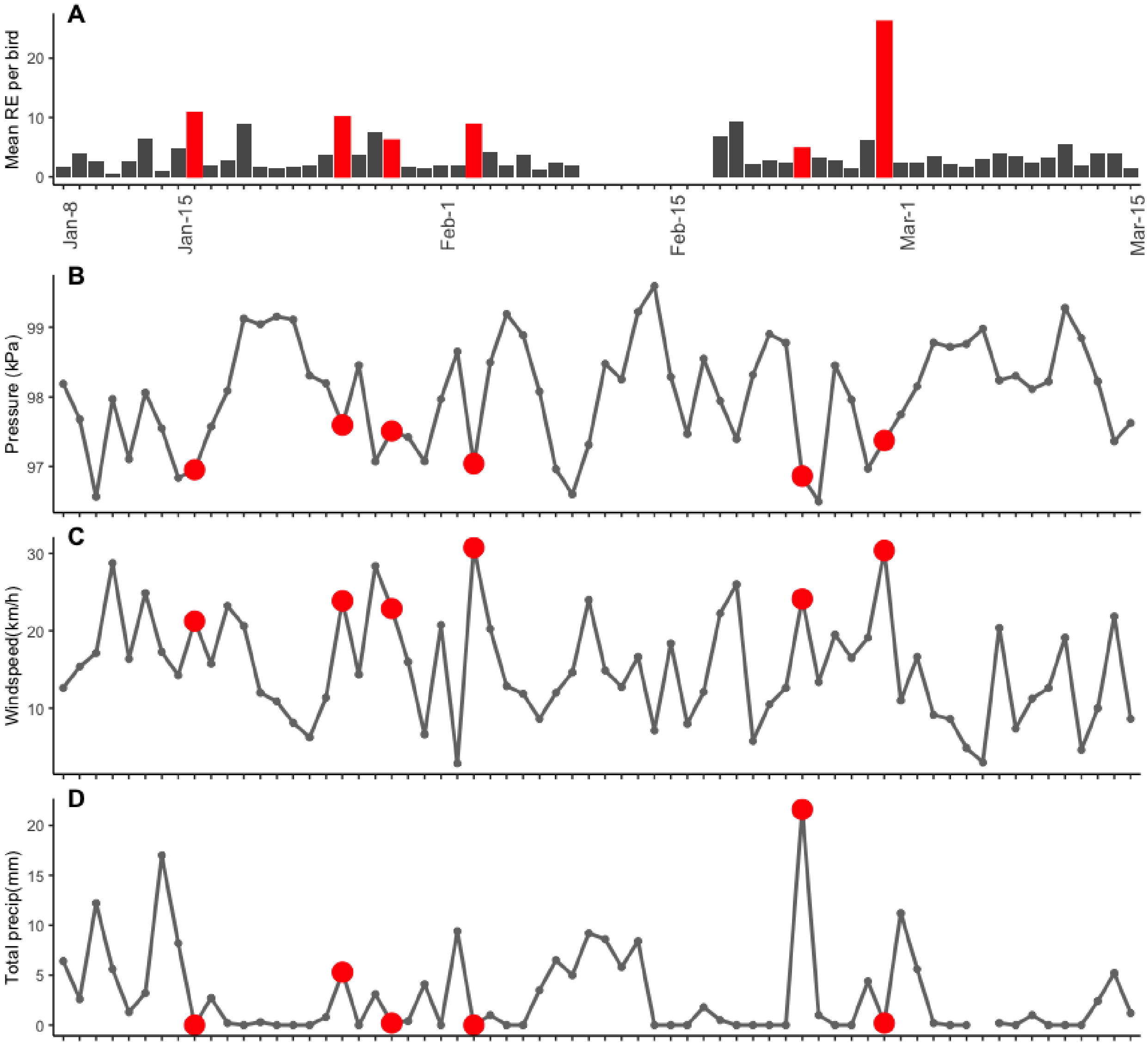


Figure 4. 7 Mean number of restless events (RE) per bird (**A**) and corresponding environmental variables of interest (**B-D**) for Winter 2016. Storm events are indicated in red.

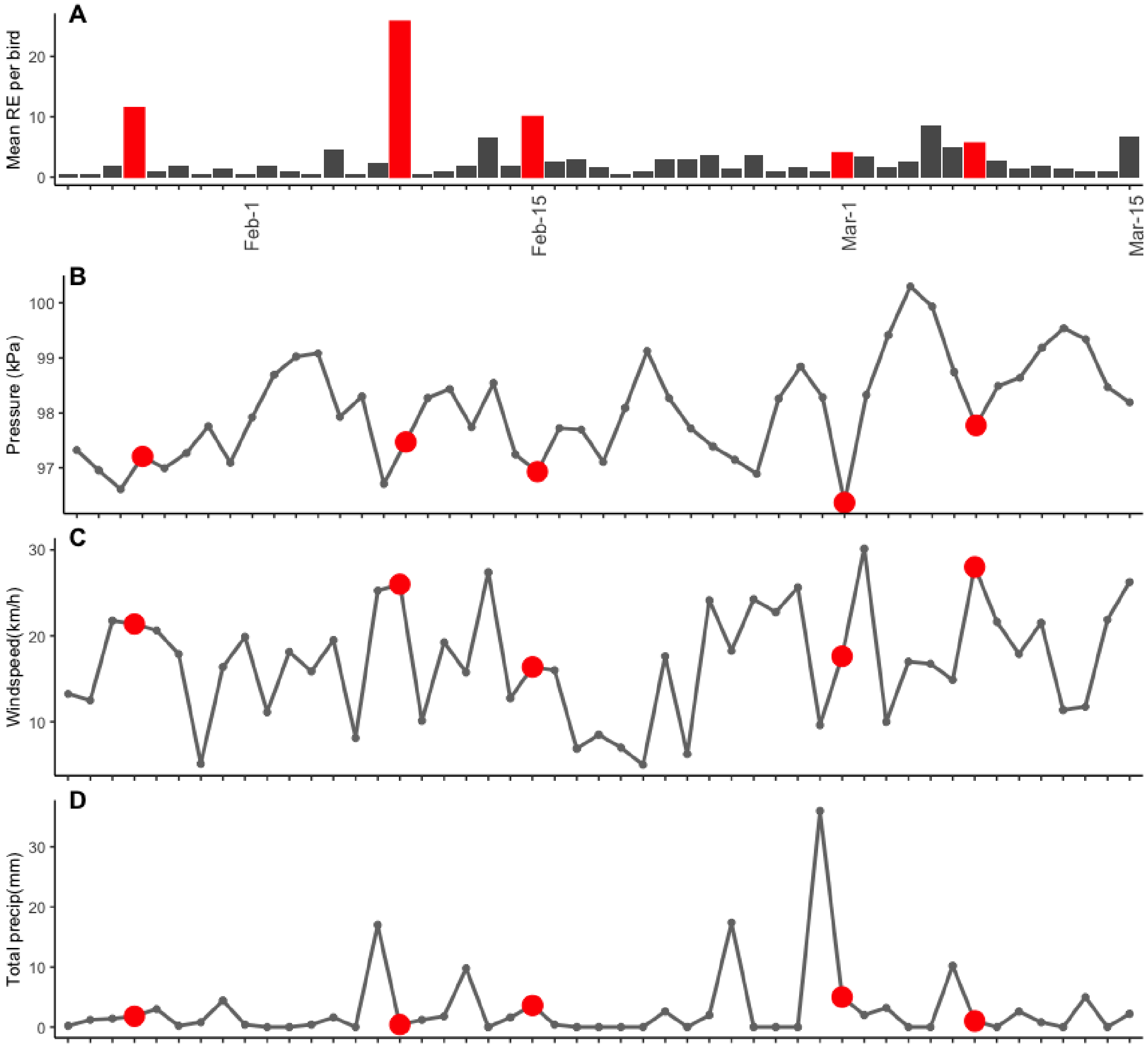


Figure 4. 8 Mean number of restless events (RE) per bird (**A**) and corresponding environmental variables of interest (**B-D**) for Winter 2016. Storm events are indicated in red.

4.4 Discussion

4.4.1 Advancements in tracking techniques

While radiotracking studies typically measure spatial patterns, temporal and behavioural studies are much less common (Dominoni et al., 2017), due in part to not being able to distinguish different behaviours using signal strength alone and therefore the need to rely on general activity level estimates (Adelman et al., 2010). However, because tagged animals at rest produce a characteristic 'flatline' of signal strength variance, this provides for an ideal baseline control to observe any behaviour occurring during this time, allowing for example, onset of activity to be directly studied (Greives et al., 2015, this study Chapter 3), or more generally, rhythmic behavioural cycles (Steiger et al., 2013). Filtering activity at signal strength variances of +/- 2 dBm before sunrise, make it possible to track sleep disturbances for studies investigating the environmental impacts on sleep, the fitness consequences of sleep, and could be extended to studies examining nocturnal restlessness. Currently, these types of experiments are 'semi-natural' – requiring enclosures and additional measuring devices (Dominoni et al., 2017; Eikenaar et al., 2014; Mueller et al., 2012; Raap et al., 2015), but this method may provide a simple and less intrusive alternative to study these behaviours directly in the wild.

4.4.2 Early morning behavioural responses to environmental conditions

In general, early morning windspeed had a significant effect on restlessness for both winter seasons. The majority of mornings of high restlessness (>10 RE per bird) occurred in cases of windspeeds of approximately 20 km/h and over (Figure 4.4). Increased windspeeds are known to increase heat loss in birds even at lower speeds < 10km/h (Mayer et al., 1982; Mayer, 1979). In laboratory studies, chickadees roosting at night are known to respond to increased windspeeds by increasing metabolic rate, which is typically accomplished by the hypothermic state (Mayer et al., 1979). However, when birds are exposed to temperatures of -10°C, and moderate winds >7.3 km/h in laboratory conditions they do not survive (Mayer et al., 1979), indicating that the hypothermic state is ineffective at high winds at maintaining metabolic rate. However, metabolic rate can also be increased by shivering thermogenesis and/or activity thermogenesis (by up to 3-5 times) which have found to be roughly equal in terms of heat production, meaning that a chickadee engaged in these behaviours is producing heat by alternate methods than the hypothermic state. This would explain why high winds are consistent with restless behaviour – as birds need to increase metabolism, but may not be able to do so via facultative hypothermia at high windspeeds.

As predicted, minimum temperature was positively related to restlessness, which suggests that on colder nights birds tend not to be as restless. This agrees with Mueller et al. (2012) study that found low temperatures to increase the length of sleep-wake cycles in free-living blue tits in winter. In addition to increasing sleep-wake cycles, lower temperatures are known to induce facultative hypothermia in chickadees, a metabolic state which results in lower energy expenditure, but impairs motion (Brodin et al., 2017). This suggests the decreased activity on cold mornings are due to either increased sleep-wake cycles and/or facultative hypothermia.

But what happens on cold and windy nights? Since the hypothermic state is ineffective in these conditions (Mayer et al., 1979), I would expect the highest degree of restless behaviour. This explains why the highest rate of restlessness (>20 RE per bird) for both seasons occurred when windspeeds were >20 km/h and temperatures were approaching -10°C, and suggests that in poor environmental conditions, activity thermogenesis is more effective than facultative hypothermia.

I also found total precipitation and snowfall to have a negative relationship on early morning restlessness, meaning that on mornings with higher precipitation, birds have decreased restlessness. This is consistent with the observation that precipitation increases roosting behaviour in chickadees (Kennedy, 1970).

I observed restlessness to vary between individuals (even of the same flock), which is typically the case on mornings of moderate restlessness (RE>5,<10), where some individuals are more restless than others (Figure 4.1). It is possible that individual variation in roosting restlessness could relate to roosting position, as a position further out on a branch would be more susceptible to the elements. While I suspected that there may be a rank effect to restlessness, especially considering that individuals of higher ranks typically outcompete lower ranks in terms of spatial resources like breeding and foraging territories (Ratcliffe et al., 2007), but found that rank had no effect in the model, meaning that regardless of rank birds are equally susceptible to early morning restless. Since resting behaviours in wild parids have been found to vary between individuals (Caorsi et al., 2019), it is possible that differences in restlessness behaviour also depend on the individual. This might account for some of the differences of REs that I witnessed at least in times of moderate restlessness, in that some individuals could be hypothermic and others more active as a way to compensate for heat loss. While birds tend to react similarly in the most extreme conditions, moderate winter conditions may represent different behavioural strategies of maintaining metabolic rate (Figure 4.1).

4.4.3 Response to winter storms

I observed 11 winter storm events over the two seasons which occurred during the early morning period and were characterised by the low pressure, moderate to high winds and precipitation consistent with Canadian winter storms (Taylor et al., 1993). Winter storms provided an interesting combination of our environmental variables of interest and resulted in high levels of restlessness (>10 RE per bird) for 4 of these storms and 5 in which there was moderate restlessness (5<RE<10 per bird), and 2 of the storms resulted in very high restlessness (>20 RE per bird; Figures 4.7;4.8). Since these storm events are related to seasonal peaks in early morning restlessness, and higher pressure changes and higher windspeeds were found to increase restlessness, I take this as evidence of a winter storm response in my population of black-capped chickadees. This finding is corroborated in laboratory experiments which demonstrate that birds respond to storm-simulated low pressures with increased movement (e.g. hops and restlessness) and feeding behaviour via a stress response (Boyer & MacDougall-Shackleton, 2020; Metcalfe et al., 2013). Since the amount of signal variation I observed in restless birds is between inactive and fully active, this resembles a restless or hopping bird which is more evidence that the behaviour I tracked is a stress response to storm conditions.

In addition, onset of activity was negatively related to pressure, indicating that low pressure events result in later onset of activity. This makes sense in the context of winter storms (a low pressure event) because if birds are indeed more restless during storms, onset in the morning is delayed, suggesting that birds may ‘sleep in’ to recover from the restless events. This has been reported in birds experiencing nocturnal restlessness (Fuchs, et al., 2006), and indicates by another behavioural measure that storms do in fact cause restlessness which impacts sleep. Conversely, the relationship between pressure and onset of activity also suggest that during days of higher pressure, onset of activity should be earlier. This was observed (Figure 4.6), and considering that birds behaviourally respond to changes in barometric pressure (Metcalfe et al.,

2013) and that high pressures are typically related with increases of bird activity, such as migratory departure flights (Elkins, 2005) suggest that higher pressures are indicative of fair weather and thus foraging can commence early. In addition, temperature change was negatively related to activity onset, indicating that larger daily temperature changes resulted in earlier onset of activity. A sharp decrease in winter temperature would therefore result in earlier onset of activity of chickadees in this dataset. This is consistent with findings that demonstrate a flexibility in parid foraging strategies such that in colder winter conditions foraging peaks are earlier in the day (Pitera et al., 2018).

If birds are showing a storm stress response, what specific behaviours are they engaged in? Typically, stress responses of birds to winter storms include: increasing foraging behaviour to build reserves (Kelly & Weathers, 2002), shivering thermogenesis (Dawson et al., 1992), and movements to sheltered areas (Kelly, 2001). To help survive winter nights, chickadees burn their fat reserves meaning that in the early morning period are close to starvation (Pravosudov et al., 2003), meaning that if a winter storm passes at this time, the need for food intake would be considerably higher. However, because winter foraging birds require post-sunrise light levels to forage (Kacelnik, 1979), it is very unlikely they could be foraging at the time I observed restlessness (3:00AM – 6:00AM). While cache retrieval typically occurs in the early morning (Brodin, 2007) and would be beneficial in this sense, this also seems unlikely for the same reason.

Considering that even moderate winds (<10 km/h) increase heat loss in parids (Mayer et al., 1982; Mayer, 1979), the high windspeeds of winter storms (>20 km/h) are a substantial threat to roosting chickadees. Since chickadees can increase their metabolic rate by activity and/or shivering thermogenesis, it is possible the restless episodes I observed are either of these behaviours.

Finally, chickadees could be behaviourally responding to storm condition and/or windy conditions by finding a more suitable roosting position, or moving to a cavity, which is a known response of chickadees to extreme conditions (Mayer et al., 1982; Smith, 1991). This behaviour is possibly identifiable in the flock radio-profiles during a winter storm on Jan 16th, 2016 (Figure 4.2). In this case multiple birds display a gradual increase in signal strength indicating movement toward the tower, which is immediately followed by a relatively stable (though still restless) position. Presumably, these were movements to safer positions, possibly a cavity or a more protected roosting position.

4.4.4 Social responses to environmental conditions

Is there a flock response to environmental conditions? Because response varied individually on different winter mornings, it was expected that flocks may also reflect such variation. Flock was significantly related to restlessness, but Tukey's post hoc test revealed that while most flocks did not differ from each other, the EF flock showed more early morning restless events than the other flocks for both seasons. Interestingly, the EF flock also had the earliest onset of activity of all flocks for both seasons (Chapter 3). It is possible that these two responses are related. Because small birds in winter burn energy reserves during cold nights, the risk of starvation is greatest in the early morning (McNamara et al., 2016; Pitera et al., 2018). In flock EF, which generally had higher rates of early morning restlessness, this suggests these birds have less reserves than the other flocks, and therefore require an earlier foraging onset to compensate for this loss.

Radiotracking studies have revealed that birds typically roost as flocks or communal groups in trees within the winter territory (Dhondt et al., 2007; Romano, 2018), and furthermore that while birds do change roosting locations throughout the season, they often reuse the same tree for months at a time (Kerstupp et al., 2015). In chickadees which typically endure cold night temperatures while roosting, it has been hypothesized that birds may huddle together for warmth (S. M. Smith, 1991). All of these suggest that roosting occurs in a social context, and that flocks may respond to environmental conditions as a group. The raw flock radioprofiles do reveal that in cases of winter storms flock-mates may react together. In the example of the winter storm on Jan 16, 2016, members of all flocks show a distinct 'bend' in their signal strength which occurred over an hour (4:30AM-5:30AM) which appears to be synchronized in the flock (Figure 4.2). This movement is interesting because it occurs over a much longer period than a simple roost reposition (see above), and therefore take this as evidence as a synchronized flock effort to seek a more protective roost position. Since storm-related shifts in movement have been observed in groups of birds (Kelly, 2001), and chickadees flocks are both highly synchronized and important for survival (Hogstad, 1989) in the winter, it is likely that in times of extreme weather stress a synchronized storm response may benefical. Regardless of how exactly flocks behaviourally respond, it is most important to note the fact that there is a flock-level storm response and one that indicates that flocks are not sleeping in the early morning hours during winter storms.

Chickadees and other winter food-storing birds are particularly at risk for the negative effects of sleep deprivation (Roth et al., 2010). These results indicate a new dimension to this problem, since harsh environmental conditions (e.g. windy conditions and winter storms) result in increased restlessness in the early morning. Birds are known to respond behaviourally to environmental temperature and pressure changes and our results indicate that morning restlessness, and changes in onset of activity are also reflected in these contexts. While it is not known exactly what a restless bird is doing, the important finding is that extreme winter conditions often produce a behavioural state which is neither sleeping nor hypothermic for a number of hours (Figure 4.2). These consequences on sleep-deprivation are furthered by the fact that in simulated winter storm experiments, birds are pushed past their ability to physiologically and metabolically compensate when storms occur twice a week (Boyer & MacDougall-Shackleton, 2020). Considering that I observed 5 instances of two winter storms occurring in the same week (Figures 4.7;4.8) and that winter storms are predicted to increase via climate change (Ulbrich et al., 2008; Yin, 2005), this represents a substantial increase of environmental stress on a bird already ‘living on the edge’ (Pitera et al., 2018).

These novel findings indicate that automated radiotelemetry is effective at tracking sleep disturbances and can quantify restlessness and possibly indicate facultative hypothermia and social roost changes. These methods provide a simple way to investigate restlessness in completely free-living birds during known rest periods, which could have important applications to Motus or other automated radiotracking studies.

There has been a clear effect of climate change on bird populations, but the mechanism of the effect and which groups are most susceptible have not reached consensus (Knudsen et al., 2011). Migratory birds in particular are often used as indicators of climate change, but due to the large travel distances, and the multiple environments they interact with make it difficult to tease out the effect of particular environmental cues (Gregory & Strien, 2010; Mason et al., 2019; James & Abbott, 2014). More ‘bottom-up’ approaches including field studies with resident birds and controlled lab studies have revealed clear fitness consequences of specific climate change factors, including spring temperature and phenology of egg-laying (Visser et al., 2003), and decreased energy stores in birds exposed to simulated winter storms (Boyer & MacDougall-Shackleton, 2020; Metcalfe et al., 2013). Additionally, I demonstrate that automated radiotelemetry can be used to study individual responses to environmental conditions consistent with winter storms in real time, directly in the field. This suggests the 'little birds in winter' may be suitable climate change indicators especially with regards to increases of extreme weather events due to climate change.

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Chapter 5

Daily activity patterns of the little bird in winter

5.1 Introduction

5.1.1 The concept of dominance

In many social animals, the position in a dominance hierarchy is correlated to behaviour, physiology, personality, reproductive fitness, habitat use, and many other factors (Creel 2001; Ekman & Askenmo 1984; Fox et al. 2009; Schubert et al. 2007; Lewden et al. 2012; Ratcliffe et al. 2007). While dominance patterns are argued to be essential in understanding social structure and behaviour, ‘dominance’ is poorly defined (Hand, 1986; Rowell, 1974) which poses a problem to its functionality as a concept. A synthesis of different perspectives yields that dominance is a pattern of interactions between two individuals which results in a predictable unidirectional outcome—there is consistently a ‘winner’ (dominant) and a ‘loser’ (subordinate) (Drews, 1993). Dominance is therefore a relative trait, and not a strategy, since individuals in a dominance hierarchy are simultaneously dominant and subordinate to others in the group, and rank changes are common. This definition has a higher descriptive value than others (Rowell, 1974; Hand, 1986) in the sense that it can be applied to broad range of social groups.

5.1.2 The social group

In many social groups, hierarchies are arranged linearly such that the alpha individual at the top is dominant over all individuals of the group, the beta is dominant over all except the alpha and so on (Chase & Seit, 2011). High-ranking dominant individuals are often larger, more aggressive and older than those of lower ranks (Chase & Seit, 2011; Smith, 1991; Tsuji & Tsuji, 2005) and maintain their position by aggressively excluding subordinates from higher-quality resources and access to mates, resulting in survival and reproductive fitness skewed in their favour (Lloyd & Rasa 1989; Richards & Course 2015). Why, then, do subordinates stay in dominance-structured groups? Simply, they should stay when the benefits of living in a group outweigh the costs of living alone. While group benefits such as increased foraging time, predator protection and survival (Olav Hogstad, 2014; S. M. Smith, 1991) have been found, estimating all individual net benefits to a subordinate can be complicated (Clutton-Brock, 1998). Some ideas have been proposed, however, that can explain why subordinates remain in a group. First, subordinates can gain a dominant position —and thus the benefits this position incurs— through either usurpation, death of the dominant, or waiting in a queue. This hopeful dominant hypothesis has gained support by researchers examining a variety of animal groups (Alberts et al., 2003; Bridge & Field, 2007; Ekman & Askenmo, 1984) and also explains the potential benefits of waiting behaviour in subordinates. A second hypothesis is that dominants and subordinates, while occupying different roles, may ultimately obtain similar levels of fitness in instances where the costs of being dominant are high. In other words, being dominant may not always be best. Considering that rank does not always predict reproductive success in the long-term (Alberts et al., 2003; Schubert et al., 2007) and that dominants fight more, spend more time searching for intruders (Olav Hogstad, 1986), have higher rates of metabolism (Bryant & Newton, 1994; Hogstad, 1987; Metcalfe et al., 1995) and can have higher levels of stress-related hormones (Creel, 2001)—the costs of being dominant can be quite high. Additionally, subordinates may obtain indirect benefits from the dominant's presence such as experience, Hogstad (1984) showed that subordinate birds in flocks with a dominant had higher survivability than flocks with the dominant removed. Ultimately, the benefits of being dominant may still outweigh the costs in most instances, but fitness differences between dominants and subordinates may be less stark than was originally thought (Lewden et al., 2012; Schubert et al., 2007), which provides indirect support for why subordinates stay in dominance-controlled hierarchies.

5.1.3 Winter daily activity in Parids

For parids, the low temperatures, low availability of food, and little daylight characteristic of winter present a real challenge to survival. Small birds have higher metabolic requirements in cold temperatures and need to build energy reserves to survive cold winter nights (Pravosudov et al., 2001). This greater need for resources is further complicated by the shorter days, which reduce potential foraging time to require food. As a result of a variable food supply, many parids such as chickadees and some species of tit have adapted to cache food for later retrieval (Lucas & Walter, 1991; D. F. Sherry, 1984). This serves to reduce the unpredictability of resources, save on energy daily energy expenditure—since resources are stored in the environment rather than the body, and finally provides a reliable food source at the end of the day to build reserves to survive the night. This means winter foragers should optimize their foraging schedules such that they cache food early in the day and retrieve it later in the day (bimodal activity) which has theoretically evolved as a response to starvation avoidance (McNamara et al., 1990; 1994). To test this in the field, Pitera et al. (2018) compared foraging schedules in flocks of mountain chickadees in variable winter ‘harshness’ conditions by recording RFID tagged chickadee at two different elevations. Chickadees in harsher conditions showed the distinct bimodal foraging schedule as predicted in McNamara (1990; 1994), while those in less harsh conditions showed an inverted ‘U’ pattern with the highest activity occurring in the middle of the day. This study provides an excellent example of how using automated tracking technology provides direct evidence of selection pressure while also illustrating the importance of factoring environmental variables into behavioural field studies. The important limitation here, however, is that this and other RFID feeder studies (Aplin et al., 2012; Farine et al., 2015) are limited to the foraging context alone (Evans & Morand-Ferron, 2019) and thereby exclude all other behaviours and contexts which flocks of birds experience, meaning that a complete daily activity pattern of individual birds in winter flocks in a natural context is still largely unknown. Since much of what is known of winter bird activity in the field is based on observations from feeders (Aplin et al., 2012; Boisvert & Sherry, 2000; Evans & Morand-Ferron, 2019; Farine, Firth, et al., 2015; Herborn et al., 2014; Hogstad, 1988; Pravosudov & Lucas, 2000; Ratcliffe et al., 2007; Smith, 1991), radiotracking the general activity pattern in free-living birds is therefore a worthy pursuit, as this will effectively test if activity at the feeder is reflective of activity away from the feeder.

5.1.4 Rank activity

It is likely that daily activity patterns of birds within winter flocks are rank dependent, which comes from a number of studies that have observed consistent rank-related behavioural differences in a number of contexts. Since dominant individuals are known to consistently displace subordinates from safe and profitable foraging patches (Desrochers, 1989; Ficken et al.,1990), subordinates are forced to explore more, which increases temporal and energetic costs, and puts them at a greater predation risk (Barta & Giraldeau, 1998; Desrochers, 1989; Fox et al., 2009). While in these areas of high predation risk, subordinates spend more time being vigilant for predators (Ekman, 1987) and are more likely than dominants to both make alarm calls, and to respond to them (Rajala, et al., 2003; Zanette & Ratcliffe, 1994), making dominants much less conspicuous under threat of predation. Dominants further exploit subordinates through scrounging, by displacing them from newly found food sources – more often discovered by subordinates – essentially using them as ‘food-finders’ (Hegner, 1984; Stahl et al., 2001). Considering the costs of being subordinate, it is not surprising then, that there is a positive relationship of rank and winter survival (Desrochers et al., 1988).

In response to being excluded from preferred resources, subordinates likely face higher daily energetic demands. In order to offset these costs, subordinates respond by foraging earlier in the morning, and later in the evening than dominants (Lahti et al., 1997), thereby increasing their daily duration of activity to offset the increased need for energy. Additionally, it has been proposed that in an effort to increase energy stores subordinates should cache more than dominants (Pravosudov & Lucas, 2000), but, the opposite trend has been found (Boisvert & Sherry, 2000; Hitchcock & Sherry, 1995; Pravosudov et al., 2003). This contradiction may in part be due to the fact that dominant-subordinate pairs were used, which does not reflect a natural linear hierarchy (Chase et al., 2002). It is also important to note that chickadee flocks rarely consists of just two birds (S. M. Smith, 1991), meaning that pair-wise dominant studies are not reflective of a natural flock of birds. For these reasons, examining daily activity in natural flocks of individually tracked chickadees could provide a new perspective about activity and social dominance in more natural and socially appropriate context.

5.1.5 Black-capped chickadee hierarchy

Black-capped chickadees form linear hierarchies in the fall and are maintained throughout the winter season until flock break-up in spring (Smith, 1991). Dominants aggressively exclude subordinates from preferred resources, resulting in fitness outcomes that are generally skewed in their favour (Table 1). However, dominants are unable to fully control group reproduction which means that flock-mates are in control of their own reproductive output and compete with one another to maximize individual reproductive fitness (Schubert et al., 2007; S. M. Smith, 1991). While being dominant clearly seems to be a favourable position, investigations from the subordinate’s perspective are needed to fully understand social structure.

The major factors that influence rank in black-capped chickadee flocks are age, sex, size and seniority. First, older male chickadees are dominant over younger males (Otter et al.,1999;

Smith, 1991) though this does not occur in females (Ramsay & Ratcliffe, 2003). Second, while males typically dominate females, field observations of flock-mates becoming mated pairs, combined with 1:1 flock sex ratios, suggest that males and females are likely paired *prior* to breakup of the winter flock— meaning that a flock should be considered a hierarchy of pairs (S. M. Smith, 1991). In other words, a flock of six is really three *pairs*: an alpha, beta and gamma.

Automated radiotelemetry has been used to successfully record individual activity patterns (Adelman, et al., 2010), as well as onset of activity (Greives et al., 2015, Our study Chapter 3) and provides an effective means of tracking flocks of individual free-living birds in a natural context (Chapter 2). While the above discussion centred around subordinates having a more active role than dominants in a number of behavioural contexts, another view is that ‘it is expensive to be dominant’ (Hogstad, 1987). Dominants have been found to have higher basal metabolic rates (Hogstad, 1987; Roskaft et al., 1986), sing earlier and for longer periods (Otter et al., 1997), cache more (Hitchcock & Sherry, 1995; Pravosudov et al., 2003) and have more aggressive encounters (Ratcliffe et al., 2007). While rank accounts for many differences in activity patterns in specific contexts, which rank expends more energy on a daily basis throughout the winter is still unknown, especially as there has been no attempt yet to record general activity levels on free-living birds in the field over a full winter season. Therefore, I hypothesized that there would be rank-related differences in daily activity of individuals in flocks, but that direction of effect was unclear.

Because lower ranks are forced away from foraging sites by dominants (Desrochers, 1989), cache further away from food sources than dominants (Lahti et al., 1998), and explore more than dominants (Stahl et al., 2001), I expected a seasonal difference in terms of spatial use in the territory. I predicted that lower ranking birds would be more often found further from the flock centre than higher ranking birds.

Theoretical modelling has predicted a bimodal daily foraging pattern in winter birds, that exists to maximize energy gain in situations of possible foraging interruption (McNamara et al., 1994). These findings have partial field support in a RFID feeder study, but only in populations of high environmental harshness (Pitera et al., 2018). However, since the sources of foraging interruptions in winter (e.g. predation), are theoretically consistent in all winter conditions

(McNamara et al., 1994), I predicted that general activity in free-tracked birds would show a bimodal pattern.

5.2 Methods

5.2.1 Rank assessment

Ranks were assessed using methods described in Chapter 2.

5.2.2 Statistical methods

To determine if lower ranks were more often found further away from the flock's centre than higher ranks over the winter season, I first calculated each flock's centroid per season. This was done by running an LDA for each flock for each day of both winter seasons, and then taking the mean centroid. The Euclidean difference was then calculated from each individual daily position from this flock centrepoint.

In order to determine general daily activity of the three ranks, I first calculated the proportion of active birds per rank. To do this, the number of birds that had signal strength variances of +/- 4.0 dBm were divided by the total numbers of birds in each rank. Similarily to Adelman et al. (2010) I used 30 mins ranges to calculate the proportion of active birds.

To compare rank differences of daily activity I used a General Additive Model (GAM) approach. GAMs are similar to General Linear Models (GLMs), but with the added ability to add smoothing terms to the model which flexibly addresses non-linear data, making them both common in ecological studies and suitable with data in time-series (Pedersen et al., 2019). GAMs can also be used with random effects, making it convenient to effectively address any conditions of non-independence, which in this case is Bird ID. To compare the difference between ranks I used a method for comparing smooth functions similar to Rose et al. (2012). I used the s(time, by=rank) function, which estimates a separate smooth for each level of rank. Difference of rank levels of activity is computed by comparing the smooths to a reference level, which is low rank curve in this case. Since proportion of birds active was non-normal and the Poisson model did not converge, I used a negative binomial model which converged successfully. This was the model structure:

$$m \leftarrow PorportionActive \sim Rank + s(time) + s(time, by = Rankclass) + s(BirdID, bs="re"),$$
$$method = 'REML'$$

All statistics were analyzed using R version 3.6.2 ‘Dark and Stormy Night’. I used the *mgcv* package in R to run the GAM models.

5.3 Results

I detected no differences between the distance to seasonal flock centroid of the three rank classes for both winter seasons. This result did not change when distances to flock centroids were analyzed per month (Figures 5.1;5.2). When viewed on an individual level, distances to flock centroids allows for a visual tracking of general seasonal movement patterns of the different ranks. (Figures 5.3;5.4).

The general activity of all ranks for both years were multi-modal in shape, with peaks at the beginning and end of the day (Figure 5.5). In winter 2016, low and middle ranks had significantly different curve shapes, while low and high ranks were not different (Table 5.1). When activity levels were compared, both high and middle ranks were significantly higher than low ranks at the end of the day, and high ranks were significantly less active than middle ranks in the morning, but more active than mid ranks in the afternoon (Figure 5.6). In winter 2017, both middle and high ranks had significantly different activity curves when compared to low (Table 5.1). There were no differences however, in amount of activity between the ranks (Figure 5.6).

Table 5.1 Differences of rank GAM curves using the low rank as reference comparison for both seasons.

Winter	*Rank*	*Edf*	*Ref df*	*Chisq*	*p*
2016	mid	1.8	2.3	25.7	<0.001
	high	2.0	2.5	3.5	0.33
2017	mid	2.1	2.6	20.8	<0.001
	high	5.9	7.0	44.2	<0.001

Edf – Effective degrees of freedom, Ref df – Reference degrees of freedom for hypothesis testing

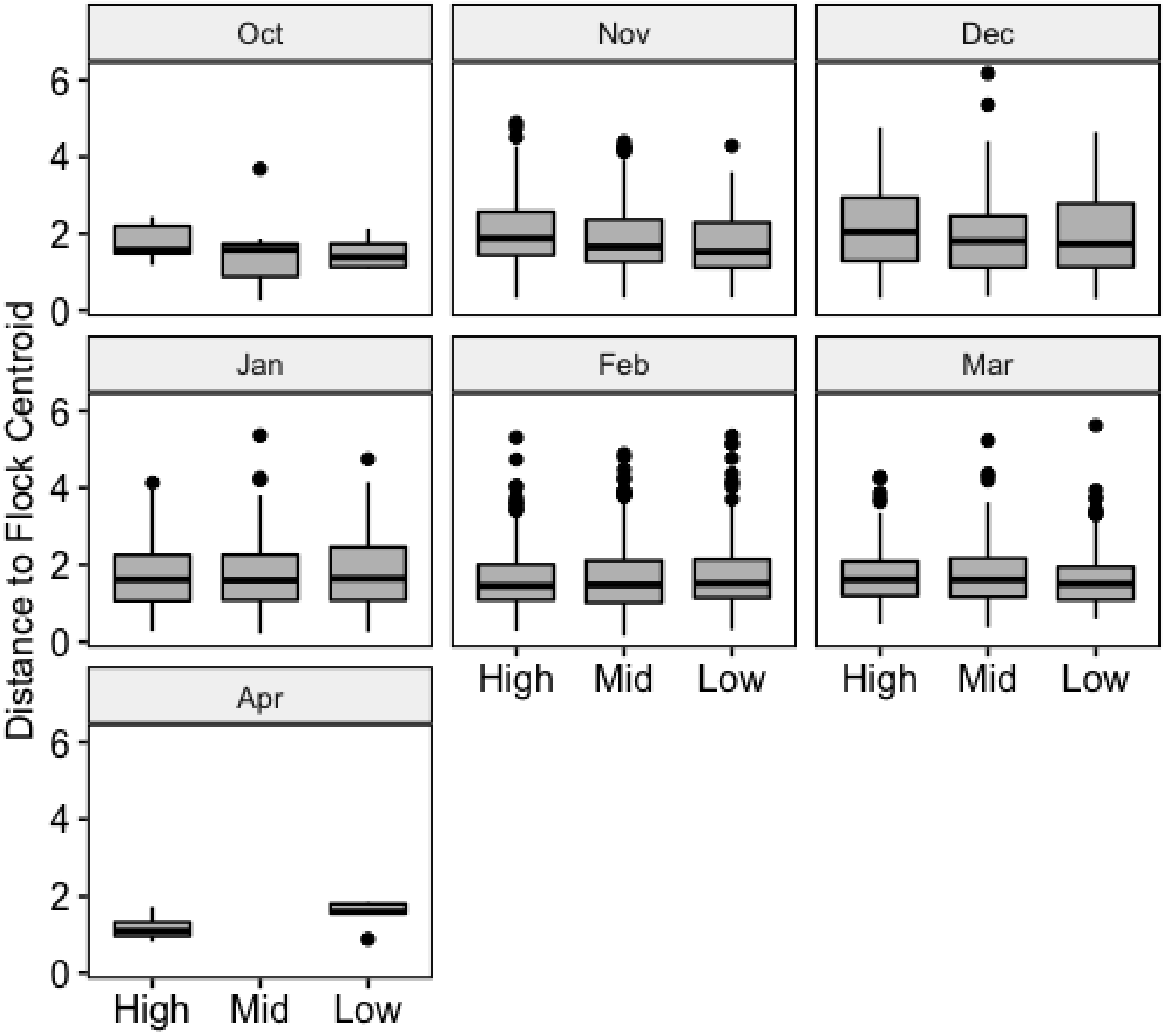

Figure 5. 1 Mean distance to seasonal flock centroid grouped by rank, for the 2016 winter season.

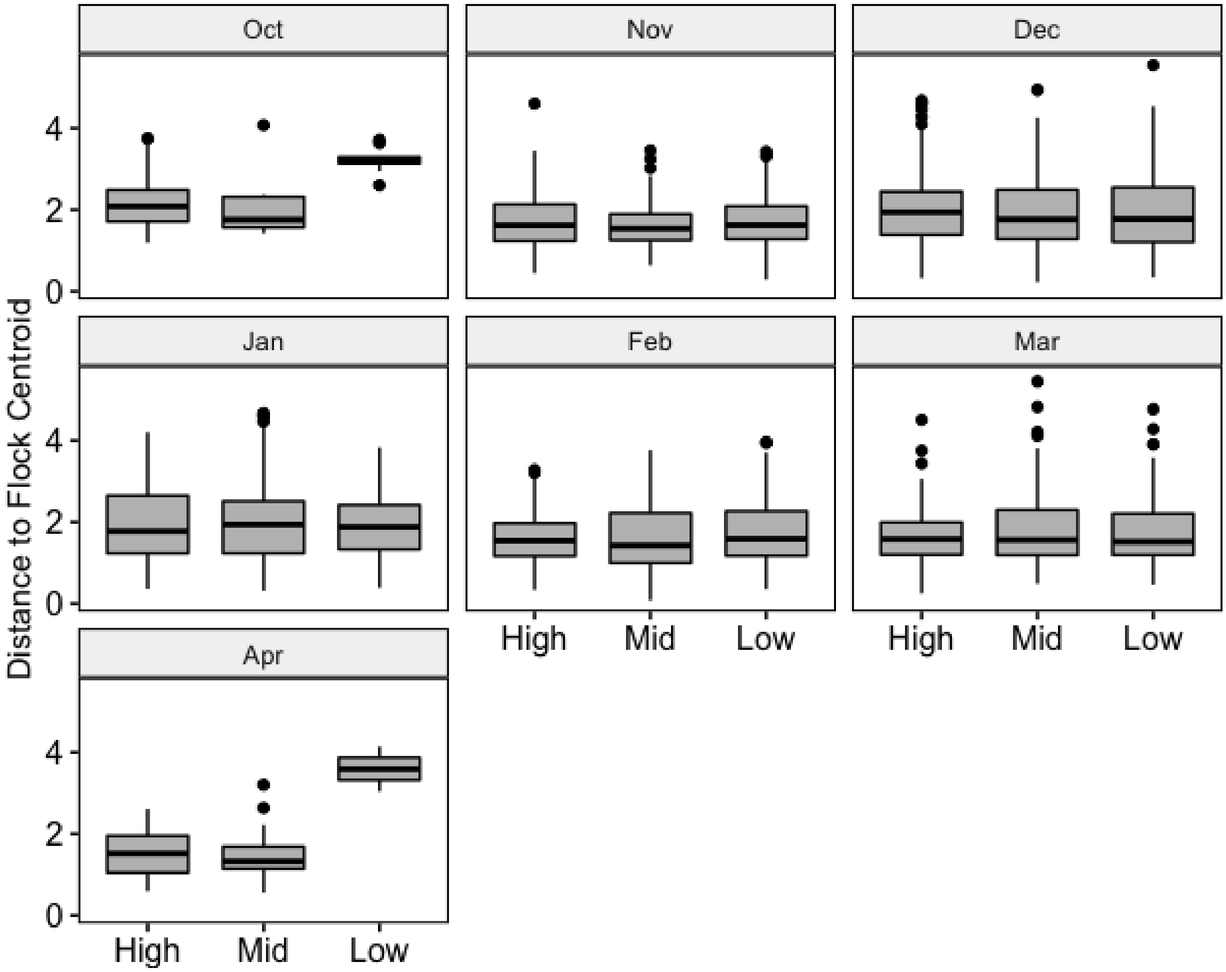

Figure 5. 2 Mean distance to seasonal flock centroid grouped by rank, for the 2017 winter season.

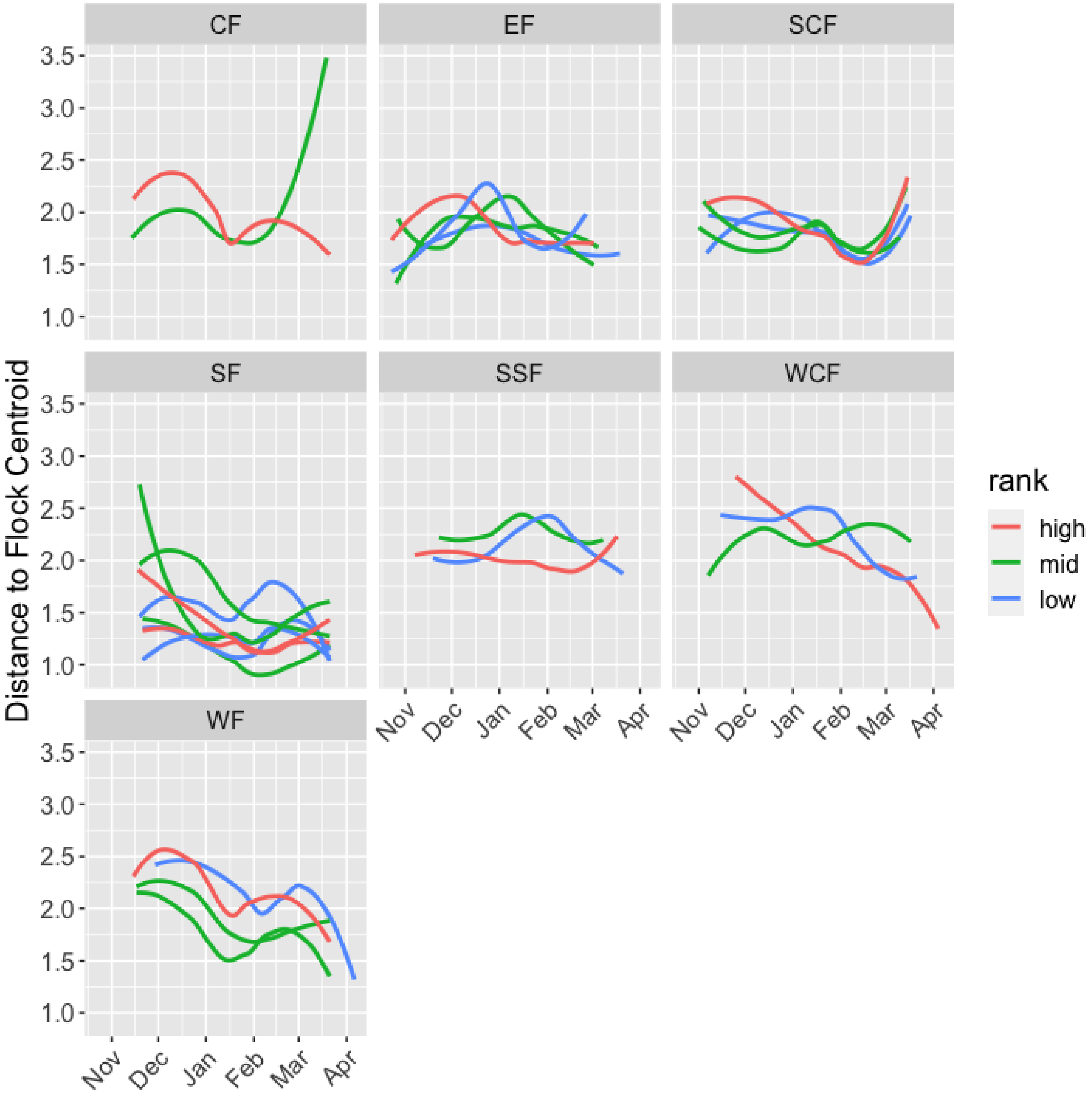

Figure 5. 3 LOESS smoothing of distances to flock centroids of ranked individuals per flock for winter 2016.

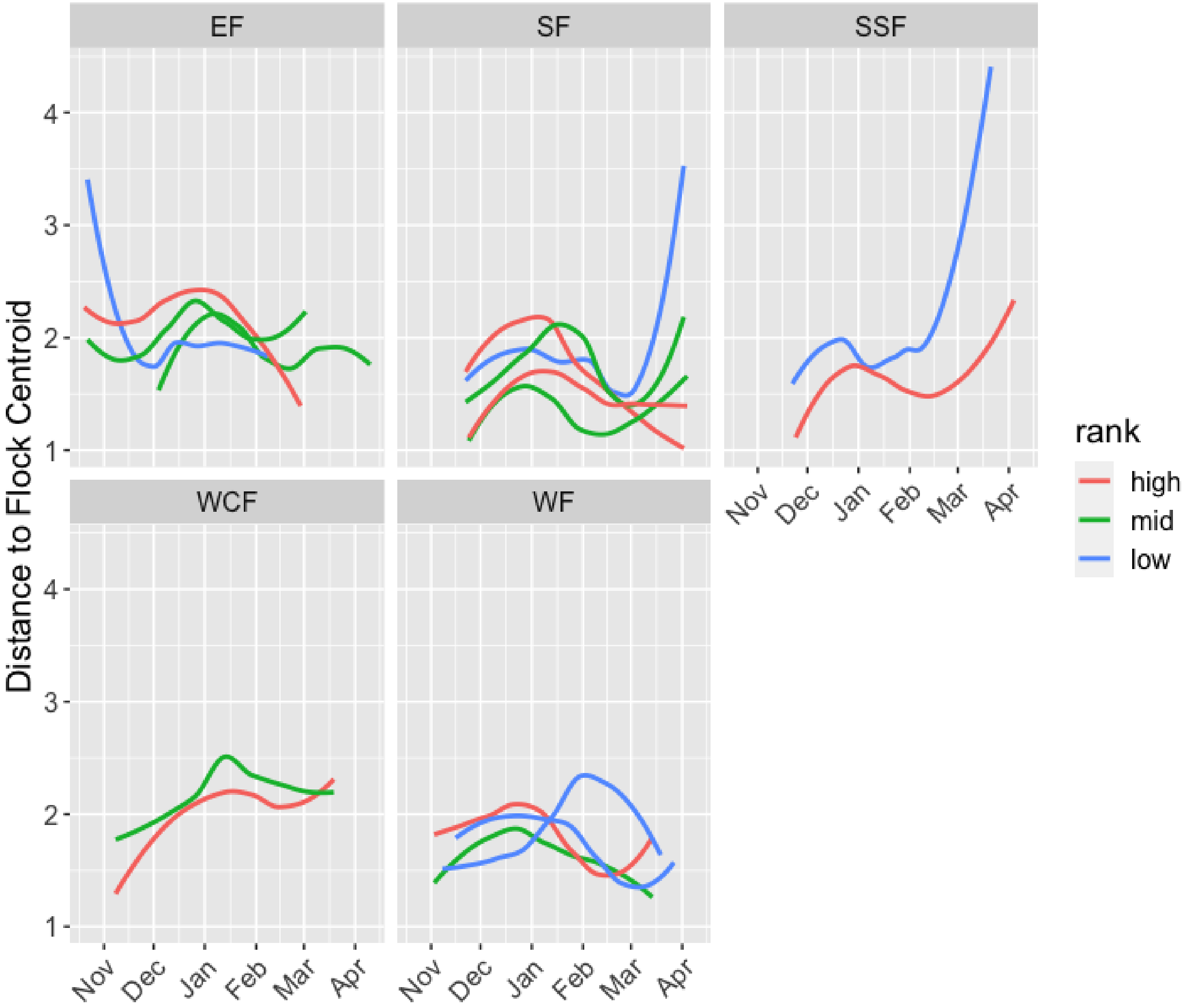

Figure 5. 4 LOESS smoothing of distances to flock centroids of ranked individuals per flock for winter 2017.

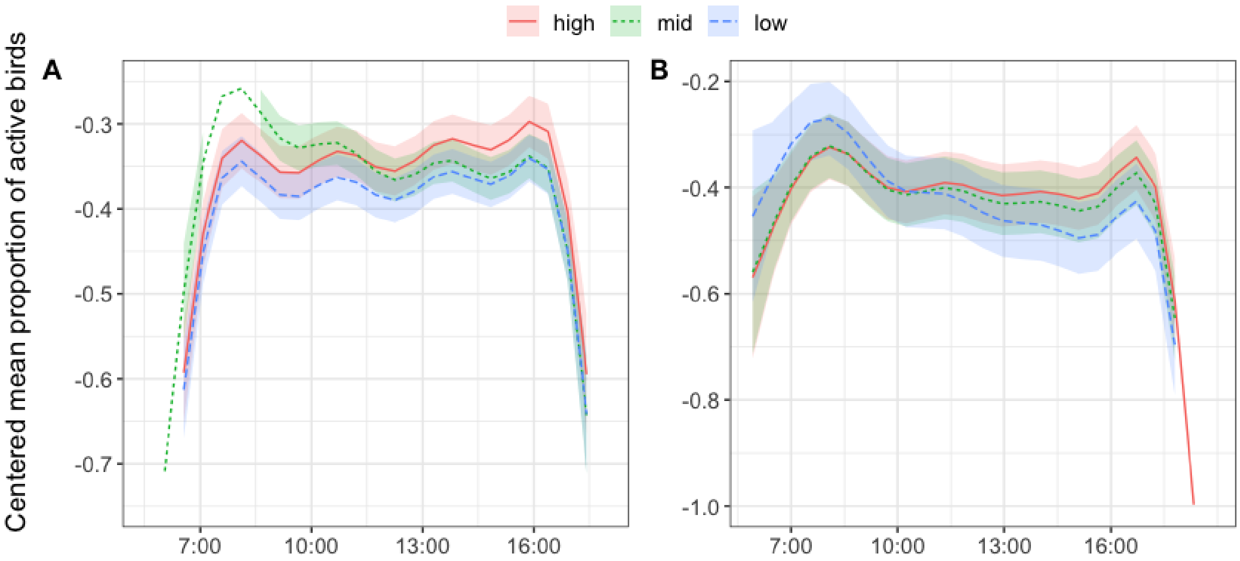

Figure 5. 5 Centred GAM smooths of mean proportion of active birds per 30 min periods, per rank, for winter 2016 (A) and 2017 (B).

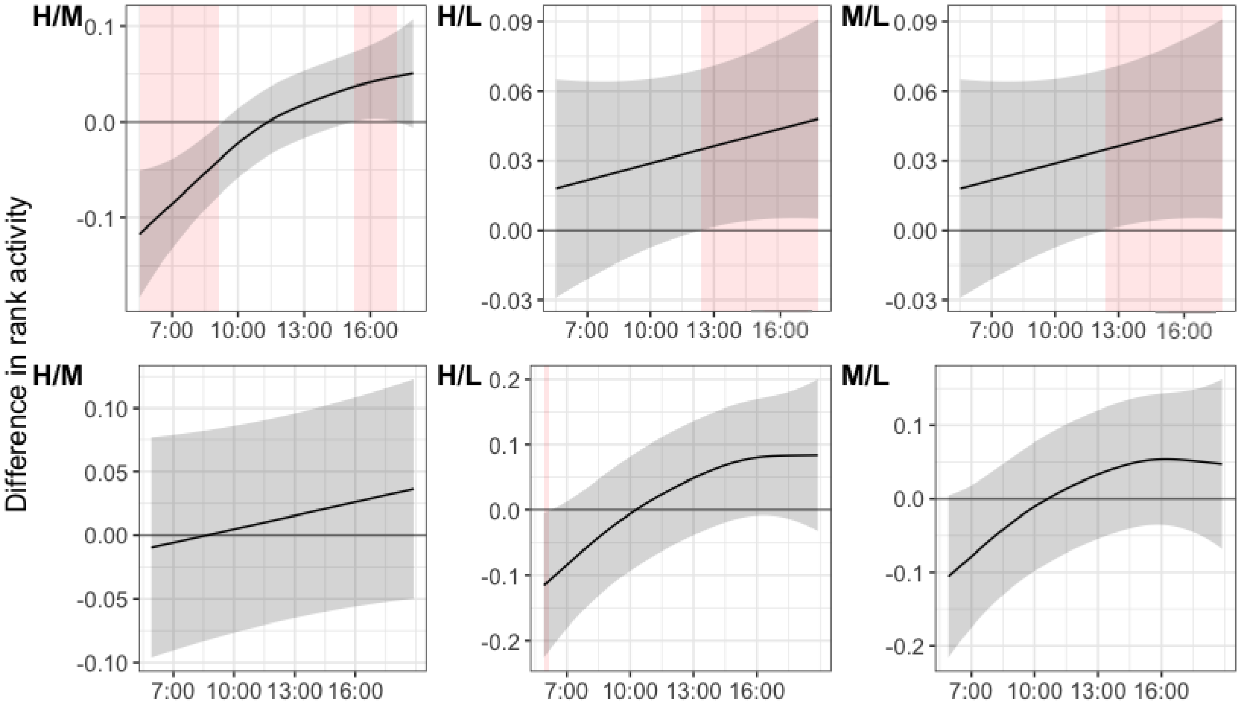

Figure 5. 6 Difference of GAM smooths of rank activity for winter 2016 (top row) and 2017 (bottom row). Significance is indicated in red.

5.4 Discussion

5.4.1 Seasonal spatial patterns of ranks

Contrary to my hypothesis, I found no rank-related differences in space use relative to the flock's seasonal centre in either field season. This pattern was also mostly consistent when distance to centroid per rank was examined on a monthly basis as well. Considering that I used data from all flock-mates for the entirety of the season to calculate a single centroid per flock, this 'flock centroid' may actually more appropriately be an estimate of the centre of the flock's territory. The lack of rank-dependent distance to centroids indicates that, regardless of rank, all birds of a flock moved within the same space of the territory centre meaning and likely remained a tightly cohesive group in their territory for the duration of the winter, which is consistent with field records (S. M. Smith, 1976). Because rank-related differences in spatial use have been observed at a microhabitat level—on different regions on a tree; (Desrochers, 1989) and caching locations relative to a feeder (Lahti et al., 1998), it is probable that the spatial resolution was too large to detect these kinds of patterns.

While no rank-related patterns were observed during the winter, the distance to flock centroid approach may be more useful at the end of the season. After fission occurs in the spring, the highest-ranking (alpha) pair typically occupies the centre of the winter territory which becomes their breeding territory (Glase, 1973). Interestingly, in April, I observed lower ranks moving away from the flock centroid, and higher ranks moving toward the centre which agrees with field observations. While it should be noted that loss of reception of tags started in late March, this still provides some support that a distance to centroid approach using radiotelemetry data is a possible way to measure individual differences in spatial use in a territorial context.

Using flock-mate distance to seasonal flock centroids also provides a novel way of visualizing how general flock structure changes through the social season, allowing the movements of individual birds (e.g. away/towards flock centrepoint) to be examined, offering a degree of 'social precision'. I contend that because this satisfies the conditions of long-term, simultaneous individual, and group-level data on a spatio-temporal scale (Silk et al., 2014), this represents a novel way to examine fusion-fission dynamics in real time, in a full environmental context. While most of what is known of fusion-fission dynamics is based on theoretical modelling (Aureli et al., 2008; Couzin & Krause, 2003). To better understand fusion-fission dynamics a field approach that collects high resolution data on individual and group-level movements is needed. Automated radiotelemetry data can address this need and furthermore be used to address specific social hypotheses. As an example, tracking rank movements in this manner has shown that while in some cases high ranking birds do move to the centre of the territory at the end of the winter as is predicted, others leave earlier (Figures 5.3;5.4), suggesting this is not always the case. Another potential application to this method is to study how flocks fuse in black-capped chickadees and other parids, which is poorly understood (Ratcliffe et al., 2007; Schubert et al., 2008). While this would require birds to be tagged earlier in the fall, how fusion occurs could be examined this way, especially since fission was successfully identified in this study, which is essentially the opposite of fusion. At least in a few instances in this dataset (WCF flock in Figure 5.3), I observed more flock-mate separation before January, at which point flock-mates get much closer together, which I expect would be an example of what flock fusion would look like earlier in the season.

5.4.2 General activity patterns

McNamara et al. (1990;1994) demonstrated that winter birds should maximize energy reserves while avoiding foraging interruptions, resulting in a bimodal activity pattern. These activity peaks represent an optimal ‘cache early and retrieve later’ response in order to avoid starvation. This model has received some field support in a RFID study with mountain chickadees, in which a bimodal foraging pattern was observed at feeders in populations at high elevations, but not low elevations (Pitera et al., 2018). Since McNamara et al. ‘s (1994) model predicts that the bimodal activity pattern should persist in situations regardless of environmental variation or food supply, I predicted I would observe bimodal activity patterns in flocks of black-capped chickadees. Instead, I observed multi-modal activity patterns with morning and afternoon peaks of activity (Figure 5. 5).

My approach of assessing general daily activity is unique in the sense that this the first automated radiotelemetry dataset which tracked freely living flocks of birds openly in the field for the entire duration of the winter. My findings support McNamara’s model in two important ways. Firstly, it supports the theoretical importance of the dawn and dusk periods of increased foraging activity, as these peaks are present when general activity was examined. In other words, if it is indeed optimal to increase foraging effort in the dawn and dusk periods, than it would be expected that these peaks would be identifiable not just in a foraging context, but across all contexts, which explains why the dawn and dusk peaks are visible on a scale of general activity. Secondly, since all activity was included from full winter seasons, this helps to support the McNamara's et al. (1994) prediction that the dawn and dusk peaks of activity is robust against seasonal variation, as overall, these peaks were consistent within and between both winter seasons.

These results also help to corroborate different methodologies in studying activity in the field. It is promising that using automated radiotelemetry analysis – namely, a signal strength variation of +/- 4.0 dBm to assess the proportion of birds active over time – agrees with the results from both a dynamic modelling approach (McNamara et al., 1990, 1994) and a RFID feeder foraging study (Pitera et al., 2018). This additionally provides an example where studying behaviour in the field using feeders is an accurate representation of what occurs away from the feeder, which is a current issue in field studies which use automated tracking technology (Evans & Morand-Ferron, 2019).

5.4.3 Rank differences in activity

In general, activity curves showed consistent rank-related differences, with the exception of the high and low ranks in winter 2016. Considering that the low ranks were significantly less active than high ranks during the evening peak, I interpret this as ranks having the same general activity pattern, but of differing amounts of activity. Ultimately, for both seasons and for the three ranks levels, general activity was rank-specific. While other field experiments have also found rank-related activity differences, these are often constrained to the level of dominants and subordinates (Desrochers, 1989; Lahti et al., 1997,1998). Because the hierarchy is linear and flocks rarely consist of two individuals (Smith, 1991), a two-level approach to flock structure is likely not representative to how all subordinates behave. The middle and low ranks (which would typically be grouped together as subordinates), demonstrate differences in activity, suggesting the importance of separating rank levels as much as possible.

In terms of amount of activity, high ranks tend to be less active in the morning, and more active in the evening. Conversely, the middle and lower ranks tend to be more active in the morning and less active in the evening. This trend was consistent in both seasons, though no significant differences of between rank activity were detected in winter 2017. Considering that the second season had 53% less birds than the first, it is likely that the sample size had an effect on the observed rank differences.

What behaviours could be occurring in this measure of general activity? It is important to note that since my measure of activity is fully automated, and occurs across all contexts, it is difficult to tease out exactly which behaviours are occurring throughout the day. That being said, it is very likely that the dawn and dusk peaks of general activity represent foraging effort. This is due to the optimal strategy of ‘cache early and retrieve later’ of starvation prevention which has been supported both in winter birds in dynamic modelling (McNamara et al., 1990, 1994) and in field as well (Lahti et al., 1997; 1998; Pitera et al., 2018). Therefore, the dusk peak represents retrieval, in which previously cached food is consumed in order to provide energy stores to sustain the birds overnight, while the dawn peak represents increased foraging and caching to provide resources for the following night. The dawn peak also coincides at the point where energy stores are lowest, meaning some retrieval of food caches occurs in order to prevent starvation. Due to the fact that it is energetically expensive to carry large energy reserves throughout the day (McNamara et al. 1990), these retrievals likely account for a much lower proportion of the dawn peak foraging effort than caching behaviours.

In this optimal view of foraging effort, my results suggest an interesting rank-difference in that middle and low ranking birds are more active than high ranks in the dawn peak and less active than high ranks in the dusk peak – suggesting that lower ranks cache more, while high ranks retrieve more. Since lower ranks are actively excluded from preferred foraging sites, their food resources are more unpredictable and therefore should respond with a higher foraging effort to maintain higher energy reserves than dominants (Brodin, 2001). While the opposite trend is typically found (Pravosudov et al., 2003; Pravosudov & Lucas, 2000; Hitchcock & Sherry, 1995), my data suggests that the higher activity peak of lower ranks may represent increased this expected foraging effort in the morning. Furthermore, this increases support to the finding that rank-related differences of foraging effort depend on the time of day (Boisvert & Sherry, 2000).

During the dusk peak, the opposite occurs in that high ranks are more active than lower ranks, which suggests that high ranks retrieve more. Considering that high ranks are structurally larger, have larger pectoral muscles (Lewden et al., 2012; Smith, 1991), and tend to have a higher basal metabolic rate, more reserves would be required to sustain their body condition, meaning that it is ‘expensive to be dominant’ (Hogstad, 1987). This would explain why higher ranks tended to have a higher retrieval rate.

This is the first study to my knowledge to track general daily rank activity patterns of multiple flocks of undisturbed black-capped chickadees through the winter. While this measure makes it difficult to know exactly what behaviours are occurring, the rank-specific activity results do suggests a temporal separation in activity peaks may be an important part in the maintenance of the hierarchy, and provides an additional evidence to both how subordinates remain in flocks of high resource competition.

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Chapter 6 – General discussion

Almost all social groups undergo the same processes. Groups begin to form (or undergo fusion) when interactions between conspecifics begin to stabilize, often taking the form of a dominance hierarchy, which reduces aggressive interactions and maintains group functionality (maintenance). Once stabilized, the group is cohesive and many behaviours (e.g. navigation, predator evasion) are completed with members acting in unison. Social groups are adaptive, since group members have increased benefits often in the form of predation reduction and increased foraging efficiency (Conradt & Roper, 2005; 2003). Eventually, group conflict rises to the point that the costs of being in a group outweigh the benefits (e.g. the breeding season) and the group undergoes fission, only to re-fuse when conditions again favour group-living (Silk et al., 2014). The processes of: Fusion, Maintenance, Cohesion and Fission are so ubiquitous that they are referred to as the social principles and are not only integral to group functionality, but also the process of social evolution itself (Bourke, 2011).

Recent advancements in the field of animal collective movement have revolutionized our understanding of social behaviour and have provided new methods of studying sociality that was simply not possible before. Dynamic modelling has simplified complex group patterns to understandable and testable group-member interactions (Couzin & Krause, 2003; A. D. M. Wilson et al., 2015), new tracking techniques have provided the ability to study cohesion of flocks of birds in mid-flight (Nagy et al., 2010; Nagy et al., 2018) and studies combining RFID tracking and Social Network Analysis have led to discoveries including: social information transfer (Aplin et al. 2012), individual differences in social connectedness (Farine, Firth, et al., 2015a), and flock responses to flock-mate loss (Firth et al., 2017). While these studies have provided essential information of the mechanisms of social dynamics, the importance of investigating the interaction of social dynamics in natural ecological social contexts cannot be overstated. SNA studies, for example, have been scrutinized for their ‘staticness’ – as they do not incorporate the dynamic aspect of social behaviour, oversimplify what defines an animal group, and are based on limited environmental contexts (Castles et al., 2014; Farine & Whitehead, 2015; Pinter-Wollman et al., 2014).

My major objective for this dissertation was to apply automated radiotelemetry techniques to address questions spanning the major social principles: Fusion-fission, Cohesion, and Maintenance (Bourke, 2011), and I organized this work around this purpose. Birds of the family *Paridae* are an excellent candidate in which to marry animal collective movement and automated radiotelemetery, as they typically do not migrate, but instead overwinter in flocks which occupy ranges which are well suited for automated tracking (Aplin et al., 2012; S. M. Smith, 1991). In temperate birds, social behaviour is strongly concentrated in the non-breeding season (Helm et al., 2006), making it the ‘key’ to understanding bird social behaviour (Boucherie et al., 2019) and highlighting the value of automated tracking studies which track multiple flocks of birds throughout the winter season to the fields of: collective animal movement, automated radiotelemetery and social evolution.

The major limitation of this work is the ability to extract various social and individual behaviours from temporal variations in signal strength (radioprofiles) alone. Radiotelemetry studies have been successful in quantifying: amount of individual daily activity, represented as magnitude of signal strength variance (Adelman et al., 2010), activity onset; represented as the first signal strength change to reach an activity threshold, following rest behaviour (Greives et al., 2015a), and tracking movement patterns (Brown & Taylor, 2017; Mennill et al., 2004). A secondary goal of this work was to examine how these existing techniques could be applied in social contexts, while simultaneously exploring the possibility of developing new ways to use signal strength to study previously unexplored behaviours and/or how signal strength can be compared among group members to address social questions in a novel way.

6.1 Summary of findings and future applications

6.1.1 Flocks can be identified and tracked using automated radiotelemetry

In collective animal movement studies, the ability to relate any findings to group functionality and evolution is dependent on how the animal group is defined (Castles et al., 2014). Using single variables (such as proximity) to identify the social ties on which entire social networks are constructed can be both complicated (Farine, 2015) and problematic (Pinter-Wollman et al., 2014). In birds, this importance is even more paramount, considering that fission-fusion rates in this group are highly variable (M. Silk et al., 2014), thus making a clear and functional definition of a flock essential. Ecological definitions of flocks on the other hand, are much more conservative and stress constant and stable membership, in which group members act cohesively (e.g. fly, roost, forage) throughout the winter (Smith 1991). The environmental contexts of flocks are important, meaning a more suitable method of defining a flock would be based on a full winter's worth of movement data.

In Chapter 2, I used seasonal positional information (extracted from the signal strength of four radiotowers) from the highest ranked (alpha) individual of flocks which could be separated via Linear Discriminant Analysis (LDA). All other birds were then compared to this training set, such that each individual's daily signal strength profile was matched to the alpha it corresponded to resulting in daily flock assignments. Essentially, each alpha's seasonal signal strength was used as a proxy of its territory, and birds in that territory were considered to be flockmates. This resulted in the identification of 7 flocks in Winter 2016, and 5 in Winter 2017 and were unbiased in the sense that the flock assignments were completed by LDA rather than by visual separation of radioprofiles. All flocks were typically associated with one alpha over the season, though this method was also effective in tracking instances of flock switches or cases when birds moved into other alpha territories. This matched with previous accounts of flocking behaviour in chickadees quite well, in the sense that chickadee flocks showed stable membership with one alpha with occasional episodes of switches (Smith 1991). My results indicated that although switches were less common than individuals staying in their home territory, they occurred at a higher rate than previous work (Smith 1991) and furthermore, often involved more than one group member. This finding suggests that automated telemetry methods are more efficient than direct observational methods in quantifying flock fission-fusion events

Chapter 2 demonstrated 'alpha-matching' as a successful and novel method of flock identification and that signal strength alone can be used to isolate and track flocks effectively, while still satisfying the important ecological, temporal and seasonal contexts all of which are known to influence social dynamics. Furthermore, this method of flock identification is superior to observational methods as all flocks are simultaneously recorded for the duration of the winter season.

The most notable application of these findings are for tracking fission-fusion events in real time, directly in the field. By using LDA in combination with long-term tracking records, it is possible to not only more conservatively define animal groups than with previous methods, but in doing so be able to isolate precisely which individual is moving, when the switch is occurring and to which relative group the individual moved.

6.1.2 Onset of activity depends on flock, and is likely a group decision

Consensus decisions evolve in animal groups to reduce uncertainty in the environment and maintain cohesion (Miller et al., 2013). In the case of chickadees which overwinter in unpredictable and harsh conditions, they have evolved flexibility in foraging schedules which optimizes foraging depending on environmental condition (Pitera et al., 2018), and thereby increases survival. Because of the importance of foraging at first light to prevent starvation in parids (McNamara et al., 1994), activity synchronization of foraging would be of adaptive significance for all individuals in the flock and thereby a situation which should result in a strong flock consensus.

In Chapter 3, I tested the hypothesis that onset of activity would be different relative to sunrise between flocks which would indicate that onset of activity is determined by flock. I examined flock onset of activity through the Winters of 2016 and 2017, by using the first occurrence of a +/- 4 dBm change in signal strength which is indicative of an active bird (Adelman et al., 2010; Greives et al., 2015a) which was used to test mean flock onset compared to sunrise. Flock-specific onset of activities were suggested by the finding that seasonal onset was different between flocks when directly compared, and also when each flock's onset was compared to sunrise. Some flocks had onset of activity at sunrise, while others were later than sunrise and one flock was earlier than sunrise. Specific instances of fission-fusion events were used to further test this finding and it was found that individuals switching out of a flock had a later onset than when in the flock, while the individual that switched into a flock had an earlier onset after the switch. These instances help support the prediction that earlier onset is beneficial, and also that it is determined by flock. This method of determining onset of activity per flock is valuable in the sense that it provides a simple way of automatically measuring daily group stability and cohesion of social groups directly in the field. When used in combination of fission-fusion events the onset of activity schedule can be used together to pinpoint times of flock instability, and therefore provide a feasible method of tracking group cohesion over time and how it changes seasonally.

It is possible that habitat structure might have an affect on onset of activity of flocks and which may account for some of the variation in flock onset of activity that I observed. This would be interesting area of further study, especially considering the importance of habitat structure on social composition in bird flocks (He et al., 2019; Lantz & Karubian, 2017), Given that the study site is partially reforested with Black Walnut, White pine and Cedars and partially native mixed coniferous/deciduous, this results in unequal patches of conifers. This patchiness likely influenced roosting areas as chickadees prefer coniferous environments (S. M. Smith, 1991). Since early morning foraging is linked to light intensity in willow tits (Kacelnik, 1979), it is possible that onset of activity could be affected by differential sunlight penetration into flock territories in winter, especially in areas with higher densities of deciduous trees after their leaves were dropped.

6.1.3 Daily winter activity has distinct peaks at dawn and dusk and is rank specific.

Rank position in winter flocks of parids can explain a variety of fitness outcomes which are skewed in favour of high ranks. High ranks have larger clutch sizes, higher rates of fledgling survival (Otter et al., 1999), more extra-pair copulations (Mennill et al., 2004), access to more profitable foraging sites (Ficken et al., 1990) and have higher quality breeding territories (S. M. Smith, 1991) than lower ranked birds. Dominants actively displace subordinates from these resources, forcing them to explore more, which increases temporal and energetic costs, and puts them at a greater predation risk (Barta & Giraldeau, 1998; Desrochers, 1989; Fox et al., 2009). To offset these energetic costs subordinates increase foraging effort earlier in the morning, and later in the evening than dominants (Lahti et al., 1997). Additionally, it has been predicted that subordinates should cache more than dominants (Pravosudov & Lucas, 2000), but, the opposite trend has been found (Boisvert & Sherry, 2000; Hitchcock & Sherry, 1995; Pravosudov et al., 2003). In light of these costs to subordinates, why do subordinates join flocks at all? Part of the answer may be due to the cost of being dominant. Dominants sing more (Otter et al., 1997), have more aggressive encounters (Ratcliffe et al., 2007) and have higher metabolic rates (Hogstad, 1987; Roskaft et al., 1986) than subordinates, suggesting that ‘it is expensive to be dominant’ (Olav Hogstad, 1987).

Taken together, which rank expends more energy on a daily basis throughout the winter is still unknown, so I used known methods of quantifying activity in radiotracked birds (Adelman et al., 2010) to test the hypothesis that there would be rank-related differences in total amount of daily activity of individuals in flocks, but that direction of effect was unclear. Dynamic programming models have predicted that in response to unpredictable food sources, a daily bimodal activity pattern is optimal in winter foraging birds, but this has found limited support in the field (McNamara et al., 1994). I furthermore predicted that all activity curves would be bimodal and would reflect the theoretical investigations of foraging activity. Spatial use of ranks was furthermore expected to be different considering that subordinates are forced away from preferred foraging sites (A. Desrochers, 1989), and often cache at farther locations than dominants (Lahti et al., 1998). I tested this by first calculating flock seasonal centroids using LDA, and then calculating distance from the seasonal, and monthly rank position from each flock's seasonal centroid.

Using daily bird distance to seasonal flock centroids revealed that spatial use was not dependent on rank throughout the season, but it may be an effective method for tracking fission-fusion events. The general activity pattern of chickadees showed distinct peaks at dawn and dusk, and agreed with theoretical studies which predict that that foraging activity would peak at these times in free-living birds in the winter. Activity patterns showed rank-specific differences at the dawn and dusk peak. At dawn, lower ranks were higher than high ranks and indicated increased caching effort, while the higher activity rate of high ranks at dusk was attributed to higher retrieval rates. Both of these findings are supported by the characteristic energy budgets of dominants compared to subordinates. Overall, the temporal separation of rank peak activity provide an explanation to how the hierarchy is maintained.

6.1.4 Environmental effects

While studying the onset of activity of flocks in Chapter 3, I noticed a number of days which had early morning spikes of activity well before sunrise throughout the population over both seasons. Since these spikes often occurred in multiple individuals and flocks, I suspected this might be due to weather effects, and were possibly interrupting rest behaviour at this time. Sleep is an adaptive behaviour that is seldom studied in the field, and sleep disruptions are particularly detrimental to parids, which rely on memory to retrieve cached food (D. F. Sherry, 1984). Birds are known to be behaviourally sensitive to weather events including changes in pressure, winds and storm events (Boyer & MacDougall-Shackleton, 2020; Elkins, 2005; Metcalfe et al., 2013). Considering weather events such as winter storms are expected to increase via climate change (Ulbrich et al., 2008), I investigated the possibility of these events to cause disruptions of rest behaviour in flocks of black-capped chickadees.

To examine sleep disruptions, I applied a filter of +/- 2dBm to all birds in the early morning hours of (3:00AM – 6:00AM) to attempt to quantify restlessness. This was selected because it is below the threshold of +/- 4 dBm of an active bird (Adelman et al., 2010; Greives et al., 2015a) and above +/- 1 dBm which is generally associated to bird at rest (personal observations). I found that the number of restless events (RE) were positively related to minimum temperature, windspeed and changes in pressure. The lack of restless in cold temperatures agreed with Mueller et al. (2012) finding that colder temperatures increased sleep duration, and that increased restlessness in birds during pressure drops was also supported (Boyer & MacDougall-Shackleton, 2020; J. Metcalfe et al., 2013)**.** Furthermore, winter storms occurred during the mornings of highest restlessness and the most likely effect of this was high windspeed (>20 km/h) which was positively related to restlessness. These findings provide the first potential method for radiotracking restlessness to my knowledge, and suggest that environmental factors can cause disruptions of sleep behaviour in free-living flocks of black-capped chickadees. Finally this work highlights the potential of parids to model the effects of extreme weather events due to climate change.

In addition to being able to identify individual restlessness, I also report the possibility of tracking flock-level responses to winter storm conditions. This was considered in early mornings where a winter storm was occurring in which flocks showed a similar response involving movement in relation to a tower in a synchronized manner, possibly to cavities or to a safer roosting position. Since birds are known to respond with synchronized movement in storms situations (J.P. Kelly, 2001), this may represent another behaviour which can be effectively radiotracked – at least in terms of nocturnal responses to environmental extremes.

An additional aim of this Chapter originally was to assess whether the environmental variables of interest had any direct social implications on roosting flock-mates. Little is known about winter roosting behaviour, beyond that birds typically roost as flocks or communal groups in trees within the winter territory (Dhondt et al., 2007; Romano, 2018), and that while birds do change roosting locations throughout the season, they often reuse the same tree for months at a time (Kerstupp et al., 2015). Because chickadees which typically endure cold night temperatures while roosting, it has been hypothesized that birds may huddle together for warmth (S. M. Smith, 1991), but there are currently no methods to investigate this in the field. I created a measure

‘Relative Roost Distance’ (RRD), to attempt to quantify how close flock-mates were to each other while roosting. This was calculated by first obtaining the mean signal strength for each individual positions during the period of (3:00AM – 6:00AM) for each individual, and then taking the maximum roost position (highest SS) is subtracted by the minimum (lowest SS) of each flock to get a relative ‘space’ that was occupied by each flock and which ideally would serve as a proxy of social proximity (Figure 6.1). To compensate for flocks roosting at different positions through the field site, I selected the single antenna and tower which resulted in the highest number of hits for each flock per day before calculating RRD. This method was not included in the dissertation due to the difficulty of being able to ground truth this as a technique. Because transmitters can vary in power according to orientation, it would need to be shown in a more controlled testing environment, that RRD could be used to accurate represent flock-mate distance in a roosting position. This would be a worthy pursuit, especially since birds at rest typically provide a stable signal strength to work with and considering that no method currently exists to measure this in the field.

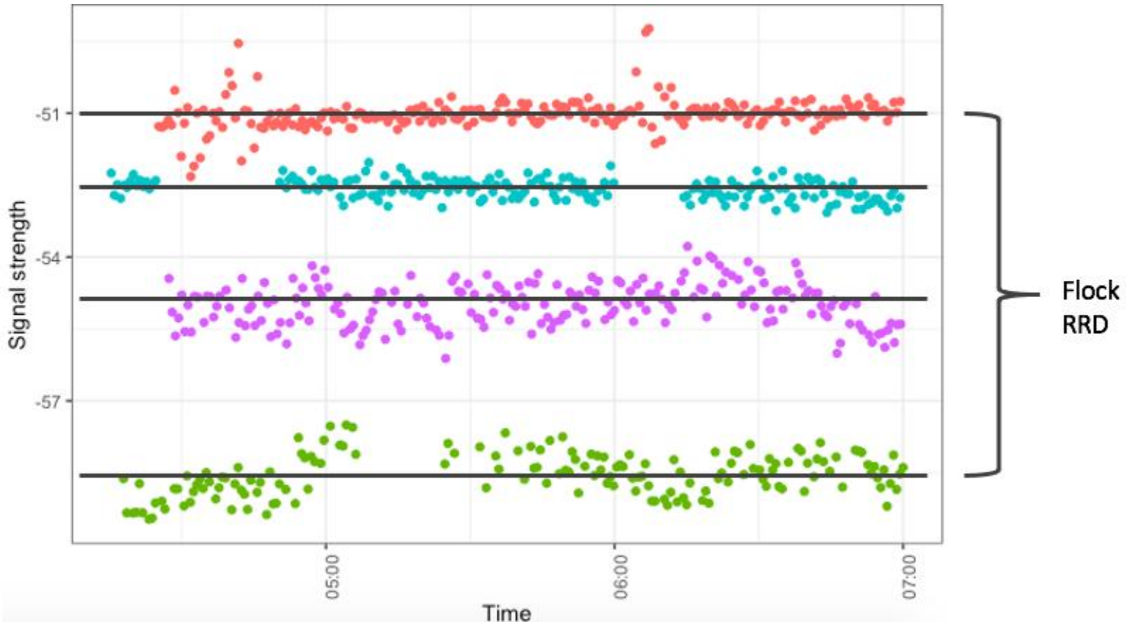

Figure 6. 1 Visual example of the calculation of flock ‘relative roost distance’ of a flock of four birds. Individual roost positions (signal strength dBm) were first averaged (black lines) for the flock, then the individual with the lowest roost position was subtracted from that of the highest determine the flocks RRD for each day.

6.2 Conclusions

The localized radiotelemetry array I used was able to effectively identify flocks, individual fission-fusion events, flock onset of activity, individual general activity, and early morning restlessness over the winter. Combining radiotelemetry individuals records with advanced statistical modelling techniques (LDA, GLMM, GAM), provided with a powerful and flexible dataset which could be adapted to examine many different aspects of sociality and beyond, including those as broad as the fundamental principles of social groups, as specific as individual sleep disturbances, and as far-reaching as the possibility of using early morning restless data as an indicator of climate change.

I strongly contend that ‘social radiotracking’ has fulfilled the need of a long-term, large, spatio-temporal, and real-time dataset to study sociality in relevant ecological and social contexts. In my opinion, it is largely the ‘re-wilding’ (King et al., 2018) aspect of our work which has been responsible for successfully and simultaneously corroborating studies as diverse as theoretical daily activity routines and behavioural responses to winter storms. I hope this work may inspire researchers in the Motus community and others to consider using local automated arrays to studying aspects of: Fission-Fusion dynamics, social dynamics, sleep monitoring, or general activity, in both new or existing projects where possible. This, and any further application of the methods described in this work will assist in the understanding the evolution of social behaviour, the adaptive value of group-living, and the creation of novel methods which are applicable to study dynamics of many different types of social animals.

The potential of the ‘little bird in winter’ for understanding many aspects of biology is truly immense and my journey into radiotracking flocks of black-capped chickadees over two winters drew a similar conclusion; the impact of this little bird in understanding the many yet unaddressed questions of social dynamics is anything but little at all.

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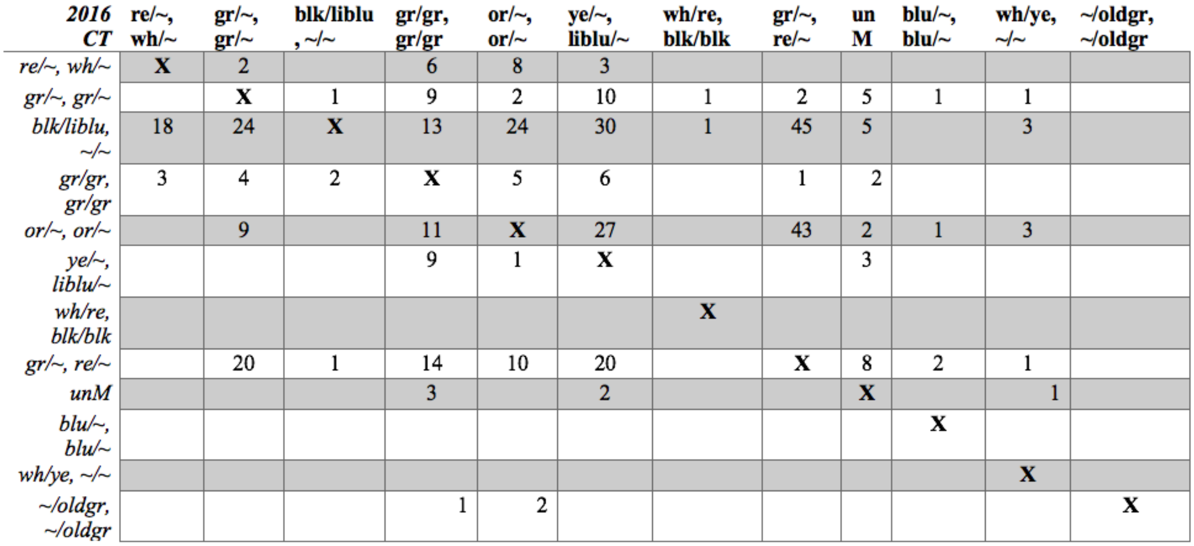
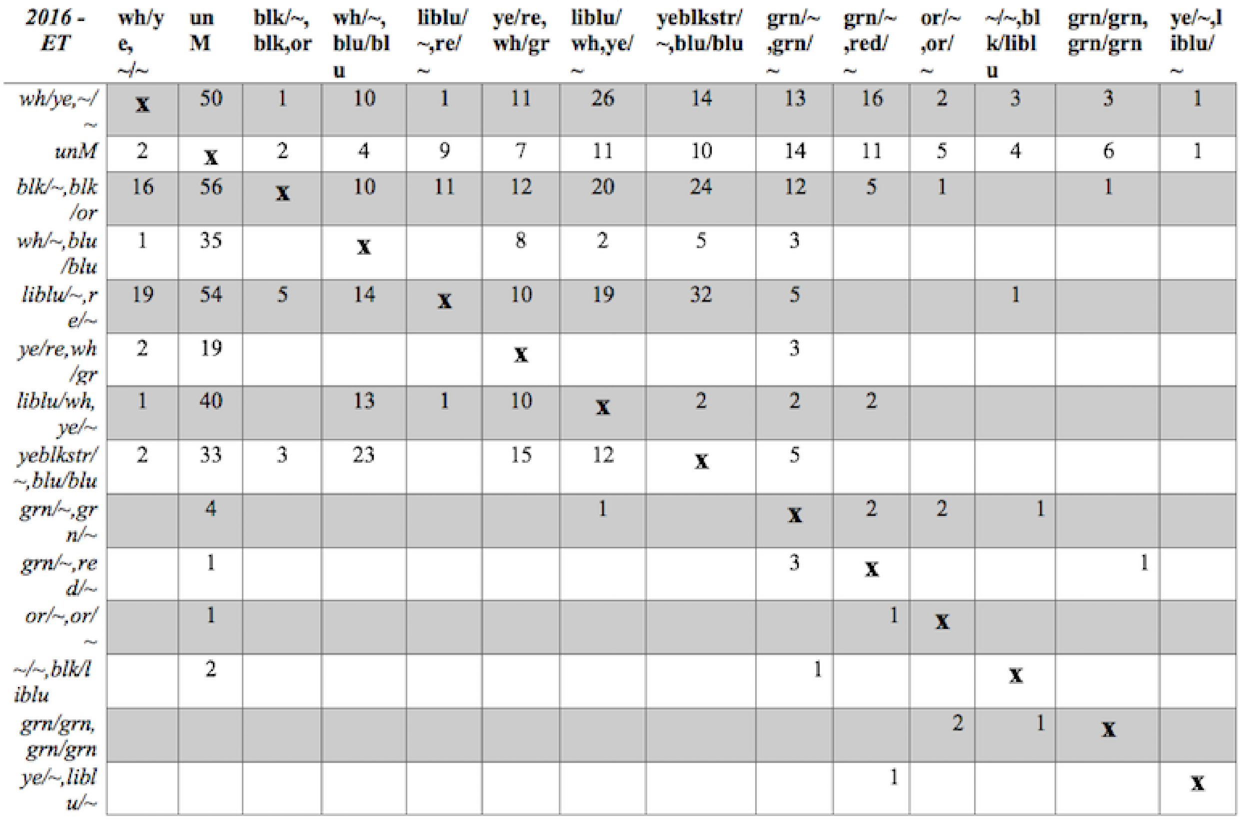
Appendices

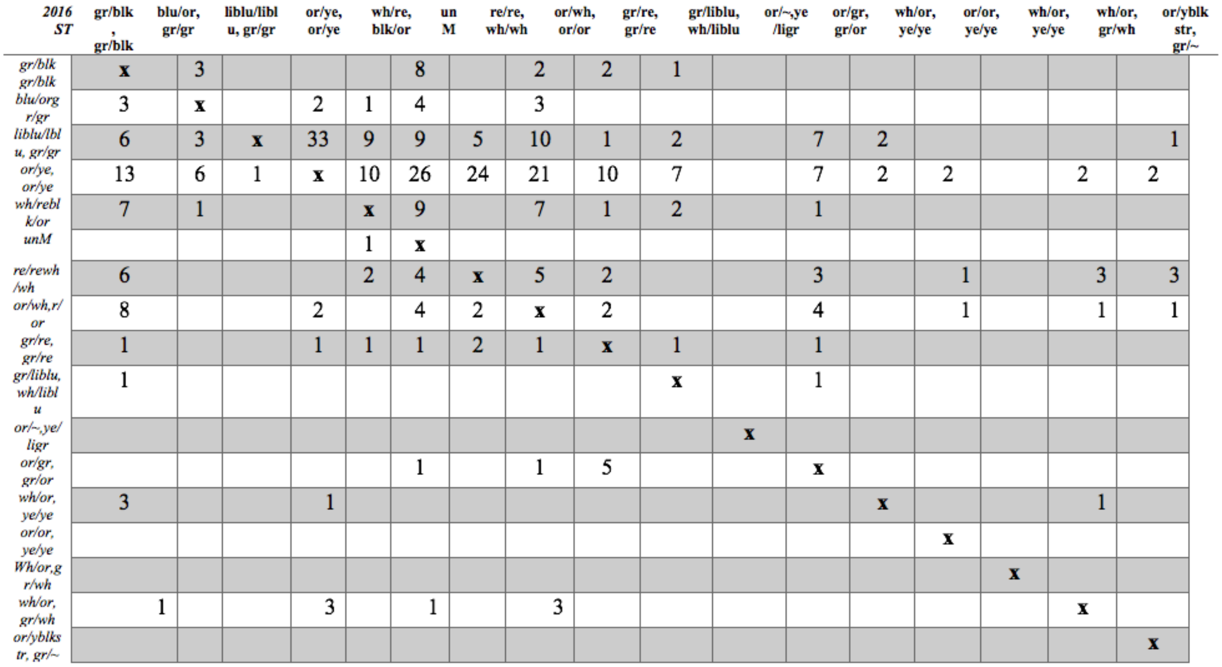
Appendix A Dominance win/loss matrices for the four dominance observation sites (CT, ET, ST, WT) for winter 2016 and 2017. Interactions are represented with winning individuals in bold (top) and losing individuals (left) in italics. Individuals are represented by four colour bands (2 on each leg) ~ denotes missing band.



2016 CT	**re/~, wh/~**	**gr/~, gr/~**	**blk/liblu, ~/~**	**gr/gr, gr/gr**	**or/~, or/~**	**ye/~, liblu/~**	**wh/re, blk/blk**	**gr/~, re/~**	**un M**	**blu/~, blu/~**	**wh/ye, ~/~**	**~/oldgr, ~/oldgr**
re/~, wh/~	**X**	2		6	8	3						
gr/~, gr/~		**X**	1	9	2	10	1	2	5	1	1	
blk/liblu, ~/~	18	24	**X**	13	24	30	1	45	5		3	
gr/gr, gr/gr	3	4	2	**X**	5	6		1	2			
or/~, or/~		9		11	**X**	27		43	2	1	3	
ye/~, liblu/~				9	1	**X**			3			
wh/re, blk/blk							**X**					
gr/~, re/~		20	1	14	10	20		**X**	8	2	1	
unM				3		2			**X**		1	
blu/~, blu/~										**X**		
wh/ye, ~/~											**X**	
~/oldgr, ~/oldgr				1	2							**X**



2016 - ET	**wh/ye,~/~**	**unM**	**blk/~,blk,or**	**wh/~,blu/blu**	**liblu/~,re/~**	**ye/re,wh/gr**	**liblu/wh,ye/~**	**yeblkstr/~,blu/blu**	**grn/~,grn/~**	**grn/~,red/~**	**or/~,or/~**	**~/~,blk/liblu**	**grn/grn,grn/grn**	**ye/~,liblu/~**
wh/ye,~/~	**x**	50	1	10	1	11	26	14	13	16	2	3	3	1
unM	2	**x**	2	4	9	7	11	10	14	11	5	4	6	1
blk/~,blk/or	16	56	**x**	10	11	12	20	24	12	5	1		1	
wh/~,blu/blu	1	35		**x**		8	2	5	3					
liblu/~,re/~	19	54	5	14	**x**	10	19	32	5			1		
ye/re,wh/gr	2	19				**x**			3					
liblu/wh,ye/~	1	40		13	1	10	**x**	2	2	2				
yeblkstr/~,blu/blu	2	33	3	23		15	12	**x**	5					
grn/~,grn/~		4					1		**x**	2	2	1		
grn/~,red/~		1							3	**x**			1	
or/~,or/~		1								1	**x**			
~/~,blk/liblu		2							1			**x**		
grn/grn,grn/grn											2	1	**x**	
ye/~,liblu/~										1				**x**

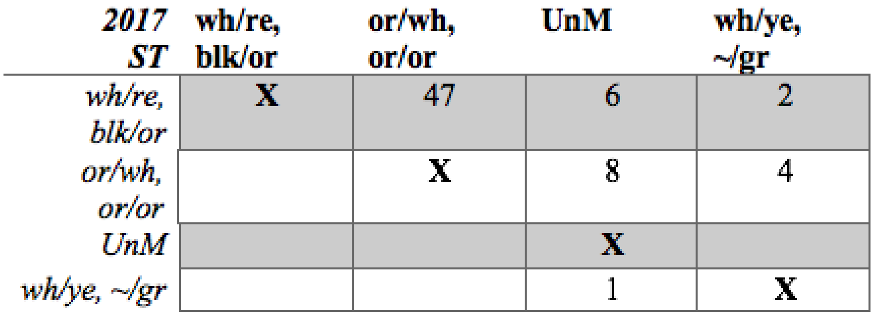


2016 ST	**gr/blk, gr/blk**	**blu/or, gr/gr**	**liblu/liblu, gr/gr**	**or/ye, or/ye**	**wh/re, blk/or**	**unM**	**re/re, wh/wh**	**or/wh, or/or**	**gr/re, gr/re**	**gr/liblu, wh/liblu**	**or/~,ye/ligr**	**or/gr, gr/or**	**wh/or, ye/ye**	**or/or, ye/ye**	**wh/or, ye/ye**	**wh/or, gr/wh**	**or/yblkstr, gr/~**
gr/blk gr/blk	**x**	3				8		2	2	1							
blu/orgr/gr	3	**x**		2	1	4		3									
liblu/lblu, gr/gr	6	3	**x**	33	9	9	5	10	1	2		7	2				1
or/ye, or/ye	13	6	1	**x**	10	26	24	21	10	7		7	2	2		2	2
wh/reblk/or	7	1			**x**	9		7	1	2		1					
unM					1	**x**											
re/rewh/wh	6				2	4	**x**	5	2			3		1		3	3
or/wh,r/or	8			2		4	2	**x**	2			4		1		1	1
gr/re, gr/re	1			1	1	1	2	1	**x**	1		1					
gr/liblu, wh/liblu	1									**x**		1					
or/~,ye/ligr											**x**						
or/gr, gr/or						1		1	5			**x**					
wh/or, ye/ye	3			1									**x**			1	
or/or, ye/ye														**x**			
Wh/or,gr/wh															**x**		
wh/or, gr/wh	1			3		1		3								**x**	
or/yblkstr, gr/~																	**x**

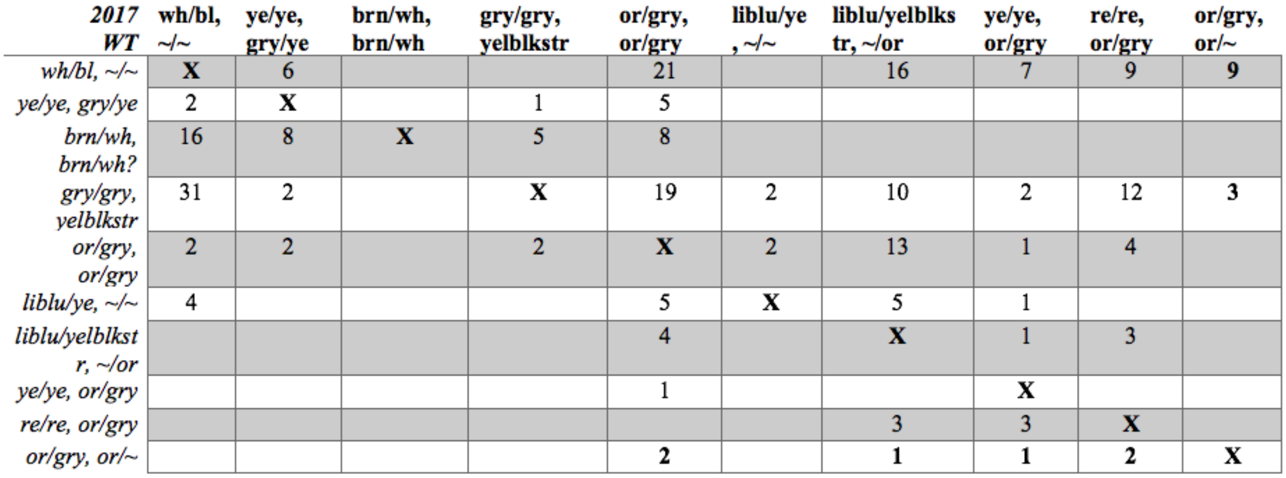
2016 WT	**~/~, yblkstr/~**	**UnM**	**wh/blk, ~/~**	**blu/yblkstr, or/~**	**yblkstr/yblkstr, yblkstr/yblkstr**	**blu/~, blu/~**	**liblu/yblkstr, ~/or**	**gr/liblu, ~/or**	**re/wh, re/wh**	**wh/re, blk/blk**
~/~, yblkstr/~	**X**	122	18	5	21	14		7	6	4
UnM	7	**X**	11	22	37	29	2	23	14	8
wh/blk, ~/~	3	100	**X**	14	8	12	1	10	4	13
blu/yblkstr, or/~		12		**X**		3		1		
yblkstr/yblkstr, yblkstr/yblkstr		4			**X**	2				
blu/~,blu/~		10			1	**X**				
liblu/yblkstr, ~/or		3				1	**X**	2	2	1
gr/liblu, ~/or		7		2	1			**X**	6	4
re/wh, re/wh		16		3	5			2	**X**	
wh/re, blk/blk		2		2				1		**X**

2017 CT	**~/gr, ~/gr**	**~/re, ~/gry**	**liblu/yelblkstr, ~/or**
~/gr, ~/gr	**X**	10	11
~/re, ~/gry	7	**X**	
liblu/yelblkstr, ~/or	2		**X**

2017 ET	**re/~, gry/~**	**gr/~, gr/~**	**wh/~, re?/~**	**gr/wh, or/wh**	**liblu/~, re/~**	**wh/~, wh/~**
re/~, gry/~	**X**	3		5		1
gr/~, gr/~	6	**X**		3		1
wh/~, re?/~			**X**	1		
gr/wh, or/wh	9	6		**X**		
liblu/~, re/~	11	3		46	**X**	1
wh/~, wh/~						**X**



2017 ST	**wh/re, blk/or**	**or/wh, or/or**	**UnM**	**wh/ye, ~/gr**
wh/re, blk/or	**X**	47	6	2
or/wh, or/or		**X**	8	4
UnM			**X**	
wh/ye, ~/gr			1	**X**



2017 WT	**wh/bl, ~/~**	**ye/ye, gry/ye**	**brn/wh, brn/wh**	**gry/gry, yelblkstr**	**or/gry, or/gry**	**liblu/ye , ~/~**	**liblu/yelblks tr, ~/or**	**ye/ye, or/gry**	**re/re, or/gry**	**or/gry, or/~**
wh/bl, ~/~	**X**	6			21		16	7	9	**9**
ye/ye, gry/ye	2	**X**		1	5					
brn/wh, brn/wh?	16	8	**X**	5	8					
gry/gry, yelblkstr	31	2		**X**	19	2	10	2	12	**3**
or/gry, or/gry	2	2		2	**X**	2	13	1	4	
liblu/ye, ~/~	4				5	**X**	5	1		
liblu/yelblkst r, ~/or					4		**X**	1	3	
ye/ye, or/gry					1			**X**		
re/re, or/gry							3	3	**X**	
or/gry, or/~					**2**		**1**	**1**	**2**	**X**

Appendix B Birds were captured under Canadian Wildlife Service permit CA 0236 and all procedures were conducted under Western University Animal User Protocols 2015-019.

AUP Number: 2015-019
PI Name: Sherry, David
AUP Title: Cognition, Behavior, And The Brain Of Birds.
Approval Date: 10/20/2015

Official Notice of Animal Use Subcommittee (AUS) Approval: Your new Animal Use Protocol (AUP) entitled "Cognition, Behavior, And The Brain Of Birds." has been APPROVED by the Animal Use Subcommittee of the University Council on Animal Care. This approval, although valid for four years, and is subject to annual Protocol Renewal.2015-019::1

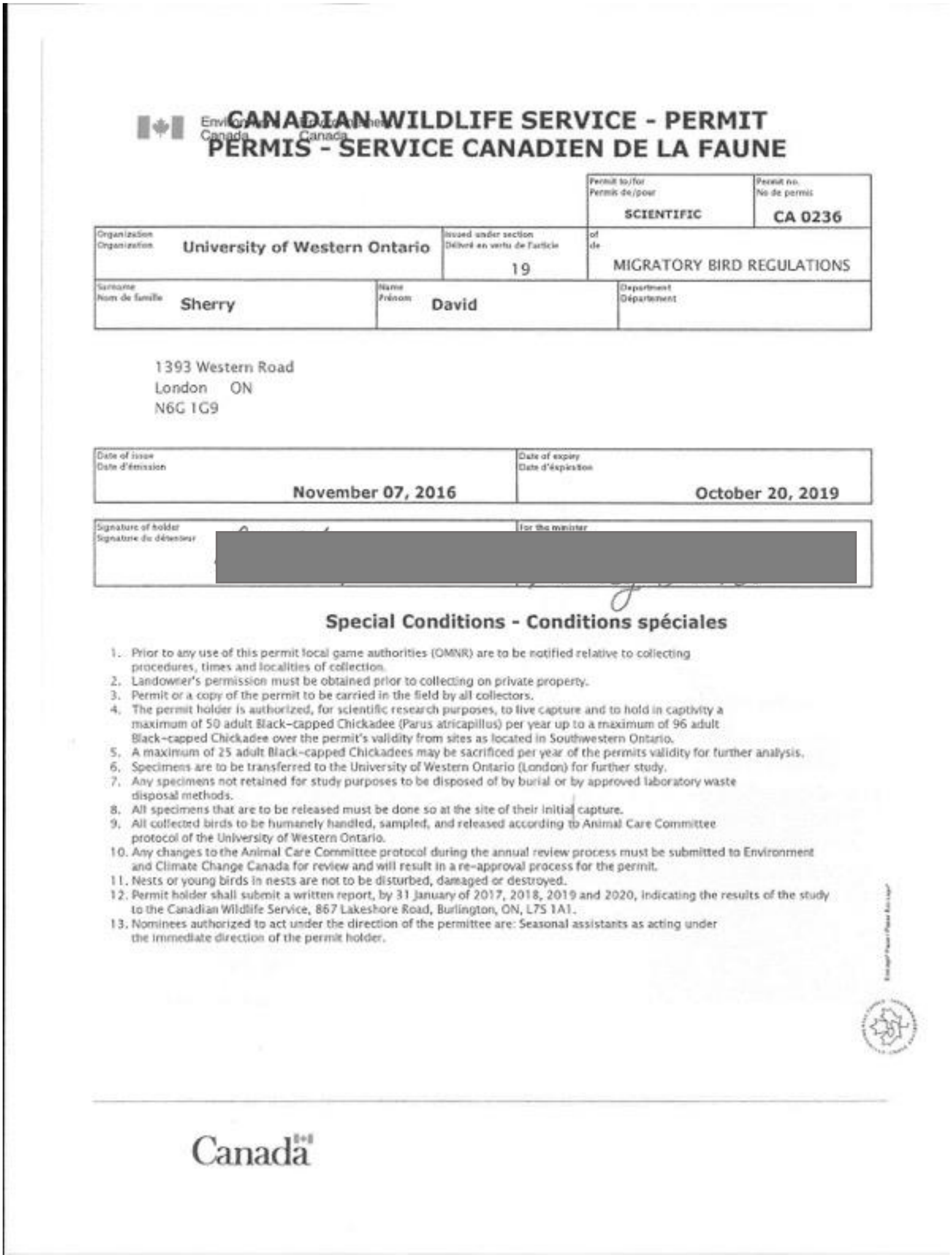
1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

Submitted by: Copeman, Laura
on behalf of the Animal Use Subcommittee
University Council on Animal Care

[redacted]

The University *of* Western Ontario
Animal Use Subcommittee / University Council on Animal Care
Health Sciences Centre, • London, Ontario • CANADA – N6A 5C1
PH: 519-661-2111 ext. 86768 • FL 519-661-2028
Email: auspc@uwo.ca • http://www.uwo.ca/animal/website/



CANADIAN WILDLIFE SERVICE - PERMIT
PERMIS - SERVICE CANADIEN DE LA FAUNE

		Permit to/for Permis de/pour SCIENTIFIC	Permit no. No de permis CA 0236
Organization Organisation University of Western Ontario	Issued under section Délivré en vertu de l'article 19	of de MIGRATORY BIRD REGULATIONS	
Surname Nom de famille Sherry	Name Prénom David	Department Département	

1393 Western Road
London ON
N6G 1G9

Date of issue Date d'émission November 07, 2016	Date of expiry Date d'expiration October 20, 2019
Signature of holder Signature du détenteur [redacted]	for the minister

Special Conditions - Conditions spéciales

1. Prior to any use of this permit local game authorities (OMNR) are to be notified relative to collecting procedures, times and localities of collection.
2. Landowner's permission must be obtained prior to collecting on private property.
3. Permit or a copy of the permit to be carried in the field by all collectors.
4. The permit holder is authorized, for scientific research purposes, to live capture and to hold in captivity a maximum of 50 adult Black-capped Chickadee (Parus atricapillus) per year up to a maximum of 96 adult Black-capped Chickadee over the permit's validity from sites as located in Southwestern Ontario.
5. A maximum of 25 adult Black-capped Chickadees may be sacrificed per year of the permits validity for further analysis.
6. Specimens are to be transferred to the University of Western Ontario (London) for further study.
7. Any specimens not retained for study purposes to be disposed of by burial or by approved laboratory waste disposal methods.
8. All specimens that are to be released must be done so at the site of their initial capture.
9. All collected birds to be humanely handled, sampled, and released according to Animal Care Committee protocol of the University of Western Ontario.
10. Any changes to the Animal Care Committee protocol during the annual review process must be submitted to Environment and Climate Change Canada for review and will result in a re-approval process for the permit.
11. Nests or young birds in nests are not to be disturbed, damaged or destroyed.
12. Permit holder shall submit a written report, by 31 January of 2017, 2018, 2019 and 2020, indicating the results of the study to the Canadian Wildlife Service, 867 Lakeshore Road, Burlington, ON, L7S 1A1.
13. Nominees authorized to act under the direction of the permittee are: Seasonal assistants as acting under the immediate direction of the permit holder.

Canada