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Social behavior among nocturnally migrating birds revealed by automated moonwatching

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ABSTRACT

Migrating birds often fly in group formations during the daytime, whereas at night, it is generally presumed that they fly singly. However, it is difficult to quantify group behavior during nocturnal migration as there are few means of directly observing interactions among individuals. We employed an automated form of moonwatching to estimate percentages of birds that appear to migrate in groups during the night within the Central Flyway of North America. We compared percentages of birds in groups across the spring and fall and examined overnight temporal patterns of group behavior. We found groups were rare in both seasons, never exceeding 10% of birds observed, and were almost nonexistent during the fall. We also observed an overnight pattern of group behavior in the spring wherein groups were more commonly detected early in the night and again just before migration activity ceased. This finding may be related to changes in species composition of migrants throughout the night, or alternatively, it suggests that group formation may be associated with flocking activity on the ground as groups are most prevalent when birds begin and end a night of migration.

Keywords: flight, group formation, migration, seasonality, social behavior

How to Cite

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LAY SUMMARY

- Birds that migrate in groups during the day are easily observed, but most bird species migrate at night when it is much harder to discern how individuals interact while flying.
- We automated an old observational method called "moonwatching" to monitor nocturnally migrating birds as they flew across the Moon, and this approach allowed us to determine how frequently they fly in groups.
- We found that group migration was generally rare at night (never exceeding 10% of birds observed), but it was especially rare during fall as opposed to spring migration.
- We observed a strong overnight pattern during spring migration wherein group migration was most frequent early in the night and then again as migration activity declined in the hours before sunrise.
- Our results suggest that group formation during nocturnal migration may be due to different species flying at different times of night or also to social activity on the ground before and after migratory flights as groups were more prevalent just after sunset and before sunrise.

Comportamiento social entre aves migratorias nocturnas revelado mediante la observación automatizada de la luna

RESUMEN

Las aves migratorias a menudo vuelan en formaciones grupales durante el día, mientras que, por la noche, generalmente se presume que vuelan individualmente. Sin embargo, es difícil cuantificar el comportamiento grupal durante la migración nocturna, ya que hay pocos medios para observar directamente las interacciones entre individuos. Empleamos una forma automatizada de observación de la luna para estimar los porcentajes de aves que parecen migrar en grupos durante la noche en el Corredor Central de Vuelo de América del Norte. Comparamos los porcentajes de aves en grupos durante la primavera y el otoño, y examinamos los patrones temporales nocturnos del comportamiento grupal. Encontramos que los grupos fueron raros en ambas estaciones, nunca superando el 10% de las aves observadas, y fueron casi inexistentes durante el otoño. También observamos un patrón nocturno de comportamiento grupal en la primavera, donde los grupos se detectaron con más frecuencia al principio de la noche y nuevamente justo antes de que cesara la actividad migratoria. Este hallazgo puede estar relacionado con cambios en la composición de especies de migrantes a lo largo de la noche, o alternativamente sugiere que la formación de grupos puede

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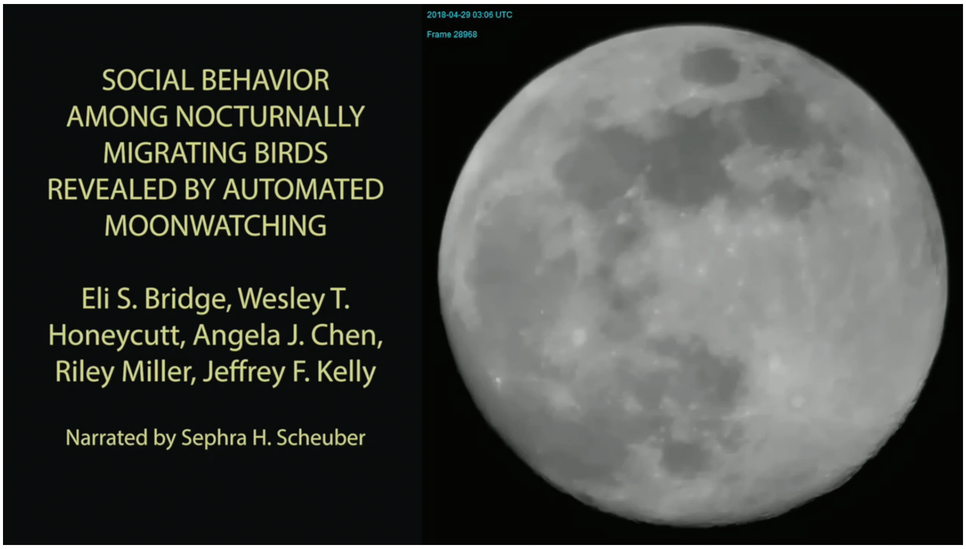
estar asociada con la actividad de formación de bandadas en el terreno, ya que los grupos son más prevalentes cuando las aves comienzan y terminan una noche de migración.

Palabras clave: comportamiento social, estacionalidad, formación de grupos, migración, vuelo

Graphical Abstract



INTRODUCTION

The familiar "V" formations of waterbirds migrating during daylight hours are an easily observed example of social behavior carried out by migrating birds. However, most migratory bird species tend to travel at night (Komal et al. 2017), when direct observations are not as easy to obtain. Despite some evidence to the contrary (Moore 1990), conventional wisdom holds that the vast majority of nocturnal migrants do not fly in groups. However, little work has been done to verify this supposition, which is likely due in part to methodological limitations.

Radar, flight-call recording, light-aided visual observation, and thermal cameras all offer insights into nocturnal migration. For example, Larkin and Szafoni (2008) examined tracking radar records with the goal of quantifying group flight behavior, and they presented evidence that nocturnal migrants frequently form diffuse groups with individuals separated by distances of up to 300 m. Similarly, flight-call recordings have been used to determine the species composition of birds aloft (Smith et al. 2014, Horton et al. 2015). However, robust inferences about group behavior based on flight calls require validated models of vocalization rates across migratory species, which is a complex and developing field of study (Smith et al. 2014, Horton et al. 2015, Gillings and Scott 2021).

Other means for discerning group migration behavior include direct observation using artificial lights (Larkin and Szafoni 2008, Huang et al. 2016), recordings from thermal cameras (Liechti et al. 1995, Horton et al. 2015), and moonwatching (Lowery 1951, Nisbet and Drury, 1969). The current study is based on moonwatching, wherein an observer with a telescope uses the Moon as a backdrop to enumerate birds passing overhead. Although moonwatching was first conceived as an observational method ~150 years ago (Scott 1881a, 1881b), it was not fully developed until the middle of the 20th century when George Lowrey derived the mathematics necessary to translate observation data into flight directions and passage rates (Lowery 1951). Nisbet (1963, 1959) subsequently refined some of Lowrey's methods and performed the first radar-based validations of moonwatching.

Although traditional moonwatching is simple and has modest equipment requirements, it has several obvious drawbacks. For instance, it is only possible when appropriate moon phases coincide with clear weather conditions. Also, it relies on the alertness and acuity of human observers who are likely to suffer some degree of sleep deprivation. In a comparison with a fixed beam radar and thermal camera, researchers doing traditional moonwatching failed to document approximately one-third of the birds detected by the other methods (Liechti et al. 1995).

To address some of these issues, we developed an automated version of moonwatching that uses a motorized mount for a spotting scope, a small video camera, and a single board computer to record video footage of the Moon for subsequent analysis using computer vision (for details see Honeycutt et al., 2020). This system, which we refer to as LunAero, not only mitigates human error and observer bias but also provides a means of assessing aspects of migration behavior that are likely beyond the ability of a person to accurately discern in real-time. Although we have not yet developed or validated the analytical workflows, LunAero footage should allow for determination of flap rates, body orientation, and even some degree of taxonomic identification.

Among the assessments possible with LunAero are precise measures of flight direction and the relative timing of bird observations. Hence, we have a means of determining whether birds are engaging in apparent group behavior during migration. While LunAero was under development, we opportunistically and sporadically collected moonwatcing footage over a 3-year period from 2018 to 2021. We analyzed a sample of this footage and used the results to test for both overnight and seasonal patterns in group migration.

There are several known differences between spring and fall migration including wind conditions (La Sorte et al. 2014, Mitchell et al. 2015), pace of migration (Nilsson et al. 2013, Horton et al. 2016), age and sex composition of populations (Ralph 1978, Woodrey and Moore 1997, Covino et al. 2020), and differing temporal patterns of species composition (Deppe and Rotenberry 2005), which could lead to corresponding differences in group migration behavior. Moreover, it is possible that group behavior wanes as the night progresses as an increasing number of individuals curtail their migration activity. On the other hand, if group formation happens during flight, it is possible that group behavior would become more widespread as the night progresses. Lacking sufficient knowledge to guide our expectations, we sought to test null hypotheses of consistent group behavior across nights and across seasons.

METHODS

We used the LunAero system (Honeycutt et al. 2020) to record footage of the Moon at sites in Central Oklahoma including the Kessler Atmospheric and Ecological Field Station (34.98°N, 97.52°W); private residences in Norman, Oklahoma (35.22°N, 97.44°W); and the U.S. Department of Energy Atmospheric Radiation Measurement Southern Great Plains Lab (36.61°N, 97.48°W). These sites aligned north to south and were all within the North American Central Flyway (Buhnerkempe et al. 2016). Much of the video footage we collected was unusable due to cloudy skies and/or technical issues with the hardware. Hence, we screened the footage to identify recordings where the video was suitable for further analysis. All footage used in our analyses were collected within 5 days of a full Moon or when the Moon was at least 66% illuminated.

The steps used to extract, filter, and validate flight paths from our video footage are described by Honeycutt and Bridge (2022). This workflow yielded a dataset wherein all detected bird silhouettes were incorporated into individual flight paths along with their screen coordinates (x and y) and timestamps. To find potential groups of birds, we first grouped all flight paths that occurred in the same video frames or within five frames of each other. Next, for each potential group, we generated a distance matrix based on flight speed (using apparent moon diameter as a reference) and on-screen flight direction in degrees. We then applied a cluster analysis to the distance matrix to group together coinciding flight paths that were very similar to each other. We applied a cutoff value of 7.5 for the cluster analysis, which we determined by comparing group designations from the cluster analysis with visual assessments of groups in the video footage. These analyses were done in R using the *dist()* and *hclust()* functions in the *stats* package (R Core Team 2021), and our code is available on the Open Science Framework at https://osf.io/bv5hj/. As a final step, we visually inspected all potential groups to verify group determinations.

For examination of temporal patterns in group behavior, we assigned each flight path to one of eight equivalent periods of time (octiles) between sunset (defined as the moment the sun sinks below the horizon) and sunrise (first appearance of the sun above the horizon) for each night of data collection. Note that the durations of these octiles differ across the different days of the year as they represent sequential portions of the night as opposed to specific time periods.

TABLE 1. Frequency of group sizes detected by automated moonwatching.

Group size	Groups in fall	Groups in spring	Total groups
2	39	6	45
3	11	0	11
4	6	1	7
5	5	0	5
6	2	0	2
10	2	0	2
11	1	0	1
13	1	0	1

To test the null hypothesis of uniform group flight activity across the night, we calculated the overall proportion of birds flying in groups within each season. We then used these proportions to generate 5,000 simulations of uniform proportions across octiles with sample sizes in each octile matched to our observed data. Observed proportions of birds in groups that did not fall within the respective 95% confidence intervals of the simulated data were considered evidence against the null hypothesis of uniformity. To test for differences across seasons, we applied a Fisher's exact test to the overall proportions of birds in groups in the spring and fall.

By focusing on the percentages of birds flying in groups, we are able to sidestep problems such as uneven sampling across different time periods. However, there is a possible bias in the methodology that relates to the position of the moon in the sky and its effect on the volume of the sky sampled by moonwatching. As a post hoc analysis, we carried out a simulation exercise to quantify the extent to which detection of group behavior may be related to moon elevation angle. This simulation indicated that moon elevation angle has a strong effect on the overall number of birds detected, but little to no effect on the proportion of birds in groups detected.

RESULTS

Our analysis included 68.85 hours of video that comprised 49.23 hours from 17 different nights in spring and 19.12 hours from 12 nights in autumn. This footage yielded 5,294 bird detections: 3,394 from spring and 1,900 from fall. These results should not be used to infer differences in the intensity of spring and fall migration as the sampling was uneven across the 2 seasons and there was considerable day-to-day variation. We report overall bird detections only to establish that there were sufficient observations to derive proportions of birds flying in groups.

Of all the birds observed, only 232 (4.4%) appeared to belong to a group. Group sizes ranged from 2 to 13 individuals and the vast majority of groups were pairs (Table 1). Our comparison of data from spring and fall indicated a clear seasonal difference in group behavior among nocturnal migrants. Although group migration in the spring was rare (216 birds in groups or 6.4%), group behavior in the fall was nearly absent, with only 16 birds detected in 7 groups (0.8%). A Fisher's exact test indicated a significant difference between these proportions ($P < 0.001$).

Comparing observed group behavior across nighttime octiles to the simulation of uniform group occurrence revealed

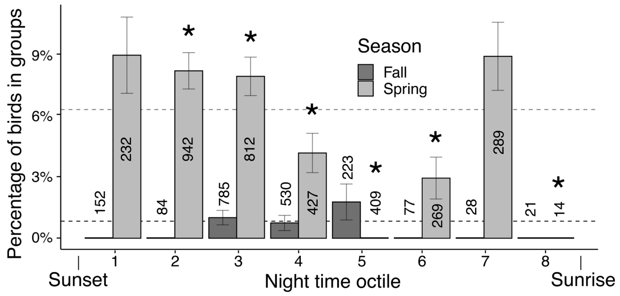


FIGURE 1. Percentages of birds flying in groups during spring and fall migration across 8 nocturnal time periods (octiles). Numbers associated with each bar correspond to the total number of birds detected. Horizontal dotted lines indicate expected percentages for spring (upper, gray line) and fall (lower, black line) under the presumption of uniform migration activity across octiles. Percentages that differ significantly from the expectation of uniformity are indicated with asterisks. Error bars show standard error.

that during spring migration group behavior was more prevalent early in the night and again as the night ended (Figure 1). There were no groups detected in last octile, but overall bird detections were also scarce during this time period, which suggests that most birds have stopped flying before or during the eighth octile (Figure 1). Based on 95% confidence intervals of the null expectation of uniformity (i.e., 6.4%) for each octile, springtime proportions of birds in groups differed significantly from the null in all octiles except 1 and 7.

Observations of group migration in the fall all occurred during the third, fourth, and fifth octiles. However, we did not have statistical support for an overnight pattern in the fall, because of the small number of groups observed. Based on 95% confidence intervals, none of the proportions of birds in groups were significantly different from the null expectation of uniformity (i.e., 0.8%).

DISCUSSION

Clear differences across seasons as well as an overnight pattern of group behavior during spring migration indicate that the null expectation of homogenously distributed group behavior across seasonal and nightly time frames should be rejected. The near absence of group behavior during fall migration was surprising. Although only a few species migrate in groups composed of related individuals (Black and Owen 1989, Alonso et al. 2004, Palacín et al. 2011, Earnst and Bart 2013, Chetverikova et al. 2017) and they are generally diurnal migrants (Komal et al. 2017), the prospect of parents accompanying their offspring on their first migration would lead to an expectation of increased nocturnal group migration in the fall relative to spring. On the other hand, there is a body of evidence indicating that the migration behavior of juvenile songbirds is often fundamentally different from that of adults in terms of timing (Yong et al. 1998, Rguibi-Idrissi et al. 2003, Crysler et al. 2016) and orientation (Perdeck 1958, Moore 1984), which would reduce the prevalence of migration of family groups.

One general explanation for group migration is the "many wrongs" hypothesis which posits that a collective navigation effort is safer and more efficient than that of an individual on its own (Simons 2004, Beauchamp 2011). Spring migration, which some studies suggest is faster, more direct, and more demanding than fall migration (Kokko 1999, Moore et al. 2005), may warrant more efficient passage, which may be facilitated by group behavior. Whereas in the fall birds may travel more in accordance to their own energetic status (Nilsson et al. 2013, La Sorte et al. 2015). It is also worth noting that there is some evidence for songbirds migrating in the spring as members of mated pairs (Greenberg and Gradwohl 1980, Willis 1987). The high frequency in which we observed groups of 2 (Table 1) may be a result of birds sustaining pair bonds during migration. However, we know of no substantiated observations of mates migrating together; whereas observations of spring arrival (Morbey et al. 2012) and at least one tracking study (Stutchbury et al. 2016) indicate that, among most songbirds, mates migrate separately.

It is important to note that not all of the birds we observed were passerines, and that species composition likely plays an important role in patterns of nighttime group migration. Although we do not have a validated workflow in place to make taxonomic determinations about the birds in our video footage, a visual review of all of the migrating groups we observed indicated that 35% of the groups (26 of 74) appeared to be composed of non-passerine species. Non-passerines also made up many of the larger groups such that at least 106 of the 232 birds detected in groups (46%) were not passerines. Note that these are minimum estimates, as there were many groups for which we could make no taxonomic classifications. Hence, changes in the species composition of birds aloft could account for overnight patterns of group migration behavior as well as seasonal differences.

Our failure to observe substantial group migration during the fall may be due, in part, to limited sampling. Although our sample from the fall included 1,900 bird observations, these came from only 12 nights for which we had video footage that was suitable for analysis. There was a high degree of variation with regard to the numbers of birds detected on these nights, yet there remains the possibility that the nights represented in our data set were, by chance, particularly unfavorable to group behavior. Hence, there is a chance that differences in the seasonal timing of spring and fall sampling could contribute to observed differences in group frequency

The overnight pattern of group migration observed in the spring may also relate to social behavior during migratory stopovers, during which migrating birds use social information (Nemeth and Moore 2007, 2014) to improve both foraging efficiency and predator avoidance (Krause and Ruxton 2002). If group behavior during migration stems from selective pressure for flocking during stopover periods (Piersma et al. 1990), then group activity would be most likely to occur at the time when birds are first departing stopover locations (early in the night) and again as they near the next stopover site (late in the night). This expectation is reflected in our observed pattern of group behavior wherein groups are more prevalent early in the night and again just before nocturnal migration ceases.

In general, our findings align with conventional wisdom that group flight behavior among nocturnal migrants is rare compared with diurnal migrants. We did not attempt to discern the diffuse groups of migrants that Larkin and Szafoni (2008) described based on their analysis of tracking-radar data. Such groups would be difficult to detect with moonwatching due to its limited window of observation. However, we did frequently observe nearly identical flight headings and speeds of different individuals that were spaced out over several minutes of video. We are uncertain about whether to interpret these observations as evidence of social interaction as opposed to the result of multiple individuals adhering to a similar behavioral program. In addition to diffuse flocks, Larkin and Szafoni (2008) report light-aided visual observations of migrating groups that were tightly clustered, and these reports are consistent with our observations.

Although our automated moonwatching method has several shortcomings, it fills an important observational gap in enabling us to observe the behavior of individual birds engaged in nocturnal migration. There are other observation methods that can provide similar data, but they often require specialized technology (e.g., tracking radar) and/or advanced optical equipment (e.g., thermal cameras) which can make the method prohibitively expensive, or at least too costly to deploy on a broad scale. As automated moonwatching progresses, we hope to automate tasks such as flap rate detection and recognition of body shapes that could further improve inferences from moonwatching by offering taxonomic classifications, assessments of wind drift, and altitude estimates. With these enhancements and additional data, we may be able to improve our interpretation of the apparent patterns underlying nocturnal group that automated moonwatching has thus far revealed.

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Ethics statement

In this study, birds were only passively observed. A description of the project was submitted to the University of Oklahoma Animal Care and Use Committee, and it was exempted from review as no animals would be materially affected by the research.

Conflict of interest statement

None declared.

Author contributions

E.S.B. and W.T.H. conceived, built, and programmed the Lunaero moonwatching system and collected all field data. E.S.B. and W.T.H. also developed the primary workflow for extracting data from video footage. E.S.B., W.T.H., and J.F.K. secured funding for the project and conceived the idea of using moonwatching data to examine group migration behavior. A.J.C. and R.M. performed initial evaluations of video footage, carried out software testing, and manually screened data to ensure accuracy. E.S.B conducted the statistical analyses and drafted the manuscript with input and editing from all other authors.

Data availability

Data and analysis code referenced in this paper are publically available on Dryad at https://doi.org/10.5061/dryad.0k6djhb62 and on the Open Science Framework at https://osf.io/bv5hj/.

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