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# Remote Time-lapse Photography as a Monitoring Tool for Colonial Breeding Seabirds: A Case Study Using Thick-billed Murres (*Uria lomvia*)

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**Abstract.**—Seabirds are important bio-indicators for marine ecosystem conservation. Monitoring at logistically-challenging seabird colonies takes extensive resources and expensive man-hours to complete. The use of remote time-lapse photography to collect population parameters at seabird colonies is a novel way to reduce researcher effort while collecting valuable data. To illustrate the applicability of this method, data were collected at a Thick-billed Murre (*Uria lomvia*) colony on Kippaku, Greenland. Time-lapse photography was used to take pictures once per hour of a predetermined study plot for the duration of the breeding season, and the pictures were then analyzed using GIS software. By using a photo-capture interval of one picture per hour during one murre breeding season, the study showed a seasonal trend in attendance peaking in the mid chick-rearing period, a diurnal trend with a small peak at ca. 07:00 hr and a larger peak at ca. 19:00 hr. The study showed that careful choice of photo-capture interval is important to reduce the possibility of misrepresenting the diurnal trend of the study species. Compared to the 1-hr photo-capture interval, intervals of 2 and 4 hr accurately depicted the diurnal trend, while a 3-hr interval showed the trend but with a misrepresentation of the first attendance peak. A 5-hr interval introduced stochastic effects that did not show the correct diurnal trend. The proposed method can be applied to colonial breeding seabirds and/or other similar systems for population monitoring. Researcher effort and costs associated with data collection for population monitoring of seabird colonies can be greatly reduced and population estimates can be drastically improved by the use of remote time-lapse photography. Received 19 February 2013, accepted 30 April 2013.

**Key words.**—breeding biology, cameras, colony attendance, count bias, investigator effort, nest attendance, photo counts, population monitoring, Thick-billed Murre, *Uria lomvia*.

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Time-lapse photography has been in use for some time, and was proposed for observing avian behavior since the technology became commercially available (Cowardin and Ashe 1965; Temple 1972; Weller and Derksen 1972; Tennyson *et al.* 1974). Most studies have focused on specific behaviors, e.g., nest predation and chick provisioning (Goetz 1981; King *et al.* 2001; Booms and Fuller 2003; Gula *et al.* 2010). The use of the technology has not been fully exploited to monitor diurnal, seasonal or long-term population trends. Some studies have used video or time-lapse photography for analyzing habitat use over daily and seasonal periods (Piatt *et al.* 1990; Lynn *et al.* 2008), but few have applied the technology in groups of gregarious birds for any purpose (Cowardin and Ashe 1965; Weller and Derksen 1972; Montalbano *et al.* 1985; Piatt *et al.* 1990). The method has not been expanded on since new technology

has been developed making the method feasible for long periods of time, for purposes such as population monitoring (Weller and Derksen 1972; Piatt *et al.* 1990; Lorentzen *et al.* 2012).

Seabirds breed in large colonies and have been distinguished as indicators of climate change and the health of marine systems (Piatt *et al.* 2007; Einoder 2009; Mallory *et al.* 2010). A very basic but essential parameter of colonial seabird monitoring is breeding population development, often measured as the number of birds attending the breeding colony. However, colony attendance can vary over the course of a day, a season or between years according to local factors, such as weather, foraging conditions and the proportion of non-breeding birds attending the colony (Birkhead 1978; Harris *et al.* 1986; Cadiou 1999; Dittmann and Becker 2003). This implies that rather detailed studies are

needed to arrive at accurate and comparable breeding population estimates. Many seabird species breed in remote places where direct observation often requires expensive travel and use of man-hours, especially if you want to gain quality long-term monitoring data that extend over full seasons. With the method being proposed here, an initial visit to setup and install the camera and then a single annual visit thereafter are adequate for collection of entire seasons worth of data, and using a camera gives freedom for researchers to collect other data while visiting a study site. The technology provides a low-cost opportunity to gain a detailed insight into the daily, seasonal and annual trends of colonial seabirds.

In this project, we propose the use of remote time-lapse photography as a tool to collect population estimates and to correct for bias in large-scale colony surveys of seabird numbers due to short-term variation in colony attendance. We test different photo-capture intervals to explore the resolution of data needed to detect diurnal variation in colony attendance correctly, and we discuss the feasibility of using remote time-lapse photography as a long-term monitoring tool for seabird colonies with possible application to other similar systems. Because of rapidly changing technology and multiple commercially available choices for equipment, this study will primarily focus on the novel benefits and uses of the proposed method instead of the hardware and software used. As a case study, we present results using one breeding season of Arctic-breeding Thick-billed Murres (*Uria lomvia*).

## METHODS

### Study Area

The study was conducted on the Arctic island of Kippaku (15 ha), Upernavik, Greenland (73° 43' N, 56° 37' W). The colony on Kippaku had approximately 17,000 Thick-billed Murres (Labansen *et al.* 2013). We used a previously established study plot where observations could be made and the placement of the camera box for long-term monitoring could be setup directly opposite (approx. 25 m) the plot. The study plot contained approximately 75 breeding pairs.

### Data Collection

We used a camera body (Canon 40D DSLR) with an industrial Compact Flash memory card (iCF 4000, 8 GB) to conduct time-lapse photography. A zoom lens (Canon EF-S 17-85 mm lens, fixed on 50 mm) was attached to the camera body, and was securely inserted with silica gel (to eliminate moisture) in a weatherproof box (GA BOX 330 x 230 x 180 mm, Rittal GmbH & Co.) securely attached to the cliff. A programmable timer (Canon TC-80N3) was used for partial data collection during the breeding season, but a custom programmable timer was developed to collect data from before the onset of the breeding season until the conclusion of the breeding season by using predetermined dates. Single pictures were taken once per hour on West Greenland Time (UTC -03 hr), and a lithium-ion battery supply was constructed to provide adequate charge for over 12 months. Photographs ( $n = 730$ ) were taken from 30 June until 30 July 2010 encompassing the end of incubation until ca. fledging of the Thick-billed Murre (hereafter murre) chicks for the case study, but the camera was left on-site to define arrival-time of individuals the following breeding season. Two 24-hr storms occurred during the study season, 14-15 July and 23-24 July, the first being more severe than the second. Pictures that were unusable because of inclement weather or investigator disturbance were discarded ( $n = 35$ ). We used ArcMap (Environmental Systems Research Institute 2008) to count all individual Thick-billed Murres present within each sub-plot for each picture regardless of breeding status.

### Statistical Analysis

We used program R (R Development Core Team 2010) for all statistical analyses. For gaps within the photo-data caused by weather or investigator disturbance ( $n = 35$ ), we used a linear interpolation (command `na.approx`; R Development Core Team 2010) to estimate the number of Thick-billed Murres present for the missing hours. An autocorrelation function (ACF) and partial ACF of murre numbers were used to determine the cyclic pattern of the data. To test the viability of reducing the use of memory card space and reducing work effort of counting murres in pictures, pictures at 2-, 3-, 4- and 5-hr intervals were autocorrelated and partially autocorrelated to observe if the diurnal cycle was similar to the once per hour sampling interval. A time-series analysis in R (command `STL`) using seasonal-trend decomposition based on Loess (Cleveland *et al.* 1990) on the photo-data was run to determine seasonal and diurnal trends. An ANOVA was run to test for the difference in numbers of attending individuals in four different breeding periods, defined as: incubation = attendance before the average hatching date; early chick-rearing = mostly hatched chicks under 7 days old; mid chick-rearing = mostly chicks between 7 and 14 days old; and late chick-rearing = mostly chicks greater than 14 days old. Each period contained approximately 5 days of attendance data once weather influences were accounted for by removing the major disruptions in attendance associated with the storms. A Fligner-Killeen ho-

mogeneity of variance test ( $\chi^2_3 = 5.349 P = 0.148$ ), a Q-Q normality plot, and a histogram of the residuals were used to check if the model adhered to the assumptions of ANOVAs. Average hatching date was determined from 32 pairs within the study plot. A Tukey's honestly significant difference (HSD) test was conducted on the ANOVA results to test for pair-wise differences and to obtain adjusted *P*-values between the breeding periods.

## RESULTS

The average hatching date was 7 July (SE = 4.36 days), and the median hatch date was 6 July. Attendance was not significantly different between the early chick period and the incubation periods (Table 1), but all other combinations between the breeding periods were significantly different according to the Tukey's HSD test (Table 1; ANOVA:  $F_{3,638} = 34.37 P < 0.0001$ ). This indicates that Thick-billed Murre attendance during the study varied significantly during the chick-rearing period, with the highest attendance occurring during the middle of the chick-rearing period and the lowest attendance during the late chick-rearing period when the young began to fledge. There were marked decreases in colony attendance during the two observed storms (wind speed average and maximum: storm one 13.9 m/s, 31.7 m/s and storm two 8.0 m/s, 22.4 m/s, and total precipitation 28.7 mm and 11.2 mm, respectively).

Thick-billed Murres showed peaks in attendance at ca. 12-hr intervals at approximately 07:00 hr and 19:00 hr. The peak occurring at 07:00 hr was less pronounced than the peak in the evening (Figs. 1 and 2). The mean difference between maximum

and minimum colony attendance was 14% (SE = 0.69%, Range = 5-25%).

The ACF (Fig. 1B) showed the highest significant lags in the cycle at 10 and 23 hr, while also exhibiting a clear pattern. The initial lags (0-3) are expected to be correlated because of the varying length of the incubation/brooding shifts of the breeders and because this is the nature of autocorrelation where short intervals are expected to be dependent with each other. The partial ACF (Fig. 1B), which more accurately describes the cycle by removing correlation associated with the previous lag, showed the highest positive significance in the cycle at 9 and 19 hr, but also had positive significance at 7, 8, and 20 hr and had weak positive significance at 18 and 21 hr. The negative part of the cycle was illustrated by negatively significant lags at 4, 26 and 28 hr and was strongly negative at 13 hr. It is important to understand that the lags (hours) should not be treated as time of day but used to determine the interval of the cycle.

The results illustrate that the once per hour photo-capture interval depicts that the time-lapse interval should match the cycle of attendance if a cycle is present, because both the highest and lowest attendance values are correctly represented by peaks at 12-hr intervals and corresponding dips match the 12-hr trend of the plotted murre attendance values (Fig. 1). The 2- and 4-hr photo-capture intervals (Figs. 3A, 3B, 3E and 3F) accurately depicted the diurnal 12-hr trend, although delayed by 1 hr compared to the 1-hr interval dataset, and showed attendance peaks at 08:00 hr and 20:00 hr. The 3-hr interval

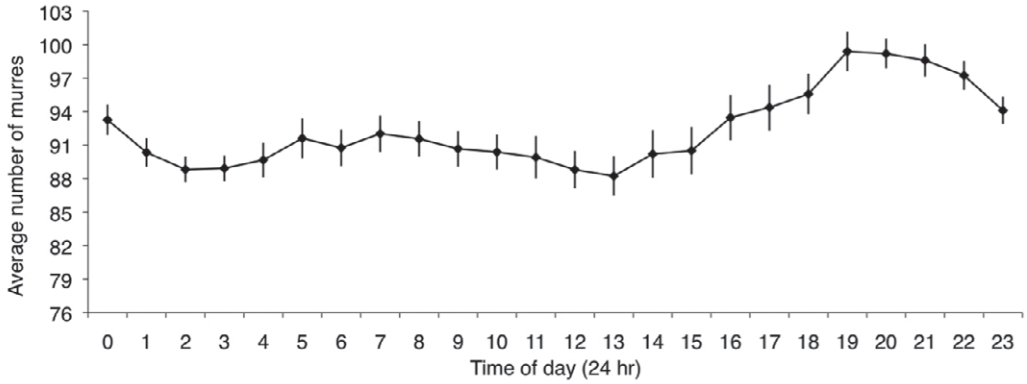
**Table 1. Summary of Tukey's HSD<sup>a</sup> test statistics comparing breeding periods for Thick-billed Murres (*Uria lomvia*), Kippaku, Greenland, 2010.**

Breeding Period <sup>b</sup>	Difference	<i>P</i> -adjusted
Early chick-rearing > Incubation	0.26	0.991
Mid chick-rearing > Incubation	3.50	0.0001
Late chick-rearing < Incubation	-5.81	< 0.001
Mid chick-rearing > Early chick-rearing	3.24	0.0012
Late chick-rearing < Early chick-rearing	-6.07	< 0.001
Late chick-rearing < Mid chick-rearing	-9.31	< 0.001

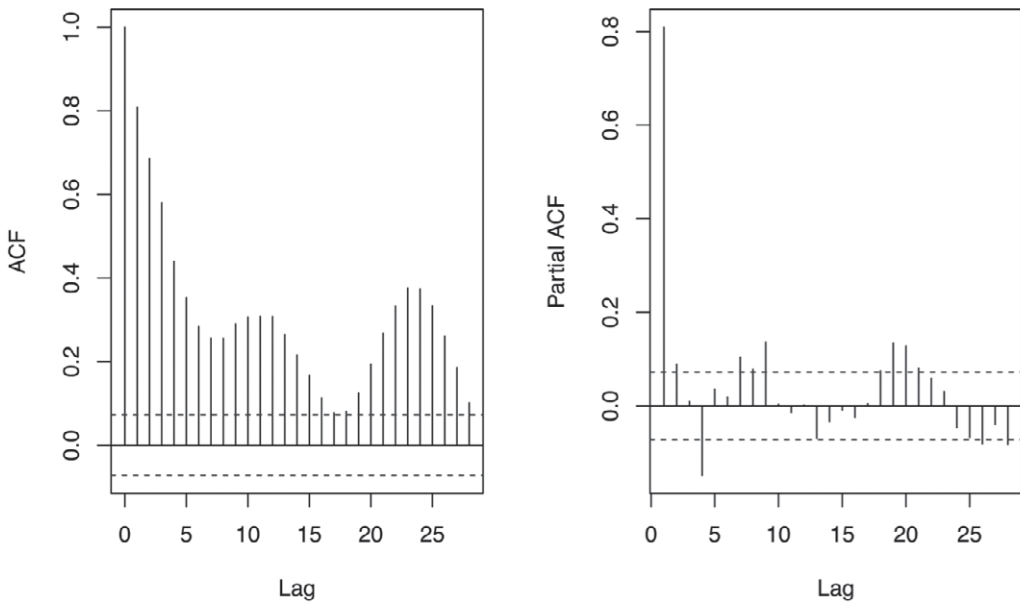
<sup>a</sup>> or < signals which parameter had the greater value.

<sup>b</sup>incubation = before average hatching date; early chick-rearing = mostly hatched chicks < 7 days old; mid chick-rearing = mostly chicks 7-14 days old; late chick-rearing = mostly chicks > 14 days old.

A)



B)

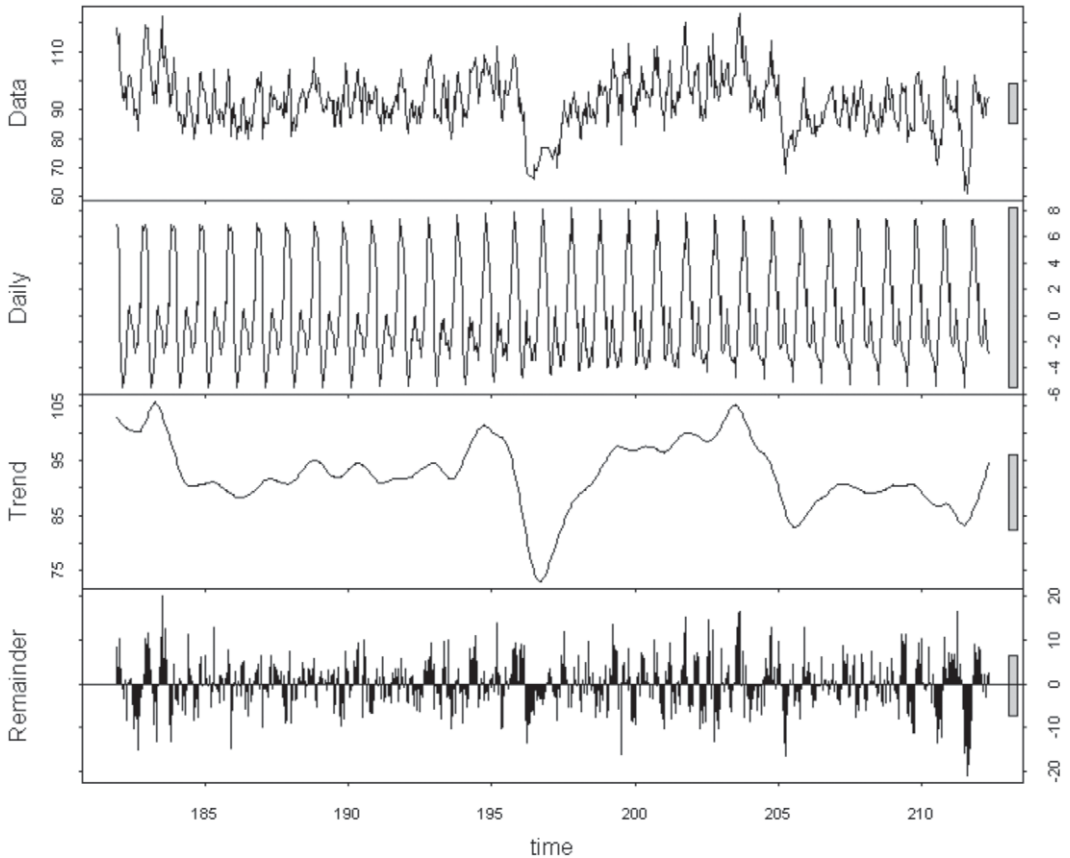


**Figure 1.** Diurnal pattern of Thick-billed Murrens (*Uria lomvia*) colony attendance on Kippaku, Greenland, 2010. A) Average number of murrens attending the colony with standard error. B) Autocorrelation function (ACF) and partial ACF of murre numbers; dotted lines = 95% confidence intervals, 1 lag = 1 hr.

(Figs. 3C and 3D) had equivalent attendance at 06:00 hr and 09:00 hr with a large peak at 21:00 hr. The similar number of attending murrens detected at 06:00 hr and 09:00 hr can also be seen in Fig. 1A where there is a dip in attendance at 06:00 hr during the morning peak in attendance that corresponds to 09:00 hr. However, the 5-hr interval was unable to maintain the depiction of the cycle by showing attendance peaks at 11:00 hr, 16:00 hr and 21:00 hr (Figs. 3G and 3H).

## DISCUSSION

The importance of establishing diurnal and seasonal trends for seabird colonies could reflect important ecological connections between the population and the marine environment (Gaston and Nettleship 1982; Harding *et al.* 2007b). Diurnal and seasonal attendance illustrates the effort spent foraging for food items that could reflect stochastic short-term changes in prey avail-



**Figure 2.** Time-series decomposition of Thick-billed Murres (*Uria lomiva*), Kippaku, Greenland. The left vertical axis is number of Thick-billed Murres, the right axis is the relative variation visualized by the gray bars and the horizontal time axis is day of the year (180 = 29 June 2010). Data = plotted raw data, Daily = diurnal cycle, Trend = Loess smoothed raw data, Remainder = residuals from the Daily plus Trend fit.

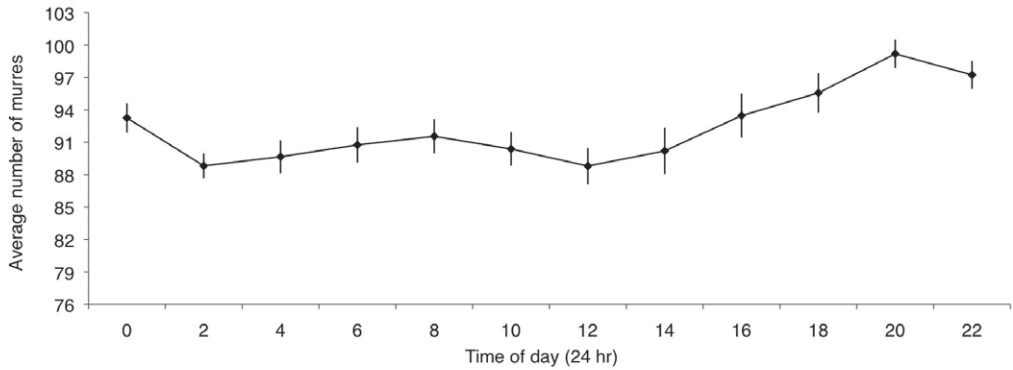
ability, long-term abundance of available food, and/or changes from incubation to chick provisioning (Burger and Piatt 1990; Uttley *et al.* 1994; Harding *et al.* 2007a; present study). For this case study, the range of 5 to 25% of maximum and minimum attendance and the low mean between maximum and minimum attendance observed for Kippaku for the 2010 breeding season suggest that the colony was doing well.

Using time-lapse photography to monitor colonies of gregarious breeding birds can depict diurnal and seasonal attendance trends with the potential to economically collect long-term population data. Correctly identifying diurnal and seasonal trends plays an important role in deciding when to collect data at colonies. For instance, if a colony

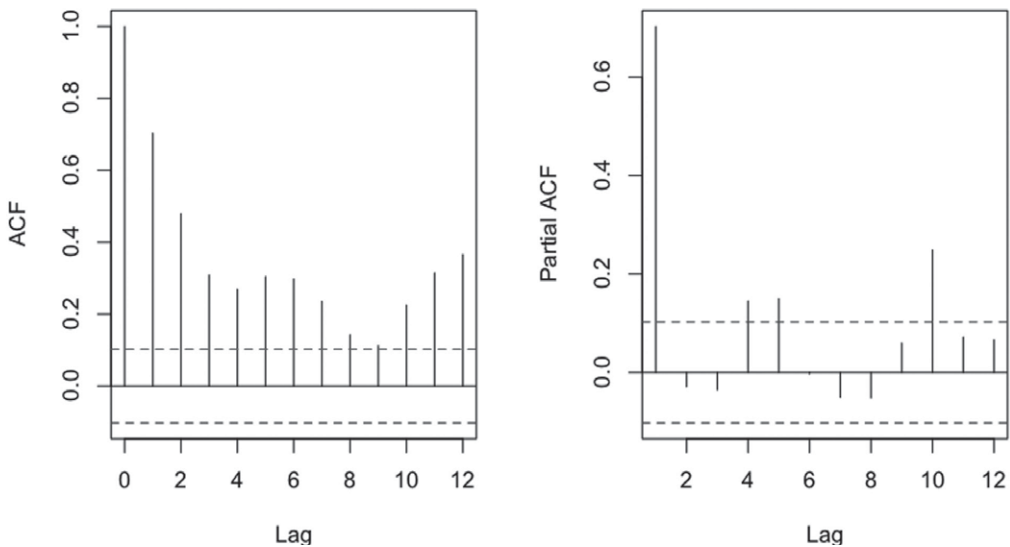
shows a peak in attendance at certain times of day then a total count of breeding birds could be underestimated if the count is not conducted during this peak in attendance, but if the diurnal pattern is known it is possible to correct for this variation by producing a standardized measurement (Cutler and Swann 1999; Mosbech *et al.* 2009). By using the proposed tool and following the same procedure in subsequent years, we could produce comparable population size estimates. In our case study, the mean difference between minimum and maximum colony attendance was only 14%, but it has been observed as high as 100% in Greenland Thick-billed Murre colonies (Merkel *et al.* 1999). This extreme difference illustrates the need to understand the diurnal colony



A)



B)



**Figure 3 A, B.** Comparison between time-lapse intervals for data collected on Thick-billed Murres (*Uria lomvia*), Kippaku, Greenland, 2010. A) Average individual attendance at 2-hr time-lapse interval with standard error. B) Autocorrelation function (ACF) and partial ACF at 2-hr time-lapse interval. Dotted lines = 95% confidence intervals. 1 lag = 2 hr.

attendance to accurately estimate population size for a study colony, and remote time-lapse photography is a cost effective tool to obtain such data.

The same issue of biased population estimates could arise if a distinct seasonal trend or event occurred during the breeding season, e.g., the large dips in attendance seen in Fig. 2 associated with severe storms. The dips in attendance during the storms show weather can affect colony attendance of Thick-billed Murres, similar to other alcids (Birkhead 1978; Slater 1980; Burger and Piatt 1990; Piatt *et al.* 1990). The ex-

ample emphasized the importance of having knowledge about the daily variation in attendance. Weather could easily account for biased counts of a colony if a storm had passed through the area some time before, as seen by the slow recovery in attendance after weather events (Fig. 2). Predation and non-weather disturbance events are also known to effect attendance levels (Schauer and Murphy 1996; Thayer *et al.* 1999; Mallory *et al.* 2009). However, the study site at Kippaku showed no breeding failures due to non-weather events in the study plot during the 2010 field season (N. P. Huffeldt, pers.

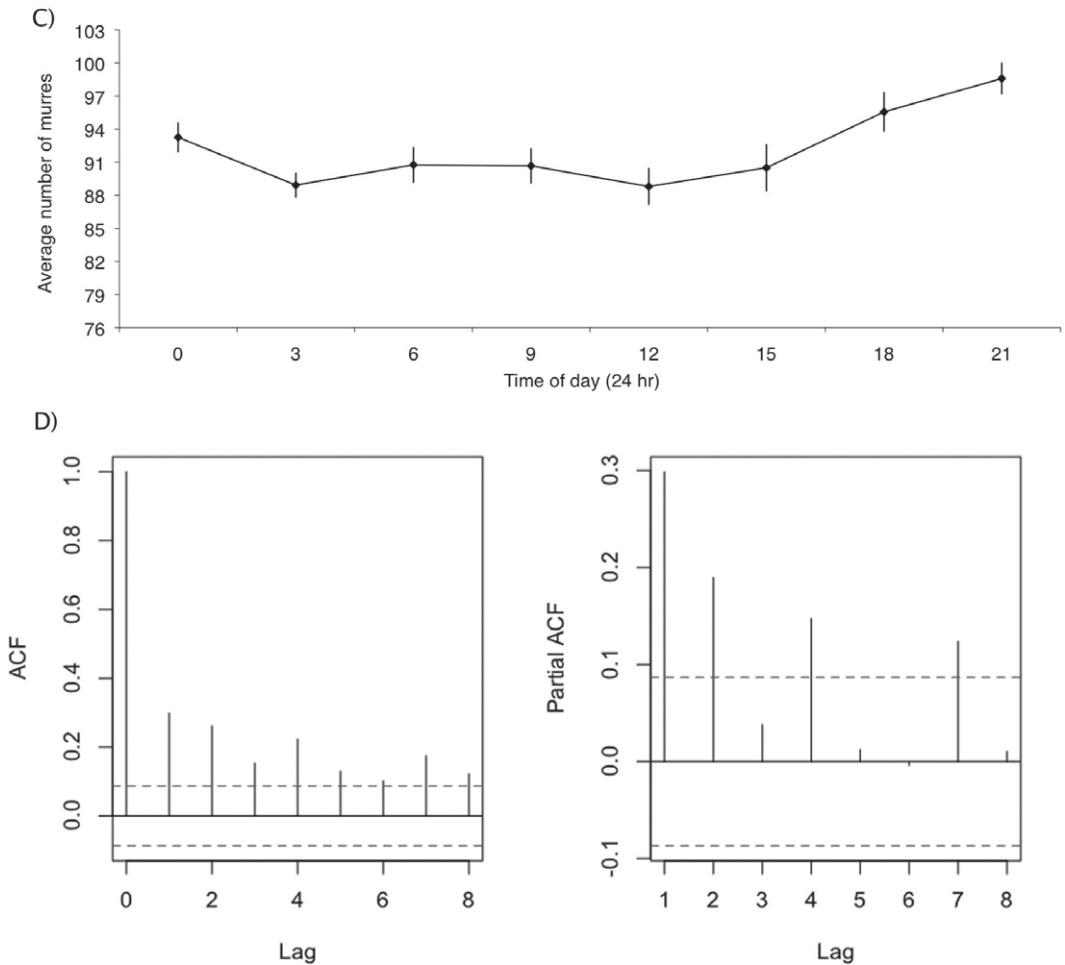


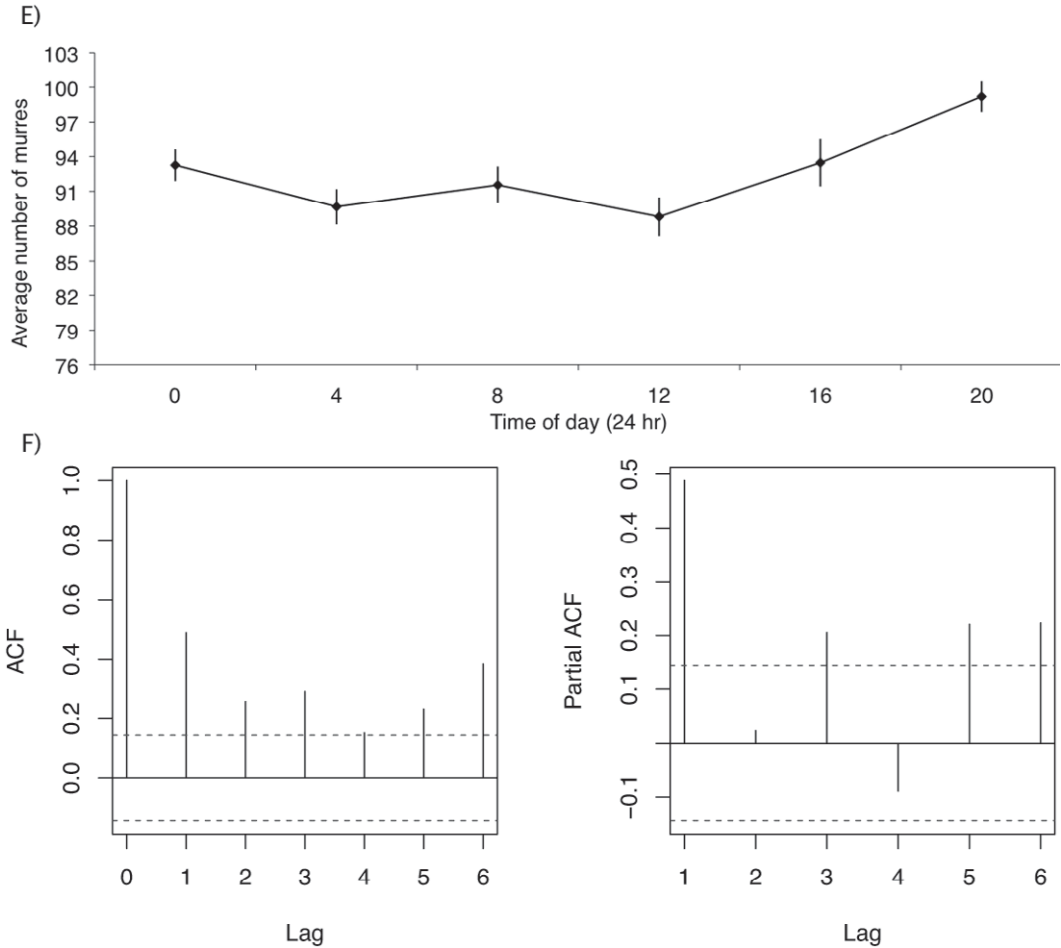
Figure 3 C, D. Comparison between time-lapse intervals for data collected on Thick-billed Murres (*Uria lomvia*), Kippaku, Greenland, 2010. C) Average individual attendance at 3-hr time-lapse interval with standard error. D) ACF and partial ACF at 3-hr time-lapse interval. Dotted lines = 95% confidence intervals. 1 lag = 3 hr.

obs.). In addition the presence of camera equipment most likely does not influence predation of nests in the Arctic including areas with mammalian and avian predators according to Mckinnon and B ty (2009).

In other members of the families Laridae and Alcidae, the arrival of non-breeders peaks toward the late chick-rearing period with a sharp decline at the first sign of fledging, with non-breeder activity related to prospecting behavior tracked over multiple years indicating the performance of a colony (Birkhead 1978; Harris *et al.* 1986; Cadiou 1999; Dittmann and Becker 2003).

Time-lapse photography could be used to identify established breeding pairs, and then using this information to determine the number of non-breeders attending the observed location. Even though the most variable component in colony attendance for some seabirds is attributed to non-breeders, it is suggested that the non-breeders follow a similar diurnal trend (Birkhead 1978; Harris *et al.* 1986). In this case study, the high attendance observed in the early and middle chick-rearing periods, and the subsequent drop in attendance during the late chick-rearing period, could be associ-





**Figure 3 E, F.** Comparison between time-lapse intervals for data collected on Thick-billed Murres (*Uria lomvia*), Kippaku, Greenland, 2010. **E)** Average individual attendance at 4-hr time-lapse interval with standard error. **F)** ACF and partial ACF at 4-hr time-lapse interval. Dotted lines = 95% confidence intervals. 1 lag = 4 hr.

ated with non-breeder activity. Further studies using time-lapse photography could be used to calculate a reasonable estimate of non-breeding individuals and thereby provide an additional parameter for colony performance. Also, understanding attendance patterns at a colony could be used for conservation and emergency response purposes, by understanding when during a 24-hr period or when in the season an environmental disaster (e.g., anthropogenic or natural) would most impact a colony, or as a regulatory tool to limit human disturbances (e.g., from tourists) during a season or diurnal period.

One can see from the example here using Thick-billed Murres that there were two peak attendance periods at approximately 12-hr intervals during a 24-hr period, the later peak being larger than the earlier peak (Figs. 1 and 2). A similar pattern with peaks at 08:00 hr and 20:00 hr was found for Common Murres (*Uria aalge*) during middle incubation period with little diurnal trend during the chick-rearing period (Birkhead 1978). The 12-hr intervals and time of the peaks correspond to the times of day when incubation/brooding shifts tend to occur between parents of Thick-billed Murre nests (Elliott *et al.* 2010; N. P. Huffeldt, unpubl.

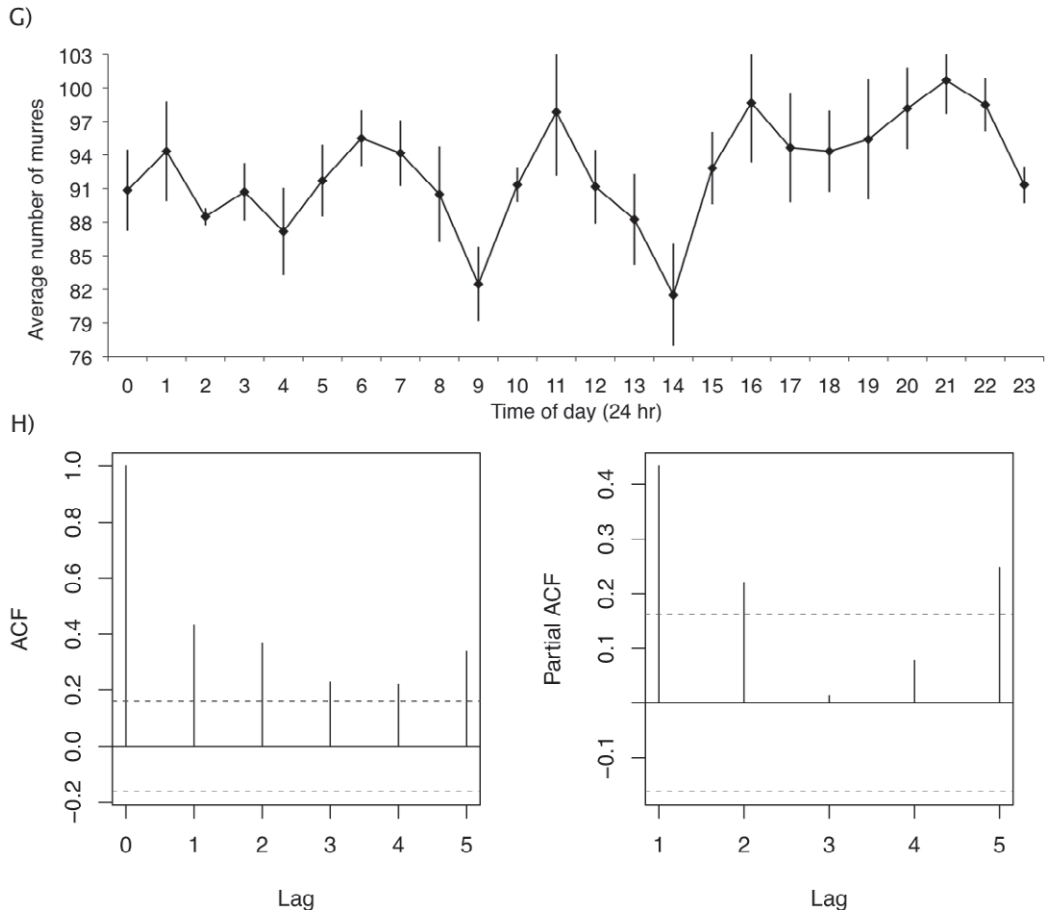


Figure 3 G, H. Comparison between time-lapse intervals for data collected on Thick-billed Murres (*Uria lomvia*), Kippaku, Greenland, 2010. G) Average individual attendance at 5-hr time-lapse interval with standard error. H) ACF and partial ACF at 5-hr time-lapse interval. Dotted lines = 95% confidence intervals. 1 lag = 5 hr.

data), and illustrates that when combined with previous knowledge or direct observation, time-lapse photography can provide additional results useful for management.

This study used only a single camera to observe a single Thick-billed Murre study plot within one colony. Inter-colony variation in attendance can exist due to colony size, location, and/or foraging conditions (Birkhead 1978; Zador and Piatt 1999; Harding *et al.* 2005; Elliott *et al.* 2010). In addition, within-colony variation and spatial autocorrelation in attendance, date of laying, and other breeding parameters can also exist (Birkhead 1978; Murphy and Schauer 1996; Jakubas and Wojczulanis-Jakubas 2011) and could be corrected with the use of multiple cameras observing additional areas of the

colony. However, the lack of additional cameras in this study is not a limitation to the method as such—the same limitation of intra- and inter-colony spatial autocorrelations and attendance differences would exist for direct observations and counts as well.

The limiting factor in time-lapse photography at the time of the study was the available memory for photograph storage and the amount of the work associated with counting individuals in the photos. Therefore, it could be necessary to increase the time-lapse interval from once per hour for long-term monitoring programs. If the study population shows a cyclic pattern, it appears to be necessary to incorporate an interval for time-lapse image capture that is divisible into the number of lags in the

attendance cycle as seen in Fig. 3 with the 5-hr interval between image capture and the apparent misrepresentation of a cyclic pattern in Figs. 3G and 3H. Even though the resolution appears to be better with a 5-hr interval because the interval samples across all hours of the day, the reduction in the sample size for each hour incorporates potential stochastic effects that become visible when compared to Fig. 1 and Figs. 3A and 3B. The 3-hr interval more accurately describes the pattern than the 5-hr interval, but the 3-hr interval misses the two highest attendance hours in the morning peak (Figs. 3C, 3D, 3G and 3H) suggesting that the peak takes place at a different interval than what is present in Fig. 1. Based on this, we recommend a 1-hr sampling interval as the most appropriate resolution to describe diurnal attendance patterns. For population monitoring over a seasonal scale, a sampling interval between 6 and 24 hr could be sufficient. This study takes one breeding season from a single colony into account for the case study, and, therefore, to implement this method in a long-term monitoring scheme a multi-year calibration should be considered to determine the appropriate interval to incorporate for this method. In addition, if the method should be used for multiple colonies, an individual adaptation of the interval/method for each colony should be considered. Other benefits and uses of using this method are that it could also be used to measure other behaviors such as individual time-budgets and feeding parameters using a shorter (minutes) interval, or colony arrival/departure and mean hatching dates using longer (days) sampling intervals, but this comes with the limitation of storage space and/or resolution, respectively.

The development of automated object-oriented photo recognition software for automatically counting seabirds could also greatly reduce the workload for each series of photographs, and should be considered as a key supplement to the proposed method. However, at this time the advancement of this technique is hindered by the complication of the drab colors of most seabirds

and the similar colors of their backgrounds (i.e., for our case study breeding cliffs and stones/rocks). Other elements of the data that could be expanded on include the use of GIS software to spatially analyze photographs, and the chronology of breeding parameters could be collected over a single season or multiple years to determine hatching success and nest failure events. Data from this method can be used to produce time-series of the precise phenology and population development of breeding seabirds, reducing the time needed to detect population changes and giving a better understanding of their biology. With the evolution of data storage, the photo system could be programmed to collect data over multiple years without data download, further reducing researcher effort.

Overall, the proposed method could greatly reduce man-hours and costs of seabird colony monitoring, while obtaining data that would have otherwise not been collected, thus improving conservation and management practices. This method could be applied to other systems that have similar characteristics.

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#### LITERATURE CITED

- Birkhead, T. R. 1978. Attendance patterns of Guillemots *Uria aalge* at breeding colonies on Skomer Island. *Ibis* 120: 219-229.
- Booms, T. L. and M. R. Fuller. 2003. Time-lapse video system used to study nesting Gyrfalcons. *Journal of Field Ornithology* 74: 416-422.
- Burger, A. E. and J. F. Piatt. 1990. Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. *Studies in Avian Biology* 14: 71-83.
- Cadiou, B. 1999. Attendance of breeders and prospectors reflects the duality of colonies in the Kittiwake *Rissa tridactyla*. *Ibis* 141: 321-326.

- Cleveland, R. B., W. S. Cleveland, J. E. McRae and I. Terpenning. 1990. STL: a seasonal-trend decomposition procedure based on Loess. *Journal of Official Statistics* 6: 3-73.
- Cowardin, L. M. and J. E. Ashe. 1965. An automatic camera device for measuring waterfowl use. *Journal of Wildlife Management* 29: 636-640.
- Cutler, T. L. and D. E. Swann. 1999. Using remote photography in wildlife ecology: a review. *Wildlife Society Bulletin* 27: 571-581.
- Dittmann, T. and P. H. Becker. 2003. Sex, age, experience and condition as factors affecting arrival date in prospecting common terns, *Sterna hirundo*. *Animal Behaviour* 65: 981-986.
- Einoder, L. D. 2009. A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* 95: 6-13.
- Elliott, K. H., A. J. Gaston and D. Crump. 2010. Sex-specific behavior by a monomorphic seabird represents risk partitioning. *Behavioral Ecology* 21: 1024-1032.
- Environmental Systems Research Institute (ESRI). 2008. ArcInfo and ArcMap v. 9.3. ESRI, Redlands, California.
- Gaston, A. J. and D. N. Nettleship. 1982. Factors determining seasonal changes in attendance at colonies of the Thick-billed Murre *Uria lomvia*. *Auk* 99: 468-473.
- Goetz, R. C. 1981. A photographic system for multiple automatic exposures under field conditions. *Journal of Wildlife Management* 45: 273-276.
- Gula, R., J. Theuerkauf, S. Rouys and A. Legault. 2010. An audio/video surveillance system for wildlife. *European Journal of Wildlife Research* 56: 803-807.
- Harding, A. M. A., J. F. Piatt, G. V. Byrd, S. A. Hatch, N. B. Konyukhov, E. U. Golubova and J. C. Williams. 2005. Variability in colony attendance of crevice-nesting Horned Puffins: implications for population monitoring. *Journal of Wildlife Management* 69: 1279-1296.
- Harding, A. M. A., J. F. Piatt and J. A. Schmutz. 2007a. Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. *Marine Ecology Progress Series* 352: 269-274.
- Harding, A. M. A., J. F. Piatt, J. A. Schmutz, M. T. Shultz, T. I. Van Pelt, A. B. Kettle and S. G. Speckman. 2007b. Prey density and the behavioral flexibility of a marine predator: the Common Murre (*Uria aalge*). *Ecology* 88: 2024-2033.
- Harris, M. P., S. Wanless and P. Rothery. 1986. Counts of breeding and nonbreeding Guillemots *Uria aalge* at a colony during the chick-rearing period. *Seabird* 9: 43-46.
- Jakubas, D. and K. Wojczulanis-Jakubas. 2011. Subcolony variation in phenology and breeding parameters in Little Auk *Alle alle*. *Polar Biology* 34: 31-39.
- King, D. I., R. M. Degraaf, P. J. Champlin and T. B. Champlin. 2001. A new method for wireless video monitoring of bird nests. *Wildlife Society Bulletin* 29: 349-353.
- Labansen, A., F. R. Merkel, M. Frederiksen, K. Falk and A. Mosbech. 2013. Monitoring af lomvier og rider i det nordlige Upernavik, 2008. Technical Report No. 90, Pinngortitaleriffik, Greenland Institute of Natural Resources, Nuuk, Greenland.
- Lorentzen, E., R. Choquet and H. Steen. 2012. Modeling state uncertainty with photo series data for the estimation of breeding success in a cliff-nesting seabird. *Journal of Ornithology* 152: 477-483.
- Lynn, J. C., S. S. Rosenstock and C. L. Chambers. 2008. Avian use of desert wildlife water developments as determined by remote videography. *Western North American Naturalist* 68: 107-112.
- Mallory, M. L., A. J. Gaston and H. G. Gilchrist. 2009. Sources of breeding season mortality in Canadian Arctic seabirds. *Arctic* 62: 333-341.
- Mallory, M. L., S. A. Robinson, C. E. Hebert and M. E. Forbes. 2010. Seabirds as indicators of aquatic ecosystem conditions: a case for gathering multiple proxies of seabird health. *Marine Pollution Bulletin* 60: 7-12.
- Mckinnon, L. and J. B ty. 2009. Effect of camera monitoring on survival rates of High-Arctic shorebird nests. *Journal of Field Ornithology* 80: 280-288.
- Merkel, F., A. S. Frich and P. Hangaard. 1999. Polarlomvien i Disko Bugt og det sydlige Upernavik. 1998. Bestandsopg relse og grundlag for fremtidig monitoring af lomviebestandene. Technical Report No. 25, Pinngortitaleriffik, Greenland Institute of Natural Resources, Nuuk, Greenland.
- Montalbano, F., III, P. W. Glanz, M. W. Olinde and L. S. Perrin. 1985. A solar-powered time-lapse camera to record wildlife activity. *Wildlife Society Bulletin* 13: 178-182.
- Mosbech, A., F. Merkel, D. Boertmann, K. Falk, M. Frederiksen, K. Johansen and C. Sonne. 2009. Thick-billed Murre studies in Disko Bay (Ritenbenk), West Greenland. In NERI Technical Report, 1-60. Department of Arctic Environment, National Environmental Research Institute, Aarhus University, Roskilde, Denmark.
- Murphy, E. C. and J. H. Schauer. 1996. Synchrony in egg-laying and reproductive success of neighboring Common Murres, *Uria aalge*. *Behavioral Ecology and Sociobiology* 39: 245-258.
- Piatt, J. F., B. D. Roberts and S. A. Hatch. 1990. Colony attendance and population monitoring of Least and Crested Auklets on St. Lawrence Island, Alaska. *Condor* 92: 97-106.
- Piatt, J. F., W. J. Sydeman and H. I. Browman. 2007. Seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series* 352: 199-309.
- R Development Core Team. 2010. R: a language and environment for statistical computing v. 2.12.1. R Foundation for Statistical Computing, Vienna, Austria.
- Schauer, J. H. S. and E. C. Murphy. 1996. Predation on eggs and nestlings of Common Murres (*Uria aalge*) at Bluff, Alaska. *Colonial Waterbirds* 19: 186-198.
- Slater, P. J. B. 1980. Factors affecting the numbers of Guillemots *Uria aalge* present on cliffs. *Ornis Scandinavica* 11: 155-163.
- Temple, S. A. 1972. A portable time-lapse camera for recording wildlife activity. *Journal of Wildlife Management* 36: 944-947.

- Tennyson, L. C., P. F. Folliott and D. B. Thorud. 1974. Use of time-lapse photography to assess potential interception in Arizona ponderosa pine. *Journal of the American Water Resources Association* 10: 1246-1254.
- Thayer, J. A., W. J. Sydeman, N. P. Fairman and S. G. Allen. 1999. Attendance and effects of disturbance on coastal Common Murre colonies at Point Reyes, California. *Waterbirds* 22: 130-139.
- Uttley, J. D., P. Walton, P. Monaghan and G. Austin. 1994. The effects of food abundance on breeding performance and adult time budgets of Guillemots *Uria aalge*. *Ibis* 136: 205-213.
- Weller, M. W. and D. V. Derksen. 1972. Use of time-lapse photography to study nesting activities of birds. *Auk* 89: 196-200.
- Zador, S. G. and J. F. Piatt. 1999. Time-budgets of Common Murres at a declining and increasing colony in Alaska. *Condor* 101: 149-152.