RESEARCH ARTICLE

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Estimating nest-level phenology and reproductive success of colonial seabirds using time-lapse cameras

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Abstract

1. Collecting spatially extensive data on phenology and reproductive success is important for seabird conservation and management, but can be logistically challenging in remote regions. Autonomous time-lapse camera systems offer an opportunity to provide such coverage.

2. We describe a method to estimate nest-level breeding phenology and reproductive success of colonial pygoscelid penguins using photographs from time-lapse cameras. The method derives from stereotypical patterns of nest attendance, where predominantly two adults are present before and during laying, but switch to one adult during incubation. The switch approximates the date of clutch completion and is estimated by fitting a smoothing spline to daily nest attendance data, identifying candidate dates that switch from two adults to one and selecting the date when the first derivative of the spline is minimized. Clutch initiation and hatch dates are then estimated from the mean, species-specific interval between laying (pygoscelid penguins typically lay two eggs) and the duration of the incubation period. We estimated these intervals for each species from historical field data. The phenology is adjusted when photographs indicate egg or chick presence prior to their estimated lay or hatch dates. The number of chicks alive in each study nest on its crèche date determines reproductive success estimates. The method was validated with concurrent direct observations for each species and then applied to a camera network in the Antarctic Peninsula region to demonstrate its utility.

3. Mean egg laying and incubation intervals from direct observations were similar within species across sites. In the validation study, the mean clutch initiation, hatch and crèche dates were generally equivalent between photographs and

direct observations. Estimates of reproductive success were identical. Applying the method to a time-lapse network suggested relatively high reproductive success for all species across the region and corroborated general understanding of latitudinal trends and species-level plasticity in phenology.

4. The method accurately estimated phenology and reproductive success relative to direct observations and appears well-suited to operationalize regional time-lapse camera networks. The estimation method should be applicable for other seabirds with stereotypical nest attendance patterns from which breeding phenology could be estimated.

1 | INTRODUCTION

Data on reproduction, including breeding phenology and nest success, are important for management and conservation of seabirds globally (Cairns, 1987; Constable, de la Mare, Agnew, Everson, & Miller, 2000; Cury et al., 2011). In particular, breeding phenology and reproductive success data from seabirds are thought to indicate general conditions of marine ecosystems (Cairns, 1987) and represent important components for the development of ecosystem-based fisheries management (Einoder, 2009). However, monitoring to collect such data can be time intensive and requires experienced field personnel, often in remote sites for extended periods of time. The commitment of personnel to the field may also necessitate spatially restricted data collection (relative to species distribution). In particular, long-term ecological studies at single sites can provide high resolution data, but population-level inference requires an assumption that such data represent regional trends. This is not always the case (e.g., Lynch, Naveen, Trathan, & Fagan, 2012). Furthermore, direct observations of nests may bias estimates of reproductive phenology or success via a variety of mechanisms (e.g. observer disturbance, predator facilitation, nest abandonment) that can ultimately result in nest failure (Carney & Sydeman, 1999). As an alternative, autonomous camera networks may provide a solution that can expand spatial coverage of seabird monitoring in a cost-effective, non-invasive way (e.g. Newbery & Southwell, 2009). Widespread application of such systems would benefit from simple methods to standardize analysis of data derived from photographic images. We report a novel method to estimate seabird breeding phenology and reproductive success using colonial pygoscelid penguins as a model, with photographs collected from time-lapse cameras. We apply the method to a collaborative, multi-national camera network that was deployed in the Antarctic Peninsula region in the austral summer of 2015/16 to monitor penguin colonies.

Remote photography, defined as "photography or videography of wild animals in the absence of the researcher" (Cutler & Swann,

1999), is commonly used for research and monitoring of seabirds around the world (Cutler & Swann, 1999), particularly for studying nest predation (e.g. Collins, Green, Dodd, Shaw, & Halsey, 2014; Davies, Dilley, Bond, Cuthbert, & Ryan, 2015), nesting activity (e.g. Weller & Derksen, 1977) patterns of attendance (e.g. Black, Collen, Johnston, & Hart, 2016; Huffeldt & Merkel, 2013; Lynch, Alderman, & Hobday, 2015; Southwell & Emmerson, 2015; Southwell et al., 2013) and to estimate reproductive success (e.g. Merkel, Johansen, & Kristensen, 2016). Another potential application of these systems is to use time-lapse cameras to estimate the breeding phenology (i.e. the timing of reproductive events, including dates of clutch initiation, hatch and crèche) and reproductive success (i.e. numbers of chicks raised to independence per nest). Such data are useful for examining factors that impact seabird populations, including climate change (e.g. Visser & Both, 2005) and fishing (e.g. Agnew 1997; Constable et al., 2000; Cury et al., 2011).

For many species, the timing of phenological events (e.g. laying or hatching) can vary inter-annually and spatially depending on local environmental conditions, but the duration of intervals between specific phenological events (e.g. duration of incubation) tend to be more fixed. Thus, estimating annual breeding phenology minimally requires identifying a reliably observed event that can be placed into a known timeline, allowing back or forward calculation of the dates of other unobserved events. Estimating breeding phenology and reproductive success from time-lapse photography among colonially nesting pygoscelid penguins may be particularly ideal, given stereotypical patterns of adult attendance at their nest during the breeding season, relatively fixed periods of time between events in the breeding cycle and fidelity of chicks to their nest from hatch until crèche (defined here as the day when the chick is first left unattended by a parent). Such characteristics provide observable indicators of major events during the breeding season from which breeding phenology and reproductive success may be estimated, even if nest contents or particular breeding events cannot be observed directly or regularly in photographs. Southwell and Emmerson (2015) demonstrated that

peak attendance of adults at the colony level was synchronized at the start of laying in Adélie penguins *Pygoscelis adeliae*. Here, we extend this idea to the nest level and develop a simple method to reconstruct breeding phenology from photographic observations of nest attendance and opportunistic verification of nest contents.

In photographs, the number of parents attending the nest and the presence/absence of large chicks are reliably observed (Supporting Information Figures S1–S3). Direct observations of specific phenological events (i.e. lay and hatch) are possible less frequently, because protective postures by adults generally preclude a clear view of nest contents in photographs. However, among pygoscelid penguins, clutch completion is typically marked by a shift in adult attendance at the nest from predominantly two birds to predominantly one (e.g. Trivelpiece & Trivelpiece, 1990; Williams, 1995). This shift is readily observable because mates alternate incubation duties to forage at sea. If the date of this shift in adult attendance is estimable, then the interval between laying (pygoscelid penguins typically lay a maximum of 2 eggs per nest) can be used to back-calculate lay dates and the duration of the incubation period can be used to forecast hatch dates. Breeding phenology and success of the nest can then be completed with observations of the crèche date and the number of chicks alive on that day respectively.

To advance the use of time-lapse cameras to provide standardized data on phenology and reproductive success, we report on: (1) a method for estimating breeding phenology from photographic records of adult attendance and nest contents at focal nests; (2) mean durations of the laying, incubation, and brood/guard periods that are necessary to parameterize the estimation procedure for Adélie, chinstrap *P. antarctica* and gentoo *P. papua* penguins from several monitoring sites around Antarctica; (3) validating the estimation method with direct observations collected concurrently for each species; (4) applying the estimation method to a remote camera network newly deployed in the Antarctic Peninsula region; and (5) a sensitivity analysis to identify the minimum number of daily time-lapse images necessary for confidence in the estimated phenology.

2 | MATERIALS AND METHODS

2.1 | Camera deployment

We used autonomous time-lapse cameras (Reconyx Hyperfire HC500 or PC800) with an expected operational endurance of greater than 1 year when deployed with 12-AA lithium metal batteries. This endurance was essential, as visits to some sites are only possible for short periods once per year. Cameras were deployed to capture a minimum of 6–12 photographs per day, taken at 30 min or 60 min intervals, between local daylight hours of 09.00 and 15.00. The cameras were positioned 1.5–2 m above-ground level on tripods or partially buried metal poles. In general, focal nests were 2–10 m from the camera and photographed at an oblique angle (between 8° and 45°) to facilitate viewing of nest contents. For each camera, experience suggests that up to 20 nests can be reliably monitored for the duration of the breeding season depending on nest density
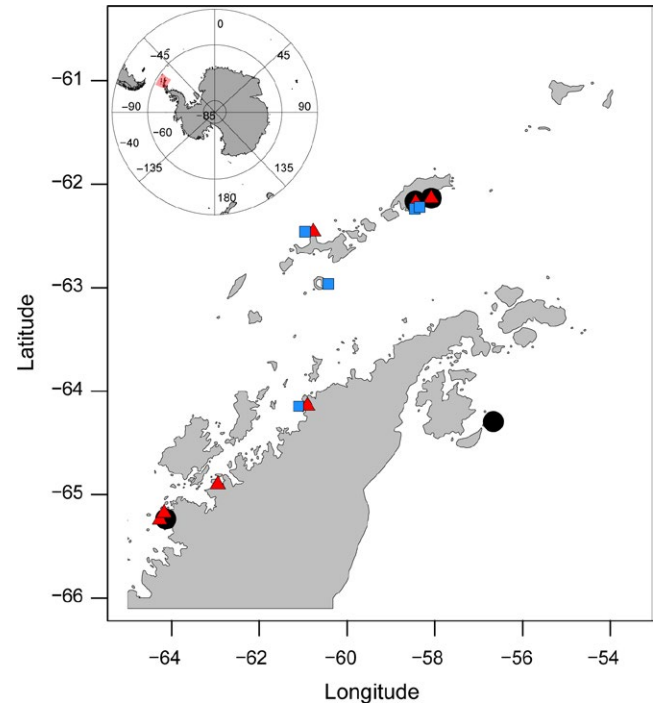

FIGURE 1 Map of the camera network sites for Adélie (black), gentoo (red) and chinstrap (blue). Inset shows the study location (red shaded polygon) relative to Antarctica

and topography. The cameras were deployed at several sites along the South Shetland Islands and Antarctic Peninsula (Figure 1). Data for the validation study (see below) were collected at Cape Shirreff, Point Thomas and Lion's Rump (Table 1). An example camera deployment is shown in Figure S4.

2.2 | Photo classification

Photographs were classified manually by teams from each site using the following protocol. Nests were selected for daily classification by identifying those which contained at least two adult birds prior to laying. From the daily set of available photographs, the maximum adult attendance at each study nest (nest attendance was defined simply as the number of adults associated with a given nest and this can be visualized in Figures S1 and S2) was recorded beginning on the date when two adults were observed attending an empty nest bowl. Daily classification of nest attendance and nest contents proceeded until nest failure or crèche was confirmed. Nest contents (the number of eggs and chicks) were identified and counted only when clear evidence of their presence or absence was visible in a photograph. On days when the nest was not visible due to nest obscurement by other birds in the foreground, iced lenses or poor visibility due to storms, fog or heavy precipitation, nest attendance was recorded as unknown. On average for each nest, all-day obscurement occurred 2% of the time across the camera network. Photographic evidence confirming a lay or hatch event was also recorded. If one photograph exhibited no eggs or chicks in the nest, but a subsequent photograph within 24 hr revealed an

TABLE 1 Data summaries from time-lapse studies during the 2016/17 field season by species and locality from the remote camera network in the Antarctic Peninsula region. Due to logistic necessity, data retrieval from the cameras at Paradise Bay occurred prior to crèche. Validation sites for each species are noted with an italicized locality

Species	Locality	Longitude	Latitude	No. cameras	Reproductive success			Breeding phenology (m day^{-1} year^{-1})		
					No. nests monitored	No. chicks crèched	No. crèched per nest	Mean lay	Mean hatch	Mean crèche
Adélie	Copacabana	−58.456	−62.175	5	50	76	1.52	10/28/2016	12/3/2016	1/1/2017
	Lion's Rump	−58.126	−62.135	5	41	55	1.34	10/28/2016	12/3/2016	12/30/2016
	Pt. Thomas	−58.462	−62.163	3	31	42	1.35	10/26/2016	12/1/2016	12/28/2016
	Seymour	−56.694	−64.295	3	24	33	1.38	11/12/2016	12/18/2016	1/8/2017
	Yalour	−64.164	−65.235	3	34	48	1.41	11/18/2016	12/24/2016	1/27/2017
Gentoo	*Cape Shirreff*	−60.789	−62.46	2	8	13	1.63	11/12/2016	12/21/2016	1/18/2017
	Cierva Cove	−60.984	−64.143	2	15	22	1.47	11/15/2016	12/22/2016	1/20/2017
	Copacabana	−58.456	−62.175	6	58	89	1.53	10/16/2016	11/23/2016	12/22/2016
	Galindez	−64.247	−65.244	3	28	41	1.46	11/29/2016	1/6/2017	2/4/2017
	Lion's Rump	−58.126	−62.135	3	19	24	1.26	10/16/2016	11/24/2016	12/20/2016
	Paradise Bay	−62.91	−64.902	3	26	NA	NA	12/22/2016	1/28/2017	NA
	Petermann	−64.189	−65.177	3	37	56	1.51	11/27/2016	1/2/2017	2/8/2017
Chinstrap	*Cape Shirreff*	−60.789	−62.46	2	10	13	1.30	11/18/2016	12/25/2016	1/25/2017
	Cierva Cove	−60.984	−64.143	3	30	50	1.67	11/21/2016	12/28/2016	1/25/2017
	Patelnia	−58.469	−62.236	2	13	16	1.23	11/15/2016	12/22/2016	1/25/2017
	Uchatka	−58.439	−62.22	2	14	17	1.21	11/13/2016	12/21/2016	1/22/2017
	Vapour	−60.504	−62.962	1	15	23	1.53	11/12/2016	12/19/2016	1/21/2017

egg or chick, the lay or hatch date, respectively, was registered as the day on which the egg or chick was observed. Similarly, the presence of crushed or partial egg shells on the nest was considered evidence of hatch, as those shells are typically ejected from the nest bowl following hatch and quickly lost to predators, winds or trampling. Crèche dates were recorded on the date when the clear association between a parent and its chicks at the nest was not distinguishable or when chicks were clearly unattended in their nest. Note that identifying the crèche date, both on the ground and in photographs, is nonetheless subjective because, without an identifying mark, movement of birds and temporary associations of chicks with other birds in the colony at this time hinder definitively tracking parent–offspring associations. We briefly discuss the time investment for manual classification of photographs later.

2.3 | Estimation of clutch initiation and hatch dates

Nest-level clutch initiation dates (CID, the date when the first egg was laid) and hatch dates were estimated from the photographic attendance and nest content data with a four-step process. Our approach assumes that nest attendance during daylight hours exhibits a switch from predominantly two birds to predominantly one bird around the time of clutch completion (Trivelpiece & Trivelpiece, 1990). The date of this shift in attendance was estimated by first fitting a smoothing spline (Chambers & Hastie, 1992), implemented with the *smooth.spline* function in R (R Core Team, 2016) with 10 *df*, to the attendance data and taking the first derivative of the fitted smooth. Next, the attendance data were differenced (lag of 1) to identify candidate dates when the observed nest attendance shifted from two to one. The switch date was selected from the candidate dates where the first derivative (slope) of the smooth was minimized. The estimation procedure is illustrated in Supporting Information Figure S5. The CID was then back-calculated from the shift date based on a species-specific mean interval between the first and second lay dates (see section below). Direct observations of nest attendance during the laying period suggest that the switch date generally occurs at the time of clutch completion by Adélie penguins, up to 1 day prior to clutch completion by chinstrap penguins, and 1 or 2 days before clutch completion by gentoo penguins (Trivelpiece & Trivelpiece, 1990). This apparent switch prior to clutch completion owes to daytime foraging of one of the mates, with subsequent returns for either clutch completion or incubation relief. We therefore adjusted the back-calculation of CID from the switch date by 0 days for Adélie, and 1 day for chinstrap and gentoo penguins to account for these stereotypical attendance patterns during the laying period (Trivelpiece & Trivelpiece, 1990). The hatch date for the first chick was then projected from the estimated CID based on a species-specific mean incubation period based on historical direct observations (see section below).

The CID and hatch dates estimated from attendance data were checked against the nest content observations and adjusted if necessary. First, if an exact lay date was observed in the photographs, we replaced the estimated CID with the observed CID.

Second, if an egg was observed in the nest prior to the estimated CID, we back-calculated a new CID from the first egg observation date. This calculation was based on the validation data (see below) which suggested that the first observation of an egg in a photograph occurred, provided the egg was observed within 1 week of the true CID, 2 ± 1.8 (*SD*) days after true clutch completion. Hatch dates were recalculated for any corrected CID. Finally, we replaced the estimated hatch date with the observed hatch date if the hatch date was considered known. The code for this estimation procedure was developed in R v 3.2.2 (R Core Team, 2016) and is available in Supporting Information Appendix S1.

2.4 | Laying incubation, and brood intervals

The intervals for estimating clutch initiation and hatch dates from the switch date derive from historical studies at two colonies per species. Laying, incubation and brood/guard interval data were collected for Adélie penguins at the Copacabana colony in the Antarctic Peninsula and at Béchervaise Island in East Antarctica (67.58°S, 62.82°E). The interval data for gentoo penguins were collected at Copacabana and at Cape Shirreff, Livingston Island. Interval data for chinstrap penguins were collected at Cape Shirreff and at Signy Island, in the Scotia Sea, (60.71°S, 45.63°W). These data were collected from daily direct observations of 40–200 nests per species per colony (e.g. CCAMLR, 2014; Hinke, Salwicka, Trivelpiece, Watters, & Trivelpiece, 2007) to determine exact lay and hatch dates for each egg or chick respectively. The observation interval used for chinstrap penguins at Signy Island varied over time, averaging 2 days (range: 1–6 days). Brood/guard interval data were not available for chinstraps at Signy Island.

2.5 | Validation study

We conducted simultaneous direct observations in photographed nesting areas for all three species to validate the phenology estimation method. Adélie penguin validation studies were conducted at the Pt. Thomas and Lion's Rump colony on King George Island with 2 cameras and 10 total nests. Validation studies for gentoo penguins were conducted at Cape Shirreff and Lion's Rump with 3 cameras and 13 total nests, while data for chinstrap penguins were collected at Cape Shirreff with 4 cameras and 20 total nests over 2 years. Within the field of view of each camera, 3–7 (*M* = 4.77) nests were observed daily by direct observation to record dates of laying, hatching, and nest failure or crèche. Photographs were manually classified as described above. Reproductive success was estimated as the number of chicks crèched per nest. Classification of the validation photographs was conducted by personnel without knowledge of the direct observations to avoid biasing the classification.

2.6 | Sensitivity analysis

The sensitivity of the estimated switch date to photograph frequency (number of photographs per day) and interval (time elapsed
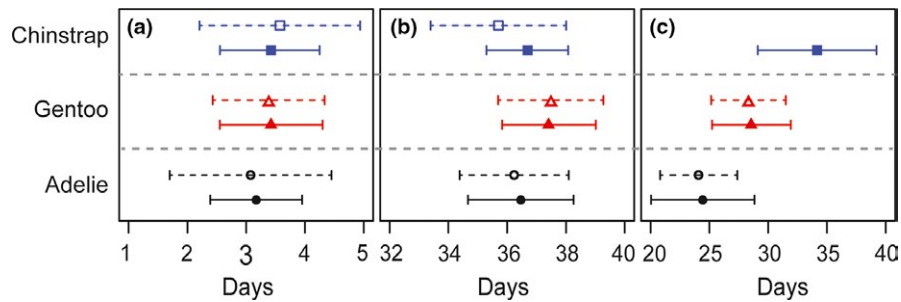
FIGURE 2 Mean and one standard deviation, in days, for the historical, directly observed intervals between (a) lay dates of egg 1 and egg 2 (b) incubation from first egg laid until first chick hatched; and (c) brood/guard phase from first chick hatched to first chick crèched for Adélie penguins from Copacabana (black solid) and Bechervaise Island (black dashed), for gentoo penguins from Copacabana (red solid) and Cape Shirreff (red dashed), and for chinstrap penguins from Cape Shirreff (blue solid) and Signy Island (blue dashed). Brood/guard interval data was not available for Signy Island

between photographs) was analysed by sub-setting the 2015/16 photographs of chinstrap penguins at Cape Shirreff and quantifying the maximum number of adults at each nest across x consecutive photographs, where x ranges from 1 to 12 for 30-min intervals and from 1 to 6 for 60-min intervals. We computed the variance of the estimated switch dates for each frequency and interval; a low variance indicates that the estimated switch date was insensitive to the chosen frequency or interval.

3 | RESULTS

Historical data on laying and incubation intervals were similar across species and sites. The mean laying interval was approximately 3 days for all species from all sites (Figure 2a) and there was no difference among species. Likewise, the incubation stage lasted approximately 37 days each species (Figure 2b) across sites. For chinstraps, a difference between Cape Shirreff and Signy Island incubation intervals was evident (0.98 ± 0.3 days [95% CI]; t_{285} = 6.47, p < .001). However, this difference was less than the mean observation interval at Signy Island and we, therefore, assume that incubation intervals for chinstrap penguins are equivalent across sites. The duration of brood/guard stages from hatch to crèche differed by species (Figure 2c), ranging from 24 days (Adélie penguins) to 35 days (chinstrap penguins).

The photograph-based estimates of breeding phenology and reproductive success were generally equivalent to direct observations. When species were combined, the mean differences in nest-level CIDs ($\bar{x}$ = 0.02 ± 0.83 days [95% CI], t_{33} = 0.05, p = .96) and hatch dates ($\bar{x}$ = 0.49 ± 0.76 days [95% CI], t_{31} = 1.32, p = .2) were not different from direct observation data (Figure 3). The mean difference between crèche dates was larger ($\bar{x}$ = −0.84 ± 0.8 days [95% CI], t_{31} = −2.15, p = .04), but within 1 day and with a median difference of 0 days (Figure 3). Species-specific differences between the dates of direct and photographic observations of CID, hatch and crèche were similarly well estimated but the observations of crèche dates in Adélie penguins suggested that direct
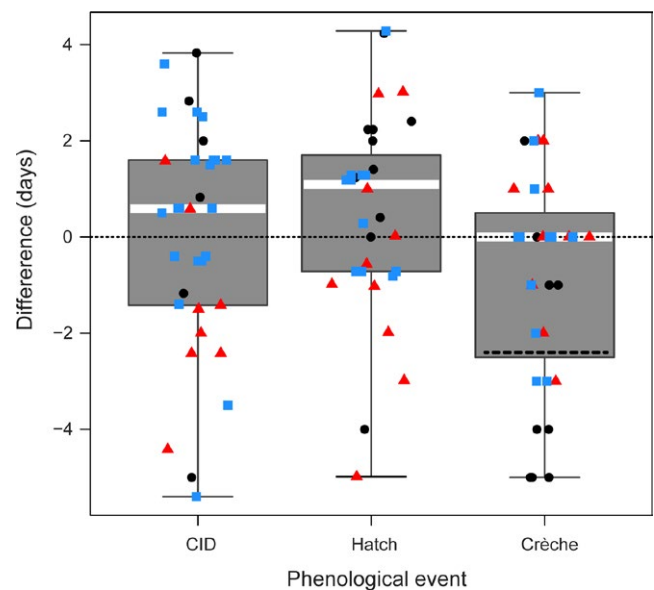

FIGURE 3 Boxplot of nest-level differences (in days) between photograph-estimated and directly observed dates for clutch initiation (CID), hatch and crèche for Adélie (black circles), gentoo (red triangles) and chinstrap penguins (blue squares) combined. The whiskers represent the full range of observed differences. The mean difference in Adélie crèche date estimates is indicated with a dashed black line. The dotted line marks a difference of 0 days for reference

observations tended to indicate crèche later than photographic observations ($\bar{x}$ = −2.4 ± 1.8 days [95% CI], t_{7} = −3.03, p = .01). All other species-specific comparisons were not significantly different. Estimates of reproductive success from photographs were identical to direct efforts, agreeing that 16 Adélie, 18 gentoo and 22 chinstrap chicks reached crèche.

Applying the estimation method to the data collected during the 2016/17 austral breeding season across the camera network revealed several consistencies. Reproductive success was, on average, relatively high for all species (Table 1). Crèche rates averaged over 1.4 chicks per nest for all species (range: 1.21–1.67; Table 1). Linear

regression models indicated that latitude explained a large proportion of the variation in CID for Adélie (R^2 = .99, $F_{1,3}$ = 602, p < .01) and gentoo penguins (R^2 = .74, $F_{1,5}$ = 14.3, p = .01), while chinstrap CID was not explained by colony latitude (R^2 = .38, $F_{1,3}$ = 1.82, p = .27), noting that the latitudinal range of chinstrap observations was smaller than for the other species (Figure 4a). The timing of phenological events across the network exhibited species-specific

FIGURE 4 Relationship of CID to latitude (a) and range of timing for clutch initiation, hatch and crèche for each species across the camera network (b)

windows (Figure 4b), with gentoo penguins exhibiting the widest range of dates for CID, hatch and crèche, while each breeding phase for chinstrap penguins showed little spatial variation.

The sensitivity analysis suggested that, for both 30- and 60-min intervals, the switch date is well estimated by ≥4 consecutive photographs per day (Figure 5).

4 | DISCUSSION

The development of a phenological estimation method and the deployment of a time-lapse network in the Antarctic Peninsula system were driven by a desire for spatially extensive ecosystem monitoring data to inform fisheries management. The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is the authority responsible for fisheries management in Antarctica. The CCAMLR coordinates a voluntary ecosystem monitoring program (CEMP) among CCAMLR Member states to monitor air-breathing predators around the continent with standardized methods (Agnew, 1997). The CEMP aims to detect changes in indicator species and interpret changes with respect to environmental variability and fishery catches and specifically includes data collection protocols for reproductive success and breeding phenology (CCAMLR, 2014). Historically, data submitted to the CEMP have been spatially restricted owing to logistical and financial constraints on field work in Antarctica. The camera network is an effort to expand the scale of monitoring to more effectively deliver advice on the status of predators for precautionary fisheries management. A standardized method is intended to streamline data collection and analysis to support the provision of management advice.

Towards that goal, we developed and validated a method for estimating phenology and reproductive success of wild pygoscelid penguins from time-lapse images. The similarity of directly observed laying and incubation intervals within each of the pygoscelid penguin species (Figure 2, see also Black, 2016) underpins the generality of the method for broad spatial application. However, we note that uncertainty in the mean durations exists (Figure 2). While the method based on the assumption of a fixed interval provides
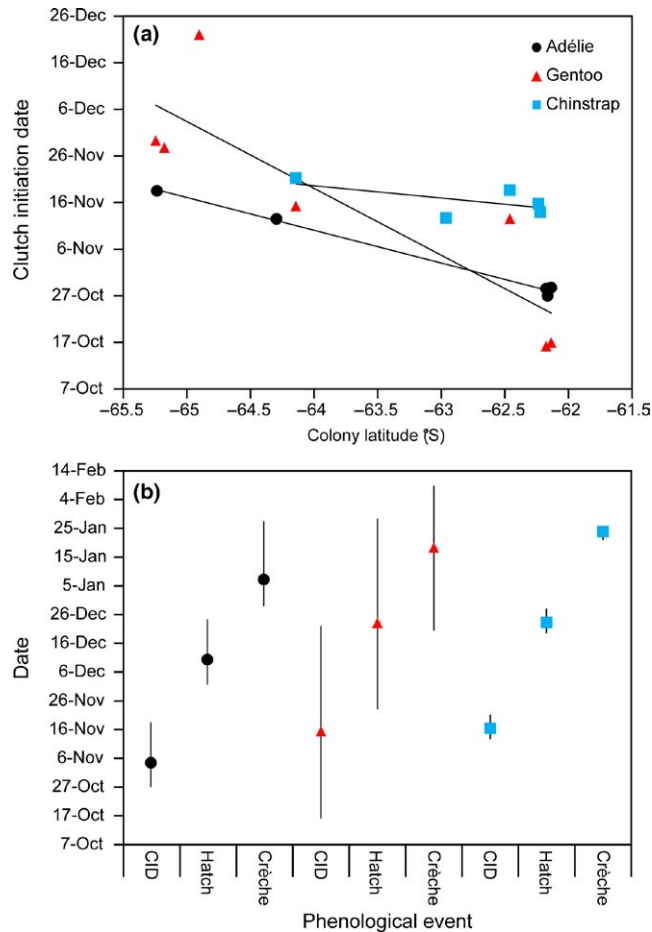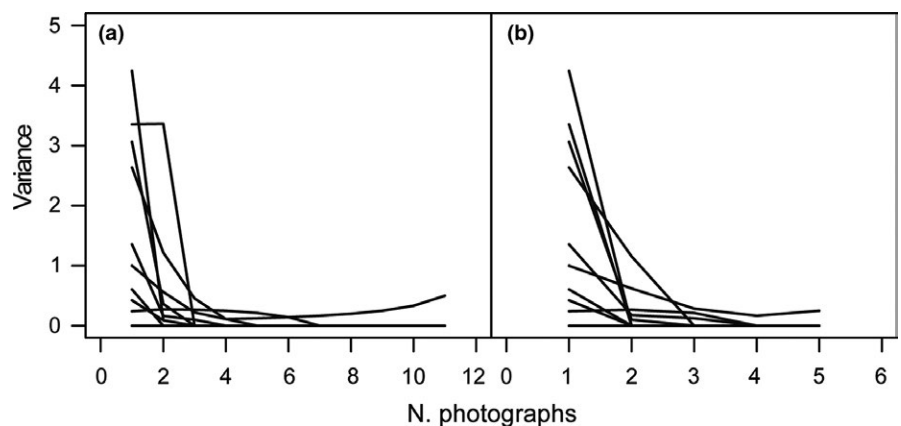

FIGURE 5 Variance in the estimates of switch date, based on the number of photographs classified, for photograph intervals of (a) 30 min and (b) 60 min. Each nest (N = 10) is represented by a line

estimates of CID and hatch in the absence of egg or chick observations, the additional information from egg and/or chick observations adds flexibility to preserve variation in laying and incubation intervals when data indicate. Across the camera network 22% of the phenology estimates were corrected based on egg or chick observations that contradicted the fixed-interval assumptions. Thus, the method takes full advantage of the variable nature of time-lapse images that may or may not record the exact timing of key phenological events. Importantly, the validation study confirmed that the signal derived from changes in adult attendance at the nest level and confirmation of nest contents can estimate CID, hatch dates and reproductive success with high accuracy for pygoscelid penguins. This suggests that the method could be parameterized with other location- and/or species-specific laying and incubation intervals, as necessary, to further extend the approach to other breeding regions or seabird species, provided images can be captured that clearly record individual nests and adult attendance in sufficient numbers. Finally, we note that the crèche dates for Adélie penguins were the only metric with a significant difference between direct and photographic observations. We regard the observed level of inaccuracy as acceptable given the subjectivity of crèche determination for both observation methods and the limited sample sizes in the validation study.

4.1 | Application to a camera network

Applying the method to a recently deployed network of time-lapse cameras demonstrated its utility across monitoring sites and research teams, and, importantly, provided results consistent with known phenological variation due to colony latitude and plasticity among the pygoscelid penguins breeding in the Antarctic Peninsula region (Black, 2016; Hinke, Polito, Reiss, Trivelpiece, & Trivelpiece, 2012; Lynch, Fagan, Naveen, Trivelpiece, & Trivelpiece, 2009). In particular, the relatively high degree of plasticity in gentoo penguins relative to Adélie penguins has been shown for inter-annual differences in phenology (Hinke et al., 2012; Juáres et al., 2013). This work extends that result to suggest intra-annual plasticity is also higher in gentoo penguins than in Adélie penguins. Similarly, while inter-annual variation in breeding phenology of chinstraps can be high (e.g. Black, 2016), the narrow window of time for each phenological event exhibited by chinstrap penguins across the camera network in 2016/17 was an unexpected, novel result. Chinstrap penguins are highly migratory (e.g. Hinke et al., 2017) and, like other migratory species, their arrival to the colony and subsequent breeding phenology may not be as strongly coupled or sensitive to local breeding conditions (Both et al., 2010). However, the interactions between migration triggers and local breeding conditions that might allow inter-annual variation in phenology (Black, 2016) but little intra-annual spatial variation as observed here remain unclear. Further monitoring will be worthwhile to assess the generality of this novel result among chinstrap penguins. With respect

to the method developed here, it is evident that integration of data collection and analysis methods can provide novel insights on spatial scales beyond focal colony monitoring.

4.2 | Advantages and disadvantages

The phenological estimation method based on time-lapse data has several advantages relative to traditional direct observations. One major advantage is the capacity to include monitoring at colonies that researchers are unable to regularly visit, as a camera can run for at least one full year without maintenance. Solar-powered options, such as those described by Newbery and Southwell (2009) can run even longer if light conditions are suitable. Such endurance enables remote sites to be monitored in a low-cost, efficient way, augmenting traditional monitoring programmes and extending the scope of data collection (e.g. Black, Raya Rey, & Hart, 2017).

The basic datum necessary for phenological estimation is adult attendance. This has three main advantages. First, photograph resolution need only be high enough for individual nests and their contents to be reliably identified. The cameras we used provided images with relatively low photograph resolution (.jpg format, 72 dpi, ca. 500 kb) that was adequate for data needs, but higher resolution or larger format photographs (e.g. Lynch et al., 2015; Southwell & Emmerson, 2015) could also be used. Second, as noted above, roughly 80% of nest-level phenologies were estimable from adult attendance data only. A primary data requirement for adult attendance may improve efficiency of data collection from images to support the estimation procedure. Nonetheless, we urge consistent identification of nest contests, as these are necessary to relax fixed-interval constraints that might mask inter-annual or spatial variation in breeding chronologies (e.g. Black, 2016). Finally, the restricted nature of the attendance data (e.g. 0,1, or 2 adults) facilitates the use of a simple statistical method to estimate breeding phenologies while accounting for uncertainty and variability in nest attendance patterns around the time of clutch completion (e.g. Figure S5).

Finally, since images for this analysis are taken during daylight hours, timing and frequency of the photographs can be optimized to achieve results without excessive picture accumulation. Prior knowledge of attendance patterns, both seasonal (Southwell et al., 2013) and diurnal (Merkel et al., 2016), would aid the design of appropriate sampling protocols for other colonial species. Necessary photographs also could be extracted from higher frequency image collection protocols if other breeding season parameters were prioritized. Foraging trip durations, incubation shifts or diurnal attendance patterns could all be estimated based on adult attendance of the nest (Huffeldt & Merkel, 2013; Lynch et al., 2015), and the phenology could be estimated from a subset of higher frequency photographs collected during the day. Thus, multiple datasets could be collected from the same images, further enhancing the efficiency of remote camera networks to provide spatially extensive monitoring data.

The photographic method also has several disadvantages. Perhaps the most important disadvantage relates to the time necessary to

generate useful data from images. A manual classification approach takes time, but has merit. Here, classifying a single nest from CID through crèche with 12 photographs per day required roughly 30 min depending on nest position and nest density, with more distant images in high-density colonies requiring greater effort to identify and track. For the full camera network with 455 nests (Table 1), we estimate that classification required 227 hrs. In contrast, a minimum field requirement for daily direct monitoring from CID through crèche would require occupancy of roughly 65 days (1,560 hrs) per site. Crowd-sourced or automated methods provide alternatives to enhance the speed of image processing, but manual classification by the analyst may provide better understanding of the behaviour being quantified, the context of prevailing environmental conditions in the colony and potential witnessing for nest success or failure (weather, predation, etc.). Such ancillary data are critical for informing inference from the data, particularly inter-annual and spatial variations that may arise in time series of phenology or reproductive success.

One important difficulty with a focal-nest approach that can negatively affect photograph classification effort (and would likely reduce the efficiency and accuracy of automated methods) is that nest identification and adult association with the nest must be clearly established and followed. This can be problematic for species like pygoscelid penguins that generally have no natural identifying marks. Movement of the camera can further complicate the continuous recognition of adult-nest associations and care must be taken during camera deployment to ensure the position is fixed and not changed during the course of data collection. Additionally, melt or accumulation of snow and changes in nest bowl integrity during the season can cause nests to shift their spatial distributions relative to each other. The analysis of attendance and nest contents must therefore account for the potential movement of the target, especially during the crèche phase when chicks begin to move beyond the deteriorating nest bowl. At present, a manual classification is well suited to such dynamics.

Finally, the phenology estimation method requires an image at the beginning of the breeding season that clearly identifies two adults and an empty nest bowl. This constraint ensures standardization of data collection. However, confirmation of this condition can take time due to large numbers of individuals in a colony, ongoing nest construction and sometimes poor conditions within the colony, such as excess snow or wet guano, that hinder identification of a nest bowl. However, once the nest location and association is determined, classification proceeds quickly.

5 | CONCLUSION

The use of autonomous data collection systems is rapidly growing in the field of wildlife biology and ecology. As the use of autonomous systems increases, standardized methods for data collection and analysis will help ensure compatible results and foster collaborations. The estimation method described here appears well-suited to operationalize regional applications of time-lapse cameras to

estimate phenology and reproductive success of wild pygoscelid penguins, a focus of ecosystem monitoring efforts in the Southern Ocean (Agnew, 1997). However, while this method was developed for and tested on pygoscelid penguins, it should apply generally to other large-bodied (e.g. >1,000 g) colonial seabirds that mate at the nest site and alternate incubation duties after clutch completion. Examples include, but are not limited to, ground- or cliff-nesting seabirds such as albatross (Diomedeidae), giant petrels *Macronectes* spp. and other fulmarine petrels (Procellariidae), boobies (Sulidae), many gull (Laridae) and cormorant (Phalacrocoracidae) species, murres *Uria* spp., as well as other penguin species including rock hopper *Eudyptes chrysocome* and *E. moseleyi* and macaroni penguins *E. chrysolophus*. Careful consideration must be given to selecting suitable aggregations of nesting seabirds for automated observation systems because terrain, vegetation and nest density may limit the efficacy of camera systems to provide such data. However, if attendance data are available, adapting the estimation method to other species or locations would simply require data on species-specific phenological intervals and stereotypical nest attendance patterns for the species and region of interest.

AUTHORS' CONTRIBUTIONS

J.T.H. and G.M.W. conceived and implemented the estimation method. J.T.H. wrote the paper with input from all authors. J.T.H.,

A.B., L.E., M.K.-A., M.J., G.M., M.S., C.S., P.N.T. and G.M.W. provided data. All authors contributed to design and support of the camera network.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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