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*Article*

# Geolocators lead to better measures of timing and renesting in black-tailed godwits and reveal the bias of traditional observational methods

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Long-term population studies can identify changes in population dynamics over time. However, to realize meaningful conclusions, these studies rely on accurate measurements of individual traits and population characteristics. Here, we evaluate the accuracy of the observational methods used to measure reproductive traits in individually marked black-tailed godwits (*Limosa limosa limosa*). By comparing estimates from traditional methods with data obtained from light-level geolocators, we provide an accurate estimate of the likelihood of renesting in godwits and the repeatability of the lay dates of first clutches. From 2012 to 2018, we used periods of shading recorded on the light-level geolocators carried by 68 individual godwits to document their nesting behaviour. We then compared these estimates to those simultaneously obtained by our long-term observational study. We found that among recaptured geolocator-carrying godwits, all birds renested after a failed first clutch, regardless of the date of nest loss or the number of days already spent incubating. We also found that 43% of these godwits laid a second replacement clutch after a failed first replacement, and that 21% of these godwits renested after a hatched first clutch. However, the observational study correctly identified only 3% of the replacement clutches produced by geolocator-carrying individuals and designated as first clutches a number of nests that were actually replacement clutches. Additionally, on the basis of the observational study, the repeatability of lay date was 0.24 (95% CI 0.17–0.31), whereas it was 0.54 (95% CI 0.28–0.75) using geolocator-carrying individuals. We use examples from our own and other godwit studies to illustrate how the biases in our observational study discovered here may have affected the outcome of demographic estimates, individual-level comparisons, and the design, implementation and evaluation of conservation practices. These examples emphasize the importance of improving and validating field methodologies and show how the addition of new tools can be transformational.

Keywords: geolocators, ground nesting, *Limosa limosa*, observer bias, renesting, repeatability, timing

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## Introduction

Long-term population studies have the power to identify changes in population dynamics over time. When combined with measurements of individual traits across different contexts, i.e. years or environments, they can also elucidate the processes underlying these changes. Such an understanding of the mechanisms underlying population change is of great value to the development of eco-evolutionary theory (Clutton-Brock and Sheldon 2010) and design of effective conservation strategies (Sutherland et al. 2004).

Imperative to long-term observational studies is the collection of data in a standardized fashion year after year or, alternatively, the ability to account for any differences in methodology that occur over time. These studies also rely on obtaining accurate measurements of individual traits, because imprecise measures can be incorrectly interpreted as change or mask the appearance of actual change. In practice, the degree to which observational studies can accurately measure empirical data is debatable (Krebs 1989, Anders and Marshall 2005), since field studies by nature always involve some degree of measurement error. Additionally, field methods are inherently both labour-intensive and invasive. Efforts to minimize these factors usually lead to studies that are both less intensive and less focused, which in turn leads to less accurate measurements. A good example of this balancing act is the number of nest visits made in studies of avian nest survival: making more frequent nest visits yields more accurate nest survival estimates (Dinsmore et al. 2002), but also increases the amount of researcher disturbance, which can influence the study subject and its nest survival (Götmark 1992, Ibáñez-Álamo et al. 2012).

Observational studies therefore benefit from efforts to obtain more accurate empirical data by developing more effective methods, by collecting data more intensively (i.e. over a focused period of time or in a particular area), and by reducing researcher disturbance. In avian demographic studies, for example, using temperature loggers to monitor nest fates has enabled more accurate estimates of nest survival while also reducing the number of nest visits (Weidinger 2006); using colour rings has enabled researchers to make more accurate estimates of productivity and survival without needing to recapture individuals (Anders and Marshall 2005); and using radio transmitters has greatly increased the accuracy of juvenile survival estimates and enables researchers to use small sample sizes while nonetheless collecting higher-quality data (Anders et al. 1997, Yackel Adams et al. 2001, but see Bennetts et al. 1999). There is still room for improvement, however. The difficulty of continuously tracking individuals, for instance, negatively affects the accuracy of survival estimates because it hampers the ability to separate mortality from emigration (Zimmerman et al. 2007, Schaub and Royle 2013). Similarly, an insufficient knowledge of the number of renesting attempts and the likelihood of producing multiple broods leads to inaccurate estimates of population productivity (Underwood and Roth 2002, Anders and Marshall 2005).

Here we focus on this latter issue and examine the accuracy of the empirical data from our long-term observational study of black-tailed godwits (*Limosa limosa limosa*, hereafter 'godwits') breeding in the Netherlands. Our observational study aims to elucidate godwit population dynamics by focusing on the relationships between the timing and location of breeding and nest survival, chick survival, natal dispersal and recruitment (Schroeder et al. 2012, Kentie et al. 2013, 2014, 2015, 2018, Loonstra et al. 2019). Accurate estimates of the timing of breeding, as well as of fecundity, productivity and survival, are therefore of great importance. However, more intensive research recently conducted in a small portion of the larger observational study area led to higher estimates of renesting propensity and a longer estimate of breeding season duration than had previously been found in the population (Senner et al. 2015a). Our team and others have spent many decades studying godwits in the Netherlands (Haverschmidt 1927, van Balen 1959, Mulder 1972, Beintema et al. 1985, Kentie et al. 2018), but the outcomes of Senner et al. (2015a) illustrated that our understanding of the renesting behaviour of godwits was incomplete and highlighted the need to examine the accuracy of our long-term empirical data.

We therefore used light-level data collected from geolocators to assess how well our field methods are able to measure three core components of population productivity: timing of clutch initiation, rates of nest loss and renesting propensity. These geolocators were deployed to study godwit migration (Senner et al. 2019, Verhoeven et al. 2019b), but because they continuously log the ambient light level and were mounted on the leg, we were also able to use them to generate estimates of incubation behaviour. Employing geolocators in this way enabled us to illuminate previously under-appreciated aspects of godwit breeding biology and helped us identify ways in which long-term observational studies can be improved through the use of novel technologies.

## Material and methods

### Fieldwork

Fieldwork occurred from March through June 2012–2018, in our 12 000 ha long-term study area in southwest Fryslân, the Netherlands (52.9643°N, 5.5042°E; Senner et al. 2015b). Starting on 15 Mar, we checked every field within the study area at least once every week for six weeks to search for nests. During this period, godwits arrive from the non-breeding areas, form pairs and establish territories. We used the egg flotation method to estimate the lay date of each nest and, consequently, their expected hatch dates (Liebezeit et al. 2007). We visited each nest three days before the estimated hatch date and, if it was still active, returned 1–3 days later to band the chicks. We also caught a portion of incubating godwits using walk-in traps, automated drop cages or mist nets placed over the nest. After capturing an adult, we individually marked it with colour rings and took a blood sample for molecular sexing. In the years after capture, we linked

marked individuals to specific nests through observations of incubating birds or by recapturing them coincidentally.

Each breeding season we outfitted 42–69 adult godwits with geolocators (i.e. 26–61% of the adults caught annually). We used geolocators from Migrate Technology, Ltd: the 0.65 g Intigeo W65A9 model from 2012 to 2013 and the 1 g Intigeo C65 model thereafter. These geolocators were attached to a coloured flag and placed on the tibia. The total weight of the attachment was ~ 3.3 g from 2012 to 2013 and ~ 3.7 g from 2014 to 2017, representing 1.0–1.5% of an individual's body mass at capture. The return rate of geolocator-carrying individuals to the breeding grounds in the year following deployment was 0.90, which is similar to their apparent annual survival rate (0.85, Kentie et al. 2016).

From 2013 onward, these geolocators were programmed to log the ambient light level for up to 26 months (i.e. up to two consecutive breeding seasons). In the years following deployment, we put considerable effort into recapturing godwits carrying geolocators. We retrieved light-level data from 129 geolocators. Of these, 22 logged for 23 months or more, while most logged only 11–22 months either because the battery ran out or because we recaptured the bird within 22 months. We also retrieved 32 geolocators that logged for less than 11 months and which thus failed to log the start of the next breeding season. We retrieved geolocators from both live and dead birds; after retrieving a geolocator from a live bird, we re-deployed a new geolocator on the same bird in all but six cases (5%).

### Inferring incubation duration and hatching success from geolocator data

The geolocators were programmed to log ambient light level every five minutes and, because they were mounted on the leg, recorded those periods of time when the geolocator was shaded during incubation (Bulla et al. 2016). To inspect the daily light patterns (Fig. 1), we used the function 'preprocessLight' from package 'BAStag' (Wotherspoon et al. 2016) in Program R (<www.r-project.org>). We manually identified the beginning and end of an individual's incubation period, as well as the number of times each individual nested within a breeding season (Fig. 1). In 111 of 151 cases, we observed an egg-laying phase denoted by 20 or more min of shading for 1–3 days, immediately followed by an incubation phase denoted by long shaded periods lasting 1–10 h. This pattern is consistent with known godwit nesting behaviour, as most godwits lay 3–4 eggs (Haverschmidt 1963, Verhoeven et al. 2019a), both females and males spend short periods sitting on the nest during the egg-laying phase, and incubation begins after the penultimate or ultimate egg is laid (Haverschmidt 1963). In the remaining 40 cases, we did not observe an egg-laying phase but did observe a clear incubation phase. Observing egg-laying phases shorter than two days or no egg-laying phase at all could be the result of females laying fewer than four eggs, birds starting to incubate earlier then the penultimate egg, males that did not sit on the nest during the laying phase, or because we were unable to accurately identify a complete egg-laying phase. Because of these uncertainties, the estimated lay date in these cases might be 1–3 days later than the actual lay date. This, in turn, might have caused us to overestimate an individual's renesting interval or to underestimate the repeatability of an individual's lay date across years. However, we do not believe these possible sources of error affected our conclusions, because 1) we use the average renesting interval across years and 2) despite being a potential underestimate, the geolocator-based estimate of repeatability was already substantially higher than the observational-based estimate.

Although our individually-specific, manual approach to analysing the geolocator data could have introduced some biases in determining the timing of laying and duration of incubation, we believe that our method was the most accurate one possible. For example, the amount of time that geolocators were shaded during egg-laying and incubation varied considerably among individuals: some individuals incubated mostly at night with only 1–2 h of incubation in the morning or evening, whereas others incubated mostly during the day, either in one long bout or multiple bouts of varying lengths. This considerable inter-individual variation meant that we were unable to quantitatively determine the onset of incubation, such as by using a threshold value for the number of daylight hours during which a geolocator was shaded.

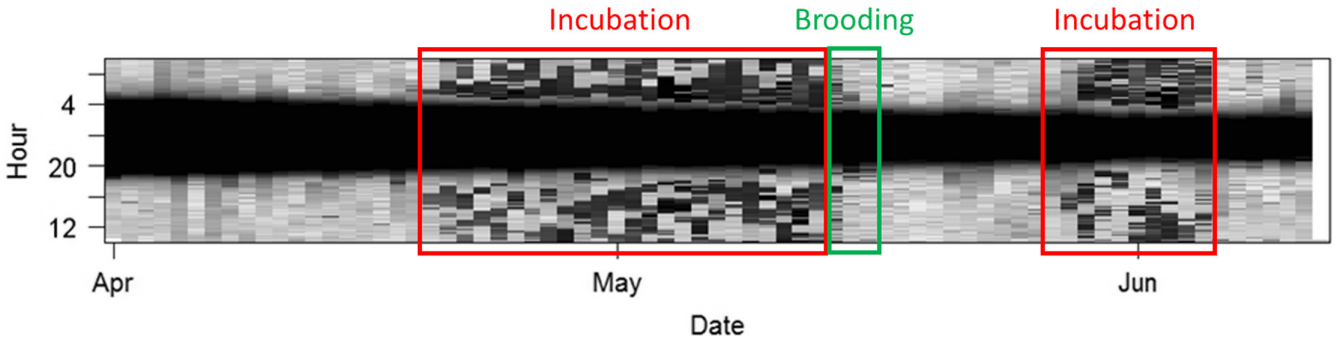


Figure 1. Ambient light level over time. Geolocators were mounted on the leg and therefore shaded during incubation, which enabled us to detect the beginning and end of an individual's incubation period and to observe the number of times each individual nested within a breeding season.

For 43 of the nests of geolocator-carrying godwits, we know that chicks hatched successfully because we observed the newly hatched chicks in the nest; the geolocator data we retrieved for these nests showed that incubation lasted between 23 and 30 days. This corresponds with the known incubation duration of godwits (24.5 days, range 22–27 days; Haverschmidt 1963). Because not all nesting attempts were identified by our observational study (Results), we lacked observational data on nest fate for some of the nests analysed in this study; we considered such nests failed if the geolocator data indicated they were incubated for 22 days or less. In most cases, it was also possible to infer chick brooding from the light-level data (Fig. 1). However, this was not failsafe, and we therefore did not use it as a measure of hatching success.

In our data we distinguish between: 1) first clutches, 2) renesting after the failure or hatching of a first clutch ('first replacement') and 3) renesting after the failure of a first replacement ('second replacement'). Replacement clutches do not include clutches laid by a godwit pair after it has successfully fledged chicks (also called 'double-brooding'); this is a behaviour we and others have never observed among godwits (Senner et al. 2015a). For all clutches we know the start of incubation; for successful clutches we know the date of hatching; for unsuccessful clutches we know the date of failure. We also had some incomplete incubation histories resulting from geolocators that stopped logging partway through the breeding season; this was the result of either 1) battery failure during the breeding season or 2) recapture of an individual during one breeding season (with one geolocator), but not in a subsequent breeding season (with a second geolocator). For this study, we collected a total of 103 incubation histories, both complete and incomplete, from 68 individuals: 39 females and 29 males. This included two males that likely each skipped a breeding season altogether, so our analyses include 101 complete and incomplete incubation histories from which we know the fate of the first clutch in a breeding season (Fig. 2).

Of these 101 first clutches with known fates, there were two cases in which it was not clear whether the bird renested or not, even though the geolocator remained operational. One female likely laid a first replacement clutch, and another female who lost her first replacement clutch likely laid a second replacement, but we cannot be certain (Supplementary material Appendix 1). We have therefore excluded these two cases from the analyses that estimated renesting propensity and probability; for these analyses we also excluded one case in which the parent was killed at the same time the first clutch was depredated (Fig. 2).

Renesting propensity and probability depend on whether the female produces a replacement clutch or not. However,

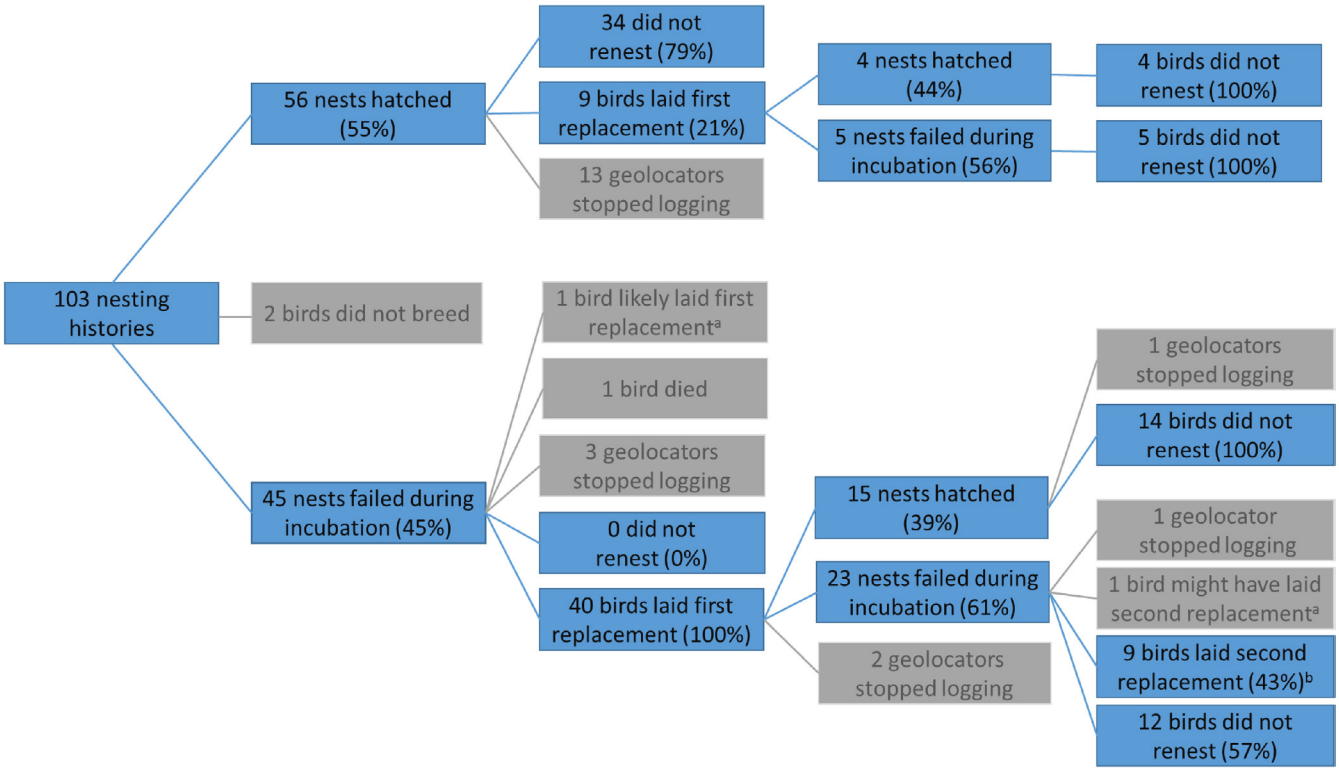


Figure 2. Flowchart of all complete and incomplete incubation histories collected with geolocators. Terminology used is defined in Material and methods. That geolocators stopped logging (including the retrieval of a geolocator during one breeding season, but not in a subsequent breeding season; Material and methods) resulted in incomplete histories (grey boxes); the presented percentages are based on complete histories only (blue boxes). As a result, the sum of blue boxes originating from the same blue box is always 100%. [a] See Material and methods for explanation. [b] Of these 9 second replacement clutches, 7 failed (88%), 1 hatched (12%) and 1 stopped logging.

since godwits are socially monogamous and share parental care (Cramp and Simmons 1983, Beintema et al. 1995), we can also infer renesting propensity and probability on the basis of males – except in those cases in which the female dies. In such cases, male geolocator data would show only that the female did not renest, not whether she was alive or not. In the cases where we retrieved geolocators from live birds, female geolocator data does not include this uncertainty. The calculated renesting propensity and probability would therefore be underestimated if the geolocator-based sample includes males whose partners died after laying their first clutch. Our results show that this scenario did not happen after failed first clutches, but it may have occurred after hatched first clutches or second replacement clutches.

## Analysis

### *Observer bias in renesting propensity*

First, we calculated renesting propensity on the basis of geolocator-carrying godwits – how many individuals laid a replacement clutch after their first clutch failed, how many laid a replacement clutch after their first nest hatched, and how many renested again after their first replacement failed. The individuals carrying geolocators were part of our long-term observational study, which enabled us to compare the found renesting propensities between the two different study methods: geolocator-based and observational.

### *Observer bias in linking an adult to a nest*

Our study set-up also enabled us to evaluate our observational study's performance in linking marked adults to nests. However, of the 101 first clutches that were laid by geolocator-carrying godwits and had known fates, eight were linked to individuals that were caught for the first time while incubating that nest. Because these individuals were unmarked prior to being caught, it was not possible to evaluate the performance of our observational study for these cases. Therefore, we could only use 93 of the 101 first clutches in our evaluation.

We used a generalised linear model with a binomial error distribution and a logistic link function to test whether the chance of linking a geolocator-carrying individual to a nest on the basis of field observations (categorized as linked or not linked) depended on whether or not the nest hatched (included as a two-level factor) or when in the season the nest was laid (included as a continuous covariate). However, there are two potential caveats to these comparisons between study methods: 1) Within our observational study, we very rarely obtained data suggesting godwits were renesting. During the proofing process of our observational study, we therefore frequently disregarded the possibility of a bird renesting. Especially in cases where an adult was linked to two nests that were close to each other in time and space, the less likely nest was sometimes permanently 'unlinked' from the adult in the database. At the time, we thought these cases resulted from mistakes made in the field, with single adults erroneously linked to two simultaneous nests. In light of our results here, however, it is likely that some of these adults were correctly linked to a replacement clutch laid soon after the previous failure. This means that the performance of our observational methods was actually slightly better than is shown by our comparison here. 2) Retrieving geolocators is of great value to our project and we therefore sometimes focused on geolocator-carrying individuals more than other marked individuals. The calculated performance of our observational study on the basis of geolocator-carrying individuals may thus be slightly higher than for all marked individuals.

### *Observer bias in the timing of laying*

Some nests of geolocator-carrying individuals found in the field during our observational study and designated as first clutches were actually second or third clutches (Results). Incorrectly assigning first and second replacement clutches as first clutches in some but not all cases has consequences for how consistent our observational study estimates individuals to be in their timing of laying (Fig. 3). Therefore, the individual repeatability of the lay date of first clutches estimated by Lourenço et al. (2011) on the basis of our observational study is likely an underestimate. To get a better estimate, we calculated the repeatability of lay date on the basis of the first clutches of geolocator-carrying birds. For this, we included individual as a random effect in the linear mixed model method of the function 'rpt' in the R package 'rptR' (Stoffel et al. 2017). The estimate made by Lourenço et al. (2011) was based on data collected in

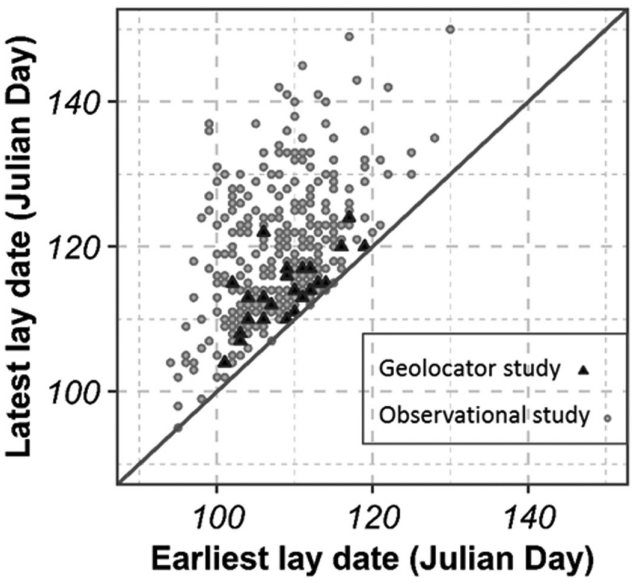


Figure 3. Individual consistency of lay date observed in our geolocator and observational studies. Here, we plotted the earliest lay date versus the latest lay date for every individual with repeated measurements for lay date. We also plotted the line x = y, which represents a scenario in which lay date is completely consistent, i.e. 100% repeatable. The observed difference in consistency between the two study methods has consequences for the estimated individual repeatability.

different years and with a different statistical method from our present geolocator-based study; we therefore estimated the repeatability of lay date based on our observational data collected during the same years as our geolocator data (2012–2018) using the same statistical method described above for our geolocator-based estimate. For this analysis we used only female lay dates because including both sexes would introduce considerable pseudo-replication from pairs comprising two marked individuals. We excluded from this analysis all nests known to be a replacement clutch on the basis of the observational study. We assessed the uncertainty of these repeatabilities with 1000 parametric bootstraps and their statistical significance with likelihood ratio tests.

#### *Renesting probability*

We also examined the chance of producing a replacement clutch, i.e. the renesting probability, as a function of the date of nest loss. This analysis yielded a 'complete separation', in which the explanatory variable (date) yielded a perfect prediction of the dependent variable (renesting probability). Further statistical estimates were therefore not required to assess or account for between-year and within-individual variation. Finally, we examined whether the renesting probability after the first clutch hatched depended on the date of hatch. For this we used a generalised linear mixed model from the R package 'lme4' (Bates et al. 2015), with a binomial error distribution, logistic link function and individual and year as random effects. Finally, we calculated the number of days between renests and plotted this interval against the date on which the earlier clutch was lost to investigate whether the renesting interval changed seasonally (Supplementary material Appendix 1 Fig. A1). We also used linear mixed models to test whether this renesting interval depended on either the number of days the previous nest had been incubated or the date of nest loss. We included individual as a random effect in these models.

#### *Comparison with van Balen*

In 1954, van Balen (1959) conducted experimental research on renesting in godwits in a 100-ha area 69 km due south of our study area (52.2366°N, 5.4184°E). After van Balen marked individual incubating godwits, he collected their eggs and studied their renesting behaviour. Following the removal of eggs, he searched the area for these marked individuals and collected their subsequent nesting attempts. He thus obtained data on the renesting propensity of godwits, the interval between replacement clutches, the distance between nests, and the initiation dates of replacement clutches. We compared his findings with our own using general linear models with a Gaussian error distribution. We obtained F-values and Chi-squared values for the significance of the fixed effect 'study' (a two-level factor with groups 'ours' and 'van Balen') of nested models with and without this fixed effect. We visually inspected the residuals to validate the model assumptions.

From the light-level data, we obtained data on renesting propensity, the interval between replacement clutches and the initiation dates of replacement clutches. We also investigated the geographic distance between an individual's first clutch and replacement clutches by taking the coordinates of both nests and calculating the distance between them with the function 'pointDistance' from the R Package 'raster' (Hijmans 2017). We used all the replacement clutches that were identified by linking a colour-marked individual to a nest as part of our long-term observational study; these include the replacement clutches of geolocator-carrying birds that were noted during the field season, but not the replacement clutches of geolocator-carrying birds that were missed by the observational study (Results). For this analysis, we log-transformed renesting distance to achieve normality.

## Results

### Observer bias in renesting propensity

The hatching success of the first nesting attempts of geolocator-carrying godwits was 55% (n = 101). After a failed first clutch, all geolocator-carrying godwits laid a replacement (n = 40, Table 1). The hatching success of these first replacements was 39%. After a failed first replacement, geolocator-carrying godwits attempted a second replacement 43% of the time (9 out of 21 times). Finally, 21% of successfully hatched first clutches were followed by a replacement clutch (9 out of 43 times); four of these attempts hatched (44%; Table 1, Fig. 2).

Of the 49 first replacement clutches identified by the geolocators (40 after a failed first clutch and 9 after a hatched first clutch), our observational study found and linked the geolocator-carrying parent in 14 cases (29%); 8 of these clutches hatched (57%). In 12 of these 14 cases, this was the first time the parent was linked to a nest that season – i.e. the geolocator-carrying parent was not linked to its actual first clutch. Our observational study therefore correctly identified the first replacement clutch as a renesting attempt in 2 of 49 cases (4%). Both cases were replacements made after the first nest failed; our observational study therefore correctly identified 2 of the 40 first replacement clutches made after a failed first attempt (5%) and 0 of the 9 first replacement clutches made after a hatched first attempt (Table 1).

The observational study correctly linked the parent to its nest in 2 of 9 second replacement clutches; one of these nests hatched and the other did not. Neither nest was identified as a second replacement: one was designated as a first clutch and the other as a first replacement. Combining first and second replacement clutches, our geolocator data identified 58 replacement clutches in total – of these, our observational study identified 2 correctly (3%, Table 1).

### Observer bias in linking a parent to a nest

In our observational study, the first clutch of geolocator-carrying godwits was found and subsequently linked to the

Table 1. Overview of the different identified observer biases present in the observational study. We simultaneously obtained estimates for the same measurements on the same individuals using both geolocators and observational methods.

| Measurement | Geolocator study | Observational study |
|---|---|---|
| Renesting propensity after a failed first clutch | 100% | 5% |
| Renesting propensity after a hatched first clutch | 21% | 0% |
| Renesting propensity after a failed first replacement clutch | 43% | 0% |
| Repeatability of lay date of first clutches | 0.54[A] | 0.24[B] |
| Range of within-individual differences in lay dates across years | 0–13 days | 0–38 days |
| Average within-individual difference in lay dates across years | 4.28 ± 2.96 days | 11.35 ± 8.10 days |
| Identifying the geolocator-carrying adult of nests with known fate | Accurate | Biased towards hatched nests and nests earlier in the season[C] |

[A] Based on 93 lay dates of 65 individuals.
[B] Based on 1334 lay dates of 650 individuals.
[C] Based on 148 clutches (93 first clutches, 47 first replacements and 8 second replacements).

geolocator-carrying parent 55% of the time (51 out of 93 cases). The probability of linking the geolocator-carrying parent to a first clutch was higher when the clutch hatched than when it failed ($\beta = 2.43$, $\chi^2 = 27.71$, df = 1, $p < 0.001$, n = 93), but did not depend on when the clutch was laid ($\beta = -0.07$, $\chi^2 = 2.66$, df = 1, $p = 0.10$, n = 93). Of the 51 first clutches to which a geolocator-carrying parent was linked based on colour rings, 39 hatched (76%); of the 42 clutches for which the link to a geolocator-carrying parent was missed by the observational study, only 10 hatched (24%).

Combining all 148 attempts with known fates (93 first clutches, 47 first replacements and 8 second replacements; Fig. 2), the probability of linking the geolocator-carrying parent to a clutch depended on whether the clutch hatched ($\beta = 1.94$, $\chi^2 = 27.36$, df = 1, $p < 0.001$, n = 148) and its lay date ($\beta = -0.06$, $\chi^2 = 13.38$, df = 1, $p < 0.001$, n = 148). Of the 67 clutches to which a geolocator-carrying parent was linked, 48 hatched (72%); of the 81 clutches for which the link to a geolocator-carrying parent was missed by the observational study, only 21 hatched (26%). The odds of linking a geolocator-carrying parent to a nest was negatively correlated with lay date, decreasing 6% for every day that passed before the nest was laid (Table 1).

## Observer bias in the timing of laying

Based on 93 lay dates of first clutches from 65 geolocator-carrying individuals, the repeatability of lay date of first clutches was 0.54 (95% CI: 0.28–0.75, $p < 0.01$, Table 1). The difference in lay date within individuals ranged from 0 to 13 days and was 4.28 ± 2.96 d on average (n = 24, Table 1, Fig. 3). Based on our observational study, which included 1334 lay dates of 650 marked females, the repeatability of lay date was 0.24 (95% CI: 0.17–0.31, $p < 0.01$); the difference in lay date within individuals ranged from 0 to 38 days and was 11.35 ± 8.10 d on average (n = 350, Table 1, Fig. 3).

## Renesting probability

The probability of renesting after a failed first clutch was 100% and therefore did not depend on the date of nest loss or the number of days spent incubating. These replacement clutches were laid following first clutches that failed under a variety of circumstances; first clutches were incubated for periods ranging from 2 to 22 days, and first clutch loss dates ranged from 18 April to 18 May. The probability of renesting after a failed first replacement was not 100% and was predicted by nest loss date: when nests failed before 19 May, all godwits renested (n = 9), whereas no godwit renested following nest failure on or after 21 May (n = 12). Our sample did not include nests lost on 19 or 20 May. We excluded from this analysis one female that likely laid a replacement clutch on 11–14 May (Supplementary material Appendix 1). Our geolocator data shows that this female lost this presumed first replacement clutch before 19 May and did not lay a second replacement clutch.

The probability of renesting after chicks hatched also likely depends on the date the chicks were lost. We unfortunately could not test for this relationship, because our geolocator data does not indicate when individuals lost their chicks. However, we could test whether laying a first replacement after a hatched first clutch depended on the hatching date of the first clutch; our analysis shows that it did not ($\chi^2 = 0.33$, df = 1, $p = 0.57$, n = 43). Lay dates of replacement clutches ranged from 25 Apr to 30 May; the latest initiation of a replacement clutch in our geolocator study was an attempt made after chicks hatched from a first nest.

The average interval between the failure of the first clutch and the beginning of incubation of the first replacement was 8.73 ± 1.84 d (range 6–16 days, n = 40), while the average interval was 9.22 ± 1.48 d (range 7–12 days, n = 9) between a failed first replacement and the start of a second replacement. This difference was not significant ($\chi^2 = 0.58$, df = 1, $p = 0.45$, n = 49). We found no correlation between the renesting interval and the date the previous nest was lost ($\chi^2 = 0.03$, df = 1, $p = 0.86$, n = 49, Supplementary material Appendix 1 Fig. A1), nor with the number of days the previous nest was incubated ($\chi^2 = 0.58$, df = 1, $p = 0.45$, n = 49).

## Comparison with van Balen

Of the 92 replacement clutches identified by our observational study, 35 were within 100 m of their previous clutch, and more than half (51 out of 92) were within 200 m. The

average distance between replacement nests was considerably higher, though, because some individuals moved large distances ($\mu = 564 \pm 1190$ m, range = 9–6496 m). Van Balen (1959) found a smaller range of distances between nesting attempts (range 80–640 m), but the average distance between nesting attempts did not differ significantly between the two studies ($F_{1,104} = 0.42$, $p = 0.52$, Table 2).

Van Balen found a 40% renesting propensity after removing a first clutch (n = 30 individuals), which is significantly lower than in our study ($\chi^2 = 39.4$, df = 1, $p < 0.001$, $n_{our\_study} = 40$, Table 2). He attributed this low propensity to the small size of his study area and the possibility that individuals moved large distances between nesting attempts, an idea that is supported by our observations that individuals can move up to six kilometres between clutches. He also found a 'complete separation,' as godwits did not replace nests lost after 20 May. The average renesting interval found by van Balen was approximately one day shorter than in our study ($7.73 \pm 2.99$ d), but did not differ significantly ($F_{1,62} = 2.98$, $p = 0.09$, Table 2). The lay dates of replacement clutches in our study (25 Apr–30 May) and van Balen's (30 Apr–27 May) were therefore very similar and not significantly different ($F_{1,71} = 0.001$, $p = 0.98$, Table 2).

## Discussion

In our sample of geolocator-carrying godwits, every individual laid a replacement clutch after a failed first clutch. Based on a comparison using data from geolocator-carrying individuals, our observational study correctly identified only 3% of the replacement clutches produced and designated as first clutches a number of nests that were actually replacement clutches. The data obtained from the geolocators also showed that our observational study linked more marked adults to hatched nests than to failed nests and linked fewer marked adults to nests later in the season. Finally, we found that the repeatability of lay dates estimated on the basis of these less accurate measurements was 0.24 (0.17–0.31), whereas the repeatability estimate using geolocators was 0.54 (0.28–0.75).

Our estimates of renesting interval and renesting distance between successive clutches were not significantly different from those found by van Balen (1959), and were also similar to the renesting interval of $12.29 \pm 2.55$ days (range 8–17 days) and renesting distance of $78.50 \pm 20.38$ m (range 27–120 m) found by Hegyi and Sasvari (1998). We also found that the date after which godwits do not replace lost clutches was 18 May, which corresponds with what van Balen (1959) found more than 60 years ago. This suggests that there is a shared and strong mechanism that determines the end of the renesting period in godwits and that this has not been altered by either habitat change or global climate change (Kleijn et al. 2010).

### Observer bias in renesting propensity

The renesting propensity of our geolocator-carrying individuals after a failed first clutch was 100%. This is higher than all previously published estimates for black-tailed godwits: 45% (Hegyi and Sasvari 1998), 41% (Schekkerman and Müskens 2000), 40% (van Balen 1959), 29% (Buker and Winkelman 1987) and 20% (Senner et al. 2015a). The differences between these studies could be biological, methodological or both. Yet, our observational study identified only 3% of replacement clutches correctly and Senner et al.'s (2015a) estimate of renesting propensity differs greatly from our own, even though both of those studies were conducted inside our study area and during the same years as our own study. We therefore believe that the differences in estimated renesting propensities among different studies are mostly due to differences in methodology. This notion is supported by two studies on Dunlin (*Calidris alpina*) conducted at a single study site in Alaska: based on an observational study from 2003 to 2006, Naves et al. (2008) found a renesting propensity of less than 5%, whereas by using radio transmitters and experimental clutch removals from 2007 to 2009, Gates et al. (2013) found that the renesting propensity of early clutches was 82–95%.

#### *Impact on estimates of fecundity*

The most important consequence of biased estimates of renesting propensity is likely their impact on estimates of fecundity. Fecundity – the number of hatched eggs per female per year – depends on both renesting propensity and nest survival. Therefore, previous studies on godwits that calculated fecundity based on previously published, much

Table 2. Comparison between our geolocator and observational studies and van Balen's (1959) study, for different population characteristics.

| Population characteristic | Geolocator study | van Balen (1959) |
|---|---|---|
| Renesting propensity after a failed first clutch | 100% (40 from 40) | 40% (12 from 30) |
| Renesting propensity after a failed first replacement clutch | 43% (9 from 21) | 25% (3 from 12) |
| The date after which godwits do not replace lost clutches | 18 May | 20 May |
| Renesting interval (first and second replacement) | 6–16 days | 5–16 days |
| Average renesting interval (first and second replacement) | $8.82 \pm 1.80$ days | $7.73 \pm 2.99$ days |
| Initiation dates of replacement clutches | 25 April–30 May | 30 April–27 May |
| | Observational study | van Balen (1959) |
| Distance between nesting attempts | 9–6496 m | 80–640 m |
| Average distance between nesting attempts | $564 \pm 1190$ m | $282 \pm 288$ m |

lower renesting propensities, have likely underestimated fecundity to varying degrees. For instance, Roodbergen and Klok (2008) assumed a renesting propensity of 0.5 and estimated nest survival to be 0.39; had they assumed a renesting propensity of 1, their estimate of fecundity would have been 25% higher. Kentie (2015, chapter 6) assumed a renesting propensity of 0.26 and estimated nest survival to be either 0.41 or 0.54, depending on the habitat type in which the nest was laid; had she assumed a renesting propensity of 1, her estimates of fecundity would have been 30% and 38% higher, respectively. These studies also assumed that godwits do not lay a replacement clutch after a hatched first clutch, which our results and those of Senner et al. (2015a) indicate is a regular occurrence, and likely means that they further underestimated fecundity.

Since fecundity is a measure of the number of hatched eggs, underestimating it leads, in turn, to an underestimation of population productivity (except in cases where all chicks die and productivity is zero). Because population productivity is an important factor in understanding population-level processes, it follows that accurate and precise estimates of renesting propensity are important for population studies. For this reason, Morrison et al. (2019) recently concluded in a study assessing the relationship between migration timing and breeding success of migratory birds that 'Empirical studies of the frequency and seasonality of replacement clutches are therefore urgently needed in order to identify the conditions in which they occur and their role as a driver of both the benefits of early arrival and the population-scale consequences of shifts in migration timing.'

#### *Impact on estimates of nest and chick survival*

Nest survival estimates are much less affected by observational performance. In most cases, the fate of a nest is independent of whether a marked individual was linked to the nest or not. However, among the 92 replacement nests identified by the observational study, there was one case in which we designated a nest as 'hatched' on the basis of later observing a marked parent linked to that nest with chicks in the field. Considering the high renesting propensity, this now appears to be a poor practice – it could be that the chicks observed accompanying an adult come from a replacement nest that was never found. As a result, our own and potentially other population-level analyses that deal with nest survival – especially nest survival as a function of date or location – are biased by the limitations of the observational methodology.

The same is true for our measurement of chick survival, which we base on whether or not adults are accompanied by chicks 25 or more days after the clutch has hatched. Because some godwits do lay a replacement clutch after successfully hatching their first clutch, the chicks accompanying the adult might actually be younger chicks from a replacement clutch. As a result, the wrong fate could be assigned to the wrong breeding attempt. Therefore, the analyses that address chick survival – especially as a function of date or location – may also be biased. Since nest and chick survival are important parameters for examining dynamics at the population level, it is critical that studies of avian population dynamics first obtain accurate and precise estimates of renesting propensity.

### Impact on conservation efforts

Underestimating the possibility that birds lay a replacement clutch can also affect the monitoring programs that evaluate population growth and the effectiveness of conservation practices. For example, a prevalent practice in the Netherlands over the past 35 years has been to use 'number of nests found' as a measure of population size or breeding density (Verstrael 1987, Wymenga et al. 2000, Oosterveld et al. 2015). In situations where birds renest after first clutches fail, this method produces an estimate of more breeding pairs than are actually present. As a result, population growth in a location with a low breeding density and low nest survival is erroneously estimated to be the same or even higher compared to a location with a high breeding density and high nest survival. Thus, using the number of nests to estimate population size or breeding density without accounting for renesting propensity has made the statuses of godwits and other bird species seem less precarious than they actually have been.

In recent years, the Dutch national monitoring program has used the ratio of adult pairs with chicks to found nests as its measure of productivity (van Paassen 1995, Nijland 2002, Nijland and van Paassen 2007). This is an improvement over methods using solely the number of nests found because it also incorporates chick survival. However, replacement clutches are not always accounted for, which introduces two types of bias: 1) more nests are found than there are actual breeding pairs, which results in a lower ratio of pairs to nests and 2) the chicks that accompany an adult might be young chicks recently hatched from a replacement clutch rather than older fledged chicks, which results in a higher ratio of adult pairs with chicks to found nests. We therefore urge monitoring programs not only to avoid using the number of nests alone to evaluate changes in population size, but also to account for renesting propensity when evaluations are based on a ratio of adult pairs observed with chicks to found nests.

It is also important for managers of nature reserves and researchers alike to consider what effect renesting can have on the length of the breeding season. We illustrate this using our research on godwits, but similar scenarios for other bird species likely exist. Our results indicate that a godwit could lose a clutch as late as 18 May and still lay a replacement clutch; that replacement clutch could, in turn, be laid as late as 16 days later, on 3 Jun. This is consistent with the latest lay date, 4 Jun, observed by Senner et al. (2015a) and the studies reviewed therein. Assuming an incubation period of 25 days and a pre-fledging period of 45 days (Loonstra et al. 2019), godwit chicks could therefore fledge as late as 13 August. Currently, the agri-environmental schemes in the Netherlands that postpone the mowing of fields to promote godwit chick survival end on 1 Jun, 8 Jun, 15 Jun, 22 Jun and 1 Jul. Similarly, most managers of nature reserves have

contracts with farmers to delay mowing until either 15 Jun or 1 Jul. And finally, our own observational study stops following adults with chicks on 1 Jul, while the national monitoring program surveys alarming pairs only from the end of May until the beginning of Jun (Nijland and van Paassen 2007). Given our results and those of Senner et al. (2015a), the timing of all of these activities should be revised to encompass the entire breeding season of godwits. This illustrates that, in order to design and evaluate conservation strategies for bird species, management organizations first need to have accurate and precise estimates of the frequency and seasonality of renesting.

***Observer bias in linking adults to a nest***

Our observational study linked more marked adults to hatched nests than to failed nests and linked fewer marked adults to nests later in the season. Thus, our observational study collects biased data on the reproductive success and lay dates of individuals, and these data are then used in subsequent between-individual comparisons: for example, when using marked individuals to relate certain individual traits – such as wintering location, arrival date or habitat use – to either reproductive success or lay date. Our observational study also designated a number of replacement clutches as first clutches, having failed to identify the actual first clutch. This compromises the accuracy of within-individual measurements. For example, our results show that calculating the repeatability of lay dates using our observational data leads to a lower estimate than does using our geolocator data. Other individual measurements – such as changes in lay date in response to environmental variation – are also affected.

Incorporating geolocators into our study has therefore been valuable; it has alerted us to these biases and allowed us to more accurately estimate renesting propensity and the probability of linking adults to nests. This, in turn, may enable us to mitigate some of the biases in our observational data. For instance, when analysing the relationship between wintering location and the lay date of first clutches, we could use the geolocation data to identify the date before which most clutches are likely first clutches and before which nests have an equally high chance of having a marked parent assigned to them. We could then use that date as a cut-off for the nests we include in the analysis.

Although in some cases we can mitigate the effects of such biases by recognizing their sources and designing our analyses accordingly, the individual nature of the underlying errors means that we cannot apply a correction to actually remove the biases. This is a pity; like other long-term studies, ours can be used to observe changes in traits and behaviours over time – but to identify the processes underlying these changes, accurate measurements of the same individuals over multiple years are required. In our case, due to the observer bias that affects these measurements, we would only be able to identify the underlying processes if the magnitude of change is larger than the error in the measurements. For example, in the case of measuring advances in lay date, the magnitude of change is usually less than one day per year (Crick et al. 1997), whereas our within-individual error is larger than that. To measure the magnitude of change, therefore, we require either better observer performance in the field or the use of more geolocators. This concept is broadly applicable: observer-based biases such as those we have encountered are inherent to observational studies in general. To identify and mitigate such biases, researchers should strive to obtain accurate estimates whenever possible. Incorporating additional data collection tools may in many cases help accomplish this.

## Conclusions

The performance of our long-term observational study in linking marked individuals to nests has limited the accuracy of our population-level estimates and introduced multiple biases to our measurements of individual traits. These less accurate measurements, in turn, impair our ability to potentially observe changes that may have occurred in our study population and to understand the mechanisms underlying those changes. Consequently, these less accurate measurements also inhibit the design and implementation of effective conservation efforts that are based on scientific evidence. The use of geolocators as an additional tool, however, has improved our understanding of the renesting biology of godwits and can help us improve and account for the limitations of our observational study. However, the use of geolocators is not a panacea; even with consistent methodological advances, no field study will ever achieve the goal of being entirely unbiased. Ultimately, part of the magic of ecology is its complexity and our permanent inability to fully understand that complexity. We can continue to develop our ecological understanding, but only by accepting the fundamental importance of undertaking regular self-assessments.

### Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c2fqz614t> (Verhoeven et al. 2020).

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*Author contributions* – MAV, AHJL, ADM, PM, CB, NRS and TP conceived the ideas and designed the methodology; all authors collected the data; MAV, AHJL, ADM and PM analysed the data. MAV, AHJL and ADM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supplementary material (available online as Appendix jav-02259 at <www.avianbiology.org/appendix/jav-02259>). Appendix 1.