Review Article title: Egg abandonment leads to biased estimates of hatching failure in birds

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Abstract

Hatching failure represents a significant and growing barrier to reproductive success in threatened birds, but its causes are often hard to identify. Egg abandonment by parents is a commonly observed phenomenon – often believed to be driven by disturbance, partial predation, and/or extreme environmental events – and is assumed to result in the mortality of viable eggs in the clutch. However, in practice it is often unclear whether abandonment is the cause of egg failure, or conversely, if parents abandon their eggs after detecting they were inviable. From a conservation management perspective, approaches to mitigating hatching failure would differ substantially depending on which of these scenarios is true. Here we draw evidence from both a systematic literature search and empirical data from a wild population of threatened birds, to show that studies rarely have sufficiently clear definitions or timeframes for

determining whether abandonment occurred, or sufficient monitoring effort to distinguish between parental abandonment as the cause or consequence of embryo mortality. By combining evidence from nest records and unhatched egg examinations, we show that parental abandonment rates are likely to be over-estimated, while other drivers of reproductive failure may be under-estimated. We provide recommendations for improving the accuracy of egg fate records, which we hope will improve the accuracy of hatching failure data and enhance the specificity of related conservation interventions.

Keywords: Hatchability; Embryo mortality; Nest monitoring; Reproductive failure; Desertion

Introduction

Egg incubation and hatching are the first major hurdles that many egg-laying taxa must overcome to achieve reproductive success (Deeming and Ferguson 1991; Du and Shine 2015). Failure of eggs to hatch is fairly common, particularly in threatened species, and has significant impacts on the stability and persistence of populations (Jamieson and Ryan 2000; Ferreira et al 2005; Brekke et al 2010; White et al 2015; Marshall et al 2023). It is therefore important that rates and causes of egg failure and loss are accurately monitored.

Egg failure and loss occurs for various reasons, including predation, damage, climatic factors, pollution, and genetic issues that impact embryo survival (Assersohn et al 2021). In addition to

these drivers, a noticeable proportion of eggs fail to hatch because they are abandoned by the parent(s), prior to or during incubation. Parents may abandon entire clutches, or a subset of the eggs (partial clutch abandonment), the latter being especially common after partial predation events (e.g., Ackerman et al 2003). We therefore use the term 'egg abandonment' to refer to the abandonment of either a subset of eggs or the entire clutch, occurring at any time between egg laying and the end of the incubation period. If the parent abandons eggs after the expected end of the incubation period, these eggs should be classed as 'failed' rather than abandoned, since they must have failed before the parent left. It should be noted that abandonment behaviour differs from egg ejection/expulsion (e.g., Lobato et al 2006), rejection, and nest sanitation (e.g., see Guigueno and Sealy 2012) behaviours, which all involve the physical removal of eggs rather than the cessation of parental care while the eggs remain in the nest.

Egg abandonment is commonly associated with disturbance, climatic and/or environmental events (see *Issues and inconsistencies in egg abandonment data collection* section below), so it is likely that abandonment is not usually related to egg quality or viability, and the majority of abandoned eggs therefore represent a random subset of those laid. Consistent with this, attempts at egg fostering abandoned eggs have previously proven successful (e.g., O'Connell et al 2015) and there is no substantiated evidence for preferential abandonment of unfertilised eggs or inviable eggs (Marshall et al 2023). The causes of abandonment are therefore mostly assumed to be independent of other drivers of either fertilisation failure or embryo mortality, and as such abandoned eggs are typically excluded from standard calculations of 'hatching failure' along with eggs that are predated or damaged (e.g., Briskie and Mackintosh 2004; Marshall et al 2023); or,

inversely, ‘hatchability’ (Koenig 1982) and ‘hatching success’ (e.g., Spottiswoode and Møller 2004).

There are three potential problems with the exclusion of abandoned eggs from hatching failure monitoring and analysis efforts. First, methods of defining and recording egg abandonment are often inconsistent and subjective, inevitably leading to inaccurate classifications of abandonment that upwardly or downwardly bias estimates of hatching failure rates (see *Issues and inconsistencies in egg abandonment data collection* section below). Second, the identification of egg abandonment may be impacted by nest monitoring effort, with the risk that egg abandonment is more commonly mistaken for other causes of hatching failure (or vice versa) when nest visits are sporadic. Third, in cases where abandoned eggs are assumed to be fertilised, abandonment is usually considered to be the cause of embryo mortality (but see Beissinger et al 2005), especially since abandoned eggs often have the potential to hatch if subsequently incubated (O’Connell et al 2015; Schacter et al 2022). It is feasible, however, that abandonment is sometimes the consequence of embryo death, rather than the cause. In birds, for example, it is well established that parent-embryo communication occurs, particularly during the late stages of egg incubation (Vince 1966, 1969; Brua 2002; Brulez et al 2015), and embryos actively respond to and modulate the incubation environment provided by their parents during development (Brua 2002; Reed and Clark 2011; Brulez et al 2015). Whilst there has been a historical under-appreciation of avian sensory abilities (e.g., as noted by Birkhead 2012; Brulez et al 2015; Caro et al 2015), recent studies demonstrate a range of sensory cues available to birds (e.g., Balthazart and Taziaux 2009; Campagna et al 2012; Caro et al 2015; Grieves et al 2022; Ziolkowski et al 2022; Mariette 2024) that might be used by parents to dynamically assess current clutch/egg viability

(see Table 1 for a summary). However, since it is known that some birds continue to incubate non-viable eggs beyond normal incubation periods (e.g., Briskie and Sealy 1988), it is likely that the ability to use sensory cues in this way, and/or the propensity to abandon eggs, varies between species.

Here, we first highlight current issues and inconsistencies with monitoring of egg abandonment in avian research projects and monitoring schemes more broadly, via a systematic review of the literature. We then demonstrate how these issues can impact our understanding of the drivers of hatching failure in a conservation context, using data from ongoing nest monitoring schemes for the United Kingdom and Ireland Eurasian Curlew (*Numenius arquata*) populations. Finally, we offer recommendations for standardising the long-term monitoring of avian egg abandonment and hatching failure to produce more accurate and informative data, which will likely also apply to the conservation management of other oviparous taxa with parental care (e.g. Pythonidae).

Table 1 should be positioned after paragraph ends on line 92

Issues and inconsistencies in egg abandonment data collection

To gain an overview of how egg abandonment is defined and measured across published bird studies, we conducted a systematic review by searching the database Web of Science on 24/10/2024 for the terms “egg”, “abandon*”, and “bird”. We excluded the terms “parasite” and “parasitism” from our search, because while egg abandonment is perhaps most intensively studied in species that experience brood parasitism, the focus of our study is abandonment by parents of their own eggs, which specifically requires better understanding from a conservation

management perspective. After restricting the search to primary literature only (i.e., excluding review papers) and removing any duplicates, this returned 141 articles. Of these, 30 were removed because they were not published in English and translation was not possible, and a further 36 were excluded because it was evident from screening the abstract or main text that they were not relevant (e.g., they did not directly study or collect data on abandoned eggs/clutches or focused on brood parasitism despite our exclusion of related terms in the initial search). We read the remaining 75 papers in detail to identify: (a) what definition (if any) of egg abandonment was used; (b) what causes (if any) of egg abandonment were cited; and (c) what rates of egg abandonment were reported. Full details of all retained studies are provided in Supplementary Material Data 1.

Of the 75 relevant studies, 43 (57%) did not provide a definition of egg abandonment for their study or describe how it was determined. The remaining 32 papers provided definitions of varying clarity, with 25 (33%) providing a definition that we considered to be sufficiently specific to enable reproducibility (e.g., the presence of intact but cold eggs in nest), but only 13 of these (17% of all identified studies) providing a conclusive timeframe for abandonment as part of their definition (e.g., “if we did not observe the breeding pair near the nest (or signs of activity) during two consecutive visits [3-4days]).''

Most (64/75; 85%) of the studies identified provided some indication of the definite or presumed cause(s) of egg abandonment. These fell into 10 broad categories (see Table S1 in Supplementary Material 1). Several studies posited multiple different causes of abandonment. Confidence in these cited causes ranged from relatively low (e.g., causes were assumed based on anecdotal

evidence or findings of other studies) to high (causes were tested directly by the study). Overall, the main drivers of egg abandonment appear to be human disturbance (31% of studies; predominantly due to farming practices and research/conservation interventions), climatic factors (19% of studies), disturbance by predators (17% of studies), and food availability (17% of studies). Notably, 4 studies confidently reported egg failure prior to abandonment, i.e., lack of embryo development was likely to be the reason the parents left the eggs.

Potential impacts of inaccurate abandonment records on breeding monitoring

Of the 75 studies identified above, 43 provided data on the proportion of clutches that were abandoned during the study period. However, one paper reported data for 9 different species/populations, so there were 51 records in total. The mean rate of egg abandonment across all records was 20%, but rates varied from 1-100%, with a median of 12%. This represents a significant loss of reproductive potential, particularly given the increasing evidence that most wild bird eggs are fertilised and therefore contain individuals that died early (Evans and Postma 2025). If egg abandonment occurred after the embryo(s) died – which it did in several studies – these losses will also have a significant impact on our understanding of hatching failure rates and drivers.

To assess the potential impact of incorrect abandonment records on quantitative monitoring of reproductive outcomes, we analysed egg outcomes recorded by various nest monitoring teams working with wild populations of Eurasian Curlew (*Numenius arquata*) across the United Kingdom (UK) and Ireland, using data collected for another study. The Eurasian Curlew (henceforth

145 “Curlew”) is a charismatic wader with around 19-27% of the global breeding population residing
146 in the UK (Brown et al 2015). Globally, the Curlew is currently classified as near-threatened
147 (BirdLife International 2017) and UK and Ireland breeding populations have seen significant
148 declines ranging from 32-96% over the last several decades (O’Donoghue et al 2019 ; Heywood
149 et al 2023). Consequently, Curlew are currently red-listed and have been proposed as the most
150 urgent conservation priority in the UK (Brown et al 2015; Stanbury et al 2021). Low global Curlew
151 productivity appears to be largely driven by nest predation (e.g., Grant et al 1999; Valkama et al
152 1999; Roodbergen et al 2012; Zielonka et al 2019), and other factors such as agricultural land-
153 use, forestry and climate warming (Franks et al 2017), but little is known about the incidence and
154 non-predation-related drivers of hatching failure across UK and Ireland populations.
155
156 Combining data from 1428 eggs, from 381 naturally incubated clutches laid in various locations
157 around the UK and Ireland, across three breeding seasons (2022-2024), we calculated the
158 percentage of all Curlew eggs recorded as abandoned to be 5.5% (although this was variable
159 across years: 2.5% in 2022, 4.0% in 2023, and 8.0% in 2024; see Supplementary Material 1 and
160 Supplementary Material Data 2 for calculation methods and data). Hatching failure rate,
161 excluding eggs that were classified as abandoned, predated, damaged and ‘unknown’ (i.e., when
162 egg outcome was unclear), was calculated as 12.9% (11.6% in 2022, 13.9% in 2023, and 13.1% in
163 2024; see Supplementary Material 1 and Supplementary Material Data 2 for calculation methods
164 and data). However, if we were to assume that all abandoned eggs died before abandonment
165 (i.e., abandonment was the consequence of embryo mortality, not the cause), recalculation of
166 our hatching failure rates including abandoned eggs (i.e., the total number of ‘failed’ plus

‘abandoned’ eggs, divided by the total number of ‘hatched’, ‘failed’ and ‘abandoned’ eggs) results in a 1.4-fold increase in our estimate of mean curlew hatching failure rates, to 18.6% (14.1% in 2022, 17.9% in 2023, and 21.7% in 2024).

While it is unlikely that all records of egg abandonment are incorrect, our experience of receiving egg samples and accompanying data has revealed that at least some degree of error is probable. For example, we frequently receive unhatched egg samples which are recorded as ‘abandoned’, but the recorded abandonment date is after the expected end of incubation (i.e., the parents left the clutch *after* it failed to hatch). Abandonment was therefore not the cause of failure, and these eggs should be included as sampling units in calculations of hatching failure rates. Confidence in egg abandonment dates is clearly dependent on nest monitoring effort, with higher frequencies of nest visits being more accurate. In many nest monitoring programmes, failed eggs left in the nest after the end of incubation may be incorrectly recorded as ‘abandoned’ due a lack of information on lay date and/or expected hatch date.

By examining the embryo developmental stages of all intact unhatched Curlew eggs using previously developed egg dissection and fluorescent microscope methods (Birkhead et al 2008; Assersohn et al 2021; Morland et al 2024), we observed that while embryo development stages were fairly consistent within the majority of reported abandoned clutches, 5/25 (20%) clutches reported as abandoned had pronounced variation in embryonic development stages across eggs. Estimated embryonic developmental differences between the least and most developed embryos within each clutch ranged from at least 3-11 days (likely conservative estimates of

duration since timing is based on Hamburger and Hamilton's (1951) embryo staging series for domestic chicken *Gallus gallus domesticus*, which has a shorter mean incubation period than the Curlew (~21 days vs ~28 days, respectively; see Table S2 in Supplementary Material 1, and also Supplementary Material 1 and Supplementary Material Data 3 for further information on methods and data). Curlew have semi-synchronised hatching, with intervals ranging from several hours to up to two days (De Jong et al 2021), but the wider developmental stage variation exhibited in several reported abandoned clutches suggests at least some eggs experienced embryo mortality before egg abandonment occurred. Our evidence suggests that 20% of reportedly 'abandoned' clutches contained eggs that experienced embryo mortality which was not caused by abandonment. If the parent(s) was able to detect embryo death/egg inviability (see Table 1 for potential mechanisms), it is possible that this subsequently stimulated egg abandonment. If it is possible to incorporate embryo staging into nest monitoring programmes, variation in the developmental stages of dead embryos within a clutch may therefore provide useful insights into the likelihood of abandonment versus other factors as the cause of failure.

Conclusions and future recommendations

There are many well-established nest monitoring programmes across the world, such as the BTO Nest Record Scheme, that collate records of breeding success across species. In general, these programmes record incidences of nest predation, damage, hatching failure, and abandonment, but what constitutes abandonment is not explicitly clear (e.g., the revised 2003 BTO Nest Record Scheme Handbook (Crick et al 2003) provides no description of how to verify abandonment). We

have shown, across a range of bird breeding studies, that there are significant inconsistencies in how egg abandonment is defined and monitored. Using empirical data, we show that eggs may be inaccurately recorded as abandoned due to ambiguous criteria and/or incomplete information on incubation dates/parental behaviour, skewing our understanding of how different factors contribute to overall rates of hatching failure.

In the ideal (but unlikely) scenario that time and resources are not limited, direct observations of parental behaviour, either via frequent nest visits or (even better) remote camera and/or nest temperature monitoring, provide the most irrefutable evidence of abandonment or 'true' hatching failure. However, monitoring effort is usually limited, and uncertainty exists in most cases. As a result, research studies and conservation monitoring programmes differ in their approach to recording the causes of egg loss/hatching failure, potentially complicating our overall understanding of the drivers of failure across species.

Examining the developmental stage of dead embryos to assess whether they died before their predicted abandonment date is one potential way to overcome the problem of limited information on incubation timing/parental care. Methods for doing this are relatively straightforward; however, because embryo staging series have not been produced for most species, this approach relies on comparison with primarily domestic chicken (Hamburger and Hamilton 1951) (precocial species) or zebra finch (Murray et al 2013) (altricial species). While zebra finches probably provide a reliable comparison for many passerine species (Hemmings and Birkhead 2016), caution should be taken when using this approach for precocial species, since

the incubation periods and late-stage developmental trajectories of many precocial birds diverge somewhat from that of the chicken (Cooney et al 2020). This may lead to some degree of error in the estimation of embryo death timings based on developmental stages.

Finally, in situations where monitoring effort is limited and assessment of embryo developmental stages is not possible, we recommend that the resulting uncertainty in egg fates is clearly documented, and that studies report hatching failure rates both including and excluding presumed abandoned eggs, highlighting the range within which the 'true' value must lie and enabling clearer assessment of the potential error in these estimations. As we found evidence that 20% of assumed 'abandoned' Curlew clutches had experienced embryo mortality prior to abandonment, it is likely that the true hatching failure rate in this species will fall much closer to the traditional calculation of hatching failure (i.e., excluding abandoned eggs). However, where the true hatching failure rates lie on this spectrum is likely to vary between species, depending on factors such as propensity to abandon (e.g., see Hanssen et al 2023) and/or their ability to use sensory cues (see Table 1) to examine current clutch viability throughout incubation. Future studies should therefore seek to obtain better understanding of how egg abandonment behaviour varies across species and the degree to which incubating birds can detect and respond to egg viability cues.

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Declaration of competing interest

We the authors provide our assurances that this work is original and has not been published elsewhere, nor is it currently under consideration for publication elsewhere. We also confirm that there are no conflicts of interest to declare.

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Table 1| Summary of sensory cues available to parental bird(s) that may be used to examine egg viability status during incubation[1,2]

Types of sensory cues	Presentation	Timing	Evidence of capacity for perception	Required test of parental response
Auditory	Embryo clicking, vocalisation and bill tapping (but can be rare or absent in some species, particularly altricial) (Vince 1966, 1969; Oppenheim 1972); parental vocalisation during incubation (e.g., Ruiz-Raya and Velando 2024).	Late incubation, after embryonic vocalisation is established (see Brua 2002)	• Embryo vocalisation elicits behavioural responses from parents during incubation (e.g., Simmons 1955; Tuculescu and Griswold 1983; Evans 1988; Evans 1990; Evans et al 1994; Brua et al 1996; see reviews in Brua 2002; Brulez et al 2015). • Prenatal parental vocalisation/other auditory stimulation exposure and eavesdropping alters pre- and post-natal development and behaviour (e.g., Woolf et al 1976; Mariette and Buchanan 2016; Mariette et al 2018, 2021; Ruiz-Raya and Velando 2024).	Manipulation of embryo auditory cues (e.g., playback experiments).
Chemical/ Olfactory	Nitric oxide (NO) and other volatile chemicals emitted by developing embryos (e.g., Ar et al 2000, 2004; Titov et al 2007).	From mid-incubation onwards, as odour profiles of inviable eggs become discernable (Webster et al 2015)	• Infertile and fertile eggs have distinguishable volatile chemicals odour profiles in Japanese quail (*Coturnix japonica*) (Webster et al 2015). • NO emittance from developing embryos passively mediates brood-patch development (although not via parental odour detection) (Ar and Sidis 2002; Ar et al 2004).	Manipulation of volatile chemical odours of eggs.
Tactile	Embryo vibro-acoustic cues; embryo and amnion motility (e.g., Vince 1969; Impekoven 1976; Wu et al 2001; Sheldon et al 2018).	Early incubation onwards, from around day 3 of incubation in domestic chickens (Wu et al 2001) and after the first quartile of the incubation period in most wild birds (Sheldon et al 2018)	• Brood patches for incubation are rich in mechanosensory receptors (see Portman 1961; Winkelmann and Myers 1961; Jones 1971) and simulation of these promotes incubation behaviour through prolactin secretion (e.g., Hall 1987; Meijer 1995; Massaro et al 2007). • Specialised beaks with mechanosensory organs evolved in some species for tactile foraging (e.g., Zweers 1973; Berkhoudt 1980; Avilova et al 2018; also see review in Ziolkowski et al 2022). • Embryos vocalise/move in response to egg turning (e.g., Brua et al 1996). • Neighbouring embryo vibro-acoustic cues used for hatching synchronicity/predation risk reduction (e.g., Vince 1969; Vince and Cheng 1970; Noguera and Velando 2019; also see review in Mariette et al 2021).	Manipulation of tactile stimulus of eggs to observe parental behavioural responses.
Thermal	Increased metabolic activity in embryos from mid-incubation, reducing in the final 20% of development period (rates and trajectories differ depending on developmental mode) (e.g., Vleck et al 1980; De Oliveira et al 2008; DuRant et al 2011).	Mid-incubation, as embryonic metabolic activity increases (e.g., Vleck et al 1980; De Oliveira et al 2008; DuRant et al 2011).	• Models based on egg cooling rate behaviours identify egg viability status with 80% accuracy, suggesting parents could assess thermal differences between viable and inviable eggs (Narushin et al 2024). • Pre-pipping embryos alter vocalisation responses when cooled (e.g., Brua et al 1996).	Manipulation of thermal properties of eggs to observe parental behavioural responses.

[1] Whilst here we mainly present summary examples specifically related to embryo-parent and embryo-embryo interactions during incubation, we do present some examples outside the context of incubation that further demonstrate birds' sensory capabilities in non-incubation contexts but could also be in turn potentially utilised in an incubation context (although not directly proven).

[2] Corresponding full reference details can be found in the 'References' section.