Summary research report

Project SS07020438

Application of Modern Biologging Tools, Data Sharing and User-Friendly Data Analysis to Optimise the Incubation of Eggs of Threatened Bird Species in Human Care

Martin Sládeček, Petr Chajma, Lucie Burešová Pešková, Kateřina Trejbalová, Iva Babováková, Michal Podhrázský, Petr Suvorov & Miroslav Šálek

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1. Introduction

Successful egg incubation is one of the key prerequisites for the long-term sustainability of bird populations under human care, particularly for threatened species, species that are difficult to breed, and those involved in conservation-breeding or reintroduction programmes. Although artificial incubation is routinely used in zoos and specialised breeding facilities, protocols for many wild bird species still rely primarily on empirical experience, general recommendations and analogies with a limited number of well-studied model species. For rare species in particular, sufficiently detailed information is often lacking on the temperature, humidity and mechanical conditions under which natural incubation takes place, and on how these conditions vary among species, husbandry contexts and modes of incubation care.

Project SS07020438 — Application of Modern Biologging Tools, Data Sharing and User-Friendly Data Analysis to Optimise the Incubation of Eggs of Threatened Bird Species in Human Care — was designed to integrate three areas that had previously tended to be used separately in avian husbandry: detailed monitoring of incubation using advanced data loggers; standardised sharing of incubation data collected during artificial incubation; and user-accessible analytical interpretation of these data. The project aimed to develop and test a suite of tools, procedures and data resources enabling practitioners to evaluate natural and artificial incubation more effectively, compare their own experience with data from other institutions and species, and make informed adjustments to incubation protocols. The outputs were designed to contribute directly to reducing losses during parent-rearing, increasing hatching success under artificial incubation and improving the quality of offspring produced by artificial incubation.

The central project output is Incubase, a web platform for managing, sharing and analysing data on avian egg incubation. The platform links records of eggs, incubation attempts, repeated measurements, hatching outcomes and other relevant metadata with analytical tools that allow users to evaluate incubation either in real time or retrospectively after an incubation cycle has ended. Its purpose is not merely to archive data, but above all to make them operationally useful. Incubase enables practitioners to assess a particular incubation case, compare it with previous experience and progressively refine decisions concerning temperature, humidity, target egg-mass loss, turning regimes, transfers between parental and artificial incubation, and the interpretation of potentially hazardous deviations.

A second key output, integrated internally with Incubase, is the public database of incubation parameters. The database collects and archives standardised information on artificial incubation, providing a basis for comparisons among species, husbandry institutions and incubation protocols. At the end of the project (30 June 2026), the database contained records for 24,543 eggs representing 470 taxa and originating from seven institutions. It already constitutes an extensive and unique data resource, and its value can be expected to increase as additional institutions participate and the volume of data grows. To raise awareness of Incubase within the international professional community, a scientific manuscript is currently at an advanced stage of preparation. It describes Incubase and the associated database in detail, together with their potential to improve breeding outcomes and support scientific research.

Another output is the Methodological Guide to Comprehensive Incubation Monitoring in Birds under Human Care, which translates experience gained before, and especially during, the project into procedures suitable for practical use in breeding facilities. The guide summarises recommendations for selecting and preparing equipment, installing data loggers in nests or surrogate eggs, minimising disturbance, downloading and checking data, interpreting measurements and subsequently using them in Incubase. It also emphasises that these procedures can facilitate the early detection of deviations from normal incubation, help identify the causes of unsuccessful parent-rearing and, in some cases, support decisions to transfer eggs to an incubator.

A further output, not envisaged when the project was prepared, is a widely applicable dataset of 3D-printable surrogate egg models. Although their development and manufacture were originally planned solely to support the collection of data on internal egg temperature and egg turning using data loggers, it became clear that practitioners had substantial demand for reproducible and affordable surrogate eggs representing a broad range of bird species. An extensive model collection was therefore developed, covering the great majority of avian egg-shape and egg-size diversity, accompanied by a detailed manufacturing protocol and a series of validation tests. Several model types are provided, both for routine husbandry use and as carriers for data loggers, as originally intended. The surrogate egg database is deposited on Zenodo, and its development and manufacturing process are described in a scientific manuscript currently in preparation.

The project also generated a unique dataset from data loggers deployed in husbandry settings, particularly records of incubation temperature profiles, humidity, parental attendance and the mechanics of egg turning. These data demonstrate that biologging can serve not only as a research method but also as a tool for operational diagnostics. It can identify situations in which eggs are not incubated consistently, undergo repeated cooling or overheating, parental care is disrupted by the surrounding environment, or the mechanical characteristics of egg turning depart from the expected pattern. Where definitive species-specific recommendations cannot yet be formulated, the data nevertheless provide a standardised framework for decision-making and for targeted further data collection. Results processed to date are presented in this report as several case studies, and publication in the scientific literature is planned.

An important component of the project was the continuous presentation of emerging outputs to the avian husbandry community, which also enabled close collaboration with a number of leading breeding institutions. This included a workshop for representatives of the principal user groups, especially zoos and other breeding institutions. The workshop, Modern Tools for Incubation Monitoring and Their Use in Avian Husbandry, was used to present working versions of the outputs, assess their clarity and obtain feedback from future users. Within the project, this was not merely an ancillary event but an integral component of implementation: comments from practitioners made it possible to refine the platform, the methodological documentation and the way in which results were communicated, ensuring that they were accessible even to users without advanced experience in data analysis. Further dissemination took place at several meetings of specialist husbandry committees in Czech and international settings.

The principal methodological conclusion of the project is that the long-term optimisation of incubation for wild bird species under human care cannot be based solely on the isolated experience of individual institutions. A more effective approach requires standardised data collection, secure and transparent data sharing, continuous quality control and accessible analytical tools capable of converting raw measurements into practically interpretable recommendations. Natural incubation provides an essential biological reference framework, whereas artificial incubation permits targeted technical control of conditions. Incubase, together with the other project outputs, creates an environment in which these two sources of information can be integrated systematically.

Practical recommendations for breeding institutions can be summarised as follows: incubation protocols should be documented in a standardised structure; incubation should be monitored with suitable data loggers in problematic or conservation-priority species; the resulting measurements should be interpreted in relation to natural incubation in the same or a related species; and the outcomes of individual incubation attempts should be shared in database form. This transforms isolated husbandry experience into a cumulative knowledge base whose value increases with every additional record.

Accordingly, this summary report treats the individual project outputs as an integrated system: data loggers provide measurements; the methodological guide standardises their use; 3D models support the technical reproducibility of work with eggs; Incubase provides data management and

analysis; the public database creates a shared knowledge resource; and scientific manuscripts integrate the main findings into the scientific literature. Their common aim is to support better-informed decisions during the incubation of eggs under human care, improve the breeding success of threatened species and establish a sustainable platform for the further development of biologging and evidence-based husbandry.

Numerous staff members from zoos and other breeding institutions contributed to the development, validation and practical implementation of the outputs described in this report. The authors particularly thank David Kodet and Barbora Lipanská (Safari Park Dvůr Králové), Aneta Ladrová, Eva Peňázová and Adéla Šmídová (Brno Zoo), Jan Kirner (Olomouc Zoo), Jan Hanel (Liberec Zoo), Václav Štraub (Zlín Zoo), and Antonín Vaidl, Pavel Kovařík and Jiří Eliáš (Prague Zoo) for their generous cooperation in testing the methods under routine operating conditions, facilitating specialised installations of monitoring equipment and providing valuable data for validation and further methodological development. The authors also thank the many other keepers and specialists who, during this project and in previous years, contributed to collecting and sharing data on avian incubation and rearing that were subsequently incorporated into Incubase. Without their long-term willingness to share experience and data, it would not have been possible to build a resource of this scale and practical value. We also thank students of the Faculty of Environmental Sciences, Czech University of Life Sciences Prague, who assisted with processing video recordings and data, especially Eliška Matějková and Monika Němcová for processing records obtained using data loggers, the results of which are presented in this report.

1.1 Theoretical background of the project: a brief introduction to avian egg incubation

An avian egg is a self-contained developmental system in which the embryo must be maintained throughout incubation within a narrow range of physical conditions that permit normal growth, gas exchange and the progressive utilisation of nutrients stored in the egg. Successful embryonic development depends primarily on four interrelated parameters: temperature, water balance governed by ambient humidity, egg turning, and sufficient gas exchange between the egg and its surroundings (Deeming 2002). Departures from appropriate conditions can slow development, cause developmental abnormalities, increase embryonic mortality or reduce hatchling condition (Webb 1987; Deeming 2002; DuRant et al. 2013).

Temperature is the most apparent parameter affecting the course and outcome of incubation. The embryo develops only when egg temperature exceeds the so-called physiological zero, below which development ceases. In birds, this threshold is approximately 23–27 °C. At the opposite extreme, there is an upper limit to thermal tolerance; temperatures above approximately 40.5 °C can cause irreversible damage to the embryo. Optimal temperatures differ among species and are rarely known precisely, but in most birds the surface temperature of an incubated egg most commonly lies between approximately 35 and 38.5 °C (Webb 1987; Deeming 2002). During natural incubation, however, egg temperature is not constant. It varies according to whether the parent is currently warming the egg, whether an incubation recess has occurred, the prevailing environmental conditions, the egg's position within the clutch and the incubation strategy of the species (Conway & Martin 2000; Boulton & Cassey 2012; Moreau et al. 2018).

The second key parameter is the egg's water balance. During incubation, avian eggs progressively lose water through the diffusion of water vapour across the shell. The rate of this loss depends primarily on shell permeability, temperature, ambient humidity and airflow around the egg. Regular weighing is therefore used during artificial incubation as a practical means of assessing whether an egg is developing along the expected trajectory. Successfully incubated eggs are generally assumed to lose approximately 12–18% of their initial mass by the time of hatching, with a loss of around 15% frequently used as a simplified universal rule. The optimum can, however, differ markedly among species (Rahn

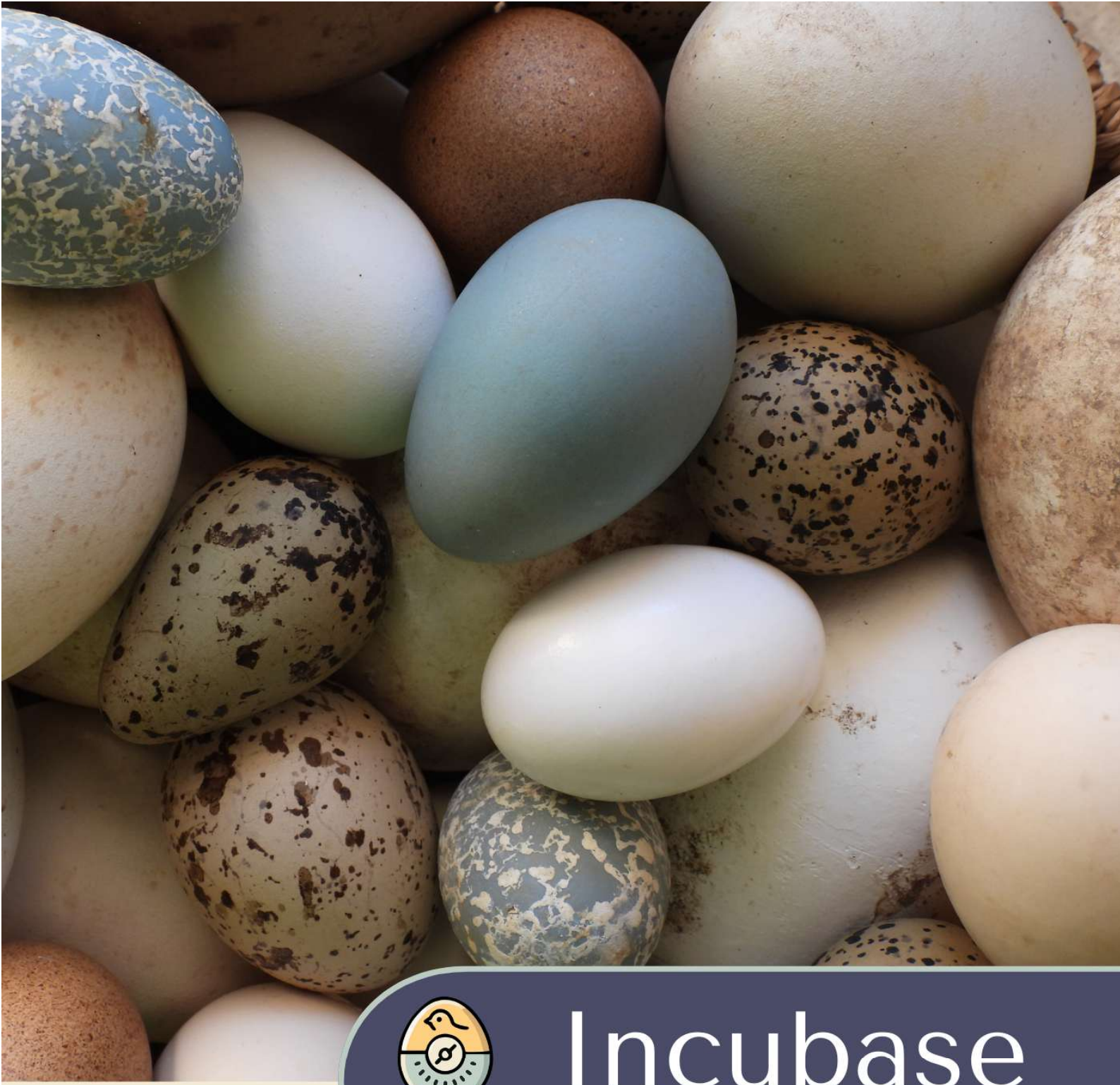
& Ar 1974; Ar & Rahn 1980; Tullett 1990), as is also clearly illustrated by the graphical outputs presented in Incupedia (Section 2.6). Excessively rapid mass loss can indicate excessive desiccation, whereas insufficient mass loss can result in fluid retention, embryonic oedema and hatching difficulties. Regular weighing followed by adjustment of incubator humidity is therefore among the most important practical procedures in artificial incubation.

The third fundamental process is egg turning. During natural incubation, parents regularly move and turn their eggs; in artificial incubators, this function is replaced by mechanical turning systems or manual handling. Turning prevents embryonic membranes from adhering to the shell, supports development of the vascular system, promotes appropriate utilisation of the albumen and contributes to the normal orientation of the embryo within the egg (New 1957; Deeming 1989; Tullett & Deeming 1987). Available comparative studies show that turning frequency is not universal. It varies among species and is associated, among other factors, with the developmental mode of the young and the duration of incubation; altricial species generally tend to turn their eggs more frequently than precocial species (Pešková et al. 2025). This is also important in husbandry practice, because a universal turning regime may not match the biological requirements of all species.

The fourth basic requirement is gas exchange. The embryo consumes oxygen and produces carbon dioxide, with exchange occurring through pores in the shell. Shell conductance to gases and water vapour is species-specific and is related to egg size, nest microclimate and incubation duration (Rahn & Ar 1974; Ar & Rahn 1980). In a natural nest, gas exchange is maintained through the combined effects of shell properties, the structure of nest material, microclimate and parental behaviour. Oxygen is not usually limiting in a well-ventilated incubator, but poor ventilation, an excessively enclosed environment or inappropriate incubator settings can impair gas exchange and negatively affect embryonic development (Tullett 1990).

Artificial incubation differs from natural incubation in that the conditions experienced by the developing embryo are determined not by the parent and nest environment, but by the technical settings of the incubator and husbandry interventions. Its advantage is the capacity for precise control of temperature, humidity, turning and ventilation. At the same time, it requires continuous monitoring because the species-specific requirements of many wild bird species remain insufficiently understood and cannot always be inferred safely from general protocols developed for poultry. From a practical perspective, regular weighing of eggs, recording incubator settings, documenting transfers between incubators, monitoring fertility and embryonic development, and recording the final incubation outcome are therefore essential.

This is precisely where systematic record-keeping and analytical support become necessary. Individual husbandry experience has considerable practical value, but without standardised recording it remains difficult to compare and only weakly transferable to other species or institutions. The database and analytical environment of Incubase are therefore founded on the principle that every egg represents a measurable developmental trajectory. If its mass, incubation timeline, incubation conditions, husbandry interventions and final outcome are recorded continuously, these data can support not only decisions concerning the particular incubation in progress, but also the gradual refinement of species-specific recommendations.



Incubase

Where Knowledge Hatches from Eggs

- Technological characteristics of Incubase and principles of data security and management
- Data collected and structure of the Incubase database
- Navigating the data and operational management of records in Incubase
- Analytical tools for optimising incubation
- Data-entry and processing validation mechanisms in Incubase
- Incupedia - A Living Encyclopaedia of Avian Incubation
- Summary of the dataset available through Incubase

2. Incubase - Where Knowledge Hatches from Eggs

Incubase (https://incubase.fzp.czu.cz/) was developed as an open web platform for the systematic management, analysis and sharing of data on avian egg incubation, and currently operates in both Czech and English. Its primary purpose is to transform the often fragmented, inconsistently maintained and difficult-to-share records held by zoo hatcheries, breeding institutions and other collections into a unified data environment that can support both routine husbandry and long-term applied and scientific research. The platform therefore functions not merely as a record archive, but as an integrated system combining standardised data entry, continuous data validation, analytical decision-support tools, inter-institutional data sharing and a continually updated knowledge base on avian incubation.

The first core component of Incubase is a database of egg-incubation parameters. It stores structured information on individual eggs, incubation histories, the incubators used, incubation conditions, fertility, embryonic development and incubation outcomes. At a general level, these data include the species, origin and identity of the egg; laying and hatching dates; egg dimensions and mass; repeated weighing records; placement in a specific incubator; temperature, humidity and turning settings; any interventions made during incubation; and the final fate of the egg. The database supports records from both artificial and natural incubation and allows the two to be compared retrospectively. A more detailed description of the database, its data structure, scope and significance as a distinct project output is provided in the following dedicated section.

The second component of the platform is a suite of intelligent analytical tools that use the entered data to provide practically applicable recommendations in real time. These tools are intended primarily for ongoing hatchery operations: they allow users to follow the development of individual eggs, evaluate mass-loss trajectories, compare a current egg with historical records from the same or a related species, and propose targeted adjustments to incubation conditions. Incubase can therefore assist, for example, in estimating an appropriate relative humidity, identifying eggs that deviate from their expected trajectories, and deciding how eggs should be distributed optimally among several incubators.

The third component of Incubase is an environment for data management, archiving and sharing. The platform enables registered users and institutions to maintain their own incubation records in a standardised format, search the available data, work with their own summaries and exports, and define the conditions under which their data may be made available to others. A key feature is the separation of individual user accounts from institutional data ownership: data are managed within an institution or breeding collection, whereas individual users may enter or edit data, or request access to a particular institution's data, according to their role and permissions (see Section 2.1.4). The platform thereby provides both the technical and organisational framework for controlled data sharing, collaboration between husbandry practitioners and researchers, and negotiation of the conditions under which data may be used for scientific or applied purposes.

The fourth component is Incupedia, an open encyclopaedia of avian incubation. Its purpose is to transform data stored in Incubase into accessible species-level summaries for animal keepers, curators, researchers and others interested in avian incubation. Species accounts summarise the information available for particular taxa, including basic egg characteristics, laying seasonality, incubation period, fertility, hatching success, recommended temperature and humidity, egg mass loss, and other parameters relevant to husbandry, especially artificial incubation. Incupedia is designed as a dynamic output: each additional validated database record can refine the species summaries, figures and practical recommendations.

Overall, Incubase integrates four levels of work with incubation data: data collection and standardisation; immediate analytical support for husbandry decisions; controlled sharing and reuse of data; and synthesis of knowledge through Incupedia. It thus creates a feedback system in which data routinely generated in hatcheries are not used only once for a particular egg, but become part of a

broader knowledge base. The value of this knowledge base will increase with the number of participating institutions, represented species and well-documented incubation cases. Incubase is therefore not merely a technical tool for recording eggs, but an infrastructural output that connects avian husbandry, the applied conservation of threatened species and research into avian reproductive biology.

2.1 Technological characteristics of Incubase and principles of data security and management

Incubase is a server-based web application designed for the long-term management, analysis and sharing of incubation data. It is built using the Python Flask framework and employs a MySQL relational database that stores records on eggs, incubation events, incubators, users, institutions and associated metadata. Communication between the application and the database is handled through the SQLAlchemy object-relational mapper, while changes to the database schema are managed through the Alembic/Flask-Migrate migration system. The application is hosted on the server infrastructure of the Czech University of Life Sciences Prague under the domain incubase.fzp.czu.cz and is served to clients through the Gunicorn WSGI server. The user interface is generated server-side using the Jinja2 templating system and employs the responsive Bootstrap 5 framework. Interactive elements, such as data tables and species searches, are implemented through client-side JavaScript components communicating with dedicated JSON API endpoints.

The application architecture separates routine user operations from processes that may take longer or place a greater load on the server. More time-consuming tasks, such as sending emails or recalculating species statistics for Incupedia, are processed asynchronously using Celery with RabbitMQ as the message broker. Statistical calculations and optimisation routines are implemented in R scripts launched from the Python environment. This integration combines a robust web and database infrastructure with the analytical capabilities of R, which is well suited to modelling incubation trajectories, evaluating egg mass loss and proposing adjustments to incubation parameters. The Incubase interface is bilingual, with Czech and English versions implemented using Flask-Babel.

Application security is addressed through user authentication, form protection, rate limiting of potentially risky requests, validation of uploaded files and separate storage of sensitive configuration data. Access to non-public Incubase functions requires user registration and login. Authentication uses a session-based login system. Passwords are stored exclusively as PBKDF2-HMAC hashes. Password recovery uses time-limited, single-use tokens sent by email; the original password is never displayed or transmitted. All HTML forms are protected against cross-site request forgery (CSRF) by cryptographically signed tokens. Sensitive endpoints are protected by IP-based rate limiting, reducing the risk of brute-force attacks and abuse through repeated requests. File uploads are restricted to permitted file types, and filenames are sanitised before storage. Database credentials, email passwords and API keys are stored outside the application in a server-side configuration file and are not included in the application's source code. Email communication uses a secure SSL connection.

The Incubase database is backed up automatically by a scheduled server script using mysqldump with the -single-transaction option. This procedure creates a consistent database snapshot without locking tables or materially restricting normal application operation. Backups follow a multi-tier retention scheme: daily backups are retained for 14 days, weekly backups for 60 days, monthly backups for one year, and annual backups indefinitely. This system provides sufficient granularity for recovery from routine operational errors while also ensuring long-term archiving of database states for auditing, reconstruction and verification.

2.1.1 Access to the platform, user structure and registration

Incubase was created as a platform for the secure maintenance of incubation records, their controlled sharing and their repeated use in husbandry, research and the development of species-specific

recommendations. A fundamental principle of the system is the separation of individual user access from institutional responsibility for submitted data. Individual users may therefore enter data into the platform, while ownership, the licensing regime (see Section 2.1.4) and decisions concerning data access remain at the level of the institution or breeding collection, which may also be represented by a private breeder.

Without registration, users can access only the public section of Incubase, principally Incupedia. All other activities require simple, free registration. Registered users can use the platform's non-public functions, search for data, submit requests for access to datasets and, once the relevant institutional affiliation has been approved, enter, edit or manage records.

2.1.2 Users, institutions and permissions management

The Incubase user structure distinguishes between an individual user and an institution. An individual user has a personal account through which they access the platform and use its functions. An institution is an organisational record representing the legal owner or manager of a breeding collection and of the data entered into Incubase. Data ownership and the applicable licensing regime are therefore assigned at the institutional level rather than solely to a particular user.

Data entered by a user affiliated with a particular institution inherit that institution's licensing and access regime. A single institution may have multiple affiliated users. The institutional administrator may approve or reject membership requests, manage access permissions, respond to data requests and, where necessary, transfer administrator rights to another user. The user account remains independent of institutional affiliation, so users can change institutions without registering a new account.

A private breeder may participate in the system in a manner analogous to an institution. After creating an individual account, the breeder establishes an institutional record representing their breeding collection and becomes the administrator of the data entered into the system. This arrangement allows zoos, breeding centres and private breeders to participate within a common data and licensing framework.

2.1.3 Ownership of and responsibility for scientific and husbandry data

Submitted scientific and husbandry data remain the property of the contributing institution or breeding collection. The operator of Incubase does not claim ownership of records entered by users, but provides the infrastructure for their management, analysis, archiving and sharing. Any use of the data in scientific publications, reports, methodological guidelines or other public outputs must comply with the licensing regime selected by the data owner and must include appropriate attribution.

The platform's terms of use also require a declaration that submitted data originate from legally held animals and lawful incubation activities. Responsibility for compliance with national legislation and international regulations, such as CITES, rests with the data provider.

2.1.4 Data-licensing regimes and data sharing

Incubase uses three principal data-sharing regimes: an open licence, a view-only regime and private data. These regimes provide a compromise between openness, scientific utility, protection of sensitive husbandry information and respect for institutional data ownership.

Open licence

The open licence is intended for institutions that wish to make their incubation data available for the broadest possible use. Under this regime, data in Incubase may be viewed, downloaded and reused, including in scientific publications, methodological documents, comparative analyses and other public outputs. Such use is conditional on proper acknowledgement of the data source and citation of the data owner in accordance with the platform's rules.

The open licence represents the highest level of participation in the shared knowledge base. The data can be used not only for species summaries in Incupedia and for the platform's optimisation tools, but also for independent analyses undertaken by other users or research teams. The data owner does not relinquish authorship or the right to attribution; openness concerns permission to use the data, not transfer of ownership.

View-only regime

The view-only regime is a compromise for institutions that wish to make their data visible to other Incubase users but do not wish automatically to permit downloading, further processing, or use in publications and public outputs. Registered users may search for and view such data within the platform, allowing preliminary comparison, assessment of the availability of records for a particular species, or contact with the data owner. The data cannot, however, be exported or used outside the platform without a separate agreement.

A user or research team wishing to use these data must request access or permission from the data owner through Incubase's standardised request mechanism. The data owner therefore remains actively involved in deciding whether the data may be used, for example, in a scientific analysis, collaborative project, publication or methodological output. This regime is particularly suitable for institutions that wish to be visible and open to collaboration while retaining control over when, to whom and under what conditions their data are provided.

Private data

The private regime is intended for data that an institution does not wish to make available to users outside its own organisation. Individual records under this regime are not directly accessible to external users and are used primarily for internal record-keeping, management of the institution's own incubators and use of the Incubase analytical tools within that institution.

Private data can nevertheless contribute to the platform's overall analytical potential. Unless they are additionally withheld, they may be included in aggregated analyses, summary statistics and visualisations presented in Incupedia without exposing individual records or identifiable details of a particular breeding event. The general existence and scope of a dataset may also be discoverable within the platform, allowing interested parties to contact the data owner and request access for targeted collaboration, a joint analysis or a co-authored output.

Temporary withholding and embargo

In addition to the three principal licensing regimes, Incubase allows data to be withheld temporarily. This mechanism protects information that is sensitive only for a limited period, such as data from the first successful breeding of a particular species or another exceptionally valuable breeding event that the institution wishes first to evaluate internally, announce or publish.

During the moratorium, the data are excluded from publicly visible summaries, cannot be discovered by other users and do not contribute to Incupedia species accounts, irrespective of the otherwise selected licensing regime. This arrangement is explicitly time-limited and allows deferred release after a specified period. The current maximum withholding period is one year.

2.1.5 Protection of personal data

Personal-data protection follows the principle of data minimisation. The platform is operated by the Faculty of Environmental Sciences, Czech University of Life Sciences Prague, which acts as the controller of personal data processed within the platform. Personal data are processed on the basis of the user's consent, expressed by accepting the terms of use during registration.

The personal data collected are limited to information necessary for system operation, principally the user's name, username, email address and password hash. The platform does not process payment information, special-category personal data, or tracking data beyond functional session cookies.

Where geolocation information is used, it relates to an institution or breeding collection rather than an individual user and is supplied manually by the user. Subscription to a newsletter and administrative communications are governed by a separate opt-in consent distinct from the basic consent to use the platform.

Deletion of accounts and preservation of scientific value

Deletion of user and institutional accounts is handled in a manner that respects users' rights while preserving the scientific integrity of specialist data. Deleting an individual user account does not automatically delete the incubation data entered by that user. In the associated records, the link to the individual user is set to a null value, thereby anonymising the original contributor while preserving the data for long-term analyses.

By contrast, deletion of an institutional account also removes the associated dataset, because records without an accountable data owner cannot be managed, licensed or made available for further use in a meaningful manner.

2.2 Data collected and structure of the Incubase database

The database of incubation parameters used by Incubase, presented as a separate Public Database project output, is designed as a relational system for the standardised recording of the complete course of avian egg incubation, from laying or registration of an egg through to its final outcome. The database collects several types of information: identification and taxonomic data; egg morphometrics and photographs; phenological data; repeated measurements during incubation; technical parameters of incubators; husbandry interventions; and outcome data. Importantly, the same structure supports records from both artificial incubation and parental incubation. This makes it possible to compare incubator conditions with biologically relevant data from parental incubation and to establish a reference framework for interpreting artificial incubation.

The database structure is organised around three principal entities: the egg, the incubator and the species. These entities are further linked to information on users, institutions, data ownership, data sharing and the species-level summaries used in Incupedia. The basic relationships among the individual tables are shown in the entity-relationship diagram in Figure 1.

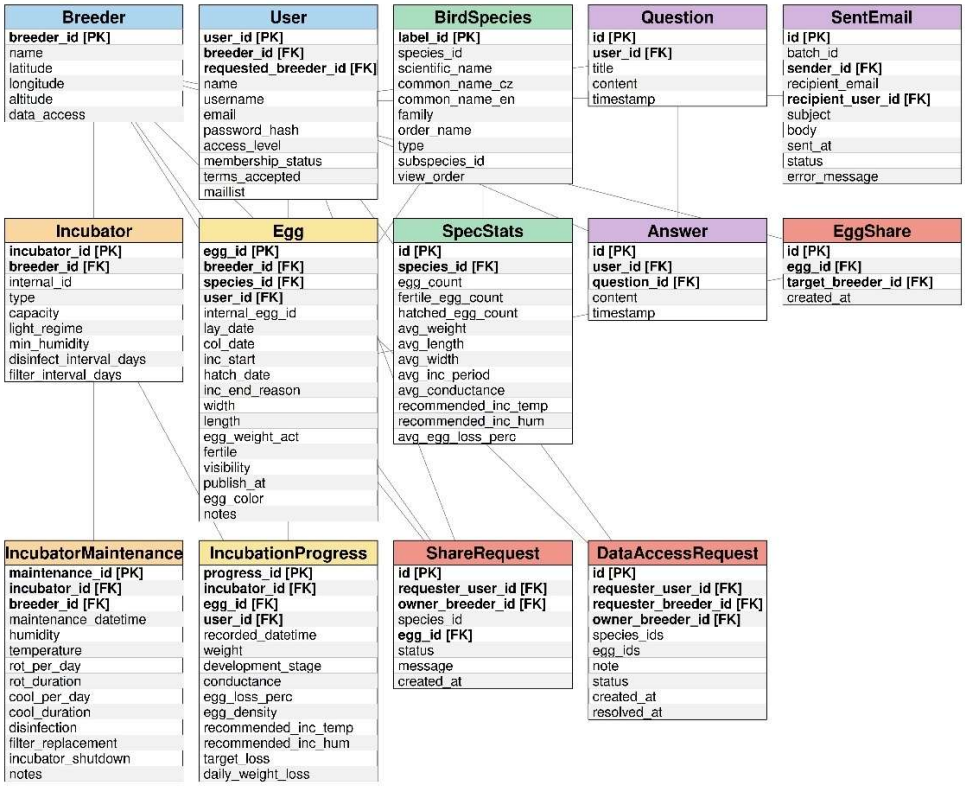


Figure 1: Entity-relationship diagram of the database.

The fundamental unit of the database is the individual egg. Each egg record stores stable information that is typically entered when the egg is registered or added during the incubation cycle as further information becomes available; part of the entry form is shown in Figure 2. These data principally include taxonomic identity, identification of the data owner, the egg's internal identifier, laying and hatching dates, parental identity, laying location, egg dimensions and mass, fertility, final incubation outcome, notes and, where available, photographic documentation. This core record may be revised and supplemented throughout incubation.

The second layer consists of repeated incubation records capturing variables that change over time. These include regular egg weighings, calculations of mass loss, assessment of fertility and embryonic development by candling or detection of cardiac activity, transfers among incubators and records of manual interventions. The database can record, for example, manual turning, cooling outside the incubator, and modifications of the shell used to regulate mass loss, such as drilling or waxing. Chick mass may also be entered at hatching. This structure allows each egg to be followed as a temporal trajectory rather than represented by a single static record.

The incubator is a separate database entity. Each incubator record contains its identifier, type, capacity and selected technical or operational parameters. The core incubator record is linked to an operational log in which changes in settings are recorded, principally temperature, humidity, turning regime, cooling and maintenance. Linking egg records to time-specific incubator records makes it possible to reconstruct retrospectively the conditions experienced by an egg at each developmental stage, including any transfers between devices.

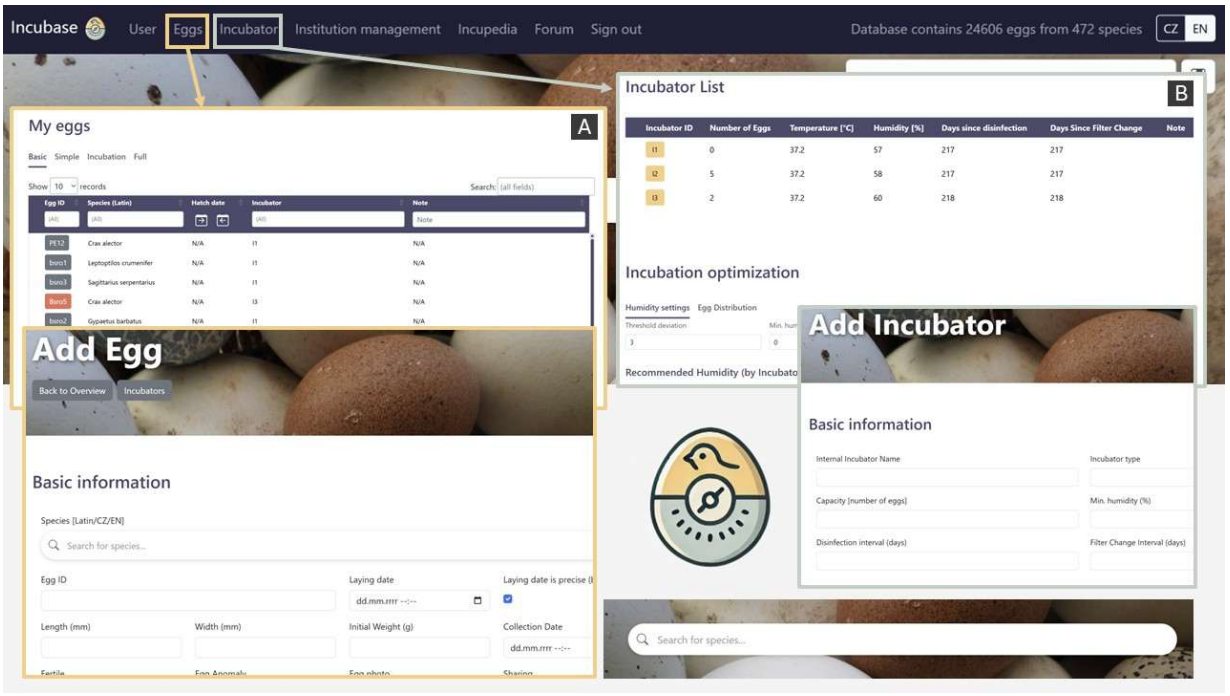


Figure 2: Incubase: (A) egg-entry form; (B) incubator record; and (C) search for information on a particular species on the home page.

The third principal entity in the Incubase database is the species, or more generally the taxon, to which a particular egg is assigned. Taxonomic identity is not entered merely as free text but is linked to a controlled taxonomic and nomenclatural list. This approach reduces errors caused by inconsistent use of names among institutions, permits reliable aggregation of records at species or higher taxonomic levels, and facilitates the import of historical datasets, which often contain obsolete names, inconsistent translations or taxonomic combinations that are no longer accepted.

Incubase is currently available in Czech and English, with the possibility of adding further languages in the future. The structure of avian nomenclature in the database reflects this bilingual operation: Czech, English and scientific Latin names are all maintained. No single nomenclatural standard is used consistently across zoos, breeding centres and private collections. The problem is even more pronounced in historical records, which may contain former species names, outdated taxonomic concepts, locally used translations or incomplete identifications.

For this reason, Incubase uses not only a simple list of currently accepted species names but a broader taxonomic and nomenclatural dictionary containing all synonyms located for each taxon in the three languages used. The IOC World Bird List v15.1 served as the principal taxonomic backbone and provides a global reference list of bird species and their official scientific and English names (Gill et al., 2025). Synonymous scientific names and alternative taxonomic combinations were subsequently retrieved through the GBIF Backbone Taxonomy and GBIF Species API, which are designed, among other purposes, to reconcile names across taxonomic sources and datasets (GBIF Secretariat, 2023; GBIF Secretariat, 2026). The list was further expanded using names and synonyms from the eBird/Clements Checklist of Birds of the World v2024, which is widely used in observation and occurrence databases (Clements et al., 2024). For taxa of particular relevance in the Western Palearctic, additional sources derived from the HBW and BirdLife International Illustrated Checklist of the Birds of the World and the subsequently updated HBW/BirdLife taxonomic checklist were also used; BirdLife International applies this checklist in its global, regional and national conservation assessments (BirdLife International, 2026).

All names obtained from these sources were subsequently deduplicated, and all synonyms were linked to a common taxon identifier. Consequently, multiple names, synonyms or language variants can

resolve to the same taxon in the database. This is particularly important during data import because it allows records entered under different names to be matched, to a substantial extent automatically, to the same currently accepted taxonomic concept. Conflicting cases, such as a name potentially referring to more than one taxon, were resolved through targeted manual review and correction or, where necessary, by manually extending the nomenclatural dictionary.

The resulting nomenclatural layer contains 48,863 unique combinations of Czech, English and Latin names for 11,507 taxa, including species, subspecies and family names. Inclusion of family-level entries is practically important because, when several species are kept together in the same facility, it may not be possible to identify an egg to species level. This may occur particularly in waterfowl and other Anseriformes, but similar situations can arise in other groups kept in mixed-species collections. In such cases, an egg can be recorded at least to family level, preventing the record from being lost and allowing it to be supplemented later or used within appropriate limitations. Conversely, where subspecies are recognised within a species and their identification is relevant in husbandry, Incubase permits egg records to be assigned to subspecies level.

The database can also record eggs produced by interspecific hybrids. For these cases, the taxonomic list includes the option "Hybrid - see note", and the parental species must be specified in the notes accompanying the record. Although the deliberate production of hybrids is generally undesirable in zoos, unintended hybridisation can occur in some husbandry situations. In the long term, Incubase may therefore also become a unique source of information on the characteristics of hybrid eggs, including their dimensions, mass, fertility and incubation outcome.

For each species, the database stores summary characteristics derived primarily from analyses of the data held within Incubase.

Individual records are subsequently aggregated for Incupedia and for the analytical tools in Incubase, with the resulting outputs stored in the SpecStats table (Figure 1). After quality control and processing, the data contribute to species-level summaries that may include egg morphometrics, incubation period, timing of laying, fertility, hatching success, typical incubation temperatures, egg mass loss and parameters relevant to humidity settings. In some cases, this table also stores information imported from other openly accessible databases that summarise existing knowledge of species life histories and other traits. These external data allow calculations and Incupedia species accounts to use parameters that are absent from, or insufficiently supported by, the primary Incubase dataset. To date, this option has been used particularly for incubation-period length, which is a key input for most calculations and optimisation procedures.

The database structure also includes tables for managing users, institutions and data sharing (Figure 1).

2.2.1 Entering data into the database

Data can be entered into Incubase in two principal ways. The first is the import of historical datasets that already exist in digital form and are converted to the Incubase structure after quality control and standardisation. Working with Czech zoos, the project team prepared and imported most of the data currently held in the database using this approach. However, such imports place exceptionally high demands on dataset preparation, which is difficult to achieve without substantial programming expertise and experience in processing large datasets. Incubase therefore does not currently provide users with a toolset for independently importing datasets in batches. Batch imports can presently be undertaken only in collaboration with the Incubase administrators.

The second, and operationally more important, approach is the continuous entry of data during routine work in the incubator facility. This reduces the risk of information loss, promotes record completeness and enables immediate use of the platform's analytical tools, for example when assessing egg mass loss or proposing adjustments to incubator settings.

2.3 Navigating the data and operational management of records in Incubase

Incubase is designed not only as a database repository but also as a working environment that supports convenient day-to-day management of incubation data. It therefore includes tools for rapid filtering and searching, identification of problematic records and preparation of summaries for a selected period.

2.3.1 Egg lists and record filtering

The principal way of working with data is through tabular lists of eggs. Users can display records in several operational views, for example as an overview of all eggs, a list of eggs associated with a particular incubator or a selection of records relevant to a particular institution. These lists are intended to provide rapid orientation both among eggs currently being incubated and within historical data. Several predefined tables are available, differing in the columns displayed: they range from a simple overview containing the egg ID, species and hatching date to a complete table containing all available columns. The individual column sets were selected in consultation with practitioners so that they would be useful in different operational contexts.

Each table provides interactive, column-specific filters and can be sorted by individual columns. Users can therefore filter records by species, internal egg identifier, laying date, incubation outcome, fertility, incubator, institution or other available fields. A universal full-text search is also available and searches the entire list across all columns. This is particularly useful in larger collections or when working with historical data, where the user may not know exactly which field contains the required information.

Such filtering supports not only routine record-keeping but also data-quality control. Users can rapidly retrieve, for example, all eggs of a particular species, eggs from a particular season, records lacking a final incubation outcome, eggs assigned to a particular incubator or cases in which essential information is missing.

2.3.2 Colour-coded egg labels

Incubase uses colour-coded labels to provide rapid orientation in the current status of eggs. Eggs with a green label are currently active and remain within the expected incubation period (Figure 2). Eggs shown in grey have already been removed from active status because they have hatched or have been recorded as dead or infertile. A red label indicates that the egg record has not been formally closed, but that ongoing viable incubation is unlikely because the egg is already well beyond the end of the expected incubation period.

2.3.3 Summary of egg care over a selected period

A separate function allows users to generate a summary of egg care for a specified period and display it within the user section. After the user selects a date range, the system creates an aggregated overview of the eggs recorded during that period. The output is a species-level table summarising key operational indicators: the total number of eggs, the number of fertile eggs, the number of chicks hatched and the number of identified females that contributed to egg laying.

This form of summary is useful for internal evaluation of a breeding season, rapid review of husbandry performance and communication among institutional staff. Its structure also directly matches the annual report submitted by all zoological gardens belonging to the Union of Czech and Slovak Zoological Gardens.

2.3.4 Relevance to day-to-day operations

Filtering, colour coding and aggregated summaries together form the operational layer of Incubase. Practitioners do not have to navigate exclusively through individual records, but can move rapidly between the details of a particular egg, a list of all relevant eggs and a summary view of an entire season or selected period. This is particularly important in institutions where many eggs of different species

are incubated simultaneously and staff need to identify quickly which records are complete, which eggs require intervention and what the overall outcome of the current breeding season is.

2.4 Analytical tools for optimising incubation

One of the key components of Incubase is a suite of intelligent analytical tools designed for the continuous optimisation of artificial incubation. Their primary purpose is to convert routinely entered operational data—particularly repeated egg weighings and records of incubator settings—into practical recommendations for day-to-day hatchery work. Incubase therefore serves not only as a passive data archive, but also provides immediate feedback on whether an individual egg or group of eggs is developing along the expected trajectory and whether the incubation conditions should be adjusted.

The optimisation tools are based principally on monitoring egg mass loss, which primarily reflects water loss through the shell and is one of the most practical indicators of whether incubation conditions are appropriate. Excessively rapid mass loss may indicate desiccation, whereas insufficient mass loss may indicate excessive environmental humidity and a risk of fluid retention. Because the optimal mass loss varies among species and remains poorly known for many of them, Incubase combines current measurements with historical records held in the database. The tools operate at three levels: the individual egg, all eggs within a single incubator, and eggs distributed among multiple incubators.

At the level of an individual egg, optimisation becomes available once the minimum required information has been entered: an approximate laying date, at least two mass measurements taken at different times, records of incubator settings and the incubation period of the species. From these data, the system constructs a mass-loss trajectory and compares it with reference records for the same species stored in the database (Figure 3). By default, the target is the median mass loss of successfully hatched eggs of that species. If sufficiently extensive species-specific data are unavailable, an estimate at the family level is used; if suitable data are lacking even for the higher taxonomic group, the system applies a general target total mass loss of 15%.

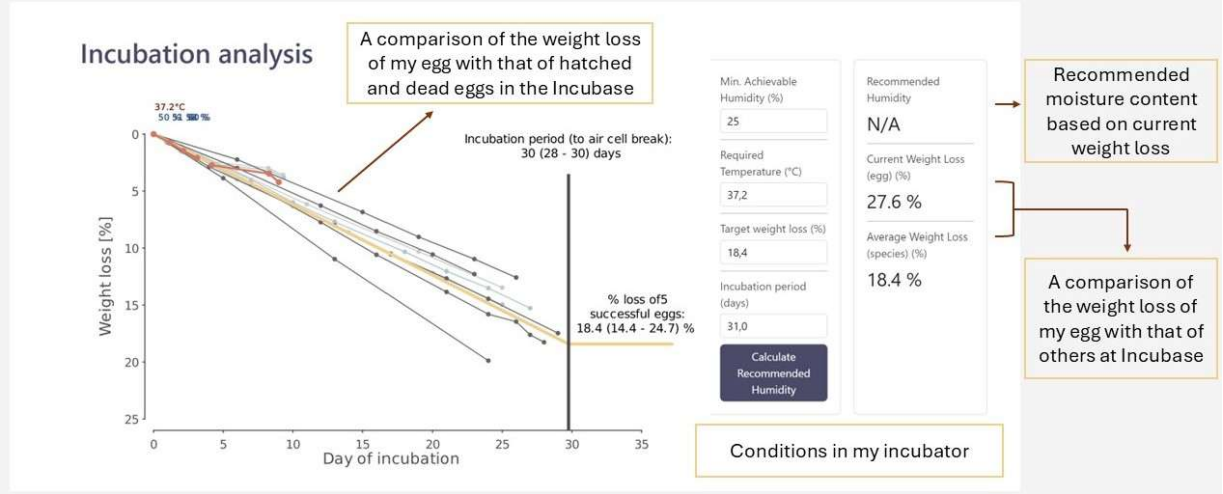


Figure 3: Optimisation at the level of an individual egg.

From the difference between the current and target trajectories, the system recommends an adjustment to relative humidity in the incubator (see Section 2.4.5), while temperature is initially held constant, reflecting the generally conservative approach of practitioners to changing incubation temperature. The user can also view the development of the egg graphically in comparison with historical records and use the optimisation calculator to test alternative scenarios, such as a different target mass loss or changes in selected input parameters, including a potential temperature adjustment. The practical output is therefore not merely a warning that an egg deviates from the

expected trajectory, but a specific recommendation for modifying the conditions so that subsequent development moves closer to the target trajectory.

The second level of optimisation considers an entire group of eggs held within a single incubator (Figure 4). This is a common practical situation because one device may contain several eggs, often from different species or at different developmental stages. For each egg, the algorithm estimates the expected final mass loss from its current developmental stage, observed trajectory and species-specific parameters. It then identifies the humidity setting that minimises the overall deviation of the group from their respective target values. The aim is therefore not to optimise the incubator for a single egg, but to identify the compromise setting that is most appropriate for the current group.

This tool is particularly useful when eggs with differing requirements or mass-loss trajectories share an incubator. Using a filter, the user can give priority to a selected subset of eggs, for example eggs of a rare or otherwise high-priority species. Eggs for which the predicted deviation from the target trajectory exceeds a defined threshold are flagged as problematic, alerting the user that transfer or individual management should be considered. The default threshold is a deviation of 3 percentage points, but it can be adjusted to the user's requirements.

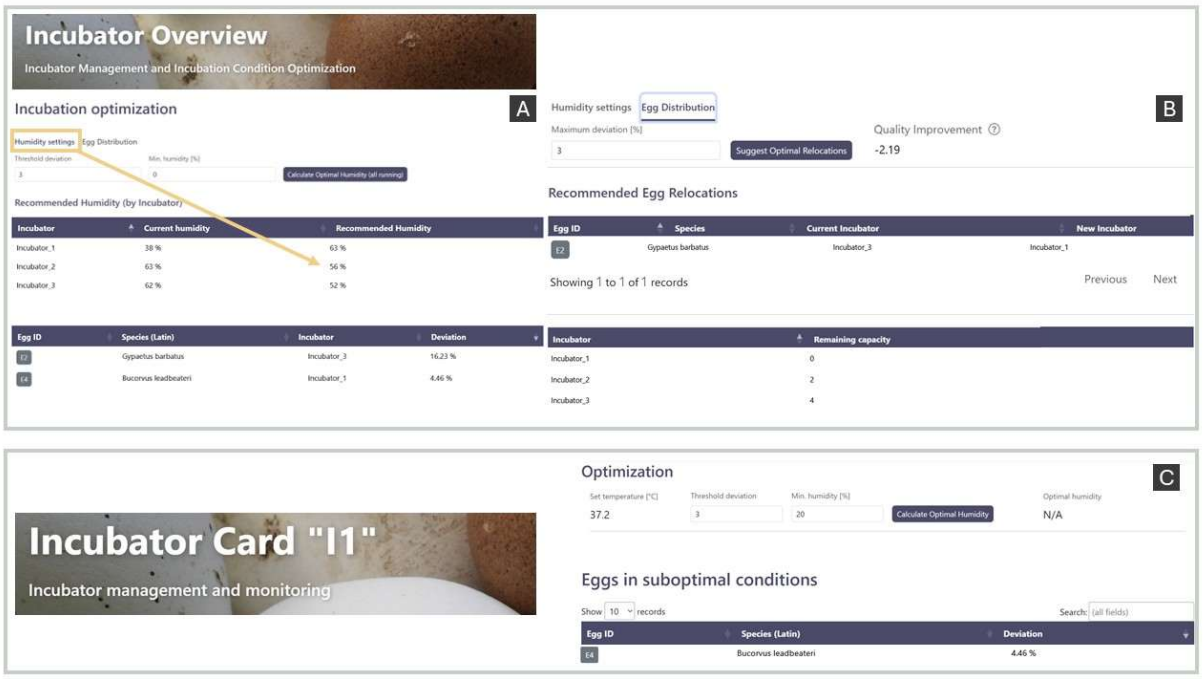


Figure 4: Optimisation of a shared incubator setting for a group of eggs.

The third level of optimisation considers multiple incubators simultaneously. The system evaluates the predicted mass trajectories of all eggs managed by the user and identifies cases in which an egg might benefit from transfer to another incubator offering more suitable conditions. This function is especially relevant to hatcheries managing many eggs, multiple species and several devices with different settings or technical capabilities. If an egg shows a substantial deviation from its optimum trajectory, the system can recommend an alternative incubator in which its expected subsequent development would more closely approach the target mass loss.

The analytical tools in Incubase are designed as powerful decision-support instruments, but they cannot fully replace the expert judgement and experience of the practitioner. Recommendations must be interpreted in the context of the species, egg age, candling results, the husbandry priority assigned to the egg, the technical capabilities of the hatchery and other information that may not be completely represented in the database. The strength of the system lies in its ability to provide a rapid and standardised calculation that would otherwise have to be performed manually or might not be available

at all. This is particularly important for species for which few eggs are available and each incubation decision may have substantial husbandry or conservation value.

The accuracy of the recommendations depends on the quantity and quality of data held in Incubase. Species-specific reference values can be used for taxa represented by extensive historical records, whereas more sparsely represented taxa require a general target mass loss. As the number of participating institutions and well-documented incubation cases increases, the reference values should become progressively more precise and the analytical tools should provide increasingly robust recommendations. Incubase is therefore conceived as a system whose practical value grows with every additional validated record. Nevertheless, even in its present form it already represents a highly robust and, above all, unique tool.

2.4.1 Computational procedures used to optimise incubator settings

The optimisation tools in Incubase are based on a simple biological principle: during incubation, an egg should lose water at a rate that allows it to reach a species-appropriate total mass loss by the end of the principal incubation phase. Because water loss depends both on properties of the individual egg—particularly eggshell conductance—and on incubator temperature and humidity, repeated weighings and incubator-setting records can be used to assess whether an egg is progressing towards its target trajectory. The computational core of Incubase therefore integrates egg morphometry, sequential mass loss, physical relationships describing water-vapour pressure and optimisation calculations for relative humidity.

2.4.2 Estimation of basic egg parameters

The basic input variables are egg length (L), egg width (W), initial or repeatedly measured mass, and the date of laying or the start of incubation. If initial mass is unknown, it can be estimated from egg dimensions. Egg volume (V) is calculated from length and width using the widely applied relationship:

$$V = k_V \times \frac{L \times W^2}{1000}$$

where V is egg volume in cm^3, L and W are egg length and width in millimetres, and $k_V = 0.51$ is the volume coefficient. The same general form of equation is used to estimate fresh egg mass, with the volume coefficient replaced by a mass coefficient. Hoyt (1979) showed that $k_V = 0.51$ is close to the empirical value for most species, although some species deviate substantially from it. In future, we therefore plan to replace this universal value in Incubase with species-specific coefficients. Egg mass can be estimated analogously (Hoyt 1979). In Incubase, estimated initial mass is expressed as:

$$W_i = k_W \times \frac{L \times W^2}{1000}$$

where W_i is initial egg mass in grams and $k_W = 0.54$. If repeated weighings are already available, initial mass can instead be back-calculated from the earliest measurement by extrapolating the estimated daily mass loss:

$$W_{i,\mathrm{pred}} = W_{\mathrm{first}} + \frac{\Delta m}{1000} \times t_{\mathrm{first}}$$

where W_{first} is the earliest measured egg mass in grams, t_{first} is the time from the start of incubation to the first weighing in days, and Δm is the estimated daily mass loss in mg/day. The resulting estimate of initial mass is constrained not to be lower than the maximum measured egg mass, because an egg should not genuinely gain mass during incubation. Egg dimensions and current mass can also be used to obtain an approximate estimate of density:

$$\rho = \frac{W_{\mathrm{actual}}}{V}$$

where ρ is density in g/cm^3, W_{actual} is current egg mass and V is estimated volume.

2.4.3 Calculation of mass loss

Regular weighing is the principal practical input for humidity optimisation. The biological basis of this approach is that eggs lose water by diffusion through the shell during incubation and that an appropriate total reduction in mass is one of the key indicators of successful incubation. Rahn and Ar (1974) described the relationship between incubation duration and water loss in avian eggs, and Ar and Rahn (1980) summarised the water balance of the egg during incubation. Practical incubation commonly uses a target loss of approximately 12–18%, with a broadly indicative midpoint of about 15%, although the optimum is species-specific, as is readily apparent from the graphs presented in Incupedia.

Daily mass loss is calculated for each relevant record, beginning with the second weighing of a given egg. The calculation compares the current mass with the nearest preceding measurement taken at least 12 hours earlier, thereby limiting the influence of short-term measurement error:

$$\Delta m_i = \frac{W_j - W_i}{t_i - t_j} \times 1000$$

where Δm_i is daily mass loss in mg/day, W_j is the earlier mass, W_i is the later mass, and $t_i - t_j$ is the elapsed time in days. Negative values are interpreted as biologically implausible mass gain and are truncated to zero. Extreme changes between successive weighings are treated as probable measurement or transcription errors and are excluded from the calculation (see below).

The current daily loss is used to predict the total mass loss that would be attained if the same rate continued throughout the principal incubation phase. In Incubase, this phase is standardised to 96% of the incubation period, approximately corresponding to internal pipping, when the hatching chick penetrates the air cell and the previously near-linear loss of water accelerates sharply. As a general approximation, an egg that has lost about 15% of its mass by this stage loses a further approximately 5% during the remaining roughly 4% of the incubation period:

$$\text{loss}_{\text{perc}} = \left(\frac{\Delta m \times 0.001}{W_i}\right) \times (IP \times 0.96) \times 100$$

where $\text{loss}_{\text{perc}}$ is predicted total mass loss as a percentage, Δm is daily mass loss in mg/day, W_i is initial egg mass, and IP is the species-specific incubation period in days. The percentage of the incubation period elapsed is calculated as:

$$IP_{\text{perc}} = \frac{t_{\text{inc}}}{IP} \times 100$$

where t_{inc} is the number of days since the start of incubation.

2.4.4 Water-vapour pressure and eggshell conductance

The rate of water loss from an egg depends on the difference in the partial pressure of water vapour between the egg interior and the surrounding air. The saturated water-vapour pressure at the incubation temperature must therefore first be estimated. Incubase uses an empirical approximation of saturated water-vapour pressure as a function of absolute temperature:

$$ln(P_g) = -\frac{5800.2206}{T_K} \backslash +1.3914993 - 4.864 \times 10^{-2} T_K \backslash +4.176 \times 10^{-5} T_K^2 - 1.445 \times 10^{-8} T_K^3 \backslash +6.5460 ln(T_K)$$

$$T_K = T + 273.15$$

where T is temperature in °C, T_K is temperature in kelvin and P_g is saturated water-vapour pressure. The result is subsequently converted to Torr. Calculation of saturated water-vapour pressure is a standard physical step when converting among temperature, relative humidity and vapour pressure; comparable relationships are described, for example, by Buck (1981).

Eggshell conductance to water vapour (G_{H2O}) expresses the ease with which water escapes through the shell. It is calculated as the ratio between daily mass loss and the water-vapour pressure difference between the egg interior and its surroundings:

$$G_{\mathrm{H2O}} = \frac{\Delta m}{P_g - P_g \times \frac{RH}{100}}$$

where G_{H2O} is eggshell conductance in mg·Torr^{-1}·day^{-1}, Δm is daily mass loss in mg/day, P_g is saturated water-vapour pressure at the incubation temperature, and RH is relative humidity in the incubator. This calculation follows the principle that water flux through the shell is proportional to the vapour-pressure difference and shell conductance (Ar et al. 1974).

If an egg has experienced different incubators or settings during incubation, temperature and humidity for the relevant period are calculated as time-weighted means:

$$\bar{T} = \frac{\sum_j T_j \times \Delta t_j}{\sum_j \Delta t_j}$$

$$\bar{RH} = \frac{\sum_j RH_j \times \Delta t_j}{\sum_j \Delta t_j}$$

where T_j and RH_j are temperature and relative humidity in interval j, and Δt_j is the duration of that interval. Short-lived changes in settings therefore receive less weight than conditions maintained for longer periods.

2.4.5 Calculation of optimal humidity for an individual egg

The purpose of optimisation is to identify the humidity at which the egg will attain its target mass loss by the end of incubation, or more precisely by internal pipping. The total target amount of water to be lost is first calculated as:

$$M_{\mathrm{target}} = W_i \times \frac{\mathrm{target}_{\%}}{100} \times 1000$$

where M_{target} is target water loss in mg, W_i is initial egg mass in grams, and $\mathrm{target}_{\%}$ is target total mass loss as a percentage.

The amount of water that remains to be lost is:

$$M_{\mathrm{rem}} = M_{\mathrm{target}} - (W_i - W_{\mathrm{actual}}) \times 1000$$

where W_{actual} is current egg mass. The optimal daily loss over the remaining incubation period is:

$$\Delta m_{\mathrm{opt}} = \frac{M_{\mathrm{rem}}}{IP \times 0.96 - t_{\mathrm{inc}}}$$

Given the eggshell conductance, the required water-vapour pressure difference can then be derived as:

$$\Delta P_{\mathrm{target}} = \frac{\Delta m_{\mathrm{opt}}}{G_{\mathrm{H2O}}}$$

and, subsequently, the optimal relative humidity as:

$$RH_{\mathrm{opt}} = \left(\frac{P_g - \Delta P_{\mathrm{target}}}{P_g}\right) \times 100$$

The resulting value is constrained by the technical capabilities of the incubator. Reducing mass loss is usually straightforward by increasing relative humidity, whereas accelerating it sufficiently without structural intervention in the shell can be difficult. Depending on the location of the hatchery and

prevailing weather, the lowest achievable relative humidity is commonly between 15 and 30%. In Incubase, the expected minimum achievable humidity can be specified separately for each incubator. If the calculated humidity is below the minimum attainable humidity of that incubator ($RH_{\min}$), the result is set to $RH_{\min}$ and the system warns that the required mass loss cannot be fully attained at the specified temperature and minimum humidity. In such cases, a modest temperature adjustment may also be considered, because higher temperature increases saturated water-vapour pressure and hence the potential vapour-pressure difference between the egg and its surroundings.

2.4.6 Optimisation of shared humidity for a group of eggs

In practice, a single incubator often contains several eggs that may belong to different species, be at different developmental stages or differ in eggshell conductance. It is therefore impossible to provide each egg with its own ideal humidity. Incubase treats this as a one-dimensional optimisation problem and uses Brent's method to identify a single shared relative-humidity value (RH^*) that minimises the deviation between predicted and target mass loss across all eggs in the incubator.

Predicted total mass loss at a specified humidity is:

$$\text{loss}_{\text{pred}} = \frac{1000(W_i - W_{\text{actual}}) + G_{\text{H2O}}\left(P_g - P_g \times \frac{RH}{100}\right)(IP \times 0.96 - t_{\text{inc}})}{W_i \times 1000} \times 100$$

where the first term in the numerator represents the water already lost and the second predicts water loss during the remaining part of incubation at the specified humidity.

The shared optimal humidity for the incubator is defined as:

$$RH^* = \arg \min_{RH \in [RH_{\min}, 100]} \text{median}_i\left(|\ \text{loss}_{\text{pred},i}(RH) - \text{target}_i\ |\right)$$

where $\text{loss}_{\text{pred},i}(RH)$ is the predicted total mass loss of egg i at humidity RH, and target_i is the target loss for the relevant species or egg. Use of the median rather than the mean makes the calculation more robust to outliers. Eggs whose deviation from the target at the shared optimal humidity exceeds a defined threshold—for example, 3 percentage points—are flagged as problematic and suitable for consideration for transfer to another incubator.

2.4.7 Optimisation of egg allocation among incubators

The most general level of optimisation proposes an improved allocation of eggs among multiple incubators. An individual optimal humidity ($RH_{\text{opt},i}$) can be calculated for each egg. If several incubators with different settings and capacities are available, the system seeks an allocation that reduces the difference between the individual optimal humidity of each egg and the humidity of the incubator in which it is placed.

In simplified form, the optimisation criterion can be expressed as minimisation of the sum of deviations:

$$\min \sum_i |\ RH_{\text{opt},i} - RH_{\text{set},a(i)}\ |$$

where $RH_{\text{opt},i}$ is the individual optimal humidity of egg i, $RH_{\text{set},a(i)}$ is the set humidity of the incubator to which egg i is assigned, and $a(i)$ denotes the assignment of an egg to a particular incubator. The calculation also respects incubator-capacity constraints:

$$n_j \leq C_j$$

where n_j is the number of eggs assigned to incubator j and C_j is its capacity.

Eggs that already fall within the tolerance band around the target mass loss remain in their current incubator. For other eggs, transfer is recommended only when the alternative placement genuinely

reduces the difference between required and available humidity. Priority is given to eggs with the largest deviations and to those with the fewest suitable alternative incubators. The procedure thus provides a practical proposal for using the available incubators so that problematic eggs can be brought closer to their individual requirements.

2.4.8 Calculation of species-specific reference values

Optimisation calculations become more accurate as the amount of data available for a species in Incubase increases. Species summaries are updated continuously as new records are added, including mean incubation period, egg dimensions, initial mass, eggshell conductance, typical mass loss of successfully incubated eggs, and recommended temperature and humidity settings. Recommended temperature and humidity are calculated as time-weighted means of incubator settings during periods in which eggs were actively incubated.

If sufficient data are unavailable for a particular species, the system can use an average derived from related species in the same family or a general default value. The user is informed of the source of the parameters used in each calculation—whether they are species-specific data or a general default estimate. This distinction is important when interpreting the recommendation: a calculation based on data from the focal species carries greater evidential weight than one based on a general substitute value.

2.5 Data-entry and processing validation mechanisms in Incubase

Incubase incorporates a multi-level system of validation checks designed to reduce erroneous data entry, detect illogical or incomplete records and alert users to situations that may affect the reliability of subsequent calculations. Checks are performed at several stages: directly while forms are being completed, during server-side data processing, when larger tables are imported and subsequently during automated calculations based on stored records. This approach is particularly important because Incubase integrates data from different institutions, species, incubators and historical sources, in which errors may occur in dates, times, masses, taxonomy or the assignment of records to institutions.

2.5.1 Access and permissions checks

The first level of validation concerns access to data and user permissions. Users must be logged in to access non-public functions and may work only with data for which they hold permission through their institutional affiliation. The system checks whether the user is a member of the relevant institution, is authorised to edit a particular egg record, is using an incubator belonging to their institution and is not accessing data owned by another institution outside the applicable licensing regime. This ensures that specialist records remain under the control of their owner and prevents unauthorised changes to data held by another institution.

The security layer also includes general safeguards standard in web applications: protection of forms against unauthorised requests, limits on repeated login attempts, validation of file types when photographs are uploaded and checks preventing dates from being entered in the future. These checks provide not only technical security but also protect the database from records whose credibility would be questionable.

2.5.2 Validation when entering an egg record

When an egg record is created or edited, the system verifies the basic completeness and logical consistency of the information entered. Assignment to a taxon and an internal egg identifier are mandatory. To ensure that the record is temporally defined, at least one relevant date must be provided. If egg dimensions are entered, length and width must be supplied together, both values must be positive and length must not be smaller than width.

An important component is validation of the chronology of the incubation cycle. The system checks that individual dates are biologically and operationally coherent: the laying date must not fall after subsequent events; parental incubation cannot begin before the egg was laid; the date on which the egg was found cannot precede laying or occur after later incubation procedures have begun; and the hatching date cannot precede the end of incubation. The permitted sequence follows the logic: egg laying → start of parental incubation → discovery or entry into the records → cooling or start of artificial incubation → transfer to a hatcher (an incubator operated in a specialised mode for the final stage of incubation) → end of incubation → hatching.

Initial mass is also subject to a specific check. It can be entered only when the date on which the egg was found or entered into the records is known. Without this temporal reference, the mass could not be interpreted reliably as either an initial or a subsequent measurement. If the user enters a hatching date, the system automatically records the incubation outcome as hatched, thereby preventing incomplete or internally contradictory outcome records.

2.5.3 Validation of ongoing incubation records

A second major area comprises records made during incubation, principally weighings, transfers between incubators and records of current conditions. Each new record must fall within the actual incubation period: it cannot be dated in the future or before the egg was laid. By default, the system uses the date and time at which data are entered. This both limits opportunities for error and encourages users to record data in real time. The system also flags duplicate records entered for the same egg at the same time.

A central validation criterion is the monotonic decline in egg mass. During incubation, an egg should progressively lose mass as water diffuses through the shell. When a new mass is entered, the system therefore compares it with both earlier and later records. The newly entered mass must not exceed masses recorded previously and must not be lower than masses recorded subsequently. This mechanism helps detect typographical errors, confusion between eggs, incorrect units, misplaced decimal separators and incorrectly assigned weighing dates.

2.5.4 Validation in incubator management

Separate validation mechanisms apply to incubator records and their operating logs. For each incubator, the system checks that essential information has been provided, including its internal identifier, equipment type and capacity. Capacity must be a positive integer. If the minimum attainable humidity is specified, it must lie between 0 and 100%. Service intervals, such as intervals between disinfection or filter replacement, are checked in a similar manner.

When entries are added to an incubator operating log, the system validates the record date and the formal validity of the temperature and humidity values. Humidity must fall within the physically and technically meaningful range of 0–100%. These checks are important because incubator settings are used in calculations of eggshell conductance, egg-mass loss and recommended humidity. An incorrect temperature or humidity entry could therefore lead to an erroneous optimisation recommendation.

2.5.5 Validation of batch data imports

For the reasons described above, Incubase does not currently allow users to import data in bulk from CSV files. A batch-import procedure has nevertheless been developed and used for historical datasets. Each import is subjected to checks appropriate to the type of data being imported. Egg imports are checked for the required columns, the presence of the relevant taxon in the database, valid data types and correct date formats. Imports of repeated records for individual eggs are checked to confirm that the egg already exists within the relevant institution, that the corresponding incubator exists and that time values use the correct format. Imports of incubator-maintenance records are checked for a valid internal incubator identifier and a correctly formatted date.

Errors are recorded separately for each row. Unless an error prevents the entire import from proceeding, the problematic row is skipped and the remaining records continue to be imported. On completion, the user receives a list of identified errors that can be used to correct the source table. This approach is particularly practical for large datasets, for which terminating an entire import because of a single erroneous row would be inefficient.

2.5.6 User warnings arising from missing inputs to optimisation calculations

A further validation layer operates after the data have been saved, when the system assesses whether all inputs required to calculate egg status and optimise incubator settings are available. If a key item is missing, the egg is excluded from optimisation calculations and the user is informed of the reason. Typical reasons include missing repeated weighings, missing mass at laying and insufficient information with which to estimate it, an unknown species incubation period, inability to determine egg age, missing initial mass, or absent temperature and humidity records for the incubator.

If species-specific reference values are unavailable, the system may use substitute sources, such as an average for related species in the same family or a general default value. The user is informed of the source on which the calculation is based. This is important when interpreting the reliability of a recommendation: a calculation based on data from the focal species carries greater evidential weight than one based on a general estimate or a value derived at family level.

2.6 Incupedia - A Living Encyclopaedia of Avian Incubation

One of the key components of the Incubase system is Incupedia, a publicly accessible encyclopaedia designed to transform individual incubation records into comprehensible and practically useful species-level summaries. Whereas the principal database and analytical tools of Incubase are intended primarily for registered users and institutions, Incupedia provides an open interface for animal keepers, curators, researchers and others interested in avian egg incubation.

Incupedia is designed as a living knowledge base rather than a static textual atlas. Data entered into Incubase that are not withheld contribute, after basic validation and processing, to species statistics that are incorporated automatically and in real time into dynamically generated species accounts. These accounts summarise the information available in the database for a particular taxon and are updated continuously as new records are added. In this way, practical experience from individual breeding institutions is progressively transformed into a shared information resource.

The basic unit of Incupedia is the species account (Figure 5). It contains taxonomic and nomenclatural information, including the scientific, Czech and English names of the species, together with its family and order. It also reports the numbers of recorded eggs, fertile eggs and successfully hatched chicks. Of particular practical importance are values applicable to artificial incubation: mass loss in successfully hatched and unsuccessful eggs, egg length and width, mass, volume and incubation period. The account may also include photographs of eggs, a graph of laying seasonality and a graph of incubation progress expressed as the change in egg mass over time. On the basis of these data, recommended incubation temperatures and humidities are provided. These define incubator settings under which an average egg of the species would be expected to follow the mean mass-loss trajectory of successfully hatched eggs of that species.

Species accounts therefore allow users to determine rapidly which values have so far been recorded for a particular species in Incubase. A keeper can compare an egg in their care with aggregated values from other institutions, for example in terms of size, incubation period, typical mass loss or incubator settings. A curator can obtain an overview of data availability for a particular taxon and of basic indicators of reproductive success. A researcher can use Incupedia as a gateway for identifying species and datasets suitable for more detailed analysis or for establishing collaboration with data owners. Incupedia is also the principal feedback mechanism through which data entered into Incubase are returned to the avian husbandry community.

An important consideration when interpreting Incupedia is that all outputs are generated from primary data, which may be incomplete or subject to inaccuracies for some species. Incupedia explicitly draws attention to this limitation. Values presented in species accounts should therefore not be regarded as definitive biological constants, but as current summaries of the records available to date. Their reliability will increase with the number of eggs represented, the breadth of participating institutions and the completeness of the information entered.

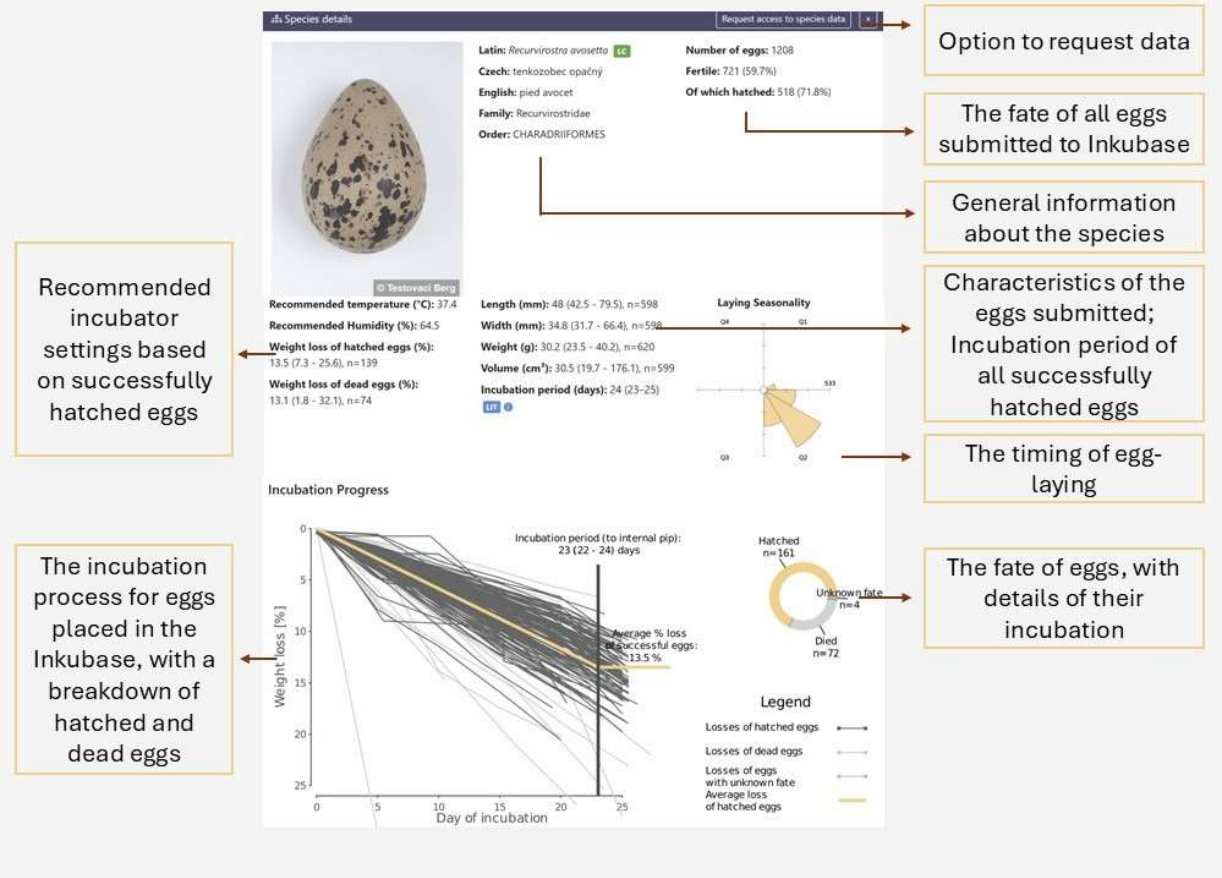


Figure 5: Example of a species account in Incupedia.

2.7 Summary of the dataset available through Incubase

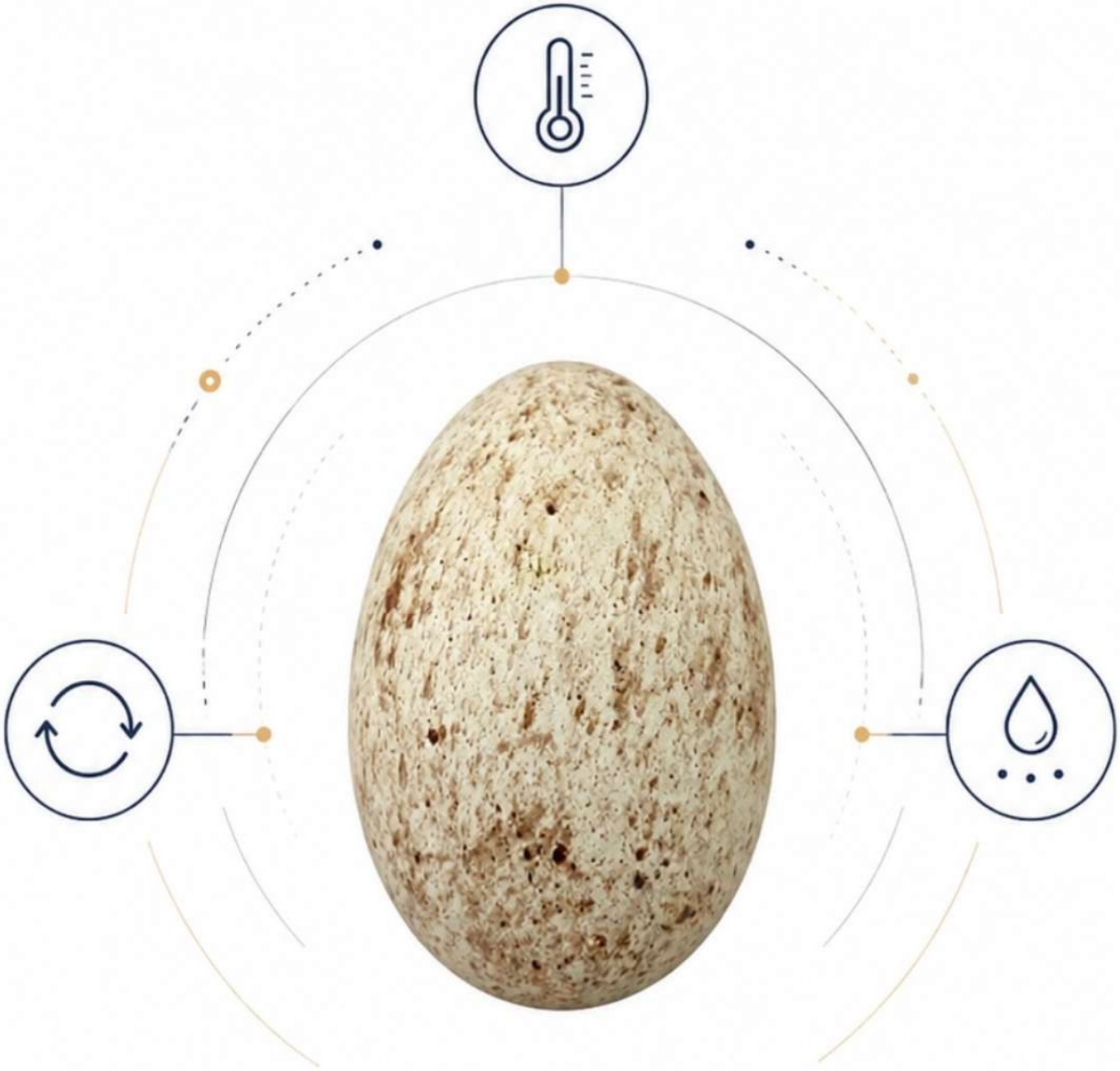
At the end of the project on 30 June 2026, Incubase contained records for 24,543 eggs representing 470 species, 73 families and 29 orders. This dataset therefore formed the data foundation of Incupedia at that time. It also included numerous taxa of conservation concern: one species classified as Extinct in the Wild, 13 Critically Endangered species, 27 Endangered species, 43 Vulnerable species and 43 Near Threatened species.

Coverage of individual data types varies among eggs, species and institutions. Fertility was recorded for 19,028 eggs representing 407 species. The final fate of fertile eggs - whether they hatched or the embryo died - was available for 11,027 eggs representing 357 species. An exact laying date was known for 12,596 eggs representing 399 species, enabling the phenology of laying under human care to be evaluated. Egg dimensions were available for 13,402 eggs representing 392 species.

Repeated egg weighings are particularly valuable for optimising incubation. These were available for 11,173 eggs representing 373 species, comprising a total of 39,770 individual mass records. Eggshell conductance could be estimated for 6,508 eggs representing 296 species because a complete set of information was available, consisting of at least two weighings, an estimate of initial mass and sufficient information on incubator settings between measurements. This component of the database has the greatest immediate value for the analytical tools in Incubase, because it enables evaluation of

mass-loss trajectories, calculation of target humidity and comparison of an ongoing incubation with historical records.

The current dataset also illustrates both the principal limitation and the potential of Incubase. Data completeness is uneven among species because the records originated from different institutions and periods, often before a standardised methodology had been introduced. Nevertheless, the dataset already covers a broad range of taxa and provides information that is difficult to obtain for many species outside human care. As use of the platform continues, the proportion of complete records can be expected to increase, especially for variables central to practical incubation management: laying dates, egg dimensions and masses, repeated weighings, fertility, incubation outcome and incubator settings.



Handbook

Monitoring natural incubation using biologging methods

- Why monitor incubation in managed breeding?
- Principal methods and procedures tested during the project
- Measuring incubation with miniature AXY5 data loggers in biomimetic surrogate eggs
- Case studies based on data collected during the project
    1. Parental incubation is not a stable incubator
    2. What can a camera reveal about sleep and preening during incubation?
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3. Monitoring natural incubation using biologging methods

This section of the summary report moves from the monitoring of artificial incubation to the opportunities offered by modern data loggers for monitoring parental incubation. A major focus of the project was the transfer of our long-standing experience from research on incubation in wild populations into managed breeding settings. This work produced not only a valuable dataset containing many unique measurements, but above all an extensive set of tested methodological procedures, presented as a comprehensive methodological handbook and delivered as a separate project output.

3.1 Why monitor incubation in managed breeding?

Although artificial incubation, discussed in the preceding section, is widely used in many breeding institutions, parental rearing remains the preferred approach in most cases. Reproductive success then depends primarily on parental behaviour. This behaviour may, however, be affected by the markedly artificial conditions of an enclosure, whether physical, such as temperature and humidity, or biotic, such as the presence of visitors or other animals. Keepers may therefore know that a bird is sitting on the nest, but without monitoring they usually do not know the actual temperature experienced by the eggs, how often incubation is interrupted, whether the parents turn the eggs sufficiently, whether both partners alternate at the nest, or whether incubation is disrupted by disturbance, unrest within the enclosure or an unsuitable microclimate. The tools described below can therefore be invaluable, first and foremost, for diagnosing why breeding attempts fail in a particular species.

A second, equally important reason for monitoring parental incubation arises when parental rearing is more successful than artificial incubation. Under favourable conditions in the wild, and excluding predation and similar causes of loss, egg hatchability may reach approximately 90% or more. Even a brief examination of the Incupedia accounts discussed above shows that artificial incubation remains less successful than parental incubation across a substantial proportion of species maintained under human care. Monitoring parental incubation makes it possible to measure the conditions under which successful incubation occurs and thereby provides an invaluable source of guidance. Parental incubation can serve as a biological reference for incubator settings: measurements reveal the temperatures attained by eggs beneath the parent, the natural extent of temperature fluctuation, the frequency of egg turning and changes in conditions across the day or during exchanges between parents. These observations can inform adjustments to incubator temperature, turning regime, cooling, humidity and the overall strategy for managing an egg. For species lacking reliable incubation protocols, monitoring parental incubation may provide some of the most useful practical data available, although this resource remains clearly underused.

The principal value of monitoring therefore lies not in data collection itself, but in improving our understanding of the causes of reproductive failure and providing evidence-based guidance for specific husbandry decisions: whether to leave eggs with the parents or transfer them to an incubator, modify the nest arrangement, reduce disturbance, alter pair composition, or use data from parental incubation to refine incubator settings.

3.2 Principal methods and procedures tested during the project

Several basic methods are available for monitoring incubation or its individual components. Each has particular strengths and limitations, and genuinely comprehensive monitoring generally requires a combination of approaches. The project team has extensive experience with a range of monitoring systems, several of which were developed specifically for this purpose. When designing and testing procedures for monitoring incubation care in breeding institutions, however, we also emphasised the broadest possible applicability of the recommended methods. The project outputs therefore focus on procedures that can be implemented entirely with commercially available equipment.

The first method uses an artificial egg, or biomimetic surrogate, containing a data logger. The surrogate resembles a natural egg in shape, size, mass and surface finish and, once placed in the nest, is incubated by the parent as part of the clutch (see Section 3.3 for details). A data logger inside the surrogate records internal temperature and, when equipped with an accelerometer and magnetometer, can also detect egg movement and turning. This method provides information directly from the perspective of the incubated egg and is especially suitable for assessing the thermal regime, turning frequency and stability of parental care. Larger surrogates can contain several data loggers positioned at different points around the egg. This arrangement provides a better estimate of incubation temperature near the actual position of the embryo and also enables the characteristic thermal gradient that develops in most eggs during incubation to be quantified.

The second method measures temperature and humidity within and around the nest. Data loggers with external probes are used, with one probe placed directly in the nest lining among the eggs and another outside the nest to provide a reference record of ambient conditions. Comparing the two records allows the incubation rhythm to be reconstructed as a sequence of incubation bouts and recesses. This method is also suitable for species whose eggs are too small to accommodate a data logger and complements data obtained from a surrogate egg. Interpretation nevertheless requires caution because the temperature measured in the nest depends on the exact position of the sensor, the depth of the nest lining and its contact with the parent's body.

The third principal method is continuous video recording of the nest. A camera reveals what is actually occurring when a data logger records a temperature change or egg movement. Video footage can distinguish incubation recesses, exchanges between partners, nest maintenance, egg turning, disturbance by other individuals, aggressive interactions, the presence of a keeper and other events affecting incubation conditions. Camera recordings can also support research into aspects of parental behaviour that are not directly related to incubation, such as when parents sleep during the incubation period, perform feather maintenance or communicate with one another.

In studies of wild birds, radio-frequency identification (RFID) has also proved highly effective for recording the presence of individually identified parents at the nest. We were unable to transfer this method to routine breeding practice, however, because no suitable commercially available system was identified.

Selection of a monitoring system must reflect not only the specific question being addressed but also the characteristics of the focal species. For disturbance-sensitive species, it is advisable to begin with the simplest possible installation, minimise the number of nest visits, perform interventions during natural incubation recesses and, when using a biomimetic measuring surrogate, reproduce the appearance and properties of a natural egg as closely as possible. For species that manipulate nest material or damage cables, equipment enclosed within the surrogate should be preferred and all other components placed beyond the birds' reach. For cavity-nesting species, a camera mounted above the nest with its power supply routed outside the nest box may be most practical. Ground-nesting species require greater attention to concealment, cable routing and installation stability.

A separate component of the methodological recommendations concerns operational procedures, without which the resulting data cannot be interpreted reliably. Every installation should record the species, identity of the pair or individual, clutch size, incubation stage, type and identification number of the equipment, data-logger settings, exact start and end times, device placement and all exceptional events. Particular attention must be paid to synchronising time across data loggers and cameras. Without accurate synchronisation, a temperature decline, egg turn or other change in the data cannot be linked precisely to a particular parental behaviour in the video record. Original files downloaded from data loggers and cameras should be archived without modification; analyses should be conducted only on copies; and all files should follow a consistent naming convention based on year, species and installation. These procedures ensure that monitoring proceeds smoothly and yields the

information for which it was undertaken. More importantly, they allow the data to be reused at any time in the future, for example in collaborative comparative studies.

Data processing is an essential but often particularly difficult stage of incubation monitoring. Freely accessible tools suitable even for users without advanced analytical expertise include online applications developed by the project team during an earlier project and subsequently adapted for commercially available data loggers. Data from surrogate eggs can be visualised and pre-processed using accelR8 (https://bergmaps.fzp.czu.cz/accelr8/), while nest temperature and humidity data can be analysed using incub8 (https://bergfzp.shinyapps.io/incub8/). Video recordings can be evaluated in the freely available BORIS software (Friard & Gamba 2016) using a predefined ethogram. The outcome is not merely a set of graphs, but a practically interpretable reconstruction of incubation that can help keepers decide whether intervention is required and, if so, what form it should take.

3.3 Measuring incubation with miniature AXY5 data loggers in biomimetic surrogate eggs

One of the most direct approaches to monitoring incubation is to place a miniature data logger inside an artificial egg that the parent accepts as part of the clutch. Such a surrogate records conditions directly from the “egg's perspective”, rather than measuring only the nest microclimate or observing parental behaviour externally. In managed breeding, this method is particularly useful for determining whether parents warm the eggs consistently, how often incubation recesses occur, whether eggs are turned regularly and how the natural incubation regime differs from conditions used in an incubator. During the project, we developed several types of 3D-printed biomimetic surrogate eggs and prepared a database of printable models covering the great majority of avian egg shapes and sizes (see Chapter 4). For data logging, we recommend the commercially available AXY5-XS logger (https://www.technosmart.eu/axy-5-xs/). Measuring 21 × 11 × 7 mm, it records temperature together with accelerometer and magnetometer data for approximately two weeks.

3.3.1 Measuring internal egg temperature

A temperature record from a data logger placed inside a surrogate egg is substantially more relevant than a measurement of nest air temperature because the surrogate is heated directly by the incubating parent and is mechanically integrated into the clutch. Nevertheless, the temperature measured within an artificial egg is not necessarily identical to the temperature experienced by the embryo in a natural egg. Within a natural egg, temperature can differ markedly between the side facing the parent and the side facing the nest substrate. This thermal gradient is particularly important because the embryo is not located at the centre of the egg. It develops on the surface of the yolk, which is less dense than the albumen, and the chalazae together with the buoyancy of the yolk maintain the embryo closer to the upper side of the egg and therefore nearer the body of the incubating parent.

This creates an important interpretative limitation: a centrally positioned data logger primarily measures the temperature of the internal volume of the surrogate, not necessarily the temperature at the location occupied by the embryo in a natural egg. For larger eggs, a surrogate with data loggers positioned closer to the shell may therefore be biologically more informative, because it captures the thermal gradient between the upper and lower parts of the egg more effectively and allows the temperature to which the embryo may actually be exposed to be estimated. The models designed for this purpose contain three laterally positioned data-logger cavities. In smaller eggs, which can accommodate only one central logger, the recorded values should be interpreted primarily as a standardised index of the egg's thermal regime, suitable for comparisons among days, pairs and species or between parental and artificial incubation, rather than as an exact absolute measure of embryo temperature.

During installation, it is therefore important to record the type of surrogate used, the position of the data logger within it and its orientation, including the precise locations of the individual sensors. In

models containing a single logger, placement should be kept as consistent as possible across repeated installations. In three-cavity models, the data loggers should be oriented with the temperature sensor facing the egg surface. This facilitates interpretation of differences among parts of the surrogate and helps distinguish genuine changes in incubation regime from artefacts caused by sensor position.

Temperature data provide several types of practical information. A consistently high temperature with brief fluctuations usually corresponds to regular incubation interrupted by short recesses or parental exchanges. Prolonged temperature declines may indicate extended nest absence, disturbance or an inability of the parent to maintain suitable incubation conditions. Repeated short fluctuations may be associated with exchanges between partners, nest maintenance, egg turning or other behaviour at the nest.

3.3.2 Measuring egg turning

A second major function of a data logger inside a surrogate egg is to record egg turning. Turning is an important component of incubation because it supports normal development of the embryonic membranes, utilisation of albumen, development of the vascular system and correct positioning of the embryo before hatching. Experimental work on poultry and studies of wild species show that insufficient or inappropriately timed turning can reduce hatchability, whereas natural turning regimes may vary substantially among species, times of day, incubation stages and ecological contexts (New 1957; Tullett & Deeming 1987; Deeming 1989; Shaffer et al. 2014; Pešková et al. 2024).

Reliable recording of turning about all three axes requires the data logger to contain not only a tri-axial accelerometer but also a tri-axial magnetometer. The accelerometer determines orientation relative to gravity, but cannot on its own describe all changes in spatial orientation reliably, particularly rotation about the vertical axis. The magnetometer adds information on orientation relative to the Earth's magnetic field. Combining both sensors therefore allows changes in logger position to be converted into changes in egg orientation in three dimensions (Pešková et al. 2024).

A fundamental requirement for a reliable record is that the logger must not move independently of the surrogate egg. If it were free to “float” within the cavity, it would record movements of the logger itself rather than genuine rotation of the egg. It must therefore be mechanically fixed within the surrogate, for example by using a precisely fitted cavity or a small amount of soft packing. The logger should also be inserted in the same orientation during repeated measurements, facilitating quality control and comparisons among installations.

3.3.3 Processing and analysing egg-turning data

Raw accelerometer and magnetometer data cannot be interpreted directly as biologically meaningful “egg turns”. A series of relatively complex steps is first required to remove noise, calibrate the sensors and combine measurements from both sensors into a description of spatial orientation. The principal steps are summarised and justified below; a more comprehensive procedure is provided by Pešková et al. (2024). The analysis is intrinsically complex, but the accelR8 application, developed during the earlier project SS01020383, guides users without advanced analytical experience through the procedure and provides graphical and summary outputs that can be interpreted readily for diagnosing husbandry problems.

Several preparatory procedures are required before analysis. Automatic calibration of the accelerometer and magnetometer should first be performed to minimise systematic measurement errors arising from heterogeneity in the Earth's gravitational field for the accelerometer and magnetic field for the magnetometer. The data are then smoothed using low-pass filters to suppress random noise and, for the accelerometer, the dynamic component of acceleration. Orientation angles, conventionally termed roll, pitch and heading, are calculated from the calibrated and filtered data. These angles describe the orientation of an object about three axes, but for general quantification of egg turning they are best converted to a quaternion representation. This combines changes in

orientation about all three axes into a single value describing the total angular change between two consecutive time steps.

Two principal types of metric are generally used in practical interpretation. The first is turning frequency: the number of time intervals during which egg movement exceeded a predefined threshold. This is typically expressed as the number of seconds per hour in which movement exceeded 1°, or alternatively 5°. The second metric is the sum of angular changes, which combines information on how frequently the egg moved with the magnitude of those movements. It is usually expressed as the sum of degrees, or occasionally radians, per hour or per day.

These metrics can subsequently be used in further analyses, although this is not always necessary for applied use in managed breeding. Even a basic visualisation of temperature, orientation angles and hourly sums of angular change can reveal whether parents manipulate an egg regularly, whether turning occurs only during exchanges between partners, whether a diel rhythm is present, or whether the egg remains entirely motionless for prolonged periods (Figure 6). Comparison with video footage can additionally establish whether changes in orientation correspond to deliberate turning with the bill, manipulation of nest material, the parent standing up or settling onto the clutch, or restlessness caused by disturbance (see Section 3.3.5).

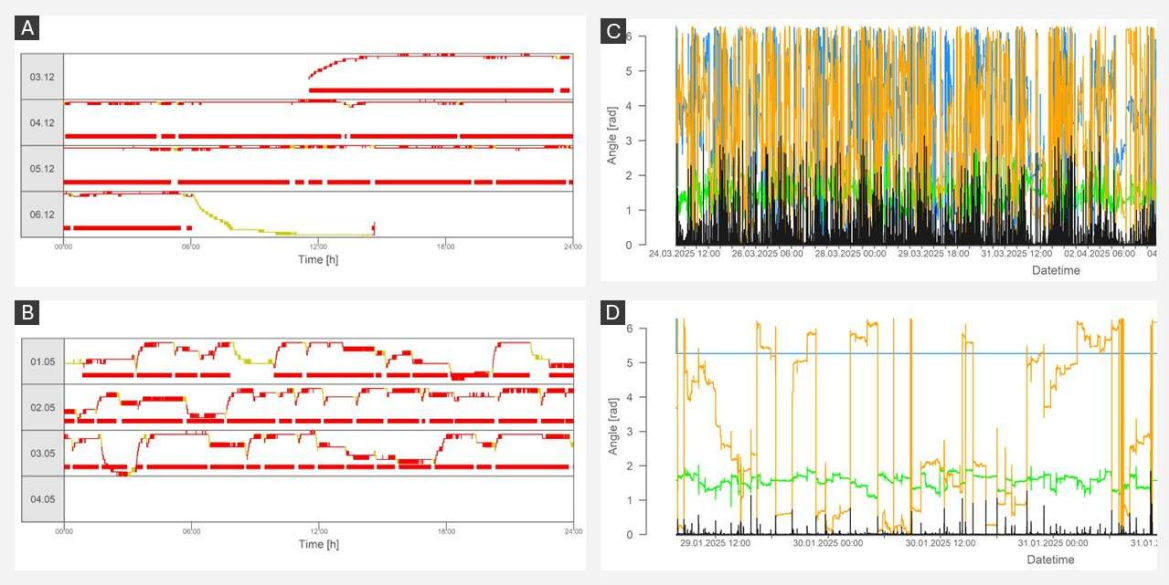


Figure 6: Examples of data visualisations obtained from multisensor data loggers in surrogate eggs used to monitor incubation conditions. Egg temperature: A) Dalmatian Pelican (Pelecanus crispus), showing a continuous incubation bout with occasional very slight temperature declines associated with interactions between individuals (Safari Park Dvůr Králové); B) Red-crowned Crane (Grus japonensis), showing temperature fluctuations and frequent alternation between incubation bouts and recesses (Olomouc Zoo). Egg turning: C) Black-headed Parrot (Pionites melanocephalus), the species with the highest measured egg-turning frequency (85.87 per hour; Olomouc Zoo); D) Dalmatian Pelican (Pelecanus crispus), the species with the lowest measured egg-turning frequency (9.91 per hour; Safari Park Dvůr Králové).

3.3.4 Measuring nest temperature and humidity with MSR data loggers

Alongside logger-equipped surrogate eggs, measurement of temperature and humidity directly within the nest and its immediate surroundings is an important component of comprehensive incubation monitoring. Several commercially available instruments can be used for this purpose. Based on our experience, the most suitable option was a multi-channel MSR data logger (https://www.msr.ch/en/product/datalogger-temperature-humidity-pressure-acceleration-msr145/), available in several configurations. The most practical versions allow simultaneous recording from two external probes, each measuring both temperature and relative humidity. One probe is placed in the nest lining among the eggs and the other outside the nest to provide a reference record of ambient

conditions. This approach is particularly suitable when the objective is to describe the parental incubation rhythm - the alternation between active incubation bouts and recesses - while also determining how nest conditions differ from the surrounding microclimate.

The principal advantage of an MSR logger over a logger placed inside a surrogate egg is its wider applicability. It can be used with species whose eggs are too small to accommodate a miniature logger within a size-matched surrogate. The body of the instrument can be concealed outside the nest itself, with only a relatively small probe inserted into the nest lining. MSR loggers are therefore suitable where information on incubation is required but the use of a logger egg is impossible or impractical. They also complement surrogate-egg data effectively: whereas the surrogate records the thermal regime from the egg's perspective, the MSR logger allows that regime to be interpreted in relation to ambient temperature and humidity. A major limitation, however, is the practical impossibility of standardising the measured temperature in relation to conditions experienced by the embryo. In most cases, the probe cannot be positioned in a way that entirely prevents movement relative to the surrounding eggs.

In a standard MSR installation, one probe is placed near the centre of the nest, ideally within the lining among the eggs or immediately adjacent to the clutch, and the second is placed outside the nest, usually within one metre. The nest probe records the microclimate of the space occupied by the eggs, while the external probe provides a control record of ambient conditions. Comparing the two time series - or, less reliably, examining the internal probe alone - makes it possible to estimate when the parent was sitting on the nest and when the clutch was unattended. During incubation, nest temperature is generally more stable and often higher than ambient temperature; during a recess, nest values gradually approach ambient conditions. Relative humidity may respond similarly to the parent's presence and the degree to which the nest is covered.

Particular attention must be paid to probe position during installation. The measured temperature is neither embryo temperature nor an exact measure of internal egg temperature; it is the temperature at a particular point in the nest. Ideally, the probe should project slightly above the lining and lie level with the eggs. In deep or loosely constructed nests it may gradually become buried, whereas species that actively rebuild their nests may pull it away from the clutch. To reduce these problems, the probe should be secured in a position that interferes as little as possible with the birds while remaining stable. In a soft substrate, inserting the probe into the lining may be sufficient; in a looser nest, the cable can be secured with fine wire, a peg or a V-shaped fixing. The cable should be routed as low as possible within the lining or substrate so that it remains inconspicuous and does not invite pulling. The data-logger body should be placed beyond the bird's reach, for example beneath the substrate, behind an enclosure structure or outside the nest box. Because many species, including parrots, penguins and some raptors, tend to damage both loggers and cables, the entire installation should be concealed as effectively as possible. Although the instrument is designed for relatively demanding conditions, it should also be protected from dust, moisture and mechanical damage using suitable packaging, such as a resealable plastic bag.

Before installation, the MSR logger is configured using the supplied software. A high sampling frequency, for example one record per second, is suitable for incubation monitoring because it captures brief recesses and rapid temperature changes. For prolonged monitoring, however, battery life and memory capacity must be considered. At a one-second recording interval, an MSR logger typically operates for approximately one month, allowing most avian species to be monitored through a substantial part of the incubation period without repeated nest disturbance.

For every installation, it is essential to record the exact start time, device identity, positions of both probes, sampling frequency, species, pair identity, clutch size and incubation stage. All nest visits, inspections, equipment changes and other events capable of producing anomalies in the data should also be documented. MSR records are often interpreted together with camera footage or surrogate-egg data, so the clocks of all devices must be synchronised as accurately as possible. Without precise temporal alignment, it may be impossible to determine reliably whether a particular temperature

decline represented a natural recess, an exchange between parents, disturbance by a keeper or a technical change in sensor position.

Temperature and humidity data can be evaluated using incub8, an application developed by the project team during the earlier project TJ02000199. It automatically detects incubation rhythms from nest and ambient sensor data and provides keepers with informative visualisations and basic quantitative summaries of practical relevance. In addition to standard visualisation, the application uses hidden Markov models to estimate with high accuracy when a parent was present on the nest and when an incubation recess occurred. Inputs are time series of temperature and, where available, humidity measured within and outside the nest. Outputs include a graphical incubation actogram and a table of predicted states that can be combined with video footage, surrogate-egg records and other data. MSR data can therefore provide not only an overview of whether incubation occurred, but also quantitative estimates of recess duration and frequency, the stability of incubation across day and night and parental responses to disturbance - all of which have considerable potential for diagnosing problems during parental incubation.

From a husbandry perspective, MSR measurements are particularly useful for pairs whose incubation pattern is uncertain. They can distinguish a situation in which a parent sits consistently but the eggs nevertheless fail to develop from one in which the clutch is repeatedly or persistently left unattended. They can also help assess the effects of ambient conditions, such as clutch overheating, nocturnal cooling, unsuitable moisture within the nest material or differences between sheltered and exposed nests. Given the extreme variation in incubation rhythms, however, it is also advisable to monitor pairs that appear to incubate normally, particularly in high-priority species. This provides a reference dataset describing how the species incubates and how variable its rhythm is, which in turn makes genuine deviations indicative of a problem easier to identify.

3.3.5 Use of video recordings in incubation monitoring

Video recording is another key component of comprehensive incubation monitoring, not least because it provides behavioural context for data obtained from loggers. A temperature or movement record may show that something happened in the nest - for example, temperature declined, an egg moved or a prolonged incubation recess occurred - but the cause cannot always be identified without visual evidence. A camera can distinguish whether the change resulted from a routine parental exchange, an incubation recess, manipulation of nest material, egg turning, disturbance by visitors, conflict with another individual, predation or a technical problem with the measuring equipment.

The principal advantage of video recording is that incubation behaviour can be observed without repeated physical inspection of the nest. This is especially important for sensitive species in which human presence may cause clutch abandonment or disruption of normal parental care. Retrospective analysis of footage can determine how long parents remain on the nest, how often they leave the clutch, whether partners alternate, which parent incubates, whether nocturnal recesses occur, how frequently eggs are turned and whether disruptive stimuli occur near the nest. In managed breeding, cameras can therefore reveal causes of reproductive failure that would otherwise remain hidden.

A suitable camera should support continuous recording, provide adequate data-storage capacity, have a reliable power supply and produce usable night-time footage. Affordable security or domestic cameras are sufficient for routine nest monitoring provided that they can store recordings on a microSD card and do not require a permanent Wi-Fi connection. Operational duration is usually determined chiefly by the capacity of the power bank and memory card. The methodological handbook identifies small cameras powered by a power bank as a practical option; with appropriate configuration they can provide continuous recordings for several days (Figure 7). More sophisticated fixed camera systems with remote transmission and a stable mains power supply can be used for species nesting on established platforms or in nest boxes. Many zoological gardens already use such systems, and their

staff are consequently more experienced in interpreting camera footage than data from other types of logger.

Figure 7: A) Complete system for recording behaviour at the nest: power bank, power cable, microSD card, camera and stand; B) camera installed beside a nest.

The camera should be positioned so that the entire nest and its immediate surroundings are visible. A field of view that is too narrow may provide detailed coverage of behaviour on the eggs but miss the arrival of the second parent, disturbance by other birds or movement of people near the nest. Conversely, a very wide view can make subtle behaviours, such as egg turning or minor nest manipulations, difficult to identify and may also hinder identification of parents, for example from leg rings. Camera placement must therefore balance the finest possible detail against the contextual information required. For cavity-nesting species, the camera can be installed above or to the side of the nest box. For ground-nesting species, stable mounting and effective concealment within the substrate, vegetation, enclosure structure or other inconspicuous environmental features require particular attention.

Minimising disturbance caused by the camera is essential. The device should be as inconspicuous and stable as possible and positioned so that it does not restrict the birds' movements. Visible cables, indicator lights or a conspicuous power bank may cause parental agitation or active damage to the equipment. Cables should therefore be routed beyond the birds' reach, fixed to the substrate, covered with substrate or nest material and darkened or otherwise concealed where necessary. Indicator lights should be disabled in the camera settings where possible or covered with opaque tape. Infrared illumination must be sufficient to resolve night-time behaviour without visibly disturbing the birds.

One of the most important steps is synchronisation of camera footage with the other data loggers. Without precise temporal alignment, it is impossible to link, for example, a temperature decline in the surrogate with the moment at which the parent left the nest, or an egg movement with a particular manipulation visible on the video. For cameras without reliable internal clocks, the display of a telephone or computer showing the exact time, including seconds and matching the clocks used by the data loggers, should be held in front of the lens at the beginning of recording; the same time should also be entered in the installation record. This procedure should be repeated after every battery or memory-card replacement and after any prolonged visit to the nest during monitoring.

Systematic evaluation of video footage is best conducted in BORIS (Friard & Gamba 2016). This software allows an ethogram - a predefined list of behavioural categories - to be created and behaviours to be recorded during video playback using keyboard shortcuts. Typical categories for incubation monitoring include parental presence at the nest, incubation, incubation recesses, exchanges between partners, sleep, feather maintenance, nest maintenance, egg turning, visits by other individuals, aggressive interactions and responses to disturbance. Some behaviours are recorded as state events with a beginning and end, such as incubation or presence at the nest. Others are recorded as point events, such as an egg turn, vocalisation or attack on an intruder. The resulting dataset is a table of events containing exact times, durations and behavioural categories.

In managed breeding, video recordings are especially useful for interpreting problematic situations. When eggs fail to develop normally, footage may show that the parent spends little time on the nest, stands frequently, covers the eggs poorly, leaves them outside direct body contact or fails to turn them. It may also reveal repeated disturbance by other birds in the enclosure, aggression between partners, disturbance by visitors or interventions by keepers at inappropriate times. Conversely, footage from consistently incubating pairs can confirm that parental care is proceeding normally, indicating that any problem is more likely to lie in egg quality, fertility or the microclimate of the breeding environment.

3.4 Case studies based on data collected during the project

The following three brief case studies examine selected aspects that could be evaluated using the dataset collected during the project in the collections of the partner organisations and other zoological gardens. They provide unique insights, not previously obtained on this scale, into several components of incubation behaviour. Their value lies not only in addressing poorly studied aspects of avian biology, but also in yielding practical conclusions applicable to the management of birds under human care.

3.4.1 Case study 1: Parental incubation is not a stable incubator

One of the most important practical benefits of biomimetic surrogate eggs equipped with data loggers is the ability to determine the temperature that an egg - and therefore the embryo developing within it - actually experiences beneath an incubating parent. Although this variable is fundamental to embryonic development and to the design of artificial-incubation protocols, it remains poorly documented for most species (Deeming & Reynolds 2015). Incubators generally maintain relatively stable temperatures of approximately 37-38 °C, whereas parental incubation is a dynamic process affected by parental behaviour, the duration of incubation recesses, exchanges between partners, nest microclimate, the position of an egg within the clutch and the particular configuration of the enclosure.

During the project, internal temperatures were measured using instrumented surrogate eggs in 56 nests of 43 bird species representing ten orders (Figure 8). Data were collected at Safari Park Dvůr Králové, Brno Zoo, Olomouc Zoo and Zlín Zoo. Where egg size permitted, surrogates containing three simultaneously recording data loggers were used, providing a more accurate estimate of the temperature actually experienced by the embryo (see Section 3.3.1). Nests were usually monitored for approximately three days, allowing routine diurnal incubation patterns, nocturnal conditions and short-term fluctuations associated with recesses or changes in parental behaviour to be recorded. A surrogate containing one or more data loggers was placed within the clutch and recorded temperature at regular intervals. Measurements were subsequently summarised by avian order and compared with temperatures commonly used during artificial incubation. To approximate embryonic temperature as closely as possible - that is, the temperature in the upper part of the egg near the brood patch of the incubating parent - the highest temperature recorded at each time point was selected from multi-logger surrogates.

The results show that temperatures measured within the surrogates were not only considerably more variable but, above all, lower on average than the standard temperatures used in incubators. Figure 8 compares mean temperatures recorded by the surrogates with those commonly used for artificial

incubation. The blue boxplots show variation among mean temperatures measured in nests within each order, whereas the red symbols indicate the approximate range of incubator temperatures used for that order, based on an informal survey of collaborating zoo practitioners. In many groups, median temperatures recorded during parental incubation were approximately 33-36 °C, whereas standard incubator settings were around 37 °C. In some orders, including certain pigeons and pelicans and their relatives, temperatures recorded under the parents were closer to those used in incubators.

These measurements have two principal applications in avian husbandry. The first is to provide reference values for species whose optimal artificial-incubation conditions are poorly known. When parents of a given species repeatedly incubate successfully, a surrogate-egg record can reveal the temperature range, degree of fluctuation and natural recess pattern typical of that species. This information can help determine whether a constant incubator temperature should be retained, controlled cooling should be introduced, or the existing incubation protocol should be adjusted cautiously.

Any modification of incubation protocols must be approached cautiously. For species in which current artificial-incubation procedures already perform well, it is probably preferable to retain them, even where they differ substantially from the conditions experienced by embryos during parental incubation. Where artificial incubation is ineffective and hatchability is low, however, the recorded values may indicate the direction in which a protocol should be modified.

The second application is the diagnosis of problems during parental rearing. For example, analysis of data from several pelican nests showed that recorded temperatures exceeded those normally used in incubators and frequently rose above 40 °C, commonly regarded as a hazardous threshold beyond which embryonic mortality may occur. This pattern was not caused by normal parental behaviour, but by the location of the nests close to a heating source. The monitoring therefore identified a clear problem requiring a specific intervention - and one that is likely to arise relatively often when parental rearing is attempted in heated indoor facilities.

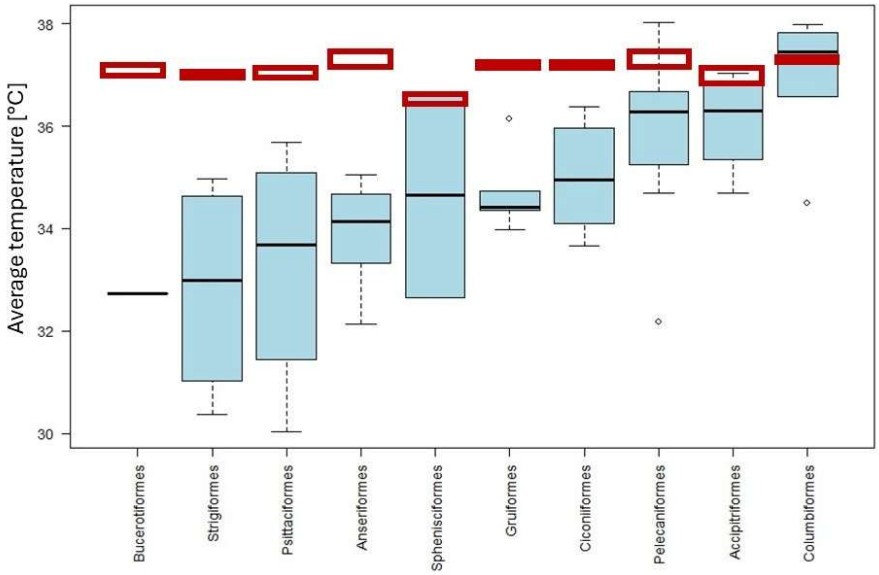


Figure 8: Comparison of mean internal temperatures measured by data loggers in biomimetic surrogate eggs with temperatures commonly used for artificial incubation in individual avian orders. Blue boxplots show values recorded in nests; red symbols indicate approximate incubator temperatures.

3.4.2 Case study 2: What can a camera reveal about sleep and preening during incubation?

This case study demonstrates that video recording is not merely a supplement to data loggers, but a highly useful tool in its own right for assessing the quality of parental care. We focused on two frequently overlooked but biologically important activities of incubating birds: sleep and preening. Both

are fundamental self-maintenance behaviours, but during incubation birds must balance them against care of the clutch, egg thermoregulation, nest defence and responses to disturbance. Sleep and preening may therefore provide useful indicators of whether an incubating parent experiences sufficient tranquillity at the nest and whether the environment permits normal behaviour.

Video recordings from 21 nests of 20 bird species maintained in zoological gardens were analysed. The dataset included species with biparental incubation, in which the two parents alternate at the nest, and species with uniparental incubation, in which a single parent cares for the clutch. Data were collected at Safari Park Dvůr Králové, Brno Zoo, Olomouc Zoo, Ostrava Zoo and the Prague Wildlife Rescue Centre. Recordings were made using compact cameras with night vision and subsequently evaluated systematically in BORIS. The coded behaviours included parental presence at the nest, incubation itself, sleep, preening and the presence of other individuals near the nest.

The results revealed pronounced interspecific differences (Figure 9). Some species, such as the African Penguin and Red-crowned Crane, slept relatively frequently at the nest, whereas sleep was recorded only rarely or not at all in others. Preening frequency also varied among species. One motivation for the study was to test the hypothesis that uniparental species would spend more time sleeping at the nest than biparental species, because a sole incubating parent has little opportunity to sleep away from the nest and must use its incubation recesses primarily for foraging. Contrary to our expectation, however, incubation system explained neither total sleep duration nor overall preening frequency. It therefore cannot be assumed that uniparentally incubating species sleep or preen more at the nest than species in which the parents alternate.

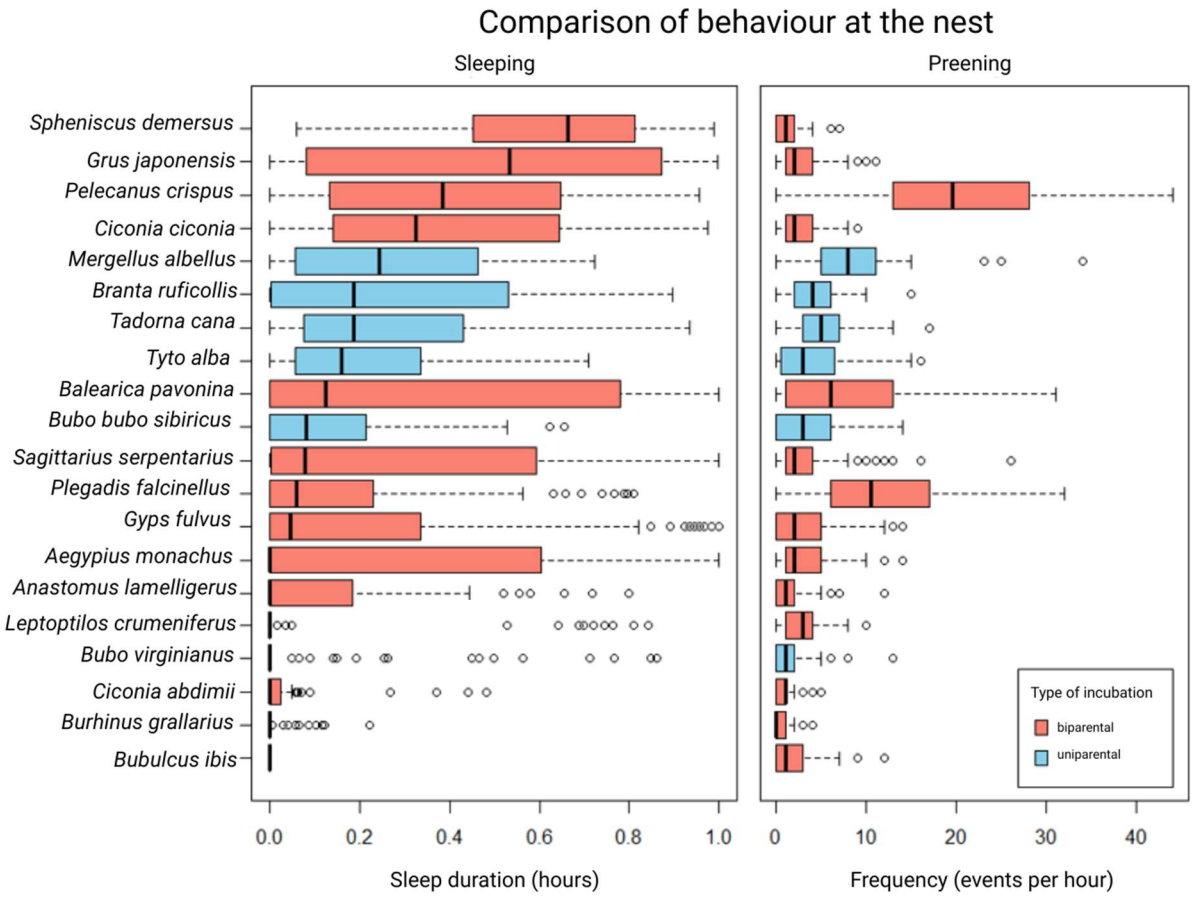


Figure 9: Variation among species in the time allocated to sleep and preening during incubation, based on monitoring in Czech zoological gardens. The time devoted to either activity did not differ consistently between uni- and biparentally incubating species, contrary to the tested hypothesis. We expected uniparentally incubating species to perform both activities at the nest, potentially at the expense of vigilance

or crypsis, whereas biparentally incubating species were expected to allocate them primarily to incubation recesses away from the nest.

A pronounced diel pattern was evident. In most species, sleep was concentrated mainly at night, although some species slept predominantly during the day or showed no strong daily sleep rhythm (Figure 10). Preening showed a weaker but discernible daytime peak, often around midday (Figure 11).

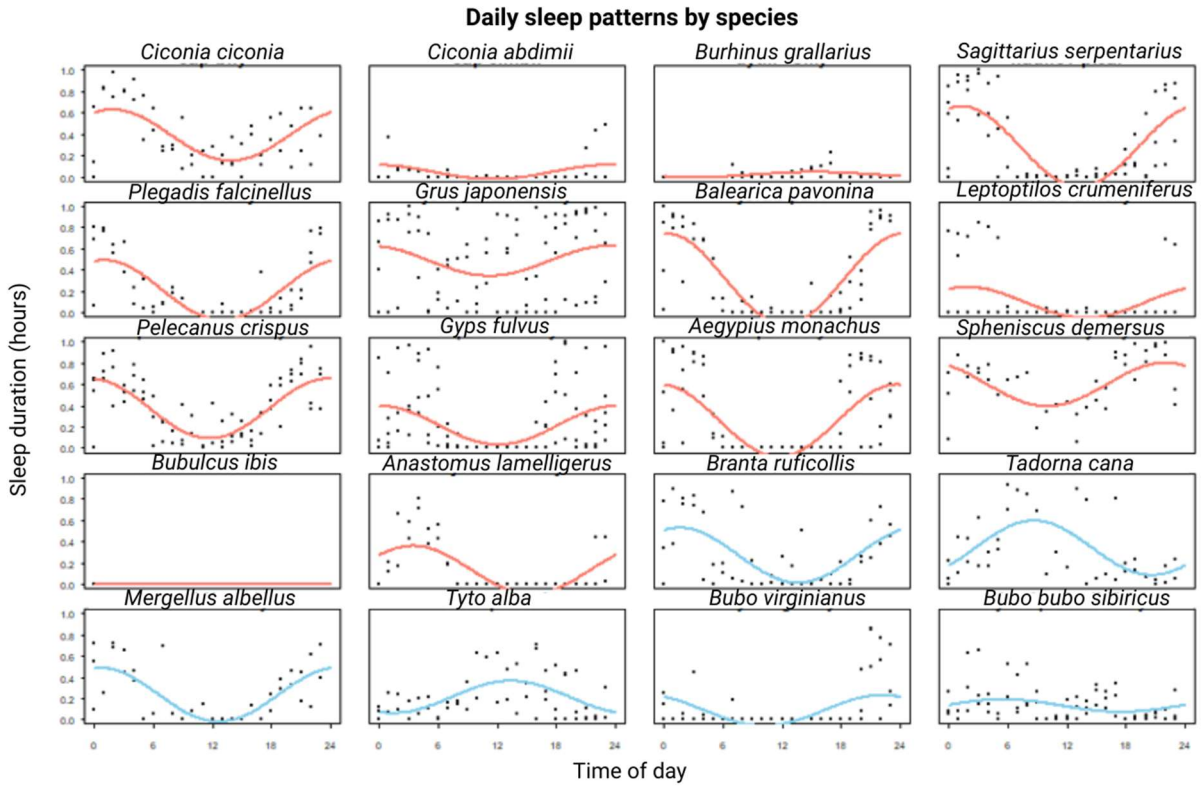


Figure 10: Distribution of sleep across the day in individual bird species. Model curves estimated using a linear mixed-effects model are superimposed; time of day was decomposed into sine and cosine components in radians, which accounts for the nonlinear appearance of the fitted relationship. The curves represent the circadian pattern of sleep.

The most important practical result was the demonstrated effect of other individuals visiting the vicinity of the nest on the amount of sleep. As the frequency of visits by other birds increased, incubating parents slept less. Disturbance therefore need not result directly in clutch abandonment: a parent may remain on the nest but become more vigilant, rest less and recover less effectively. The effect of disturbance on preening depended on the incubation system. No clear effect was evident in biparental species, whereas in uniparental species a higher visitation rate reduced preening. This suggests that a parent without regular relief from a partner may suppress less urgent activities during disturbance in order to maintain greater vigilance.

Several important husbandry conclusions follow. Tranquillity around the nest matters even when the bird does not leave and the eggs remain covered. Disturbance deserves particular attention in uniparentally incubating species because these parents have less opportunity to shift rest and self-maintenance to periods away from the clutch. Shared enclosures should therefore be assessed individually during incubation: visits by other individuals may represent a normal social context for some pairs, but may disrupt resting behaviour and reduce the quality of parental care in others.

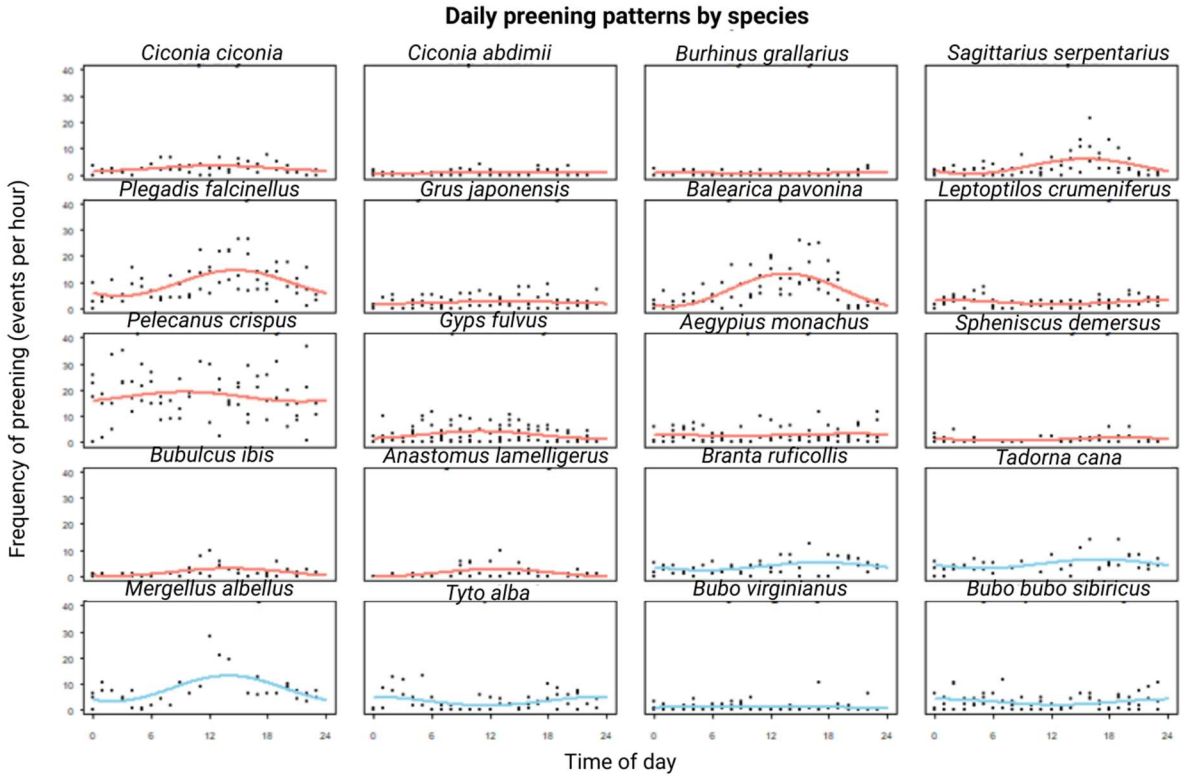


Figure 11: Distribution of preening behaviour across the day in individual bird species. Model curves estimated using a linear mixed-effects model are superimposed and represent the circadian pattern of preening.

3.4.3 Case study 3: How birds actually turn their eggs

Egg turning is an important component of incubation care. It supports normal embryonic development, prevents embryonic membranes from adhering to the shell, promotes albumen utilisation and helps maintain suitable conditions within the egg (see Section 3.3.2). Despite its importance, little has been known about the specific movements by which parents turn their eggs. It is often assumed that birds deliberately reposition or roll eggs with the bill. Combining precisely synchronised data from biomimetic surrogate eggs containing data loggers with simultaneous video recordings allowed this assumption to be tested much more directly.

The study included 40 nests of 32 bird species from 20 families and combined data from birds maintained in zoological gardens in the Czech Republic with data from wild birds in Arctic, temperate and subtropical regions. A biomimetic surrogate egg containing a data logger equipped with a triaxial accelerometer and magnetometer was placed in each nest. The logger recorded the timing and magnitude of egg movement; a change in egg orientation of 1° within one second was defined as the minimum movement event (see Section 3.3.2). The nest was simultaneously filmed, allowing the parental behaviour responsible for each movement to be identified. By combining the two methods, deliberate egg manipulation could be distinguished from movements arising incidentally during routine incubation behaviour and from movements caused by environmental factors, such as wind.

Of more than 40,000 analysed seconds associated with egg movement, movements that were apparently incidental - that is, not primarily directed at turning the egg - accounted on average for 76.2% of all events, although variation among nests was extremely large (Figure 12). Deliberate egg manipulations accounted for 18.8%, whereas passive movements caused by environmental factors such as wind represented only 2.5%. In most species, egg movement was therefore predominantly a by-product of routine parental behaviour at the nest: settling onto the clutch, standing up, shifting or wriggling on the nest, stepping, changing body position and manipulating nest material.

Deliberate manipulations were nevertheless mechanically more effective. The mean angular change during a deliberate movement was 0.160 radians, or approximately 9.2°, compared with 0.065 radians (3.7°) for incidental movements and 0.021 radians (approximately 1.2°) for environmentally induced movements. Deliberate events were therefore less frequent but turned the egg through a larger angle on each occasion. After accounting for both frequency and magnitude, however, incidental movements still made the largest contribution to total egg turning, representing approximately 65.1% of total angular displacement, whereas deliberate movements contributed approximately 33.0%.

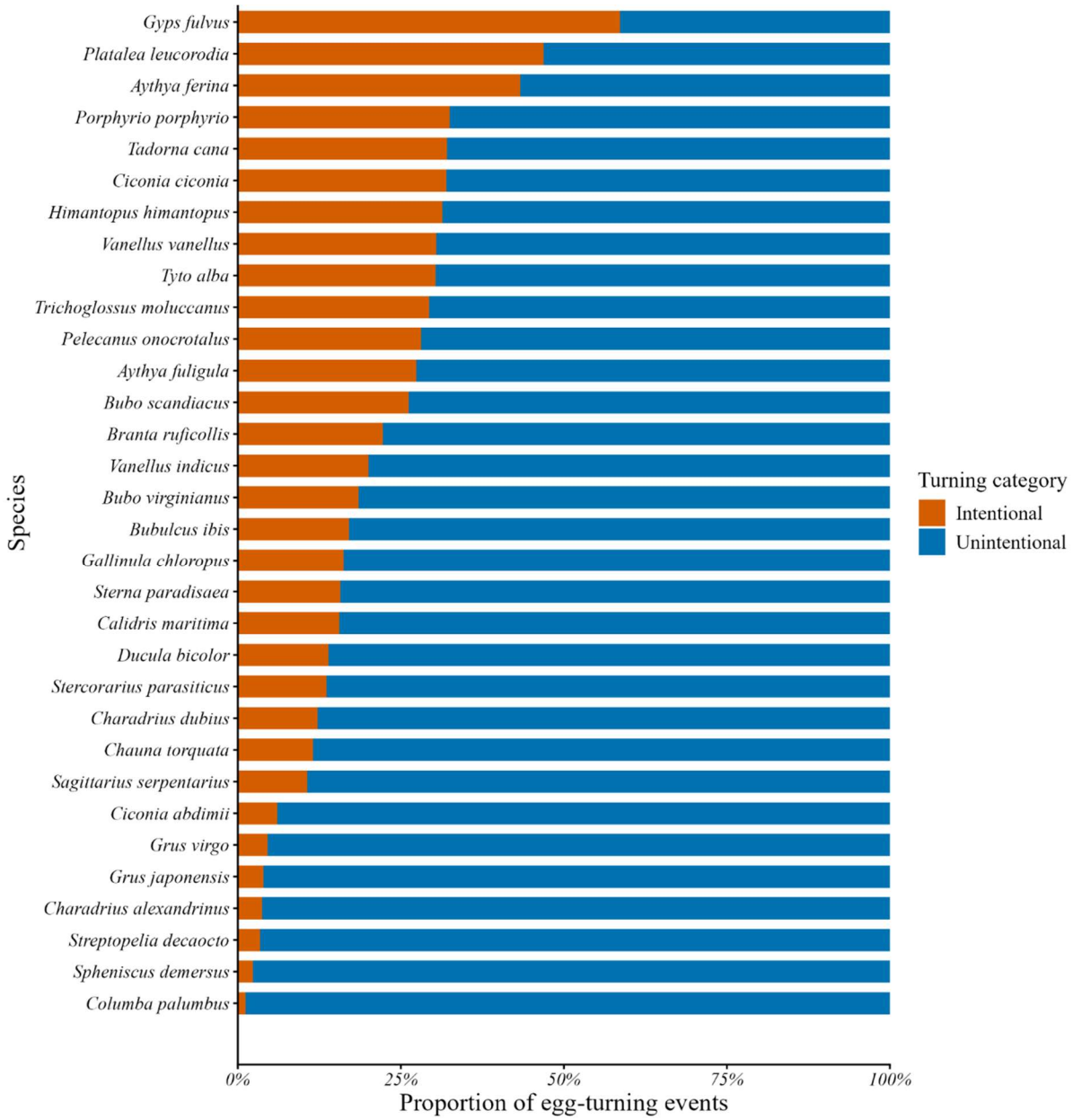


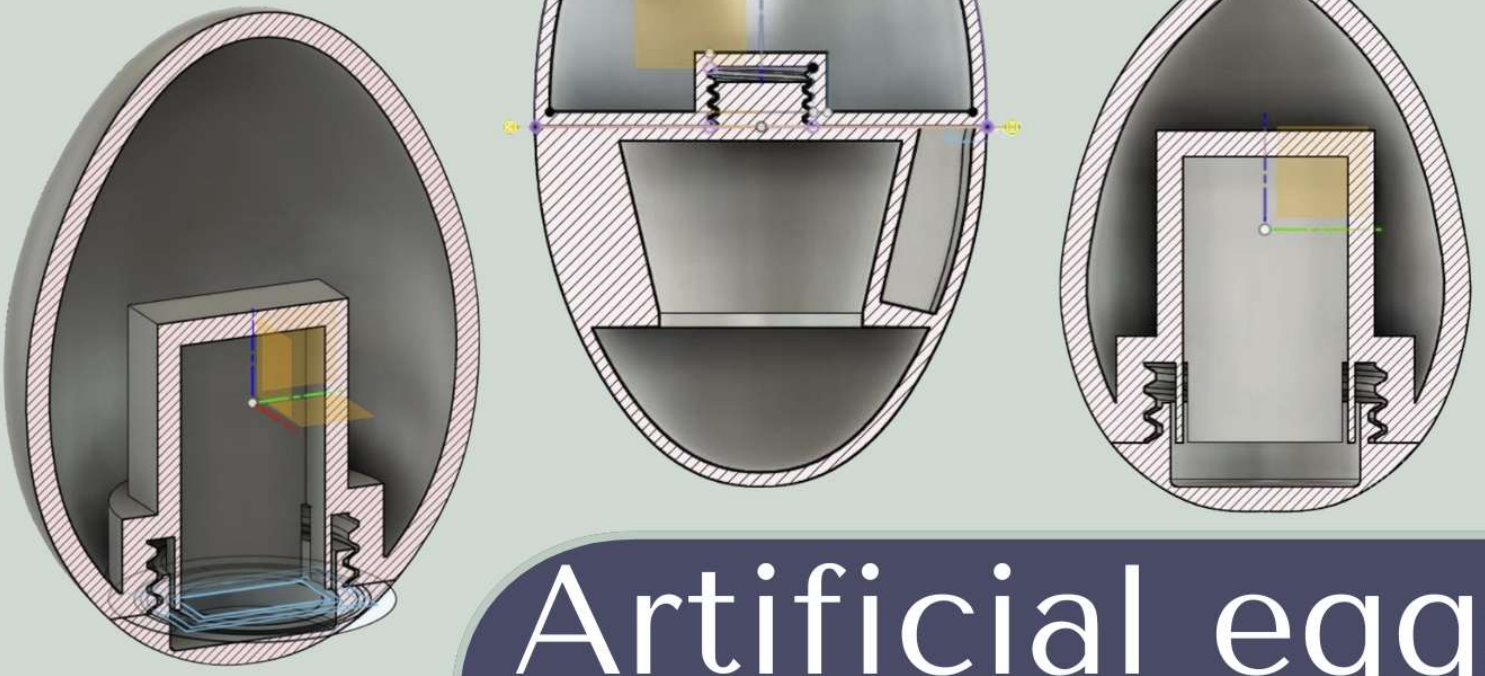
Figure 12: Proportions of egg-turning events in selected species, classified as intentional movements - deliberate turning with the bill - and unintentional movements arising as a by-product of other activity at the nest.

Clutch size was the only biological factor examined that was statistically significantly associated with the proportion of deliberate egg turning. Species with larger clutches showed a greater proportion of deliberate manipulations. In a large clutch, small body movements may not affect all eggs equally, making targeted manipulation with the bill more important. Body size, developmental mode of the young, uni- versus biparental incubation, whether the data originated from wild or captive birds, and the frequency of incubation recesses did not clearly explain interspecific differences.

Contrary to the prevailing assumption, the study therefore shows that deliberate egg turning, although a highly specialised form of parental care, is not necessarily the dominant mechanism through which eggs receive this essential component of incubation care.

The direct practical implications are less immediate than those of measuring egg temperature, humidity or mass loss, but the study nevertheless yields several useful husbandry conclusions. Normal incubation involves numerous small movements. A parent that remains completely motionless on the clutch and does not change position for prolonged periods may not provide the eggs with the same mechanical regime as a parent that regularly settles, stands, changes body position and manipulates nest material.

Overall, this case study demonstrates that the tools developed during the project can provide new insights even into apparently familiar components of parental care. Egg turning is not simply deliberate manipulation of an egg, but the complex outcome of the parent's entire incubation behaviour. For managed breeding, this finding is important because it highlights the value of natural, calm and undisturbed behaviour at the nest: even subtle movements that would pass unnoticed during routine inspections may form a significant component of care for the developing embryo.



Artificial eggs

Development and production of biomimetic surrogate eggs

- Model construction
- Mass and thermal properties of biomimetic surrogate eggs
- Coverage of avian egg morphospace and selection of representative surrogates
- Structure of the public Zenodo database of biomimetic surrogate eggs

4. Development and production of biomimetic surrogate eggs

This section describes in detail the development and production of biomimetic, 3D-printed surrogate eggs: artificial eggs designed to reproduce the natural eggs of individual species as closely as possible in shape, size, mass and incubation-relevant thermal properties. This work was initially regarded only as a component of the methodological development required for measuring incubation, and no separate project output was originally planned. During the project, however, it became clear that the surrogates could provide substantially broader benefits in managed breeding and that their use as standard husbandry eggs could offer practitioners considerable practical and financial advantages. We also recognised that the existing set of printable models already encompassed a substantial proportion of the overall variation in avian egg size and shape. We therefore systematically filled the remaining unrepresented regions of avian egg morphospace and developed a comprehensive set of models from which a suitable surrogate can be produced for virtually any bird species, while allowing for the usual degree of intraspecific variation in egg size and shape. The models were designed not only as carriers for data loggers, but also for broader routine use in avian husbandry. The resulting outputs include a complete and detailed production protocol for several types of surrogate tailored to any bird species, and, above all, a database of 409 printable models containing a suitable egg for virtually any extant bird species. In addition to the public-database output, this work formed the basis of a scientific manuscript describing the database and production process in detail.

4.1 Model construction

The basic dimensions of each model were derived from species-specific egg length and width obtained from Incubase, collaborating zoological collections or available comparative datasets on avian egg shape (Stoddard et al. 2017). Where multiple measurements were available for a species, the median value was used as the modelling target. Egg shape was reconstructed from suitable lateral-view reference photographs. The photographs provided the template for the egg profile, whereas the absolute size of the model was scaled to the measured dimensions.

The models were constructed in Autodesk Fusion. The workflow consisted of reconstructing the longitudinal egg profile, revolving it around the longitudinal axis and generating a three-dimensional solid. For hollow and research models, a shell, an internal filling chamber and, where applicable, cavities for data loggers were subsequently created. Standard wall thickness was set to 2 mm, representing a compromise among mechanical strength, printability, restriction of filling-material leakage and minimisation of undesirable thermal insulation. Wall thickness was increased in the largest models to improve mechanical stability.

4.1.1 Types of surrogate egg

Up to four model variants were created for each species, depending on egg size:

1. Solid husbandry model - a simple model printed as a solid or partially infilled body. It is available for eggs of all sizes and is intended primarily for routine husbandry, visual replacement of an egg or management of nesting behaviour.

2. Fillable shell model - a hollow model designed to be filled with an inert material, most commonly ultrasound gel, so that its mass and thermal capacity approximate those of a real egg. This variant is available for eggs at least 15 mm long. Compared with the solid model, it reduces printing time and filament use, although it requires an additional filling material.

3. Research model with one data-logger cavity - a model with a central internal cavity, a closable access port and space for one miniature data logger. It is intended primarily for recording internal temperature and egg movement. This variant is available for eggs at least 25.7 mm long and 19.3 mm wide. The spaces between the internal logger housing and the shell are also filled with an inert gel.

4. Research model with three data-logger cavities - a model accommodating three data loggers in lateral cavities positioned closer to the shell. It is intended principally for measuring temperature gradients and temperatures nearer the egg surface, which may better represent the position of the embryo during the first part of incubation. This variant is available for eggs at least 45.1 mm long and 33 mm wide. The spaces between the internal logger housings and the shell are likewise filled with an inert gel.

In larger models, the logger compartment is accessed through a screw cap, usually positioned at the blunt pole of the egg (Figure 13). In smaller eggs, where a conventional thread cannot be used, the model is divided into two parts and closed using a custom locking mechanism (Figure 14). Thread and joint tolerances were adjusted to accommodate the normal dimensional deviations associated with fused-filament fabrication (FFF).

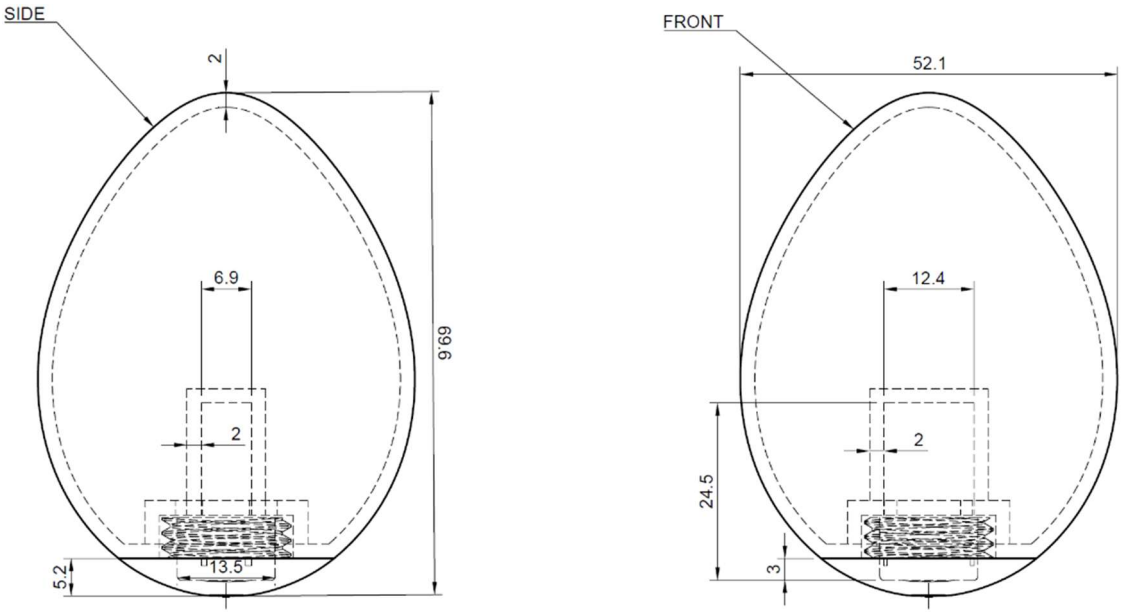


Figure 13: Lateral and frontal views of a single-logger surrogate egg for the African Penguin Spheniscus demersus; dimensions are in millimetres.

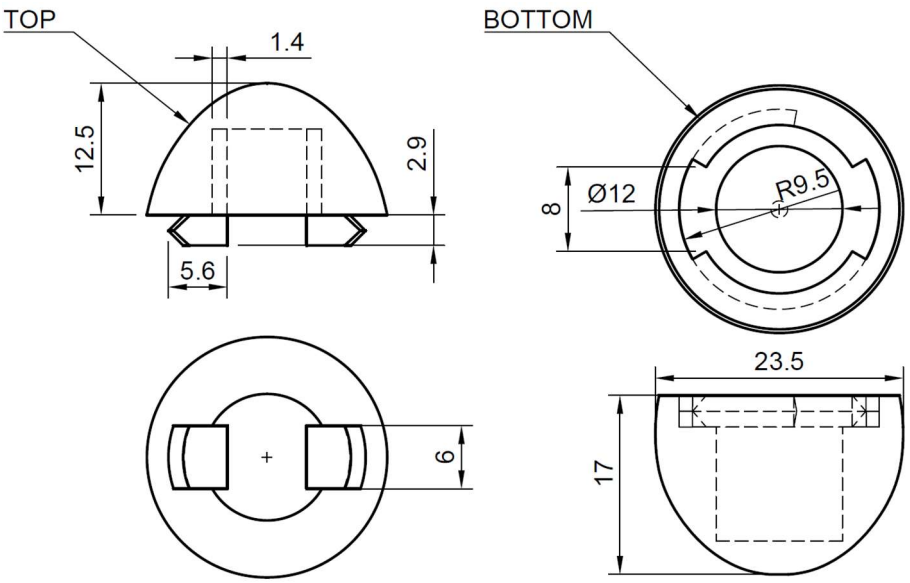


Figure 14: Frontal and basal views of a small single-logger surrogate egg for the Pygmy Falcon Polihierax semitorquatus; dimensions are in millimetres.

4.1.2 Materials and procedures for printing and filling

The models are designed for widely available FFF/FDM 3D printers. Suitable printing materials are non-toxic, mechanically durable and thermally stable filaments, particularly PETG or PLA. A light-coloured, ideally white, filament is convenient for subsequent surface finishing. A layer height of no more than 0.2 mm is recommended to obtain a sufficiently continuous and detailed surface. A standard 0.4-mm nozzle, at least three perimeters and, for fillable models, settings that improve watertightness - such as staggered internal seams or a slightly increased extrusion multiplier - are used to improve strength and reduce leakage. For large eggs, at least six perimeters are advisable to provide sufficient structural resistance.

For fillable models, printing should be paused at approximately 95% of the final egg height, immediately before the cavity is closed. The filling material is then added in an amount that produces the required mass and thermal properties. In the tested procedure, the most suitable material was commercially available ultrasound gel diluted with water to approximately 55% gel by volume. This mixture provides an appropriate combination of density, viscosity, thermal behaviour and low cost. Another inert, non-toxic liquid with similar density and thermal properties may also be used, including commonly available personal lubricating gels, but the final mass and watertightness of the model must always be verified before use.

4.1.3 Sealing, surface finishing and painting

After printing, every surrogate must be inspected visually, particularly for leakage, thread quality, correct seating of the closure and deformation of the data-logger cavities. Minor leaks can be repaired with cyanoacrylate adhesive or by locally fusing the material at low temperature. Surface irregularities are removed by fine sanding or filing, after which the model is coated with a primer.

For safety reasons, only non-toxic, water-thinned acrylic paints are used. The aim is not to reproduce every individual eggshell marking exactly, but to approximate the overall visual appearance of the natural egg of the species (Figure 15), which may be important for parental acceptance. The base coat is generally applied by airbrush, using paint diluted with water at a ratio of approximately 1:3, and repeated two or three times as required. For spotted eggs, an additional, more strongly diluted paint, approximately 1:5, is applied by splattering from an airbrush or comb. For species whose eggs normally have a worn, soiled or cryptic appearance, such as pelicans, highly diluted brown or black paint at approximately 1:10 can be applied manually, allowed to dry partially and then gently washed off so that only faint residual staining remains. Before placement in a nest, the completed model must be fully dry, non-tacky and must not release pigment.

Careful painting and overall visual fidelity are particularly important in species sensitive to egg appearance or where acceptance of a surrogate is uncertain. Following appropriate surface treatment, the surrogates were generally accepted well by incubating birds. Nevertheless, the suitability of each specific model should be verified before it is used with live birds.

Figure 15: Comparison of egg shape and coloration between natural eggs (top) and corresponding biomimetic surrogate eggs of six bird species. In every case shown, the surrogate was accepted by the parents.

4.2 Mass and thermal properties of biomimetic surrogate eggs

The surrogate eggs were designed not only to reproduce the external shape and size of natural eggs, but also to approximate their mass and thermal behaviour. These properties matter for two reasons. First, they affect the probability that parents will accept the surrogate and the way in which birds manipulate it within the nest. Second, they determine how faithfully a surrogate containing a data logger records the thermal conditions that would be experienced by a natural egg.

Model mass was set according to the estimated fresh mass of the egg of each species. This was calculated from egg length and width using the standard relationship for estimating avian egg mass described by Hoyt (1979). Because egg mass changes during incubation (see Section 2.4.3), the target surrogate mass was set at the midpoint between the estimated mass of a freshly laid egg and its mass immediately before hatching begins. The mass can nevertheless be adjusted for particular research applications. For solid husbandry models, target mass was achieved by modifying the percentage infill used during 3D printing. For each species, the infill setting was selected to bring the predicted mass of the printed model as close as possible to the target mass of the natural egg. In shell and data-logger models, the plastic components were printed at high strength, especially around cavities, threads and closures, and the remaining mass was supplied by an inert filling material. The recommended amount of filling for each model is provided in the accompanying mass-configuration table.

A commercially available ultrasound gel diluted with water to approximately 55% gel by volume was validated as a practical filling material. The mixture was selected because it combines suitable density, viscosity and thermal properties with low cost and ready availability. In fillable models, final surrogate mass can therefore be adjusted relatively easily to match the target mass of the natural egg. Before use with birds, however, the mass of the completed surrogate must always be checked, because it may vary with printer accuracy, filament type, slicer settings, the amount of filling, adhesives, sealing and surface finishing.

Thermal properties were assessed in a laboratory validation using models corresponding to Domestic Chicken and Japanese Quail eggs. For each egg type, five natural eggs were compared with five

corresponding filled, single-logger surrogate eggs. The eggs were subjected repeatedly to phases of heating, cooling and equilibration at room temperature (Figure 16). Temperature in the natural eggs was measured with a probe inserted into the egg, whereas temperature in the surrogates was recorded by a data logger placed in the central cavity.

The validation showed that filled, single-logger surrogates reproduced the principal heating and cooling trajectories of natural eggs reasonably well. Mean rates of temperature change were generally similar between natural eggs and surrogates during the individual monotonic phases. The surrogates therefore provide a biologically relevant record of thermal dynamics that is substantially closer to the conditions within a natural egg than a simple measurement of the surrounding air temperature. This supports their use for monitoring incubation-relevant thermal conditions in nests and for comparisons between parental and artificial incubation.

At the same time, surrogate eggs responded to changes in ambient temperature slightly faster than natural eggs. This difference was most evident in smaller eggs and is probably associated with the internal data-logger cavity, which reduces the effective thermal capacity of the model relative to a homogeneous natural egg. A faster response is not necessarily only a disadvantage. For some purposes, including the detection of brief incubation recesses, the return of a parent to the nest, rapid microclimatic changes or small egg movements, greater sensitivity to environmental change may improve the temporal resolution of the record.

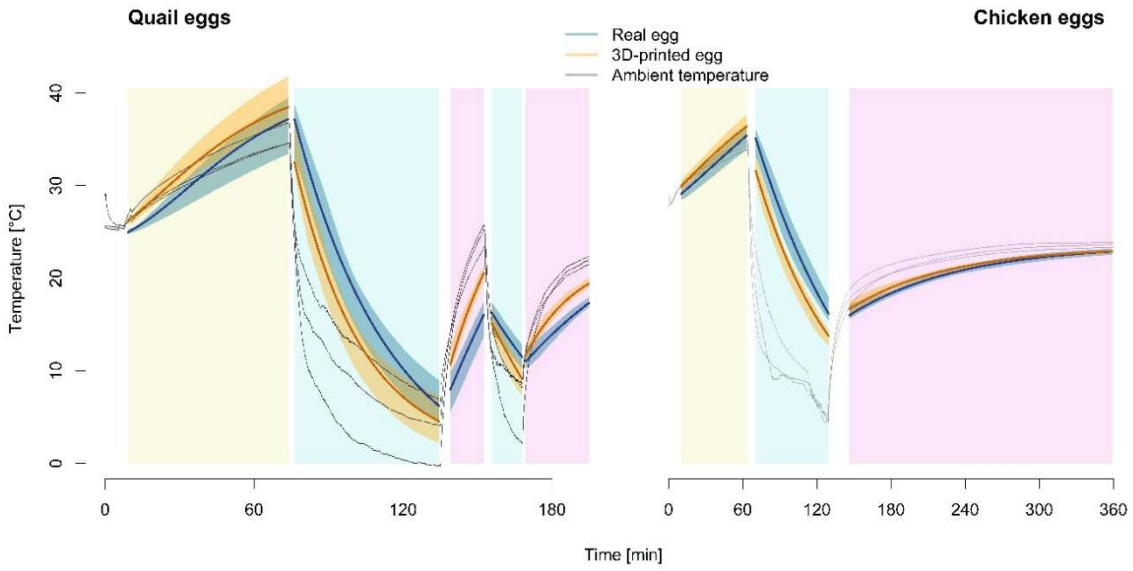


Figure 16: Temperature trajectories measured at the centre of natural eggs (blue), biomimetic surrogate eggs (orange) and in the ambient environment between the eggs (grey) during the thermal-validation experiment. Heavy lines show population-level predictions obtained from nonlinear mixed-effects models: a Gompertz model (beige block), an exponential-decay model (light-blue block) and an exponential-growth model (pink block). Hatched bands show the range of fitted individual-egg curves for the five eggs tested in each group.

4.3 Coverage of avian egg morphospace and selection of representative surrogates

The purpose of the biomimetic-surrogate database was not to create a separate model for every bird species. Such an approach would be technically inefficient and unnecessary in practice because many species lay eggs of very similar size and shape. The development strategy was therefore to cover as much avian egg variation as possible using a limited number of representative models. For this purpose, an egg morphospace was defined: a multidimensional space describing the principal differences in egg size and shape among bird species.

The morphospace was defined by three variables: egg length (L), asymmetry (A) and ellipticity (E). Egg length represents overall size, whereas asymmetry and ellipticity describe shape. Asymmetry indicates the extent to which an egg departs from a symmetrical ellipsoid and how far the point of maximum width is displaced along the longitudinal axis towards the blunt pole. Ellipticity describes relative elongation, that is, the relationship between egg length and width. Egg width was not used as a separate morphospace axis because, in the shape model applied here, it is derived from length and ellipticity. This approach follows the comparative parameterisation of avian egg shape developed by Baker (2002) and Stoddard et al. (2017), which permits comparisons across a broad diversity of bird species.

The shape of each surrogate was quantified from the longitudinal egg profile generated during modelling. The profile represented one half of a longitudinal egg section and was imported into R as a set of coordinates (x_i, y_i), where x_i denotes the position of a point along the longitudinal egg axis and y_i its radial distance from the axis of rotation. To permit comparisons among eggs of different sizes, the coordinates were first normalised. The longitudinal coordinate was transformed to the interval $[-1,1]$ as follows:

$$x_{\mathrm{norm},i} = 2 \times \frac{x_i - x_{\min}}{x_{\max} - x_{\min}} - 1$$

where $x_{\min}$ and $x_{\max}$ correspond to the two egg poles. The radial coordinate was standardised relative to half the egg length:

$$y_{\mathrm{norm},i} = \frac{y_i}{L/2}$$

where L is egg length. This produced a dimensionless egg profile in which position along the egg is expressed relative to the two poles and profile width is scaled to egg length.

The resulting profile was fitted with the two-parameter geometric egg-shape model of Baker (2002):

$$\hat{y}(x) = T(1+x)^{\frac{1}{1+\lambda}}(1-x)^{\frac{\lambda}{1+\lambda}}$$

where $\hat{y}(x)$ is the modelled radial distance of the profile at position x, and T is the relative maximum egg width:

$$T = \frac{B}{L}$$

The parameter λ determines egg asymmetry. A value of $\lambda = 1$ corresponds to a symmetrical egg, whereas departures from this value indicate displacement of the shape towards one pole. Parameters T and λ were estimated by nonlinear least squares, identifying the values that minimised the sum of squared differences between the observed normalised egg profile and that predicted by the model:

$$\sum_{i=1}^{n} \left(y_{\mathrm{norm},i} - \hat{y}(x_{\mathrm{norm},i})\right)^2$$

Shape indices used to define the morphospace were subsequently derived from the estimated model parameters. Asymmetry was calculated as:

$$A = \lambda - 1$$

and ellipticity as:

$$E = \frac{1}{T} - 1$$

Because $T = B/L$, ellipticity can also be written as:

$$E = \frac{L}{B} - 1$$

where B is egg width and L is egg length. Higher ellipticity therefore corresponds to a relatively more elongate egg. The resulting asymmetry and ellipticity values are comparable with the parameterisation used in the reference dataset of Stoddard et al. (2017).

The quality of the fitted shape model was assessed using the normalised fitting error (ε). This compared the observed and modelled profiles after radial distances had been standardised by their equatorial radii, ensuring that the resulting error was independent of absolute egg size:

$$\varepsilon = \frac{7}{n} \sum_{i} \left(\frac{r_{\text{actual},i}}{r_{\text{actual,eq}}} - \frac{r_{\text{model},i}}{r_{\text{model,eq}}} \right)^2$$

where $r_{\text{actual},i}$ is the observed radial distance at point i, $r_{\text{model},i}$ is the corresponding model prediction, $r_{\text{actual,eq}}$ and $r_{\text{model,eq}}$ are the equatorial radii of the observed and modelled profiles, respectively, and n is the number of profile points. Strongly pyriform eggs, typical particularly of some shorebirds, were not described adequately by the Baker model and were therefore evaluated separately using a simplified procedure based only on length and ellipticity.

To determine whether a surrogate could also be used for species other than the focal species from which it was constructed, biologically realistic tolerance limits were required. These were derived from the observed intraspecific variation among eggs stored in Incubase. The calculation included 7,814 eggs from 80 species and was restricted to species represented by at least 40 measured eggs. For each species s, the 5th and 95th percentiles of egg length were calculated:

$$P_{5,L,s}, P_{95,L,s}$$

and the usual range of length variation was expressed relative to the mean egg length of the species:

$$R_{L,s} = \frac{P_{95,L,s} - P_{5,L,s}}{\bar{L}_s}$$

where $\bar{L}_s$ is the mean egg length of species s. The range of ellipticity variation was calculated analogously for each species:

$$R_{E,s} = P_{95,E,s} - P_{5,E,s}$$

where $P_{5,E,s}$ and $P_{95,E,s}$ are the 5th and 95th percentiles of ellipticity calculated from egg length and width using $E = L/B - 1$. The interval between the 5th and 95th percentiles was treated as the usual range of intraspecific variation.

The acceptable deviation between a natural egg and a surrogate was then defined as half the mean intraspecific range of variation across species:

$$\tau_L = \frac{1}{2} \bar{R}_L$$

$$\tau_E = \frac{1}{2}\bar{R_E}$$

where τ_L is the tolerance for egg length and τ_E is the tolerance for ellipticity. The resulting tolerances were approximately 8% for egg length and 0.10 for ellipticity. Because asymmetry could not be derived directly from the routine dimensional data stored in Incubase, the ellipticity tolerance was also applied to asymmetry. This choice was supported by several published studies that quantified intraspecific variation in both traits (Taff et al. 2022; Bichet et al. 2025) and indicated that variation in asymmetry is, if anything, greater than variation in ellipticity. We therefore regard the selected tolerance as conservative.

A species was considered covered by a given surrogate when its mean position in morphospace fell within the tolerance region of that model, that is, when the following conditions were met:

$$\left| \frac{L_{\text{species}} - L_{\text{model}}}{L_{\text{model}}} \right| \leq \tau_L$$

$$\left| E_{\text{species}} - E_{\text{model}} \right| \leq \tau_E$$

$$\left| A_{\text{species}} - A_{\text{model}} \right| \leq \tau_A$$

Each surrogate therefore represents not merely a single point in morphospace, but a tolerance region within which its use can be regarded as biologically realistic. This made it possible to identify which regions of avian egg morphospace were already covered by the available models and where additional representative surrogates were required.

The representativeness of the original model set was evaluated against the reference egg-shape dataset of Stoddard et al. (2017), which contains approximately 1,400 bird species and, to the best of our knowledge, is by far the largest and phylogenetically most comprehensive available dataset providing the required egg traits at species level. For each species in the reference dataset, we determined whether its mean morphospace position lay within the tolerance region of at least one available surrogate. Species meeting this criterion were classified as covered. Under these criteria, the original set of 80 focal-species models covered approximately 60.5% of the species in the reference dataset. Unrepresented regions of morphospace - combinations of egg size and shape for which no suitable model was available - were then identified.

Unrepresented regions were filled using two approaches. For small eggs, particularly those shorter than 25 mm, which were entirely absent from the original set because they cannot accommodate a data logger, the morphospace was divided into a regular grid based on length, asymmetry and ellipticity. For every occupied grid cell, the focal species in the Stoddard et al. (2017) dataset closest to the cell centre was selected and a representative model was created. These small models were produced principally as solid husbandry surrogates; where egg length was at least 15 mm, a fillable shell variant was also added.

For larger eggs, candidate models were selected according to the principle of maximum incremental coverage. Each species not yet covered was temporarily treated as a candidate for a new surrogate, and the number of additional uncovered species that would fall within its tolerance region was calculated. This produced a coverage matrix identifying the species represented by each candidate model. New models were then selected sequentially so that each added model covered the greatest possible number of species not previously represented. To avoid unnecessary redundancy, a model was created only when it uniquely represented at least three species in the reference dataset, including the candidate species itself.

This procedure produced a final set of surrogates for 129 focal species (Figure 17), comprising 409 digital models in different construction variants. Reassessment against the reference dataset showed that, within the defined tolerance limits, a suitable model was available for 98.2% of the species represented in the reference morphometric dataset. The database therefore does not merely cover the 129 species for which direct models were produced; it provides a practical surrogate-selection system for the overwhelming majority of bird species and is consequently a genuinely general-purpose resource.

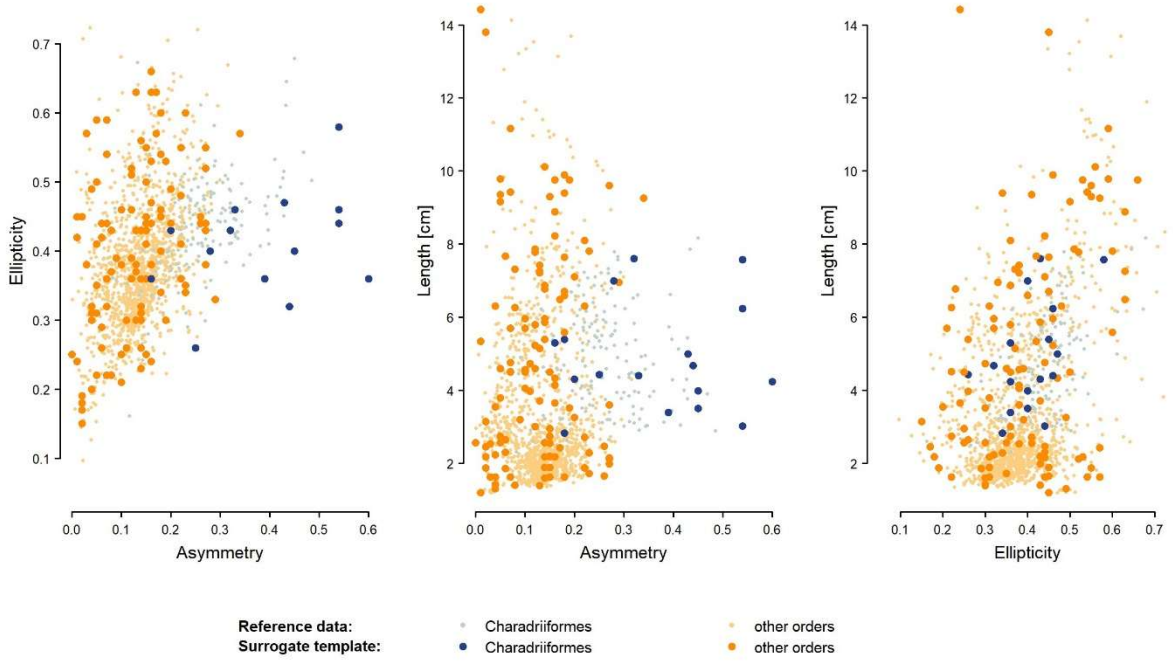


Figure 17: Coverage of avian egg morphospace by the biomimetic-surrogate dataset. The three panels show pairwise projections of egg asymmetry, ellipticity and length for species in the reference dataset (light symbols) and surrogate-egg models in the final dataset (dark symbols). Species were considered represented when their mean morphometric position fell within the predefined tolerance of at least one surrogate model. Species in the order Charadriiformes are shown separately from all other orders because they include markedly pyriform eggs evaluated using a modified parameterisation (see text).

4.4 Structure of the public Zenodo database of biomimetic surrogate eggs

The database of biomimetic, 3D-printed surrogate eggs is deposited as a publicly accessible archive on Zenodo under DOI 10.5281/zenodo.18955995. It is released under the Creative Commons Attribution 4.0 International licence (CC BY 4.0), which permits unrestricted downloading, reuse, modification and redistribution of the models and associated data provided that the source is cited appropriately. The archive is designed to provide users not only with the 3D models themselves, but also with all supporting information required to select, print, fill, finish and validate them, and to adapt them for additional species where necessary.

The core component of the database is the compressed archive biomimetic_surrogate_egg_models_v1.zip / DataS1.zip, which contains several groups of files. The largest component is the stl_models/ directory containing the 3D models in STL format. These files provide printable surrogate geometries for 129 focal bird species. Depending on egg size, up to four construction variants are available for each species: a solid husbandry model, a fillable shell model, a research model for one data logger and a research model for three data loggers. Where a model is divided into multiple components, such as upper and lower parts, each component is stored as a separate STL file. File names are standardised and contain the scientific species name, model type

and, where applicable, the model component, for example Genus_species_modeltype_part.stl. Model types are identified by the codes solid, shell, 1L and multi.

A second major component is the metadata accompanying the individual species models. The table species_metadata.csv contains basic information for the focal species for which models were constructed directly. For each species, it provides target egg length and width in millimetres, estimated egg mass, the shape parameters asymmetry and ellipticity, taxonomic classification and the names of the STL files available for each model type. This table is the principal link among the biological species, its morphometric parameters and the corresponding printable files.

The table surrogate_species_selection.csv is central to using the database for species lacking a directly constructed focal model. It links species in the reference avian egg-shape dataset to the closest available surrogate models. For each target species, it provides the scientific name, family, order, egg shape and size parameters, the number of suitable available models and a ranked list of the closest models. Users therefore do not have to select a surrogate by visual judgement alone, but can identify a model that falls within the defined tolerances for egg size and shape.

A separate table, mass_distribution.csv, contains the information required to achieve biologically realistic surrogate mass. For each model it provides the target egg mass, the estimated mass of the plastic components under standardised printing settings, the recommended amount of filling for shell and data-logger variants, and the optimised infill percentage for solid husbandry models. This table is particularly important because shape alone is insufficient: approximation of natural egg mass is also necessary for parental acceptance, appropriate manipulation within the clutch and realistic thermal dynamics.

The database additionally contains files associated with the assessment of morphospace coverage and model validation. The file morphospace_coverage.csv, or its equivalent, summarises the data used to evaluate how effectively the set of surrogates represents variation in avian egg size and shape. The file thermal_validation.csv contains the results of laboratory tests comparing temperature trajectories in natural eggs and filled, data-logger surrogate eggs. These validation data document that the principal heating and cooling patterns of the surrogates resemble those of natural eggs, although the models may respond slightly faster to rapid temperature changes.

The archive also includes README.txt, which describes the database structure, file-naming conventions, the meaning of the individual model variants, recommended use and citation instructions. The code/ directory supports reproducibility and future development of the database and contains the R scripts used to calculate egg-shape parameters, evaluate morphospace coverage, select supplementary models and analyse the thermal-validation experiment.

The database uses formats intended to be readily accessible in commonly used software. Model geometries are stored as binary STL files, which can be opened in slicers and CAD programs used for 3D printing. Supporting tables are stored as UTF-8-encoded CSV files, using decimal points and NA to denote missing values. These formats permit direct use in spreadsheet applications, R, Python and other analytical environments.

Overview of project outputs

Incubase - a platform for managing, sharing and analysing incubation data

Public database of incubation parameters within Incubase

Methodological guide to monitoring incubation in managed breeding

Database of 3D models of biomimetic surrogate eggs

Workshop

Summary reserach report

5. Overview of completed and planned project outputs

The individual outputs are described below according to their current status. The project designations O1, O2 and S1 are distinct from the classification of results under the national evaluation methodology. Manuscripts that have not yet been accepted do not constitute formally reportable publication outputs; they will acquire this status only upon acceptance or publication.

5.1 Incubase - a platform for managing, sharing and analysing incubation data

Brief description: Incubase is a bilingual web platform for the standardised entry, management, validation, searching and analysis of data on avian eggs, incubation trajectories and the incubators used. The platform includes analytical tools for assessing egg-mass loss and optimising incubation conditions, as well as a public knowledge component called Incupedia.

Type / formal status: Project output O1, classified as type O (other). This is a completed and operational output that will continue to be maintained and developed after the end of the project.

Availability: The platform is available at https://incubase.fzp.czu.cz/. Incupedia is publicly accessible without registration. Data entry, management of non-public records and use of the analytical tools require free registration.

Target users: Zoos, breeding centres, wildlife rescue centres, private breeders, hatchery staff, animal-collection curators and researchers.

5.2 Public database of incubation parameters within Incubase

Brief description: The relational database collects standardised data on individual eggs, their morphometry, repeated weighing, incubation conditions, fertility, embryonic development and incubation outcome. On 30 June 2026, it contained records for 24,543 eggs representing 470 taxa.

Type / formal status: Project output S1, classified as type S - a specialised public database. The output is complete, although its content will continue to expand.

Availability: The database is made accessible through the Incubase platform at https://incubase.fzp.czu.cz/. Access to individual records is governed by the licence and access regime selected by the data owner.

Target users: Breeding institutions, coordinators of breeding and conservation programmes, researchers and specialists in avian reproductive biology.

5.3 Methodological guide to monitoring incubation in managed breeding

Brief description: The methodological guide summarises procedures for selecting and installing data loggers, biomimetic surrogate eggs, external temperature and humidity probes, and cameras. It also addresses device synchronisation, measurement documentation, data management, data processing and biological interpretation.

Type / formal status: Project output O2, classified as type O - other result.

Availability: Czech and English versions will be published electronically and made freely available. The anticipated publication site is the website of the Behavioural Ecology Research Group at the Faculty of Environmental Sciences, Czech University of Life Sciences Prague: https://www.fzp.czu.cz/cs/r-6899-projekty-a-spoluprace/r-6923-projekty/r-20308-vyuziti-modernich-nastroju-biologgingu-sdileni-a-uzivatelsky-privetive-analyzy-dat-pri-optimalizaci-inkubace-vajec-ohrozenych-druhu-ptaku-v-lidske-peci/o-projektu.html

Target users: Staff of zoos, breeding centres and wildlife rescue centres, private breeders, curators and researchers.

5.4 Database of 3D models of biomimetic surrogate eggs

Brief description: This originally unplanned output comprises 409 printable models based on 129 representative bird species. The data package contains several construction variants, metadata, resources for selecting a suitable model, production procedures and the results of physical validation.

Type / formal status: An originally unplanned project output classified as type S - a specialised public database. Additional models may be added if a future need arises, but the current version was designed to cover the overwhelming majority of avian egg variation and is therefore essentially universal in its applicability.

Availability: The database is publicly available in the Zenodo repository (https://zenodo.org/records/18955995; DOI: 10.5281/zenodo.18955994).

Target users: Zoos, breeding centres, wildlife rescue centres, private breeders, research teams and educational institutions using 3D printing.

5.5 Workshop

Brief description: The workshop "Modern tools for monitoring incubation and their application in managed breeding" introduced the first version of the Incubase platform, methods for monitoring parental incubation and the production of 3D-printed surrogate eggs to the professional community. Participants gained practical experience with the platform and provided feedback on the outputs under development.

Type / formal status: Completed implementation, educational and dissemination activity classified as type W - workshop.

Availability: The workshop was held on 20 August 2025 at the Faculty of Environmental Sciences, Czech University of Life Sciences Prague. Presentations and other materials were provided both to participants and to interested individuals who were unable to attend.

Target users: Zoo staff, private breeders, curators and researchers.

5.6 Summary research report

Brief description: The summary research report brings together and interconnects all major project outputs within a single methodological and applied framework. It summarises the biological foundations of incubation, the development and functions of the Incubase platform and its database of incubation parameters, opportunities for monitoring parental incubation, the production of biomimetic 3D surrogate eggs, and practical knowledge acquired in breeding facilities. Through case studies, it demonstrates how the project outputs can be used to optimise artificial incubation, diagnose problems in parental care and investigate incubation biology. The report also defines priorities for future development, particularly expansion of the user base, data sharing and construction of a feedback loop between practitioners and researchers.

Type / formal status: Formal project output classified as Vsouhrn - a summary research report. The document constitutes the completed overarching output of the project.

Availability: The report is freely available electronically from the website of the Behavioural Ecology Research Group at the Faculty of Environmental Sciences, Czech University of Life Sciences Prague: https://www.fzp.czu.cz/cs/r-6899-projekty-a-spoluprace/r-6923-projekty/r-20308-vyuziti-modernich-nastroju-biologgingu-sdileni-a-uzivatelsky-privetive-analyzy-dat-pri-optimalizaci-inkubace-vajec-ohrozenych-druhu-ptaku-v-lidske-peci/o-projektu.html

Target users: Staff of zoos, breeding centres and wildlife rescue centres, private breeders, curators and coordinators of breeding programmes, researchers, conservation practitioners and the funding provider.

6. Conclusions and priorities for future development

The project clearly demonstrated that effective refinement of procedures used to incubate the eggs of threatened and husbandry-demanding bird species cannot, in the long term, be based solely on the isolated experience of individual institutions. Collaboration and inter-institutional data sharing offer enormous potential. Realising this potential requires the integration of standardised data collection, effective data sharing, user-accessible analysis and the continuous translation of acquired knowledge back into practice. The project succeeded in creating an interconnected suite of tools that enables this approach: an extensive database of incubation parameters; the Incubase web platform with analytical functions and the publicly accessible Incupedia; a methodological guide to monitoring parental incubation; a database of biomimetic 3D surrogate-egg models; and unique datasets on temperature, parental behaviour and egg-turning mechanisms. An equally important outcome is that these outputs were not developed merely as academic products, but were designed and validated in close collaboration with staff of zoos and other breeding institutions.

The central long-term project output is Incubase as a shared data and knowledge infrastructure. By the end of the project, it already contained data on more than 24,000 eggs representing hundreds of bird species. In addition to recording these data, the platform enabled assessment of egg-mass loss, recommendations for modifying incubation conditions and the creation of continuously updated species summaries in Incupedia. Subject to the relevant licensing conditions, Incubase data are also available to the scientific community. The value of such a system is neither final nor static. On the contrary, it will increase with every additional participating institution, every new and well-documented incubation case, and the increasing completeness of data on incubation trajectories and outcomes. Completion of the technical development therefore represents only the first step towards realising the project's full applied potential.

In the next phase, it will be essential to focus on implementation and active dissemination of the outputs among potential users. Awareness of Incubase, Incupedia, the methodological guide and the database of 3D models must continue to increase, while practical barriers to their use are reduced. This will require presentations at professional meetings, workshops and training sessions, direct communication with zoos and coordinators of breeding programmes, and continuing technical and methodological support for newly participating institutions. International dissemination will be particularly important, because expansion beyond the Czech context can substantially increase the taxonomic coverage of the database and generate sufficiently robust datasets even for rare species for which each individual institution handles only a small number of eggs.

A key task is the gradual development of a functional user ecosystem in which the individual groups have clearly defined and mutually complementary roles. Practitioners and breeding institutions will be the principal data providers and, at the same time, the recipients of practical recommendations. Researchers, ideally with the direct involvement of the husbandry community, will use and analyse the data in scientific work and translate them into broader biological understanding, species-specific reference values and methodological recommendations. The administrators of Incubase must maintain the technical stability of the system, protect data ownership, provide transparent licensing conditions and continue to develop an effective infrastructure for translating analytical results into a form that can be readily applied in husbandry practice.

The creation of a well-functioning feedback loop must be a fundamental principle of future development. Data generated during routine hatchery work must not end merely as archived records or source material for scientific publications. Through Incubase and Incupedia, the results of analyses

based on practitioners' data must be returned to the data providers in the form of refined reference values, accessible species summaries, warnings of potentially hazardous deviations and specific recommendations for modifying incubation procedures. This return of knowledge will be the main incentive for long-term user participation and, at the same time, the mechanism through which the quality of recommendations will progressively improve.

Scientific manuscripts already prepared on the Incubase platform, biomimetic surrogate eggs and mechanisms of parental incubation will form an important component of this process. Their publication will raise awareness of the outputs within the scientific community, support their expert validation and attract researchers interested in using the data in their own projects. In addition to publishing the results, it will be necessary to continue validating analytical recommendations against new data, extend species-specific reference values and systematically assess whether the proposed procedures genuinely improve hatching success and the quality of reared offspring.

The project therefore created not merely a collection of individual outputs, but the foundation of a long-term infrastructure connecting husbandry practice, applied research and biodiversity conservation. Its future success will depend primarily on the number of active users, the quality of shared data, long-term technical sustainability and the capacity to translate new knowledge back into the routine work of practitioners. Maintaining this circulation among data, scientific understanding and practical decision-making is the most important task for the project team following completion of the project.

7. References

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