

**Temporal dynamics of parental care in wild jackdaws:
Insights from a novel continuous monitoring approach**

Marçal Pou-Rossell

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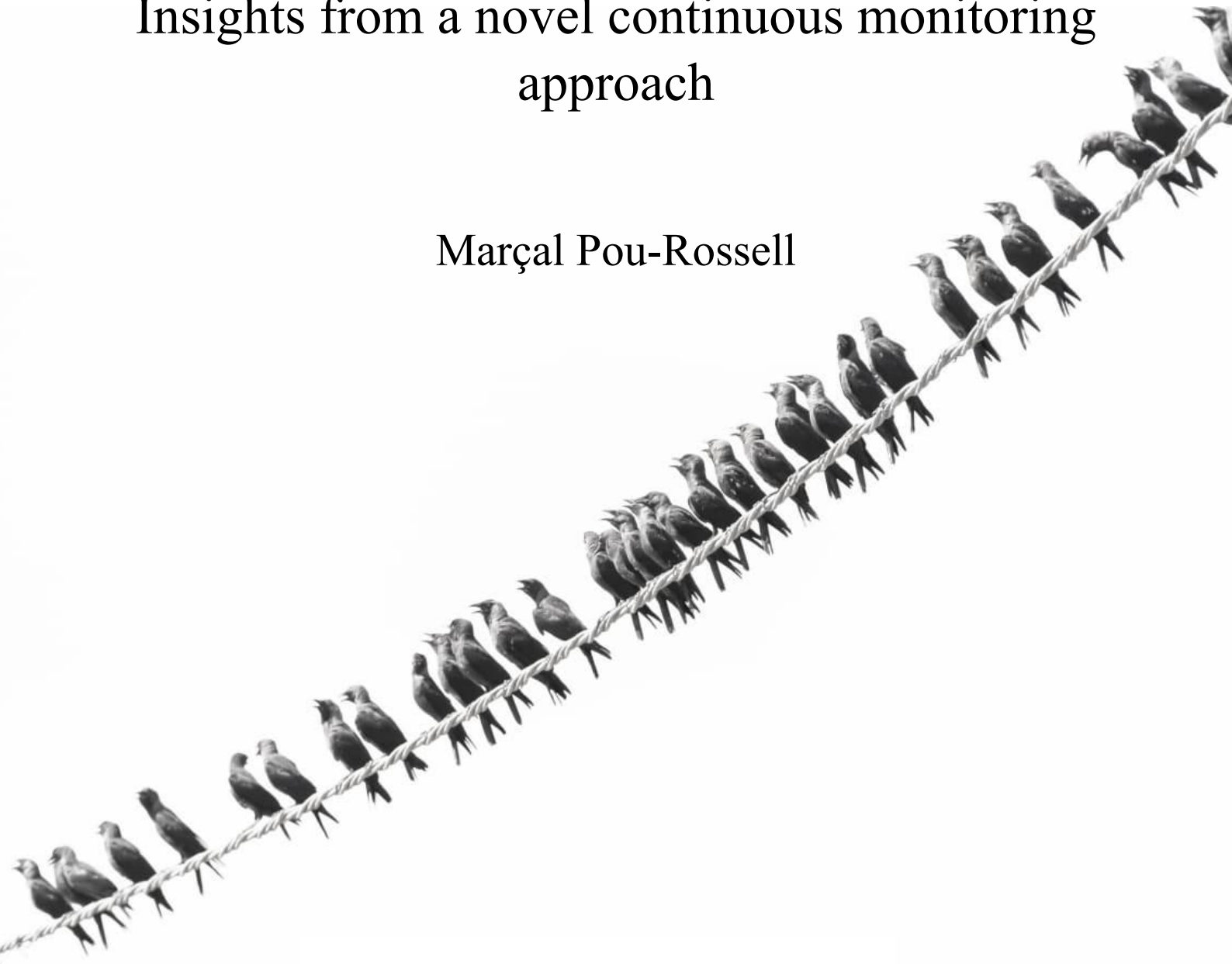
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Insights from a novel continuous monitoring
approach

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April 2026



UAB

"I am sure that in some instances they were watching, smelling, hearing, and studying me as closely as I was observing them."

Marc Bekoff, 1997

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Summary

Parental care is a central component of the life history of many animals. Although investing in offspring can enhance their survival, especially when young are born undeveloped, it can be costly for parents and limit their future reproduction. The decisions about how much time and energy to invest can also generate conflicts between parents and offspring, and between parents themselves. Because parental care directly and indirectly affects fitness, it has important ecological and evolutionary consequences. Yet we still know relatively little about how parental effort unfolds through time and how care is distributed between pair members as constraints shift across the breeding cycle. A major reason is that collecting parental care data in the wild remains logistically and technologically challenging, so parental behaviour is often quantified only partially across the breeding season through brief snapshots of parental effort. This makes it difficult to estimate parental investment accurately, as parental care comprises multiple behaviours expressed across distinct breeding stages. In this thesis, I address this gap by investigating the temporal dynamics of biparental care across the breeding season in wild jackdaws (*Corvus monedula*).

I begin by showing that methods used to quantify parental care are highly heterogeneous and often rely on short, stage-restricted observation windows. To overcome these limitations, I then describe an automated monitoring system based on Raspberry Pi single-board computers and custom computer vision algorithms, which enabled the continuous, fine-scale quantification of parental care across the full breeding season. Using this continuous behavioural data, I demonstrate that partial monitoring approaches can bias behavioural estimates relative to those derived from continuous datasets by simulating the most common monitoring designs identified in the literature. Finally, by continuously monitoring multiple jackdaw pairs from nest building through incubation to offspring provisioning, I show how biparental care changes within and across breeding stages. I further show that additive metrics of care (e.g., whether at least one parent is present), can obscure biologically meaningful differences among pairs in how care is temporally organised, which become apparent when considering joint attendance (i.e. the simultaneous presence of both parents).

Taken together, this thesis demonstrates the value of continuous monitoring for understanding parental care as a dynamic process structured over time. It provides new empirical insights into how biparental care varies across breeding stages and among pairs, highlights the importance of how behaviour is measured and sampled, and offers a practical framework for long-term behavioural monitoring in the wild.

Acknowledgements

Han passat moltes coses durant aquests últims anys de la meua vida, des que vaig decidir embarcar-me en el repte de la tesi doctoral. Miro enrere, amb perspectiva, i em fa feliç veure que he pogut dedicar tot aquest temps a fer una cosa que m'apassiona, a formar-me professionalment i, sobretot, a créixer una mica més cada dia. Moltes persones han format part d'aquest viatge i res d'això hagués estat possible sense el suport, ajuda i companyia de moltes d'elles.

Dani, vas confiar en mi des que vaig entrar al teu despatx fa uns anys per les pràctiques de grau. Vas obrir-me les portes al projecte de la gralla i em vas permetre conèixer què és el que volia fer en un futur. Des de llavors, durant tots aquests anys, has apostat sempre per la meua formació com a científic i t'has esforçat en fer-me pensar. M'has donat la llibertat per explorar les meves inquietuds i he entès que la ciència és tenir curiositat i motivació per entendre allò que no entenem. Tot i que aquesta llibertat m'hagi portat alguns bloquejos mentals i una mica d'estrès a vegades, t'agraeixo molt que m'hagis transmès aquesta visió de la ciència en una actualitat científica on sembla que només importi la producció d'articles. De tot cor, gràcies.

Jolle, sempre he sigut una mica hacker, però mai hagués arribat a fer el que hem aconseguit fer en aquest projecte si no fos pel teu acompanyament constant i la teua supervisió. No puc imaginar-me aquesta tesi sense tu. Gràcies per transmetre'm la teua passió, per introduir-me al món dels Raspberry Pi, per promoure la meua creativitat i per ensenyar-me a gaudir del procés. Admiro la teua capacitat descomunal per veure alternatives a totes les situacions desfavorables, sempre amb una visió constructiva de les coses i amb una actitud juganera cap a la feina, i cap a la vida. Estic eternament agraït pel teu suport, per la teua disposició i per obrir-me els ulls cada vegada que m'he encallat durant aquests anys. Gràcies per ser un gran mentor, per la part professional i per la part personal. Ets un gran amic. Et desitjo el millor futur a Catalunya, a tu, a la Sophie i a la meravellosa família que teniu. A tots dos, Dani i Jolle, he après molt de vosaltres i espero poder seguir treballant junts molts anys més!

Les llargues campanyes de camp a Lleida van començar amb tu, Mar. Penso en tu cada vegada que entra un nou estudiant de pràctiques i m'adono de la paciència que vas tenir amb mi. Tot això també és mèrit teu. Aina, has estat una peça clau pel meu creixement i la meua evolució durant la tesi. Ets una lluitadora i res t'enfonsa, gràcies pel teu suport i per totes les converses que m'han

ajudat a mantenir la motivació per fer les coses ben fetes. He tingut molta sort de trobar-te a tu, i a en Yuri de rebot! Gràcies per tots els consells i per la vostra amistat!

Totes les hores al camp s'han fet més fàcils amb vosaltres, Aina, amb la Laura i l'Ale, i ara també amb en Francis. Gràcies per totes les vegades que heu hagut de desconnectar cables amb videotrucada i remenar els RPi quan jo no hi era. També formeu part d'aquesta tesi! Guardo molt bons records tots junts al camp, tantes hores al cotxe compartint música i reflexions, i tantes hores cuinant a Mas de Melons... ho trobaré a faltar. Endavant amb les vostres tesis!!!

No sé què haguéssim fet sense el suport de Mas de Melons, d'en Jose, en Sebastià i de tot l'equip. Però especialment a tu, Lluís. Sempre amb un somriure, disposat a ajudar amb el que calgui. Gràcies per fer-nos la feina una mica més fàcil! També als “gralleros” del CTFC, Gerard, Carlos, Francesc i David. Gràcies per facilitar la burocràcia sempre que ha calgut i per compartir la vostra experiència amb mi! També dono gràcies a totes les converses amb vosaltres, Ferran, Laura, Lica, Oriol, Joan... Ha estat genial poder compartir aquest temps amb vosaltres durant la tesi. Molta sort amb els vostres projectes!

Malgrat haver dedicat molt temps al camp i al “teletreball” (soldant electrònica al meu taller i connectant cables a plaques solars i bateries de cotxe per dissenyar una instal·lació elèctrica solar, muntant caixes niu i dissenyant trampes automàtiques per capturar gralles), estic molt agraït d'haver-me creuat amb totes les grans persones amb qui hem compartit passadís durant aquests anys. Al CREAF sempre hi ha bon ambient. He treballat molt, però també he tingut temps per gaudir amb companys del CREAF. M'enduc molts bons records del despatx -150 amb en Víctor, en Fer, l'Anaïs, en Javi, la Xin, l'Eladio, en Filipe, Ruo Chen i molts més que hi han anat passant. Els riures entre passadissos, l'hora de dinar i els cafès, i els llegendaris “Juernes” a l'Irish amb la Susana, en Xavi, Carlos i Alba, en Gonzalo, els Jordis, en Mati, la Cinta, en Marc, en Luca, la Brenda, la Lucia, en Dani, en Ruben, i molts més noms que no m'hi caben en una pàgina. Gràcies per tots els moments junts, per escoltar i per compartir. Gràcies a la meva comissió de seguiment pel seu suport i els seus comentaris sempre positius, Sergi, Pilar, Enrique i Lluís.

During my last year I've been very welcomed in the ABEClab, thanks to Jolle, Jacob, Jesús and all the master students, Amanda, Milan and Anna. I'll really miss our annual hiking sessions! Però al CEAB també m'han acollit grans persones com si fos un més del centre: Dani, Txell, Fede, David, Pol i molts més, gràcies per escoltar les meves xerrades tan sovint, per mostrar sempre un gran interès en el meu projecte i per tots els vostres consells i comentaris. Us desitjo el millor!

I remember my days in Falmouth as a big highlight of my thesis. I had an amazing time with you Alex, Guill, Jordan, Tristan and specially Luca. Thank you all for being so welcoming and making my time there so enjoyable and productive. I'm really looking forward to seeing you soon in coming conferences!

Estic molt agraït pel finançament que he aconseguit del Departament de Recerca i Universitats de la Generalitat de Catalunya per fer la tesi, a en Dani per l'extensió del meu contracte durant un temps extra i poder acabar la tesi amb condicions, i per les beques per anar a congressos internacionals de l'Association for the Study of Animal Behaviour (ASAB) i la International Society for Behavioural Ecology (ISBE).

Poder combinar la tesi amb el SEMICE ha estat una mica complicat a vegades. M'ha costat molt fer un pas al costat per continuar la meva carrera científica, perquè al Museu de Ciències Naturals de Granollers sempre hi he trobat una família. Sou molt humans i un entorn així costa molt de trobar. Marc, Lúdia, Ignasi, Oriol, Carme, Adrià, Carmeta, Maria, Laura, David, Eric, César i molts altres... Gràcies per fer-me sentir com a casa i per tot el vostre suport durant aquest temps. Tot i que potser vindré a fer algun futbolí de tant en tant, us trobaré a faltar!

Gràcies a la Janis per escoltar totes les meves històries sobre les gralles i els micro-ordinadors sense perdre la paciència. Gràcies per fer-me costat sempre durant tot el procés i fer-me riure quan ho he necessitat. Gràcies Roger, perquè malgrat la distància sempre t'he sentit a prop. També a la Martina, Tomeu, Gina, Uri, Baixas, Sergi, Alma, Trini, Amanda, Nicu, Carles, Altí, Laia, Berta, Eloi, i a la llista de noms interminable d'amics que m'han fet agafar forces sense saber-ho quan ho he necessitat. Em sento molt afortunat de tenir-vos al meu costat!

Tot això va començar de petit. Al Montseny, a casa, amb la família. L'estima per la natura és una cosa que s'aprèn, i jo l'he après de vosaltres, pares. Gràcies per transmetre'm la vostra passió pels animals i per permetre'm sempre triar el camí que he volgut, amb el vostre suport incondicional. No seria on soc sense vosaltres i us estic eternament agraït. També a tu, Arnau. Ets el meu exemple en moltes coses i, gràcies a tu, els ocells van entrar a la meva vida. Totes les hores dedicades a la fotografia junts, al hide del camp d'en Pere o al delta, han fet créixer la meva curiositat i la meva passió pel comportament animal. T'admiro i t'ho agraeixo. També a tu, Tuli, per mostrar-me el camí d'entrada cap a la ciència. Ets un gran exemple a seguir, no perdis mai els teus principis!

I tu, Núria, ets el pilar que m'ha aguantat cada vegada que m'he enfonsat. Has cregut en mi sempre i has confiat en mi inclús quan jo en tenia dubtes. Gràcies per aguantar els meus horaris tan inestables, que depenen del treball de camp o de la meva inspiració fins les tantes de la nit. Gràcies

per forçar-me sovint a sortir del bucle laboral i fer-me connectar de nou amb la vida (encara que a vegades em costi una bona estona adonar-me'n!). Gràcies per recolzar-me absolutament amb tot i per fer-me sentir que no estic sol, perquè sempre et tinc al meu costat. La nostra vida ha donat moltes voltes durant aquest procés, però no m'imagino cap altra vida. Ara tinc ganes de veure cap a on ens porta el futur, el nostre futur, junts.

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Chapters 2 & 4

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Chapter 3

Pou-Rossell, M., Sol, D., & Jolles, J. W. (2025). A centralised multi-unit recording system for automated, off-grid animal observation and environmental monitoring. *Methods in Ecology and Evolution*, 16, 2335–2344. <https://doi.org/10.1111/2041-210X.70129>

Chapter 5

Pou-Rossell, M., Sol, D., & Jolles, J. W. Temporal dynamics of biparental care across the full breeding cycle in wild jackdaws. *Manuscript in preparation*.

Chapter 1

General introduction

Animals constantly make decisions that shape their survival and reproduction. One of the most consequential decisions animals face is how much care to invest in their young. By devoting time and energy to raising offspring, often while being exposed to risks, parents can dramatically increase offspring survival, but frequently at the cost of reducing their own condition, survival, and future reproduction. These trade-offs make parental care a central topic in behavioural ecology, linking *what* animals do to *why* they do it, and asking *how* behaviour is shaped by constraints and *how* it evolves.

Parental care shows enormous diversity across animals. In many species, particularly most invertebrates, offspring receive no care beyond the nutrients initially provided in the egg. In other species, however, parents actively improve offspring survival by protecting them from predators, food limitation, parasites, and other hazards. Mammals and birds are familiar examples, as they often provide complex forms of care before and after birth or hatching, including embryo nourishment, defence, brooding, and food provisioning. Yet parental care is also present in amphibians, reptiles, fishes, arthropods and other invertebrate groups. The expression of parental care is also extraordinarily diverse across species, ranging from minimal attendance to prolonged, energetically demanding care by one parent, both parents, or even additional group members in cooperative systems. This variation has made parental care a central topic in evolutionary biology, with relevance to life-history evolution, sexual selection, social behaviour, and family conflict and cooperation.

Parents may differ in their optimal level of investment depending on their sex, condition, mating opportunities, certainty of parentage, and expected future reproduction, generating conflict over who should provide care and how much. At the same time, care decisions are constrained by ecological factors such as predation risk, food availability, weather, and the timing of reproduction in seasonal environments. In species breeding under narrow seasonal windows or unpredictable conditions, parents must continuously adjust care to changing circumstances while balancing current offspring demands against self-maintenance and future breeding opportunities. Understanding parental care therefore requires integrating evolutionary theory with the temporal and physiological constraints under which behaviour is expressed.

Parental care is inherently dynamic. Rather than a fixed trait, it involves a variety of behaviours expressed over extended periods of time, often across days or weeks, and shaped by changing reproductive needs and environmental conditions. The form and amount of care can vary across an individual's lifetime, among breeding attempts, within a single breeding season, and even

within the same day. For example, parental effort may shift across breeding stages as offspring develop and their needs change, or as the relative contributions of carers are renegotiated. Fine-scale fluctuations can also emerge in response to temperature, rainfall, predation risk, food availability, or partner behaviour, producing short-term variation in how care is provided. Capturing parental care as a dynamic process is therefore essential for understanding how parents adjust their investment through time under changing constraints, but also how it translates into reproductive consequences.

To build a complete picture of parental care, one would ideally follow parents continuously throughout the entire reproductive cycle. This monitoring should involve many pairs and be carried out at a temporal resolution fine enough to capture within-day fluctuations. Such an approach would allow us to observe not only how much care parents provide, but also how they distribute effort over time, how they adjust to offspring needs, and how they respond to their partners and the environment. In most field studies, however, achieving this level of temporal coverage is challenging. Breeding sites are often remote, and limited personnel time, logistical and technological constraints, and the need to minimise disturbance typically force researchers to rely on partial and temporally restricted sampling. As a result, key behaviours are often sampled unevenly, limiting our ability to understand how parental decisions change through time.

My thesis tackles this gap by combining methodological, technical, and empirical approaches to better capture the temporal dynamics of parental care. It integrates a review of existing approaches, the development of an automated monitoring system for continuous, long-term recording in the wild, and the collection of high-resolution data from of a colony of wild jackdaws (*Corvus monedula*) monitored across the entire breeding season, from nest building to fledging. Together, these components provide a framework to study parental care as a temporally structured process.

This introductory chapter lays the conceptual and methodological foundations of the thesis. I frame parental care as a dynamic, multi-layered process shaped by trade-offs, social interactions, and temporal constraints. I then review common approaches for quantifying animal behaviour and explain why many standard methods struggle to capture fine-scale temporal dynamics. Finally, I summarise the key gaps addressed in this thesis, provide an overview of the chapters, and introduce the jackdaw study system and monitored breeding population.

1.1 The multiple layers of parental care

Parental care is commonly defined as any behaviour performed by a parent aimed at increasing the survival and future reproductive success of one's offspring (Clutton-Brock, 1991; Royle et al., 2012; Stearns, 1976; Trivers, 1972; Williams, 1966). The term *parental investment* additionally includes the costs to the parents in the equation, defined by Trivers (1972) as 'any investment by the parent in an individual offspring that increases the offspring's chance of survival at the cost to the parent's ability to invest in other offspring'. The broad functional definition of parental care has been highly productive in behavioural ecology, but it also raises important conceptual questions. For example, whether a behaviour qualifies as parental care may depend on how we define both care and parent: is a parent necessarily a genetic parent, or can it be a social parent, helper, or host individual caring for unrelated young, as in brood parasitism? Likewise, if parental care is tied to offspring, when does it begin? Only after hatching or birth, or already during nest building, egg formation, incubation, and other pre-hatching investments that directly affect offspring development and survival? These questions are not merely semantic, they shape how care is measured, compared across species, and interpreted in relation to theory.

In birds, parental care encompasses a wide range of behaviours spanning multiple reproductive stages, from nest construction and warming the eggs during incubation to extensive post-hatching investment through provisioning, brooding, and protection against predators and harsh weather. Such care is particularly important in altricial species, whose young hatch in a relatively helpless state and depend heavily on adult investment until fledging, and often well beyond departing the nest (Mock, 2022). Because parental care can be costly in time and energy, a large literature has examined how parents adjust investment in response to reproductive demands (e.g., clutch size and brood-size manipulations; Gow et al., 2013), environmental conditions (e.g., experimentally increased predation risk; Hua et al., 2014) and parental state or condition (e.g., manipulations of workload or condition, including partner removal or wing clipping; Mainwaring & Hartley, 2020; Serota & Williams, 2019).

Across species, parental care is organised in different care systems, including no post-hatching care, uniparental care (maternal or paternal), biparental care, and cooperative care, and the identity of the main carer may also change across breeding stages. These systems differ in how the costs and benefits of care are distributed, but all involve fitness trade-offs between parental investment and opportunities for self-maintenance, survival, and future reproduction. They also generate potential conflicts at multiple levels, including parent–offspring conflict (because offspring may

benefit from more investment than is optimal for carers) and, where care is shared, conflict among carers whose fitness interests overlap but are not identical (Royle et al., 2016; Trivers, 1972, 1974). In cooperative breeders, for example, care decisions may additionally be shaped by relatedness, dominance, and group stability (Adams et al., 2015; Remeš et al., 2015). Together, these perspectives suggest that parental care is not simply the sum of two (or more) individual efforts, but a pair-level (or group-of-carers-level) process emerging from repeated behavioural adjustments across time, throughout the different stages of the breeding season, highlighting the extensive challenges of quantifying parental investment.

Plasticity of parental care

Given the broad temporal coverage of parental care, we expect some plasticity in the way parents make decisions along the breeding cycle, shifting their investment rapidly with changing conditions. At shorter time scales (within days or across days within a breeding stage) parents may adjust behaviour rapidly as local conditions change. Indeed, evidence suggests that that animals provide parental behaviour changes in response to individual condition, brood demand, partner behaviour, food availability, predation risk and weather (Arct et al., 2025; Caro et al., 2025; Johnstone & Hinde, 2006; Matysioková & Remeš, 2018; Wilson & Nussey, 2010). Decisions are also expected to change substantially at larger time scales (across the breeding season) because the functions and constraints of care are different in each stage (Mock, 2022). Investment begins with decisions about when and where to breed and how much to allocate to nest construction, followed by stage-specific trade-offs such as maintaining incubation constancy while meeting self-maintenance needs, balancing brood care with provisioning after hatching, and whether to prioritise offspring quality or quantity (e.g., brood reduction strategies; O'Connor, 1978). Consequently, parental care is constrained differently at different stages and changes through time as the reproductive cycle progress. Finally, parental behaviour can also vary in consistent ways among individuals and pairs at longer time scales (across breeding attempts), some tending to invest more than others in caring for their offspring. However, such differences are not necessarily stable across contexts, as the same parent may show different investment patterns when paired with different partners, under different environmental constraints or as an individual's state changes across the lifespan (Hammers et al., 2021; Magrath et al., 2007; Meade et al., 2011)

Capturing the temporal dynamics across the breeding season is important because different breeding stages contribute to reproductive performance in different ways, and global summaries

of parental care can conceal that stage-specific complexity. Reproductive success is often reported as the number of fledglings produced, or as offspring condition at fledging. However, processes operating early in the breeding attempt, such as nest construction and incubation, can also influence later outcomes through carry-over effects. For example, they may shape hatching success and initial brood size, which in turn may affect early chick condition (Mueller et al., 2019). If parental care patterns differ across stages, similar overall breeding outcomes may emerge through different combinations of stage-specific investment. Conversely, focusing only on late-stage measures risks underestimating variation across individuals and pairs, understating the fitness relevance of early-stage behaviour, and overlooking how early decisions may constrain or facilitate parental performance later in the season.

Distribution of biparental care

In biparental systems, each parent may benefit if the partner contributes more, yet both risk reduced fitness if total care falls below that what offspring require. Theory on negotiation and compensation proposes that parents may adjust their effort in response to the effort of their partner, often resulting in partial compensation or conditional decision rules shaped by information and constraints (Hinde & Kilner, 2007; Johnstone et al., 2014; Johnstone & Hinde, 2006). Parent-offspring conflict can further modulate these dynamics, as offspring benefit from higher levels of investment than are optimal for parents, and offspring signals may alter the provisioning responses of carers (Burford et al., 1998; Moreno-Rueda et al., 2009; Tarwater et al., 2009). Hence, reproductive success depends not only on how much care is delivered, but also on how partners coordinate their contributions.

The behaviour expressed by each parent is shaped not only by its own state, but also by the strategy of its partner and the interaction dynamics between them (e.g., responsiveness to partner effort; Hahn et al., 2025; Hinde, 2006). The distribution of care between carers is especially relevant in socially monogamous species with strong pair bonds and repeated breeding, where partners may benefit from stability, cooperation, and mutual predictability (Griffith, 2019; Hahn et al., 2025). Moreover, when the demands of offspring rearing exceed the capacity of a single parent, the loss or removal of one parent can lead to partial or complete breeding failure (Iserbyt et al., 2019; Mariette & Griffith, 2015), highlighting the fitness consequences of effective biparental care.

However, parental care is still often conceptualised as additive effort, quantified as the total care provided by both parents combined (e.g., summed provisioning visits, total brooding time, or overall nest attendance). While such measures are informative, they can overlook a key dimension

of biparental care: how partners organise their effort relative to each other across time and tasks. Pairs may coordinate through synchronisation (arriving together or overlapping in nest-related activities), alternation (taking turns in provisioning or incubation-related roles), or division of labour (consistent specialisation across tasks, contexts, or times of day). Crucially, different coordination patterns can have distinct functional consequences even when total care is similar, by affecting efficiency, exposure to predation, information exchange, or the balance of costs between partners (Johnstone & Hinde, 2006; Royle et al., 2012). These considerations suggest that selection may act not only on individual parental effort, but also on the pair's behavioural organisation as a cooperative unit (Björklund & Gustafsson, 2013). Yet explicit quantification of coordination strategies, particularly how they shift across breeding stages as constraints and benefits change, remains largely unexplored due to methodological limitations that hinder continuous monitoring.

1.2 Methods used to quantify parental care

Recognising parental care as dynamic and stage-dependent, one would require behavioural data with sufficient temporal coverage to capture within-day variation, stage transitions, and repeated interactions between carers. Advancements in our understanding of how parental care unfolds through the breeding season directly depends on how well we can observe and quantify behaviour through time. This makes methodology a limiting step in many systems. The following section reviews the main approaches used to quantify parental care and discusses why common sampling designs often struggle to capture fine-scale temporal dynamics in wild populations.

The foundation of behavioural ecology is direct observation. Classic field studies relied on prolonged nest watches and focal follows, with researchers recording behavioural events by hand alongside contextual information on weather, predators, food availability, and social interactions. Such observations remain invaluable for interpreting behaviour, generating hypotheses, and detecting patterns that may be missed by automated systems. However, traditional observations face constraints that are especially limiting for parental care research. Observations are often restricted to specific hours of day, under favourable weather conditions and they are very labour intense, which significantly reduces temporal coverage, limits sample sizes and can bias monitoring towards accessible nests or convenient periods. Standardising protocols across observers also requires extensive training, and even with careful standardisation, observer effects and differences in detectability can introduce measurement error (Naguib et al., 2023). These

limitations are not merely logistical: when parental behaviours show strong temporal structure (e.g., diel rhythms in provisioning or stage-specific changes in attendance; Corbani et al., 2014; Kidd et al., 2015; Knapton, 1984), restricted sampling windows can systematically influence behavioural estimates and the biological conclusions drawn from them.

Technological approaches have greatly expanded the range of parental care metrics that can be quantified and improved the temporal resolution at which behaviour can be monitored in the wild. Bio-logging devices such as GPS loggers and accelerometers are especially valuable for quantifying how parental care interacts with space use and effort away from the nest, for example by characterising foraging trips, time budgets, and activity patterns that reflect energetic expenditure during different breeding stages. Proximity loggers and emerging technologies such as network-based tracking (e.g., crowd-sourced beacon networks; Farine et al., 2024) can complement this by capturing patterns of association and co-attendance, which may be informative for understanding the social context and help increase detection probability. These approaches are most powerful when the research focus is on movement, activity, or social interactions at broad spatial scales. However, they typically require capturing individuals and attaching devices, which may affect behaviour and compromise future reproductive success (Gillies et al., 2020). In addition, the durability of these loggers is constrained by their size and battery life, limiting their use in smaller species or when long-term, high-resolution sampling is required.

For parental care at fixed reproductive sites, Radio Frequency Identification (RFID) systems using Passive Integrated Transponders (PIT tags) provide a widely used alternative (Bonter & Bridge, 2011; Iserbyt et al., 2018). PIT-tag setups at nest entrances can record individual visit events at very high temporal resolution, making them particularly useful for quantifying provisioning rates, parental visit schedules, and diel patterns in nest attendance. While PIT tags are comparatively small and can be less intrusive than heavier loggers, RFID typically records detections within a limited antenna field rather than continuous behaviour, so additional assumptions or complementary sensors may be required to infer time spent inside the nest, incubation bout structure, or fine-scale interactions between carers and offspring

Finally, image-based monitoring (e.g., trail cameras, CCTV, and nest-box cameras) can collect long time series with rich behavioural detail, including incubation posture, brooding, prey deliveries, partner exchanges, and interactions that are difficult to infer from event-based detections (Cox et al., 2012; Gunn, 2022; Sabine et al., 2005). Recent advances in automated

recording systems increasingly allow these datasets to be collected and processed at scales that were previously not feasible. However, automated monitoring is often constrained by power requirements, data storage, and the substantial effort required for video processing and annotation, particularly when high temporal resolution is required. Recent advances in computer vision now provide an efficient solution to process image-based data, reducing reliance on manual annotation while retaining behavioural richness. Hence, for questions that require continuous, long-term monitoring across breeding stages at fine temporal resolution, these automated image-based approaches provide a particularly promising route.

Across these approaches, a persistent trade-off is that methods that are non-invasive and scalable often provide limited behavioural detail, whereas methods that capture rich behavioural context are difficult to sustain across long periods, breeding stages, and multiple nests. In addition, these systems are often costly, further limiting the feasibility of large-scale, intensive monitoring. Together, these constraints help explain why continuous, fine-scale monitoring across entire breeding seasons remains uncommon, despite its importance for understanding the temporal dynamics of parental care.

1.3 The persistent challenges of behavioural inference

A central motivation for this thesis is that behavioural metrics are often presented as direct estimates of parental care, but in practice they are typically inferred from incomplete and uneven samples that may incorrectly represent parental behaviour. Even when behaviour is recorded directly (e.g., by observation or video), sampling is often temporally restricted. Studies may report the same metric (e.g., nest attendance), yet differ substantially in observation duration, time of day, and number of sessions, despite parental behaviour being structured in time. Such uneven sampling can increase noise (imprecision) and bias behavioural estimates (systematic error) if monitored periods are not representative of the underlying behaviour. A second challenge is that modern technologies often measure proxies for behaviour rather than behaviour itself (e.g., detections at an antenna, movement signatures, or visual classifications of an action), so inference also depends on how observations are translated into behavioural states. These challenges imply that robust parental care research requires explicitly linking behavioural questions to sampling decisions and assumptions, and quantifying how these choices shape the estimates used for biological inference. While both issues remain important, the main focus of this thesis is on the

methodological problem of temporal under-sampling and how it can distort behavioural estimates and the inferences drawn from them.

Several studies have highlighted the limitation of short or selective observation windows (Brereton et al., 2022; Lendvai et al., 2015; Margulis & Westhus, 2008; Schwagmeyer & Mock, 1997), but there has been no quantitative overview of how parental care is currently measured across contemporary studies. Without such an overview, it is difficult to assess the representativeness of prevailing approaches, identify systematic gaps in temporal coverage, or determine where improved reporting standards would most strengthen comparability. Moreover, the scarcity of continuous reference datasets has precluded a systematic evaluation of how methodological decisions translate into bias and uncertainty in parental care estimates. Because fine-scale continuous datasets remain rare, the temporal dynamics of parental care within and across breeding stages are still poorly described. Improving temporal coverage would help move beyond static summaries of ‘investment’ towards a dynamic view of parental decision-making, strengthening links between behaviour and fitness across reproduction. Recent technological advances now allow these gaps to be addressed for the first time, enabling continuous, long-term, and synchronous monitoring of multiple individuals or pairs in wild populations.

1.4 Thesis outline

My thesis aims to first identify common approaches to quantify parental care in the literature and to develop and apply a flexible approach for continuous monitoring of parental care (and other applications beyond parental care) to overcome the shortcomings of partial sampling. I then use this system to collect a continuous dataset on wild jackdaws (*Corvus monedula*) to test how selective sampling affect behavioural estimates when compared to continuous monitoring. Finally, I describe the temporal changes in parental care across the breeding season in this system. Even though this thesis is presented as a collection of papers, the work that originally formed a single manuscript has been divided into Chapters 2 and 4 to improve the logical chronology of the dissertation. This structure allows the thesis to separate more clearly the descriptive overview of current methodological practices from the empirical assessment of how those practices affect behavioural estimates after describing the methodological approach to collect such continuous dataset.

In **Chapter 2**, I aim to identify common practices in avian parental care quantification. I start by providing a quantitative assessment of how parental care is measured in contemporary avian

studies. I review and classify the main methodological choices made across the literature (e.g., which breeding stages are monitored, observation durations, time-of-day coverage, and what behaviours are quantified). I discuss their limitations, highlight sources of limited comparability across studies and propose a practical reporting framework to improve transparency and reproducibility.

Chapter 3 forms the methodological core of this thesis. I describe the automated monitoring system that I developed to acquire continuous, long-term data on parental care in the wild, based on Raspberry Pi single-board computers combined with computer vision algorithms. As a proof of concept, I deployed the system in a jackdaw colony over three years, which allowed me to evaluate and optimise power supply, data storage, maintenance, and data processing. The results confirm that the system provides a replicable and adaptable solution that supports high-resolution monitoring of multiple nests across the entire breeding season.

In **Chapter 4**, I use the continuous dataset to evaluate how selective monitoring designs influence estimates of parental care. I simulate sampling schedules that reflect common observation regimes identified in **Chapter 2**, and then compare the resulting behavioural estimates with those derived from continuous monitoring. This allows me to quantify when partial sampling yields robust inference and when it is likely to introduce bias or noise.

In **Chapter 5**, I truly use the full depth of the continuous dataset to characterise the temporal structure of parental care and how it shifts across the breeding season. Focusing on stage-specific dynamics, I quantify overall parental nest attendance and distinguish it from biparental simultaneous attendance across nest construction, incubation, and provisioning. I first describe how attendance patterns shift across breeding stages, quantify among-pair variation and the consistency of pair strategies through time. The aim is to provide a comprehensive assessment of how nest attendance is structured across reproduction and identify when additive measures of parental care may obscure meaningful variation on how care is distributed within the pair.

In **Chapter 6**, I summarise the main conclusions of the thesis, discuss limitations, and outline directions for future work.

1.5 Study species and general approach

Birds provide an exceptional system for studying parental care because parental care is often prolonged, behaviourally diverse and structured in clear breeding stages, spanning nest

construction, incubation, and post-hatching offspring care. Many species exhibit biparental care, creating opportunities to examine how carers allocate their effort across time and how it relates to reproductive performance. I focused on the Western Jackdaw (*Corvus monedula*) as my study species, an intelligent bird with a bi-parental care strategy, particularly well suited to these questions.

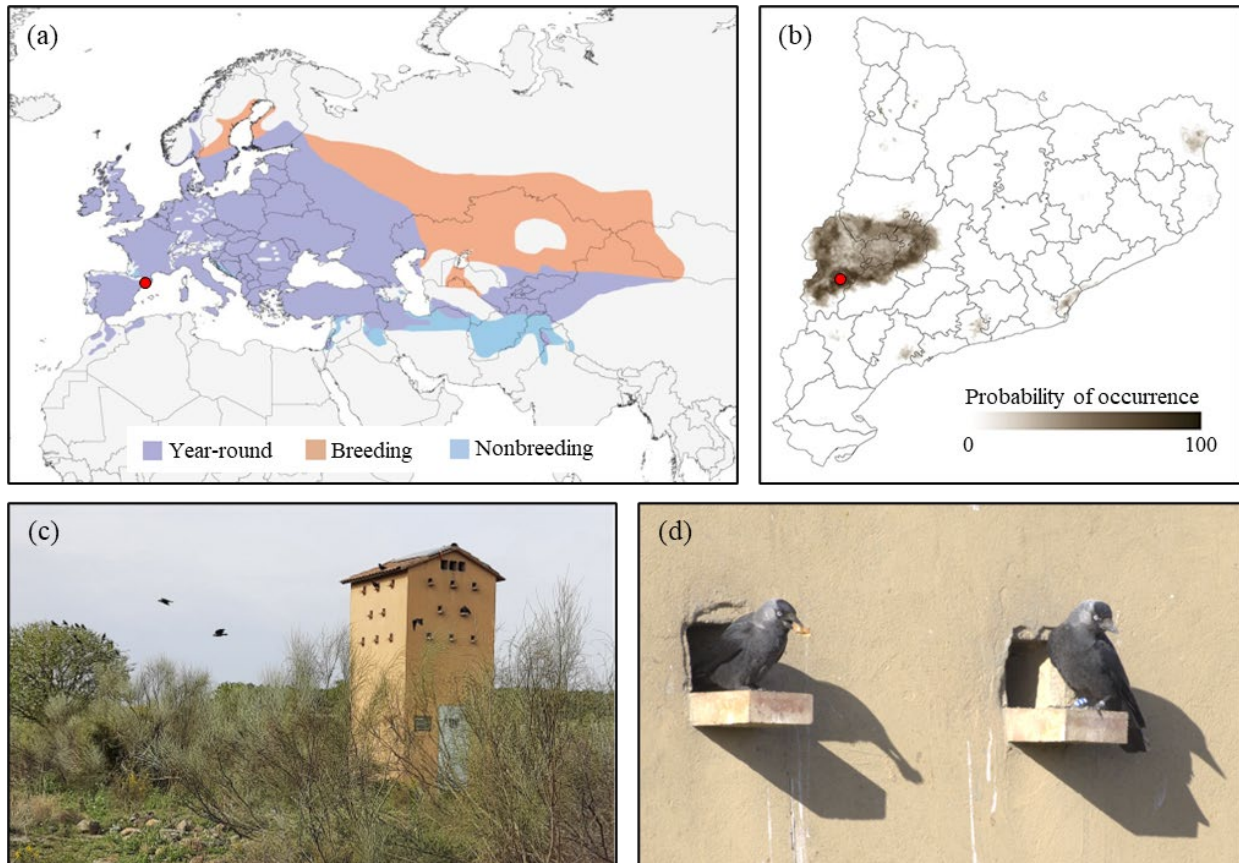


Figure 1.1 Study system and species. (a) World distribution of the study species, the Western jackdaw (*Corvus monedula*), as of 2024 (Madge & de Juana, 2024). (b) Distribution of the species in Catalonia based on records from 2015–2018 (ICO, 2026). Red dots locate the nesting tower this thesis is focused on, shown in (c). (d) A close-up photo of two marked individuals in two neighbouring nests in the focal tower.

The Western Jackdaw (hereafter jackdaws) is a small corvid widely distributed across Europe, extending into western Asia, with some occurrences as well in northwestern Africa (Fig. 1.1a; Madge & de Juana, 2020), occupying a broad range of open and semi-open habitats, including farmland mosaics, woodland edges, villages, and urban areas. Jackdaws are highly social, and outside the breeding season form large flocks and communal winter roosts that may include thousands of individuals (Dibnah et al., 2022; Jolles et al., 2013). During the breeding season, they typically nest in colonies and form socially monogamous pair bonds that are often maintained

across years, breeding in cavities such as crevices, buildings or nest boxes (Henderson et al., 2000; Röell, 1978). Jackdaws' remarkable intelligence and behavioural flexibility have made them an attractive model for studies of cognition and behaviour (Arbon et al., 2023; Dibnah et al., 2022; Greggor et al., 2016; Kings et al., 2023).

In Catalonia, NE Spain, the species is currently classified as “Vulnerable” due to local declines associated with anthropogenic habitat alteration (García & Blanco, 2023). In western Catalonia, however, the species is doing well in part thanks to conservation actions that increase cavity availability, including the installation of artificial nest boxes and nesting towers across the landscape (Figs. 1.1b–c). This thesis draws on a long-term monitoring programme of jackdaws breeding in these towers, located in an agricultural landscape in the province of Lleida. Each tower contains ~30 nestboxes of similar structure and building materials, which facilitates repeated, standardised monitoring across years. The behavioural data analysed in this thesis come from continuous monitoring deployed in one focal tower, *Roca Guilla*.

Since 2015, these towers have been monitored every breeding season and detailed fitness-related data acquired, including for each breeding attempt the laying date, clutch size, hatching dates, brood size, fledging date, and chick condition at standardised ages, while banding both adults and fledglings every year (Fig. 1d). This dataset shows that jackdaws typically produce a single brood per year; clutch size is typically around 4–5 eggs, with incubation performed mainly by the female and lasting roughly ~19–22 days on average (varying among nests and years), and altricial nestlings remain in the nest for ~32–35 days before fledging. As cavity nesters that readily breed in nest boxes, jackdaws are particularly well suited to the aims of this thesis, allowing continuous monitoring with minimal disturbance and standardised conditions across nests. Moreover, as long-lived, socially monogamous birds with stable pair bonds and biparental care with clear sex-specific roles across breeding stages (Hahn et al., 2021; Kings et al., 2023; Lockie, 1955; Röell, 1978), this species provide excellent opportunities for investigating temporal dynamics of parental care not only as total pair effort, but as a pair-level behavioural organisation.

Chapter 2

Parental care in passerine birds: a review of sampling methods

Abstract

Parental care, defined as any parental behaviour aimed at improving offspring survival, is a central topic in evolutionary ecology. Accurately quantifying parental care is essential for understanding variation in parental investment, yet current methodological approaches are highly variable and often rely on limited sampling across reproductive stages. Despite decades of research and important technological innovations facilitating wildlife monitoring, many studies still rely on short observation periods, selective sampling times, or observations during limited breeding stages. Despite important progress, there is still no consensus on best practices for monitoring parental behaviour. To address this gap, we first reviewed recent empirical studies on avian parental care to identify typical sampling designs, behavioural metrics used, and reporting practices. Our results highlight that parental care has been quantified notably partially across the breeding season: mainly in the morning, for two to three hours during two to three days, mainly during the offspring provisioning stage, while other stages of the breeding season are largely overlooked (nest building, incubation, post-fledging). Our results also highlight a lack of standardised protocols or guidelines for monitoring parental behaviour in birds, resulting in substantial variation in sampling designs, observation durations, and reporting detail. While some convergence exists, such as a common focus on morning observations over two to three days, heterogeneity in methods remains high, posing challenges for replication and comparisons across studies. Emphasising the need for greater methodological transparency, we propose a reporting checklist with key considerations to encourage more consistent and comprehensive reporting of study design.

2.1 Introduction

Parental care, defined as any parental behaviour that enhances offspring survival at a cost to the parents' future reproduction (Clutton-Brock, 1991; Royle et al., 2012), is a major determinant of reproductive success. Across animals, parental care can occur before offspring are born, during early development, and until independence, from incubation and provisioning to protection and teaching (Clutton-Brock, 1991). Its expression is remarkably diverse, from species that provide no care, such as many reptiles, to those with prolonged biparental or cooperative care, such as some mammals and many birds. By linking parental investment directly to fitness outcomes, research on parental care has shaped foundational theories such as parent-offspring conflict (Trivers, 1974) and inclusive fitness (Hamilton 1964a,b), and has illuminated the trade-offs between current and future reproduction (Clutton-Brock, 1991; Royle et al., 2012; Stearns, 1976; Trivers, 1972; Williams, 1966). Parental behaviour is therefore considered as a cornerstone for understanding the evolution of life histories and mating strategies.

Given its central importance, it has been a longstanding goal in the fields of behavioural and evolutionary ecology to understand how and why the amount, timing and type of care provided varies within and across species (Clutton-Brock, 1991; Klug & Bonsall, 2010; Stearns, 1976; Trivers, 1972). Empirical work has shown that current diversity of parental strategies reflects the conflict between parents and parents-offspring over optimal investment, shaped by offspring dependency, environmental hazards, and life-history constraints (Clutton-Brock 1991; Westneat and Sherman 1993). Despite important theoretical and empirical advances, accurately quantifying parental care in wild populations remains challenging. Continuous, non-invasive observation across the full reproductive cycle is therefore rarely feasible, and most studies rely on short, selective observation windows. In many cases, this is not simply a logistical compromise, but a design choice aligned with the specific biological question being asked. For example, studies interested in the trade-off between nestling provisioning and parental self-maintenance may justifiably focus on the stage when offspring demand is highest, whereas studies of incubation behaviour or nest construction may target entirely different parts of the breeding cycle. Such targeted sampling can therefore be entirely appropriate and highly informative when it is matched to a clearly defined question. However, restricted sampling comes with important limitations when researchers aim to estimate overall parental effort, in which case partial observation may introduce both random noise and systematic bias if the sampled periods do not adequately capture the temporal structure of behaviour. Moreover, parental care is not a unitary trait, but a suite of

dynamic behaviours that change across the breeding cycle and vary with environmental conditions, offspring needs, and the state of the parents themselves (Amininasab et al., 2016; Kulaszewicz et al., 2018; Simmonds et al., 2017). Thus, focusing on short, selective observation windows can miss biologically meaningful information.

Although several papers have discussed the limitations of short and selective observations (Brereton et al., 2022; Lendvai et al., 2015; Margulis & Westhus, 2008; Schwagmeyer & Mock, 1997), there has been no comprehensive, quantitative overview of how parental care is actually being measured in contemporary studies, and which methodological decisions are most commonly made. Without such an overview, it is difficult to evaluate the representativeness of prevailing approaches, identify gaps in temporal coverage, or determine where improved methods would most increase comparability across studies. A structured assessment of current practice is therefore necessary for (i) identifying heterogeneity and most common practices for parental care quantification, (ii) designing future studies that balance feasibility with robust behavioural estimates, and (iii) improve comparability across systems.

Here, we address this gap by assessing two decades of research on passerine birds, identifying common methodological practices, including the metrics used to quantify behaviour and the periods of the breeding cycle most frequently monitored, revealing substantial gaps in temporal coverage. As the literature in parental care is huge, we did not do an exhaustive systematic review of the literature, but rather randomly sampling the recent literature to illustrate common approaches currently used in the field. Passerines provide an ideal model, as their altricial offspring require extended care and their frequent use of nest boxes facilitates detailed, non-intrusive monitoring (Lambrechts et al., 2010). At the same time, even in nest-box systems, comprehensive monitoring can be logistically demanding, which makes them a useful case for understanding how researchers compromise between ideal sampling and field constraints. In addition, studies differ widely in the stages they monitor, the duration and timing of observations, and the particular behaviours they quantify, from incubation constancy and nest attendance to visit rate, prey delivery, or nest-building effort (Savage & Hinde, 2019). This methodological heterogeneity is often justified by the diversity of biological questions in the literature, but it also complicates comparisons across studies and can obscure true biological patterns. Our assessment therefore aims to describe methodological variation with sufficient resolution to identify prevailing practices, and to pinpoint where studies diverge most strongly in their design choices and reporting.

The goals of this study are threefold. First, we quantify the most common methodological approaches used to study parental care in cavity-nesting passerines, including the behavioural metrics used to represent parental effort, the temporal windows that are most frequently monitored, and key elements of sampling design such as the tools used for the observations. Second, we evaluate the extent of heterogeneity and incomplete reporting across studies, highlighting which methodological details are frequently omitted despite being essential for reproducibility and for meaningful comparison among studies. Third, building on the patterns identified in the review, we propose a practical checklist for standardised reporting of parental care methods. The purpose of this checklist is not to enforce a single “best” design, but to promote clarity about *what* was measured, *when* it was measured, and *how* sampling decisions were implemented, thereby improving transparency and comparability in future work on parental behaviour.

2.2 Methods

Literature selection criteria

We conducted a comprehensive literature search in Google Scholar and Scopus to identify empirical studies quantifying parental care in cavity-nesting passerines. To capture a broad range of terminology, we included variations of *parental care*, *parental workload*, *parental investment*, and *parental behaviour*, in combination with the terms *rate*, *attendance*, *quantif** and *visit**. This ensured selection of studies that quantified parental behaviour empirically, while excluding theoretical works and those focused solely on life-history traits (e.g., timing of reproduction, clutch size). We focused on cavity-nesting passerine birds as they represent a well-studied group in parental care research and are particularly amenable for such research because of their altricial offspring requiring prolonged care and minimally invasive monitoring in nest boxes. Accordingly, our search string was: ((“*Parental care*” OR “*Parental effort*” OR “*Parental behaviour*” OR “*Parental investment*” OR “*Parental workload*”) AND (“*Rate*” OR “*Attendance*” OR “*Quantif**” OR “*Visit**”)) AND (“*Passerine*” OR “*Nest box*” OR “*Nest-box*” OR “*Cavity*”).

After initial sorting and manual screening for empirical studies in Google Scholar we retained 100 papers for further inspection. Given that Google Scholar does not allow filtering by author-provided keywords, we relied on broad searches followed by manual screening. To ensure consistency, we replicated the search in Scopus using the same string but limited the selection to

papers that listed keywords such as *parental care*, *parental effort*, *parental investment*, *reproductive effort*, or *reproductive behaviour* to avoid those centred exclusively on specific breeding stages (i.e. incubation or provisioning). This Scopus search yielded 437 papers. After removing unpublished and duplicate works, as well as papers older than 20 years to reflect current methodologies, we obtained 403 unique studies between 2005 and 2024. From these, we randomly selected 100 for detailed review. After going through all 100 papers, we excluded studies lacking quantitative data on parental care (e.g., theoretical, review, or methodological papers), and those based on experimental manipulations (e.g., show a predator to increase risk perception and compare parental behaviour before and after perturbation). We also removed a few non-passerine studies missed in initial filtering, yielding a final set of 51 papers that we used to characterise methodological practices across study designs, observation protocols, and behavioural metrics.

In-depth assessment of selected studies

We quantified methodological approaches of the selected 51 studies by carefully going through the methods section of each paper using a list of predetermined metrics (explained below). When methodological details were incomplete, we consulted related papers from the same project cited for additional information when available. In these cases, we combined information from both sources while prioritising the data used in the focal paper's analyses if methods deferred (e.g., different sample sizes reported in the focal paper than in the citation). Here, we describe the different metrics extracted from each study during in-depth assessment, together with our considerations when extracting each metric (see Appendix A for the full dataset extracted; Table A.1).

Monitoring approach used for behavioural observation

For each paper we documented all monitoring approaches used to quantify parental behaviour, including indirect methods (e.g., temperature sensors to quantify incubation bouts with egg temperature oscillations). When multiple methods were combined, we selected the method providing more data as the main method (e.g., RFID working continuously but also video-recordings at some point, or many focal observations combined with few video-recordings).

Time of the day

We estimated the within-day time period during which parental care data were recorded by taking the maximum time range reported. Thus, when multiple observation lengths were used (e.g., two or four hours depending on the age of the chicks), we noted the maximum length of observations.

Likewise, when the observation period was reported as a range, we used the maximum observation duration stated (e.g., when the authors describe that they recorded data for one or two hours, starting at 0700–0900, we noted the schedule as 0700–1100). Several studies reported their monitoring times qualitatively (e.g., “morning”, “dusk” or “sunrise”) instead of providing time intervals. To ensure consistency, we standardised the time categories as follows: morning = 0700–1300; afternoon = 1400–2100; dusk = 0700; dawn = 2100; sunrise = 0800; and sunset = 2000.

Breeding stage period

From each paper we extracted the duration of the sampling (number of sampled days) and when in the breeding season the sampling occurred. The latter was recorded considering the dates the monitoring took place relative to the laying date of the first egg (for the incubation period) and the hatching date of the first egg (for the provisioning period). When multiple consecutive days were monitored, we documented the full period from the first to the last stated day, assuming daily monitoring unless otherwise specified (e.g., every other day). In cases where breeding pairs were monitored at different dates, but the overall period monitored was continuous, we recorded it as a continuous period, even if only a single day was monitored per nest. This approach likely overestimates the duration of monitoring reported in the papers, but we opted for a more optimistic quantification of the methods to standardise the reviewing process.

Number of observations per pair

We used mean number of observations per pair when specified. However, when the number of observations per pair was not specified clearly, we assumed that observations were conducted daily during the stated monitored period for all pairs. If the authors stated that each pair was monitored for example an average of 1.5 hours without providing information about the number of observations, we assumed only one observation per pair was done during the monitored period.

Observation sessions duration

When specified, we selected the average duration of the observations. Even when a more extensive dataset had been collected in the study, we only considered the data included in the final analysis. For instance, if a study recorded nests for three hours each morning but ultimately analysed only one hour, we documented the one-hour period. This would be the final data contributing to the results and we believe only these data should be considered as the method, regardless of the total amount of data collected (e.g., using continuous video recording but manually scoring part of the videos due to logistical limitations).

Number of years

For each paper, we recorded the study's duration, limited to the period during which parental care was quantified, and the timing of data collection to represent the age of the data at publication year. The former provides an indication of research quality, as longer studies generally yield more robust results, while the latter can reflect technological advances. As the year of publication does not necessarily reflect field work, we calculated the difference between the earlier year monitored and the year of publication.

Number of pairs

We documented the number of breeding pairs used in each paper. For studies on cooperative breeding species, we used the total amount of individuals divided by two to estimate the number of "pairs" used for the study. In studies that don't specify the number of pairs monitored to quantify parental behaviour, we assumed that they used all the nests in the study area even though all nests might be used to collect reproductive success data and only a subset is used to quantify parental behaviour).

2.3 Results

Study system characteristics

Our random selection of papers from the literature successfully represented the 20-year period window (Fig. 2.1a). The average delay in publication from the final year of data collection was 5.35 years (SD = 3.39; Fig. 2.1b), with datasets being up to 21 years old at the time of publication. With some exceptions, there generally was a good correspondence between year of data collection and paper publication, indicating that studies are recent enough to provide the current state of the art. On average, studies spanned a data collection period of 2.39 years (SD = 2.24; Fig. 2.2a). While most papers documented the total number of nests used to measure reproductive success, the fraction of nests that were actually monitored for parental care was often unclear. For the papers that did report this metric ($n = 47$), the mean was ≈ 54 nests (SD = 36; Fig. 2.2b).

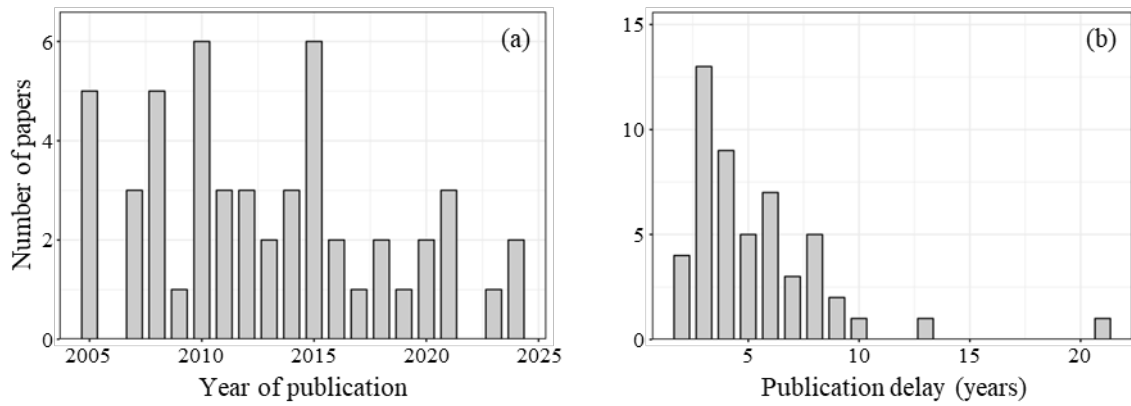


Figure 2.1 Year of publication and publication delay from data collection of the selected studies. (a) Number of papers by year of publication. (b) Difference between the year of publication and the year when data were collected, representing the delay in publication from the final year of data collection, to represent the age of the data at publication year.

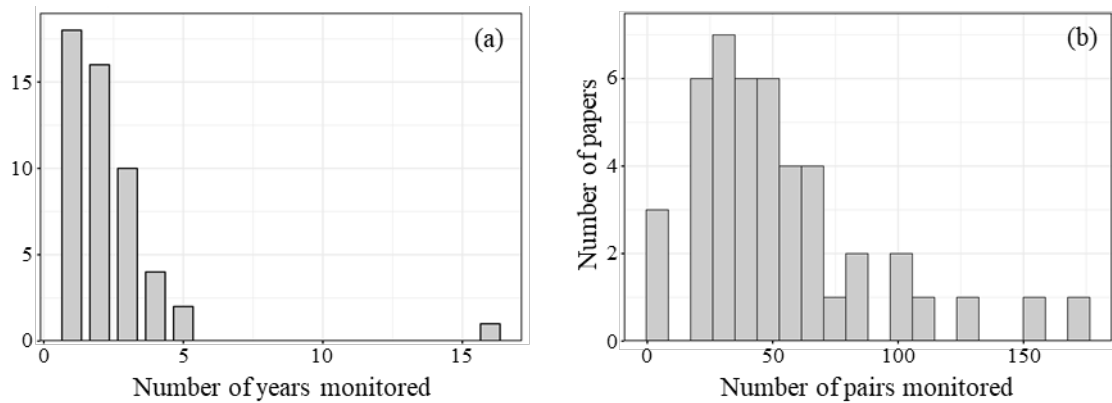


Figure 2.2 Number of years and number of pairs monitored in the selected studies. (a) Number of years when parental care was monitored in the reviewed studies. (b) Number of pairs being monitored in the reviewed studies.

Of all papers assessed, excluding two that were done in captivity, a total of 34 different species from 13 bird taxonomic groups (e.g., thrushes, tits, sparrows, wrens) of free-living populations were studied. By far tits and thrushes were the most common, with 13 and 11 papers respectively (Fig. 2.3).

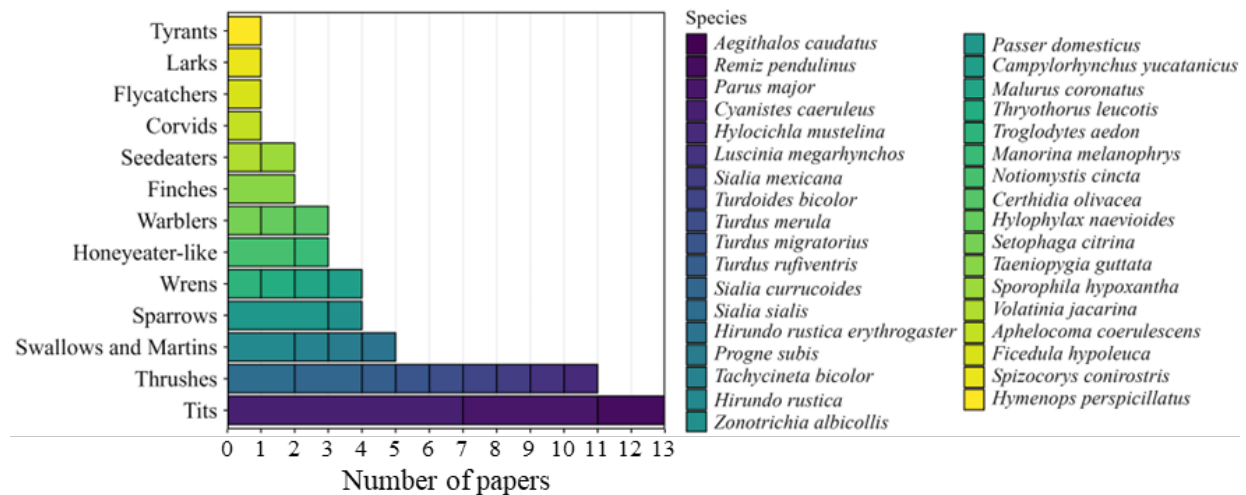


Figure 2.3 Number of papers by species within each bird group.

Methodological practices identified in the literature

The 51 reviewed studies used a wide range of data collection methods often used in combination (Fig. 2.4a), with video recording being the most common (32 papers), followed by focal observations (22 papers) and RFID-based systems (7 papers). Clarity and completeness of methodological reporting also varied substantially across studies. In terms of reporting when monitoring was performed, most papers specified exact days within the breeding cycle, but seven provided only broad stages. Similarly, while 36 studies gave precise start times, a large proportion used time ranges (26 papers) or used vague terms such as “morning” (four papers), and 11 papers did not provide any timing information. Similar ambiguity occurred in reporting how often nests were monitored, with only five studies sampling twice per day and twelve not stating the observation frequency. Likewise, the justification of methodological choices was often insufficient, and absent in 13 studies, with sample sizes being unclear in six cases. Lastly, the definitions of the behaviours being quantified were not always consistent, with for example four papers labelling “provisioning rate” (i.e. frequency of food delivery to offspring) while counting only visits in the nest regardless of food provisioning.

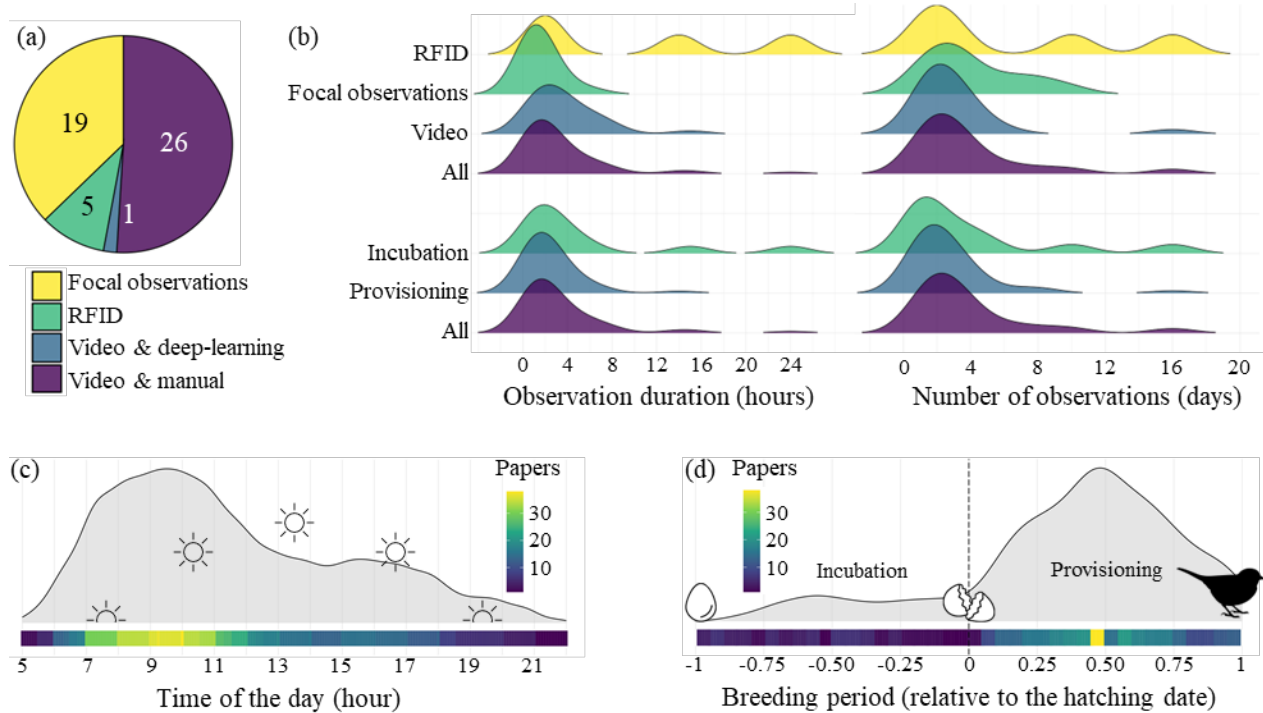


Figure 2.4 Common approaches used to monitor parental care in passerines. (a) Pie-plot showing the number of papers for each primary monitoring method. (b) Density distribution of papers by observation duration and number of days, separated by method and breeding stage. Colours match those of the monitoring methods in (a). (c) Monitoring effort across the time of day. (d) Monitoring effort across the breeding season, from egg laying to chick fledging (nest building and post-fledging not included). To facilitate comparisons, the X-axis shows relative breeding stage duration: -1 = first egg laid, 0 = first egg hatched, +1 = fledging. Negative values indicate incubation; positive values indicate nestling provisioning. Horizontal bars below (c) and (d) indicate the density of papers monitoring each period.

In terms of study design itself there was again substantial variation across studies, first of all in terms of the timing and frequency of monitoring, both as duration (Fig. 2.4b) and time of day (Fig. 2.4c). Specifically, observation sessions ranged from under an hour to full-day coverage, with most studies sampling for about 2.5 hours/day for two to three days per nest. Overall data collection was strongly biased towards the morning hours (typically 0700–1200 hours). In terms of the breeding stages considered (Fig. 2.4d), nearly all studies focused on the chick provisioning period (48 of 51), only 13 examined the incubation stage, and just one addressed nest construction or post-fledging periods. Of these, ten monitored both incubation and provisioning, 38 focused only on provisioning and three focused only on incubation. Finally, in terms of the behaviours quantified, nestling provisioning rate (i.e. food delivery rate) was the most frequently measured

variable (31 of 51 papers), followed by visitation rate (i.e. frequency of visits; 22) and nest attendance (i.e. percent of attended time; 17).

2.4 Checklist for standardised methods reporting in parental care research

To improve transparency, comparability, and reproducibility in parental care research, we provide a checklist (Table 2.1) of key methodological information that we believe should be reported when quantifying parental behaviour. This checklist was motivated by our literature assessment, which revealed substantial inconsistencies in how methodological details are described across studies, often without providing enough detail for readers to fully understand how estimates were obtained or to compare them reliably across studies. As a result, it is often difficult to evaluate whether apparent biological differences among studies reflect variation in parental behaviour or simply differences in sampling design. Our purpose is not to impose a standardised protocol, but to encourage more explicit and consistent reporting of the design choices underlying parental care estimates. We hope it will be used as a practical guide by researchers when planning and writing studies. The checklist is organised into thematic categories and includes detailed explanations and examples to guide consistent reporting.

Table 2.1 Checklist for standardised methods reporting in parental care research.

Reporting item	Details to report
Study system characteristics	
1 Study location	Provide a brief description of the study site and its habitat, including approximate coordinates or region.
2 Number of years monitored	State the years during which data were collected and specify whether all years were included in analyses.
3 Describe the species studied	Identify the species monitored and summarise key reproductive traits relevant to parental care (e.g., type of parental care, incubation length, time to fledging, mating system).
4 Sample size	Report the total number of individuals/pairs/nests monitored and clearly differentiate between those monitored and those included in behavioural analyses.
Monitoring method	

5	Method or tool used	Describe all methods used for behavioural monitoring (e.g., focal observations with binoculars, video recording, RFID). If multiple methods were combined, explain how they complement each other. If a method is used to validate another method but not for data collection for the behavioural analysis, specify this clearly.
6	Method protocols	Provide sufficient detail about the procedures to enable replication: observation distance, acclimation delay after installation or observer arrival, environmental conditions affecting monitoring (e.g., light, weather), and any observer training and consistency checks.
7	Observer reliability or automation accuracy*	Report how observer reliability or automated detection accuracy was tested and validated (e.g., repeated observations, cross-validation with manual data)

Observation schedules across the day

8	Time of day monitored	Report exact observation times (e.g., 0800 to 1100 h UTC +1) or a clear range of start times and durations if variable. If multiple observation sessions are conducted in a day, provide details for both sessions. When reporting “sunrise to sunset”, note adjustments for changing daylight hours and also state time of the day where possible.
9	Duration of observation sessions	Report the duration of observation sessions. If not fixed, report the mean and variation (e.g., SD or range) and note if duration varied systematically among individuals or breeding stages.
10	Distribution of observations across the day	Describe how observation periods were distributed throughout the day for the entire dataset. If times differed among individuals or sites, summarise this variation clearly (e.g., half of the nests were monitored for 3h starting at 07:00h UTC +1 and the other half for 3h afterwards, starting at 10:00h UTC+1. Two observation sessions were conducted in two consecutive days alternating the time schedules, so all boxes had an early and a later observation session across the day).

Breeding stage monitored

11	General breeding stages monitored	Specify which stages were monitored (e.g., nest construction, incubation, chick provisioning, post-fledging) and whether multiple stages were combined in analyses.
12	Specific parts of a breeding stage	Report the exact days or relative timing of observations (e.g., days after laying, hatching or fledging). Clarify how day zero was defined. If timing varied among individuals, describe this variation (e.g., 3 observations sessions were conducted between the day 5 and 10 after the laying of the first egg).
13	Frequency of observations	Describe how observations were distributed within the monitored period (e.g., single, daily, alternate days, sporadic) and note any deviations due to weather or logistical limitations.

13	Visualisation of sampling schedules*	When possible, include a figure or table visualising the temporal distribution of the data (e.g., time of day on the y-axis, observation days on the x-axis) to illustrate coverage across the breeding cycle.
Behavioural quantification		
14	Metrics extracted from observations	List and define all behavioural variables measured, including units, using objective terminology and specify whether multiple metrics were derived from the same observations. (e.g., we quantified visitation rate as the number of visits in the nest per hour, and nest attendance as the total % of time at least one individual attended the nest during the monitored period).
15	Assumption justification*	Explicitly justify any assumptions used to infer behaviours (e.g., proportion of visits representing provisioning events) and discuss their potential effect on interpretation.
Final data used for analysis		
16	Sample size for analysis*	If the sample size for data collection differs from the sample size for data analysis, report both numbers and explain exclusions.
17	Filtered data for analysis*	Describe any data filtering (e.g., exclusion of low-light periods or technical failures) and justify these decisions. Clarify the final dataset used for behavioural analysis.
Data availability		
18	Open data*	If possible, make data open to allow a better understanding of methodological constraints and increase transparency, replication and comparability.

**Items marked with an asterisk are recommended but may not apply to all study types*

2.5 Discussion

Our literature review highlights a lack of standardised protocols or guidelines for monitoring parental behaviour in birds. As a result, studies differ substantially in sampling design, observation duration, and the level of methodological detail reported. While some convergence exists, such as a common focus on morning observations over two to three days, heterogeneity in methods remains high, posing challenges for replication and comparisons across studies. Such variation is not inherently problematic, as ecological factors and logistical constraints often necessitate different approaches. However, the rationale for selecting sampling schedules is often insufficiently justified, complicating the interpretation and limiting cross-study comparisons.

Crucially, methodological decisions about when and how parental care is monitored can introduce both noise and systematic bias in behavioural estimates. Biases are particularly evident in the

temporal scope of existing research. All stages of parental care, from nest building and incubation to provisioning and nest defence, represent critical components of parental investment shaped by different selective pressures (Klug & Bonsall, 2010, 2014; Wang et al., 2023; Wiebe et al., 1998). Yet, our selective review shows that most studies focus narrowly on the nestling provisioning period. Although provisioning is strongly linked to offspring growth and fledging success (Killpack & Karasov, 2012; Yoon et al., 2016), it provides only a partial picture of overall parental investment. This temporal restriction is not unique to birds; similar constraints occur in mammals and other taxa where parental effort is context-dependent and varies across reproductive stages (Stockley & Hobson, 2016; Webb et al., 1999). Even within the provisioning stage, monitoring often further concentrates on a limited subset of days and specific times of day, increasing the risk that estimates capture a non-representative part of parental behaviour.

Recent technological advances in behavioural monitoring offer practical tools to overcome this strong temporal focus in parental care monitoring and expand temporal coverage and reduce reliance on short observation windows, thereby overcoming many logistical constraints that historically justified partial monitoring. Automated systems, such as continuous video monitoring or RFID-based tracking, are increasingly feasible and have already been applied successfully in field studies (Hentati-Sundberg et al., 2023; Iserbyt et al., 2018; Jolles, 2021), opening new opportunities to quantify parental care at finer temporal scales across a broader portion of the breeding cycle, although practical constraints remain.

While there might never be a single standard protocol suitable for all study systems, there is substantial room for standardisation in methodological reporting. To address this issue, we developed a concise reporting checklist that summarises key descriptors of study design and methodological detail required to interpret, reproduce, and compare parental care estimates across studies. The checklist provides a practical tool to improve consistency, transparency and comparability, and it aligns with broader initiatives that promote rigour and openness in animal research, including the ARRIVE guidelines (Percie Du Sert et al., 2020), the STRANGE framework (Webster & Rutz, 2020), and the ASAB/ABS Guidelines for ethical and methodological standards (ASAB Ethical Committee/ABS Animal Care Committee, 2023).

Overall, this work encourages more careful evaluation of how parental care is measured and reported, helping to move the field towards more coherent and reproducible research, improve comparability across studies, and deepen our understanding of how parental investment shapes fitness and life-history strategies.

Chapter 3

A centralised multi-unit recording system for automated, off-grid animal observation and environmental monitoring

Pou-Rossell, M., Sol, D., & Jolles, J. W. (2025). A centralised multi-unit recording system for automated, off-grid animal observation and environmental monitoring. *Methods in Ecology and Evolution*, 16, 2335–2344. <https://doi.org/10.1111/2041-210X.70129>

Abstract

Automated monitoring is transforming ecological and behavioural research by enabling accurate, long-term data collection and processing with minimal intervention, especially in remote or logistically challenging environments. However, monitoring multiple organisms or sites simultaneously poses substantial logistical hurdles, including the need to coordinate, optimise, and verify performance of numerous monitoring units. We present a flexible, centralised approach for multi-unit monitoring based on single-board computers. Unlike conventional systems that rely on replicated, independent units, our design uses a parent–child configuration to coordinate autonomous data collection, synchronisation, and power management. The parent unit allows for remote control of all child units while maintaining the ability to configure each one individually. We outline the core principles of this centralised multi-unit system and discuss key challenges and considerations. As a proof of concept, we deployed a centralised system to simultaneously monitor 14 nests of a colonial bird, the Jackdaw *Corvus monedula*, throughout the breeding cycle. Over four months, the system autonomously collected high-resolution, second-by-second data from multiple nests with minimal intervention. Using a deep-learning based computer vision pipeline, we extracted detailed behavioural metrics on parental effort and coordination, showcasing the system’s capacity to generate rich, fine-scale data. By integrating centralised control, efficient power management, and remote data handling, our open-source, low-cost approach offers a versatile and robust solution for continuous, non-invasive field monitoring in both accessible and remote areas. It is adaptable to a wide range of ecological applications, from monitoring long-term forest canopy dynamics to analysing fine-scale animal behaviour. To facilitate replication and adaptation, we provide full documentation for system setup, configuration, and data processing.

3.1 Introduction

The past decades have witnessed a surge in technological developments and their subsequent adaptation and integration in ecological research. From high-definition cameras to automated tools and sensors, it is now possible to study organisms in the laboratory and field with unprecedented detail and control (Dell et al., 2014; Geissmann et al., 2017; Hughey et al., 2018). Automated monitoring provides significant advantages over direct observation and manual data collection by enabling the collection of high-resolution data across extended time periods, while minimising observer-related biases associated with human perception, disturbance, and fatigue. Open Electronics integrated with sensor modules (see Oellermann et al., 2022) have played a key role in the technological revolution of automated monitoring systems, owing to their flexibility, adaptability and low cost (Barlow & O'Neill, 2020; Droissart et al., 2021; Jolles, 2021; Lennox et al., 2023). Microcontrollers and single-board computers (SBCs) such as Arduino and Raspberry Pi have for instance been used for high-resolution microclimate monitoring (Mühlbauer et al., 2023), the study of forest canopy dynamics (Wilkinson et al., 2021), Arctic plant phenology (Yang et al., 2023), cultural selection in wild-caught birds (Chimento et al., 2021), and the reproductive behaviour of nesting birds (Prinz et al., 2016). Despite all progress, a major challenge that remains is the capacity to collect data from numerous spatially distinct points of interest, such as different organisms, different parts of a habitat, or patches of the environment, especially in remote or logistically challenging environments.

Large-scale monitoring systems have been successfully implemented in controlled environments such as labs and greenhouses. Applications range from real-time fly tracking and large-scale plant phenotyping to multi-individual fish monitoring, using tens to nearly 200 SBCs in coordinated setups (Geissmann et al., 2017; Jolles et al., 2017, 2019; Martorell-Barceló et al., 2021; Tausen et al., 2020). In contrast, ecological field monitoring typically relies on standalone units, each powered, programmed, and maintained independently. Although some recent work has used tightly clustered multi-unit setups to monitor a single location (e.g., Chimento et al., 2024), the use of synchronised, multi-unit systems for distributed data collection across multiple sites remains limited. Scaling such systems for long-term, autonomous operation introduces additional challenges, including efficient synchronisation across units, long-term power management, and remote control with minimal manual intervention.

Here, we introduce a novel approach for a centralised multi-unit monitoring system for ecological and behavioural field research, based in Open Electronics. We begin by outlining the core

principles of a centralised multi-unit system scheme, where a single parent unit manages and synchronises multiple replicated child units. We then describe our proof-of-concept deployment, using multiple Raspberry Pi SBCs to autonomously capture continuous image and sensor data from wild colonial bird nests throughout the entire breeding season. Next, we evaluate its performance, identify operational challenges, and assess its efficiency and reliability. Additionally, we demonstrate the type and scale of data such systems can generate using a computer vision and deep learning pipeline. Finally, we discuss the main technical challenges and design considerations for adapting the system to different research goals and environmental conditions. To support replication and adaptation, we provide step-by-step guides for building and programming our system, and adapting the design to different needs, along with open-source tools for image processing (see Appendix B.4 and associated GitHub repository; Pou-Rossell & Jolles, 2025). Our goal is to offer a practical, open-source, and cost-effective solution for scalable ecological and behavioural monitoring in the field, particularly suited for long-term, autonomous deployments in remote and logistically challenging environments.

3.2 Principles of a centralised multi-unit system

A centralised multi-unit monitoring system consists of a single monitoring unit (the *parent*) that manages a network of peripheral sensor units (*children*). The defining feature of this approach is that the parent unit coordinates all scheduling, synchronisation, power control, and data transfer. Child units are connected to a shared power supply and can be activated or deactivated by the parent as needed to conserve energy. This setup reduces hardware redundancy, simplifies configuration, and enables consistent, time-aligned data collection across units. Both parent and child units can be employed with multiple sensors (e.g., cameras, temperature loggers, microphones), but the system-level logic is centralised. The units can communicate via a local network, and when combined with internet connectivity, the system supports automatic data transfer, real-time remote configuration and malfunction detection, making it ideal for long-term, off-grid deployments with minimal manual intervention. This framework provides a flexible basis for designing and deploying synchronised, energy-efficient monitoring systems in diverse field settings and is particularly useful for ecological and behavioural field studies that require coordinated and simultaneous data collection across multiple spatially distinct observation points.

3.3 Proof of concept: Field deployment

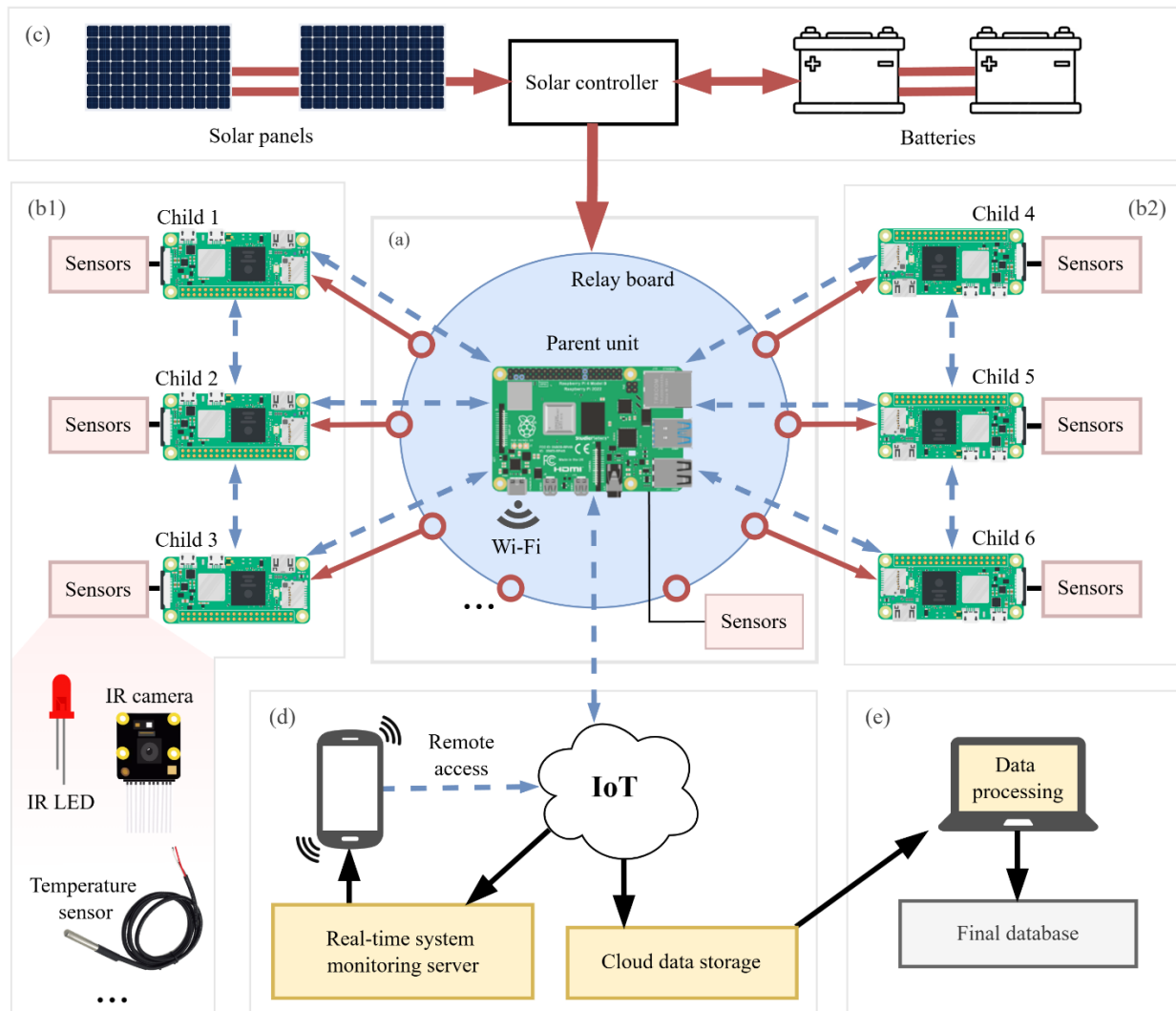


Figure 3.1 Schematic representation of our proof of concept. (a) The central parent unit and relay board controlling (b) multiple child units powered via shared power lines (red arrows). (c) The external power system includes solar panels, batteries and a power controller. Both parent and child units were equipped with a video camera and temperature sensor for data collection. (d) Wireless connectivity (4G/Wi-Fi, indicated by blue dashed arrows) enables time synchronisation from the parent, as well as real-time sharing of system updates, cloud-based data transfer, and remote access. (e) Collected data was processed using an automated deep-learning pipeline.

To demonstrate the feasibility of a centralised multi-unit monitoring system in the field, we implemented a proof of concept (see Figs. 3.1–3.2) to quantify parental care behaviour in wild jackdaws (*Corvus monedula*), a small socially-breeding corvid native to the Western Palearctic, throughout the complete breeding cycle. Accurately measuring parental care is essential for testing

key ecological and evolutionary theories, such as the cost of reproduction or parental investment theory (Clutton-Brock, 1991; Trivers, 1972), but remains challenging in wild populations. Direct observation can disturb natural behaviour, while existing tracking technologies (e.g., battery-powered video-recording, RFID tags) may not capture continuous or comprehensive data across the entire breeding season.



Figure 3.2 *Centralised monitoring system to study reproductive behaviour in wild jackdaws. (a) Nesting tower equipped with solar panels. (b) Single child unit installed inside a dust-proof plastic box on top of a nest-box. (c) 12V batteries wired in parallel powering the system through the custom relay board controlled by the parent unit. (d) Inside view of the tower, including (i) the parent unit, (ii) child units, (iii) the custom relay board, and (iv) batteries (covered under a plastic).*

In our long-term study area in the countryside of central Catalonia, NE Spain, jackdaws nest in dedicated breeding towers (Fig. 3.2). These towers are very basic, there is no insulation, and openings expose the inside to dust, wind, and large temperature fluctuations, and are equipped with nest boxes to accommodate up to 20 breeding pairs each. In one of the towers, we installed

a 14-unit system (1 parent, 13 child units), each unit associated with a separate nest-box, to record the parental behaviour and temperatures in each nest.

As the core units of our system we used Raspberry Pi single-board computers (Raspberry Pi Foundation, Cambridge, UK; hereafter RPi), nowadays one of the most widely used Open Electronics in biological research (Jolles, 2021). As the parent unit we used a RPi 4B+ and as child units we used the RPi Zero 2W model. We chose a more powerful RPi model for the parent unit for its better connectivity and increased processor speed due to extra tasks for centralisation, while for the child units the model was selected for its lower power consumption. Every unit contained a wide-angle infrared RPi camera (Keyestudio, China) with a zenith view of the nest box as well as a DS18B20 temperature sensor (AZ-Delivery, Germany; Fig. 3.2b). A 940nm IR LED diode (ams-OSRAM, Austria) in the top of the box, powered via the GPIO pins of the associated RPi, provided constant lighting. The parent unit controlled the child units using a 16-channel relay board (AZ-Delivery, Germany; Fig. 3.2d) and contained a 4G HUAWEI E8372h-320 USB dongle (Huawei Technologies Co., Ltd., China) with a SIM card to enable connection to the mobile network and provide internet access to the system via a local Wi-Fi network. To continuously power the electronics, we used two 12V solar panels (290W), linked up and charging two 12V batteries (180Ah) wired in parallel. We used AWG22-graded power cables of up to 5m in length to connect the child units to the relay board. To protect the electronics from dust and potential water seepage, we enclosed them each in a plastic box or plastic bag.

We programmed our system to automatically turn on and off on a daily basis based on sunrise and sunset times: every day it powered on 2 hours before sunrise and shut down 2 hours after sunset. We used *pirecorder* (Jolles, 2020) to schedule all units to record grayscale image sequences at 1 fps at a resolution of 640×480 pixels, which assures small image size (~20 kb each) while maintaining necessary image quality to identify image details. Each day, all the images recorded that day were converted to a compressed video. In parallel, a csv file was automatically generated containing the timestamps of all recorded images to later link video frames with its corresponding time of capture. The temperature sensor was programmed to collect the temperature inside the nest box every five minutes and store it in a csv file using a Python script and *cron* job. All data was then automatically transferred to a Google Drive folder via wireless internet. Additionally, the parent unit continuously tracked performance of all units and shared real-time status from all units in a public web server, while allowing malfunction notification automatically (see section 3.6).

The total cost of this system, including the solar system and batteries, all RPi's and cameras, a 4-month SIM card contract and all other electronics and hardware (excluding nest-boxes) was €2,012. This represents a remarkably low investment compared to commercial monitoring systems, which are often several times more expensive and less customisable. Further detailed information of expenses, component lists, installation guidelines and software are provided in Appendix B and the associated GitHub repository (Pou-Rossell et al., 2025). All field procedures received ethical approval from the *Servei de Fauna i Flora* of the *Generalitat de Catalunya* under permits SF/0018/22, FUE-2022-02968268 and SF/68/2024.

3.4 System performance

We first conducted a pilot deployment of the system in 2022 to optimise camera positioning, system setup, and software configuration. During its implementation in 2023, even though all units successfully collected data across the complete breeding season, we identified and resolved three main issues: (1) programming errors in the initial recording schedules, resulting in missing afternoon data and corrected by updating the scripts remotely; (2) instances of overheating and shutdown in some child units due to resource-intensive video conversion and insufficient ventilation, which we addressed by improving the conversion pipeline and adding aeration holes to the enclosures; and (3) power interruptions during unexpected prolonged cloudy conditions, which triggered automatic rebooting once solar input resumed, which was mitigated by installing additional batteries.

After additional refinements, we installed a final, improved version on 1 March 2024. The system was programmed to operate continuously for four months until 1 July (when all offspring had already fledged), capturing images at 1 fps from sunrise to sunset each day while simultaneously recording temperature data at 5-minute intervals. Battery capacity was estimated to sustain operation for up to three days without solar input. However, during prolonged cloudy conditions, the system occasionally shut down for an entire day to allow the batteries to recharge. Once the batteries were fully charged again, it automatically resumed operation as scheduled. Additionally, in the event of unexpected system reboots caused by overheating or resource overload, the units automatically resumed recording immediately, preventing significant data loss.

During deployment in 2024, all but one unit functioned continuously, meaning they remained responsive and capable of recording, throughout the breeding season, successfully collecting video and temperature data with minimal intervention. On average, including the underperforming

unit, the units successfully recorded data in 114.86 ± 8.93 days out of the total 123 days deployed, with occasional downtime on individual days due to power insufficiency (see Appendix B; Fig. B.5). Excluding days where the units were entirely inactive due to insufficient power, they recorded on average 94.21% of the time they were expected to. Including all non-operational periods, the units recorded 86.13% of the total expected time across the four-months period. The underperforming unit, although missing 35 days during the late breeding season due to SD card corruption, still recorded 56.73% of the four-month installation, and 85% of the expected recording time on those 88 days operating correctly. Each unit recorded on average 6.5 million images, which were continuously converted to compressed videos, yielding approximately 9 GB of video data (totalling 129 GB across all units). Temperature readings resulted in over one million measurements per unit.

Overall, our system demonstrated high reliability and robustness under field conditions and required minimal intervention over a four-month deployment. While one unit underperformed due to hardware damage (see Appendix B; Fig. B.5, child unit 8) and we still had some local power miscalculations on extended cloudy conditions, the system's modularity and built-in recovery features ensured consistent operation across the majority of units. We identified only one hardware issue during the 2024 deployment: recycled jumper wires used to power the RPi's via the GPIO pins had poor contact stability, likely due to deformation of the male ends when secured into the screw lock connector distributing battery power. This caused intermittent voltage drops below the RPi's operating threshold, leading to erratic behaviour, spontaneous shutdowns, or restarts. Based on the pattern of recording gaps, we estimate this issue accounts for the small amount of random downtime observed during the season (see Appendix B; Fig. B.5). To overcome possible system underperformance, future improvements could include expanded battery storage, adaptive scheduling based on forecasts of solar inputs and automatic battery voltage monitoring. Additionally, the use of soldered or crimped connections instead of screw lock wire connectors when powering the RPi through the GPIO pins should allow a more consistent input voltage. The collected videos offered valuable insights into nesting activities, interactions with conspecifics, offspring behaviour, and predation events, details that could be overlooked if observations were limited to specific days, hours or breeding stages.

3.5 Image-based analysis pipeline

To demonstrate how large, high-resolution image datasets, like those produced by our system, can be automatically processed to extract quantitative information, we developed a computer vision pipeline using deep learning (see also Barré et al., 2017; Chan et al., 2025; Chimento et al., 2024; Koger et al., 2023). Specifically, we used a YOLOv8 algorithm, chosen for its optimal balance of speed, accuracy, and resource efficiency (Jocher et al., 2023), to extract detailed parental care metrics by training a custom model to detect individual jackdaws in the nest boxes and infer their body position and orientation. Then, using an automated Python pipeline, we extracted positional data for every bird detected in each frame across the millions of recorded frames and saved results to individual datafiles for further analysis. Full details of our processing pipeline are provided in the Appendix B.4 and GitHub repository (Pou-Rossell et al., 2025).

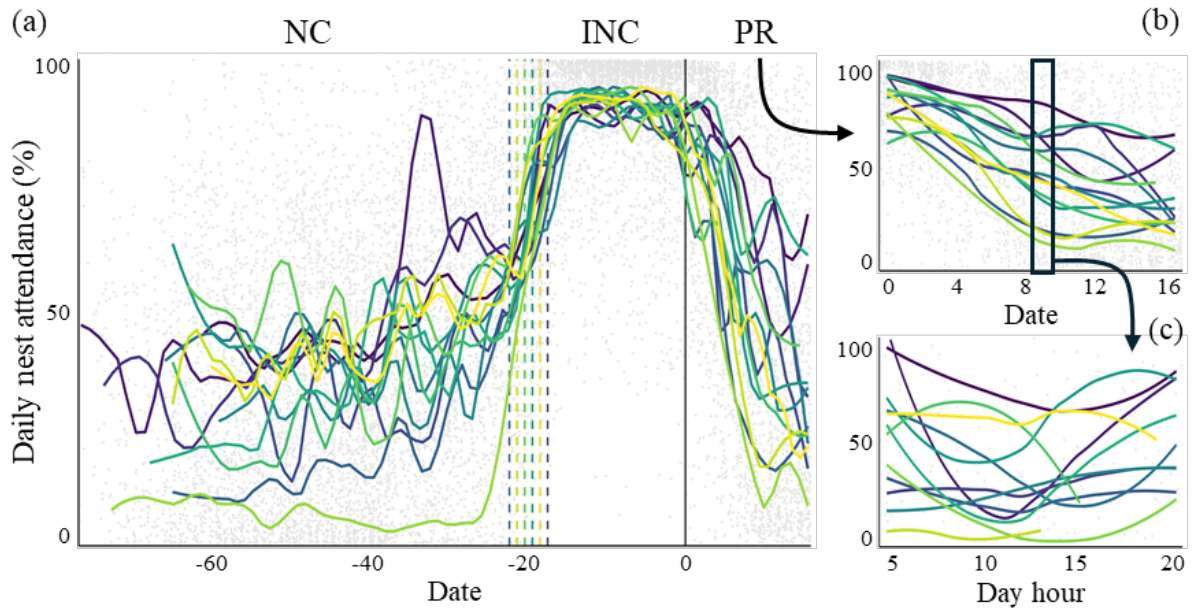


Figure 3.3 *Patterns of nest attendance by adult jackdaws across different timescales, illustrating the temporal resolution achievable with our system.* The percentage of daytime in which at least one individual was in the nest is shown for (a) the entire breeding period, (b) the nestling food provisioning period, and (c) a single day randomly selected from the post-hatching phase. Data is from 2023 and was extracted from video using our YOLOv8 pipeline. Lines were smoothed using a ‘loess’ function. Some data gaps are present, but no interpolation or estimation was applied; the figure shows only the available raw data (see Appendix B.3 for data availability). Different coloured solid lines represent individual nest boxes. Dates are relative to the hatching ($x = 0$), defined as the first hatched egg. Laying and hatching dates were detected by manual video observations. Abbreviations: NC = Nest construction stage, INC = Incubation stage and PR = Chick provisioning stage.

Our analysis extracted over 35 million bird detections for the 14 monitored jackdaw pairs over the whole recording period, encompassing more than 650,000 nest visits. This extensive dataset allowed us to accurately measure parental care investment for each of the breeding pairs, from sunrise to sunset, on a second-by-second basis, throughout the different stages of their reproductive cycle (Fig. 3.3). While pairs exhibited broadly similar patterns of daily nest attendance, the precision of our data revealed subtle differences in their investment in parental care. For example, although overall nest attendance remained consistently high during incubation, the frequency of nest visits varied substantially among pairs, with some attending frequently and others only sporadically. Our data also uncovered variation in partner coordination, such as tightly alternating visits indicative of active turn-taking. Beyond enabling accurate estimates of parental investment and conflict, the data collected by our system also allowed us to estimate subtle differences among nests in the duration of each reproductive stage and synchronisation of offspring development, as well as capturing instances of nest predation, egg repositioning after loss, sibling competition, and conflicts with other jackdaws. Such fine-scale behavioural and life history differences, detectable only through continuous and synchronised monitoring, offer valuable insights into how individual and pair-level strategies relate to reproductive success, shaping the demography and evolutionary dynamics of the population. While a detailed analysis of these patterns will be the focus of future work, our proof-of-concept combined with an efficient processing pipeline underscores the capacity of centralised multi-unit recording systems to facilitate high-throughput, long-term quantification of large image datasets, with broad applicability to other sensor types and ecological questions requiring similar temporal and spatial resolution.

3.6 System adaptability and configuration considerations

The centralised multi-unit system approach is designed to be highly modular and adaptable to different field conditions, sensor types, and research questions. Below, we outline key considerations for system assembly and configuration.

Core unit

A monitoring unit primarily consists of a SBC that manages multiple sensors for data collection. Among other SBCs such as Arduino, Asus Tinker Board, or Raspberry Pi clones such as Orange Pi, RPi micro-computers provide a power-efficient solution at low cost, benefiting from a wide

range of compatible sensors, high processing capabilities, and extensive programming flexibility, all supported by a large and active community (Jolles, 2021). While various RPi models exist, the RPi Zero 2W, with its low power consumption, is the most suitable choice for off-grid applications where energy efficiency is crucial. However, higher-end models may be preferred when greater computational power is required or when additional connectivity ports are needed on the main board. Most RPi models have a port to connect a dedicated camera and an array of general-purpose input/output (GPIO) pins that can be used to communicate with a wide range of sensors and electronics, from LEDs and buttons to servos, motors, Real Time Clocks (RTC) for time synchronisation across units and power relays (see Appendix B; Fig. B.1). The integration of a camera sensor should be relevant to most applications. RPi come with their own Linux-based operating system (Raspbian OS) and all data, including the OS, is stored on a micro-SD card, widely available with huge storage capabilities at low cost. This is a great benefit over physical hard-drives, as SD cards have a tiny footprint and do not contain moving parts (for cloud data store possibilities, see below).

When deploying monitoring units outdoors, it is essential to protect electronic components from environmental influences such as rain, humidity, dust, and heat. For example, humidity could affect the operation of precision equipment, such as Real-Time Clocks, leading to subtle timing discrepancies between units while requiring periodic recalibration. Housing the electronics in a weatherproof junction box, with external power supplied via MC4 connectors offers reliable protection against rain and moisture. However, even in dry climates or when placed under cover, dust can accumulate over time and interfere electronic components, potentially causing malfunctions. To mitigate this risk, all electronics should be enclosed, ideally in a sealed box, or at a minimum in a protective plastic bag. It is also important to prevent overheating, especially for more powerful SBCs, which generate significantly more heat than low-power models. This can be achieved by using heatsinks, allowing for ventilation, and positioning units in well-shaded areas. In hot environments, keeping components cool is critical to avoid system failures and unexpected shutdowns.

Optimal power conservation and centralised control

To ensure continuous monitoring over long periods of time in off-grid applications, solar power provides a cost-effective solution in most scenarios, although alternative power solutions can be used if that is not feasible (e.g., hydro power or simply extended battery storage). By controlling the individual channels of a relay board, the parent unit can turn on or off the child units when

desired, thereby minimising their power consumption such as when they would otherwise be idle (see Appendix B.1 for details). To optimise the power consumption of the parent unit itself, power management boards like the PiJuice (Pi Supply, Bells Yew Green, UK) enable programmatic control and scheduling of its on-time, and connect to the top of the RPi. In particular, it can enable the uninterrupted supply of power for continued system functioning after shutdown, during which it remains active in an ultra-low power state using its built-in battery. It can power the system back on at scheduled times instead of demanding researchers to physically be there, ensuring autonomous and continuous system operation. In this way, the parent unit can be programmed, for example, to operate only during daylight hours to conserve battery at night, or to only run 5 minutes of every hour to take specific measurements. Thus, when the parent unit is activated by the PiJuice, it can automatically power on the child units using the relay board, synchronising all units' operation. Additionally, power management boards like the PiJuice can be programmed to automatically power on the RPi once the battery reaches a sufficient charge level after depletion, offering continuous operation even after periods of low solar input with no intervention. Similarly, the system can be programmed to be in standby for days, weeks or months, which can for example be useful when weather conditions are sub-optimal to generate enough solar energy. It is also feasible to schedule recordings that change with time, such as daily changes in sunrise and sunset times, to optimise the use of solar energy.

A centralised multi-unit system works particularly well for clustered monitoring units. It can also be used for widely dispersed monitoring locations (e.g., beyond ~50m from the central unit) but constraints in communication range and extended wiring requirements need to be overcome. For example, while extended power cable length may lead to voltage and amperage drop, this can be minimised by using thicker cables and configuring a higher input voltage to the buck converter to compensate for the expected voltage drop. Power over Ethernet (PoE) technology can further simplify deployment by providing both data and power through a single Ethernet cable, for distances up to 100m, particularly useful when child units are distributed across a site but still accessible via cable. However, PoE infrastructure comes with higher power demands and added hardware requirements and may not be feasible in most field locations. It is always essential to ensure that cables are waterproof and shielded from sunlight and potential damage, such as by encasing them in PVC conduits buried underground.

Connectivity

Connectivity between the parent and child units allows for time synchronisation, unit control and system updates. Having a working internet connection furthermore enables real-time monitoring of system performance, crucial for detecting issues like power failures and data storage problems (for which various solutions exist, see below), and facilitates automatic data uploads to cloud storage. While both wired and wireless setups can be used to create a local area network (LAN) among units, a wireless setup is generally preferable in field settings, where deploying physical cabling and network switches is impractical and adds power demands. The parent unit can be configured to act as a wireless hotspot to enable communication between units, and the range can be extended to over a hundred meters using a Wi-Fi extension antenna or USB stick. This makes it feasible to install child units tens to over a hundred meters apart, even in open outdoor settings, rather than keeping them within the same structure.

For internet connectivity, mobile internet is typically the most straightforward solution and can be provided by a USB modem with a SIM card, providing connection to mobile networks. Many modern hotspot devices support simultaneous connections of up to 16 units, such as the HUAWEI E8372h-320 dongle (Huawei Technologies Co., Ltd., China). In areas where mobile coverage is limited or absent, satellite internet (Whytock et al., 2023) or long-range radio (e.g., LoRa; Rebaudo et al., 2023) can serve as alternatives, albeit with higher costs, limited bandwidth and potential latency constraints. When power availability is less constrained, a wired ethernet LAN may be preferred for its faster and more stable data transfer. Once internet connectivity is established, units can be remotely controlled using Secure Shell (SSH) for command-line access or remote desktop solutions like Virtual Network Computing (VNC) for a graphical interface. Cluster SSH tools are useful to control all child units at the same time with simultaneous command executions from the parent RPi, efficiently centralising coordinated multi-unit operation.

Automated data collection

The system can be programmed to run completely autonomously, with units to turn on and off when desired, and perform a series of tasks at predetermined intervals. In most cases daily routines may be preferred, such as powering on, collecting data, performing necessary conversions, backing up files, and then powering off at specific times in the day. Such task automation can be easily managed through bash and Python scripts, which can be triggered at fixed times, dates, or intervals using utilities like *cron*. These routines can be furthermore programmed to change with

time or in response to environmental factors (e.g., changes in daylight hours or cloud cover). For example, parent wake-up and relay activation schedules can be set to change at a daily basis to power on the whole system aligned with changes in sunrise and sunset, thereby saving solar energy. Such automation ensures reliable and long-term operation, even under harsh weather, with minimal manual intervention.

RPi cameras can be operated using native RPi packages such as *Picamera* or *libcamera*, allowing to write custom recording scripts and also dedicated packages exist for scientific use such as *pirecorder* (Jolles, 2020), which help with customising camera settings, recording parameters, and scheduling recordings. In applications requiring long, continuous recording periods, using image or video sequences instead of long videos minimises the risk of data loss in the event of unexpected shutdowns, and allows for uninterrupted data collection over long periods. For instance, images can be captured at sizes as small as a few kilobytes each, managing storage use effectively. These sequences can later be converted into a single video file using customisable compression settings via the *ffmpeg-python* package, deleting the raw sequence files to free storage use afterwards. By automatically uploading and cleaning up data, the system can operate long-term without running out of space on the SD card.

Uptime and performance monitoring

Continuous performance monitoring ensures that all units function optimally and any issues are detected quickly. Each monitoring unit can share its real-time status with the central unit, allowing researchers to check important operational data, such as CPU load, available storage, sensor functionality, and network connectivity. Various options exist for enabling such up-time and performance monitoring, the most versatile of which is a local webserver that provides a centralised view of the status of all devices, which can be accessed from any web browser. In practice, the parent RPi hosts a local web server that collects and displays performance data from itself and all child units, which are sending data at standard intervals (e.g., every 5 seconds) to the parent via the local network. To enable the information to be shared on the internet remotely, a gateway service such as *Ngrok* can be used to publish the local web server to the internet, enabling real-time monitoring from any location. At the same time, all performance monitoring is continuously stored in a logfile, allowing to check from errors in the past even in scenarios with no internet connection. In addition to real-time status checks, periodic diagnostics can be scheduled to automatically detect potential malfunctions. If any issues are detected, such as a malfunctioning sensor, low storage space, or data backup problems, the units can send instant

alerts via email, enabling quick intervention to minimise data loss or downtime. This performance tracking system is highly customisable, allowing specific performance checks tailored to the needs of the project, ensuring problems are identified and addressed before they highly impact the data collection process (see GitHub repository for real-time performance monitoring used in our proof of concept).

3.7 Conclusion

Our centralised multiple-unit monitoring approach provides a reliable and versatile solution for coordinated, long-term ecological and behavioural data collection. By implementing a centralised ‘parent–child’ configuration, our setup synchronises monitoring across units, optimises power usage, and enables remote system uptime and performance monitoring, facilitating autonomous data collection over extended periods. Our proof-of-concept demonstrates practical feasibility under real-world field conditions. Across the 14 deployed units, our system operated with minimal intervention over four months, achieving high uptime and delivering continuous, high-resolution video and sensor data. The system’s adaptability in both hardware and software makes it suitable for a wide range of ecological applications, from fine-scale behavioural tracking to distributed environmental monitoring. Its robustness supports long-term deployment in remote field settings. When combined with automated data extraction tools such as computer vision and deep-learning, centralised monitoring opens up new possibilities for high-throughput, non-invasive research in the wild. Taken together, the proposed framework offers a flexible, affordable, and scalable alternative to conventional field monitoring methods, with potential to advance the capabilities of field-based ecological research.

3.8 Data availability statement

Full step-by-step guides for setting up a multi-unit system, programming the electronics and customising software functionalities can be accessed via <https://doi.org/10.5281/zenodo.16354887> (Pou-Rossell & Jolles, 2025) or in the following repository: <https://github.com/mpourossell/Centralised-Multi-RPi-Recording-System>.

Chapter 4

Addressing noise and bias in
parental care quantification using
simulated partial sampling from
continuous monitoring

Abstract

Quantifying parental care in the wild often requires sampling decisions that trade temporal coverage for feasibility. However, parental behaviours are strongly structured in time, both within days and across breeding stages, meaning that restricted observation windows may distort estimates of parental effort. Here, we evaluate how partial monitoring designs influence two widely used metrics, nest visitation rate and nest attendance, using a continuous, high-resolution dataset of parental behaviour from a passerine. We simulated realistic sampling schemes that varied in time of day, number of observation days, observation duration, and breeding stage, reflecting common constraints in field studies. These simulations allowed us to assess how different monitoring choices affect behavioural estimates. We show that restricted or selective sampling can systematically bias estimates relative to those derived from continuous data, introducing substantial error in behavioural metrics. While common approaches may be sufficient to detect broad-scale patterns (e.g., among colonies or populations), thereby supporting commonly used approaches, they often lack the resolution needed to detect variation among individuals or pairs, which is critical for evolutionary inference. Importantly, sampling schemes that preserve mean behaviour at the population level can still alter variance and relative ranking among pairs, reducing the ability to detect individual differences. Together, these results demonstrate that study design can strongly shape conclusions about parental investment and provide empirical guidance on how to minimise bias when continuous monitoring is not feasible.

4.1 Introduction

Parental care is a core component of the life history of many species because it translates parental decisions directly into offspring survival, thereby strongly influencing fitness (Clutton-Brock, 1991; Royle et al., 2012; Stearns, 1976; Trivers, 1972). Robust quantification of parental behaviour is therefore essential for testing ecological and evolutionary predictions about variation in parental investment within and among populations. In wild populations, however, parental care is often quantified only partially. Such partial sampling is not necessarily inappropriate, but it is potentially consequential given that parental behaviours are strongly structured in time.

In Chapter 2, we show that studies of parental care in passerines exhibit substantial heterogeneity in sampling schedules, with a strong concentration of effort within narrow windows of the breeding cycle and day. These patterns are understandable given field constraints, and monitoring requirements may differ across systems and species, but they highlight the possibility that commonly used designs capture a non-representative subset of parental behaviour. Parental activity varies across the breeding cycle (e.g., nest building, incubation, provisioning), within the diel cycle, and in response to environmental conditions such as weather (Amininasab et al., 2016; Kulaszewicz et al., 2018; Simmonds et al., 2017). As a result, monitoring schedules that capture only a subset of this temporal variation may yield estimates that are not representative of overall parental effort, both within specific reproductive stages and over the entire breeding cycle. Moreover, restrictions in sampling schedules may introduce noise (random error or imprecision) and/or bias (systematic error) in the quantification of parental behaviour. Although several papers have discussed the limitations of short and selective observations (Brereton et al., 2022; Lendvai et al., 2015; Margulis & Westhus, 2008; Schwagmeyer & Mock, 1997), a systematic evaluation of how methodological decisions affect estimates of parental investment remains lacking.

To address this gap, we used a continuous, high-resolution dataset of parental behaviour in jackdaws (*Corvus monedula*) collected across the entire breeding season, using a recently developed automated video monitoring system combined with AI-based behavioural extraction (Pou-Rossell et al., 2025; Chapter 3) to evaluate the consequences of partial monitoring. We restricted analyses to the provisioning period and generated simulated subsets that emulate commonly applied observation schedules, explicitly varying time of day, observation duration, number of monitored days, and timing within the breeding stage. By comparing the behavioural estimates quantified from these simulated subsets with the ones from the complete dataset, we quantified the noise and biases introduced by alternative sampling designs, and assessed how

different methodological decisions influence conclusions about individual variation in parental investment.

4.2 Methods

Continuous parental care data collection

To assess how methodological choices influence behavioural estimates, we used a high-resolution dataset on parental care of wild jackdaws monitored across the complete breeding season, as described in Chapters 1 and 3. We recorded the behaviour of 14 pairs breeding in nest boxes in an artificial tower in Lleida, Spain, from 15 March to 15 July during the 2023 breeding season. Further details on the study system and monitoring setup are provided in Chapter 3. Jackdaws provide bi-parental care, and in this population, females typically lay three to seven eggs from late April to mid-May, incubation lasts 18–22 days, and chicks fledge 32–35 days after hatching.

Parental activity was continuously monitored using a solar-powered, automated video system based on Raspberry Pi computers (Pou-Rossell et al., 2025; detailed in Chapter 3), which captured synchronised images from inside all nests at one frame per second, continuously from sunrise to sunset, every day, across the full breeding season. A custom YOLOv8 computer-vision model (Jocher et al., 2023) was trained to automatically detect birds across all frames, allowing each frame to be classified according to the number of adults present in the nest (0, 1, or 2 individuals).

From these frame-level classifications, we derived two pair-level metrics: nest attendance, defined as the proportion of time the nest was occupied by at least one parent, and visitation rate, defined as the number of transitions from an unattended to an attended nest per hour. Because jackdaws are monomorphic and individuals could not reliably be distinguished by the model, analyses were restricted to pair-level measures rather than individual specific behaviour. Although the computer vision model performed with high overall accuracy, it increasingly confounded adults with fledglings from day 16 after hatching onwards. To avoid misclassification, all post-hatching analyses were therefore restricted to the first 14 days after hatching. The system was installed before nest construction, ran autonomously with minimal intervention, and was removed after fledging. Detailed visualisations of data distribution are available in Appendix B.3

Simulation of partial monitoring approaches

From the complete dataset, we created subsets that replicated the most common sampling schedules identified in the literature. This allowed direct comparison between partial and full sampling schemes, focusing on the most studied breeding stage, the nestling provisioning period (see Chapter 2). We first evaluated how four dimensions of sampling schedules commonly varying across avian parental behaviour studies affect behavioural estimates when examined individually: (1) time of day, (2) breeding stage, (3) number of days observed, and (4) observation duration. Each subset was thereby compared to the complete dataset (Fig. 4.1). We then tested two combined scenarios to assess how multiple methodological dimensions interact: (5) a typical design using the most frequent monitoring decisions for each dimension, as identified in our literature review, and (6) a pseudo-random schedule design, in which monitoring times and durations were randomly drawn within the commonly used ranges of the typical design (see Appendix C for further information). This pseudo-random approach introduced natural variation among pairs, mimicking the flexible and heterogeneous monitoring routines often reported in empirical studies. Together, these scenarios enabled us to test whether noise and bias associated with methodological decisions persist, or accumulate, when several temporal constraints are applied simultaneously.

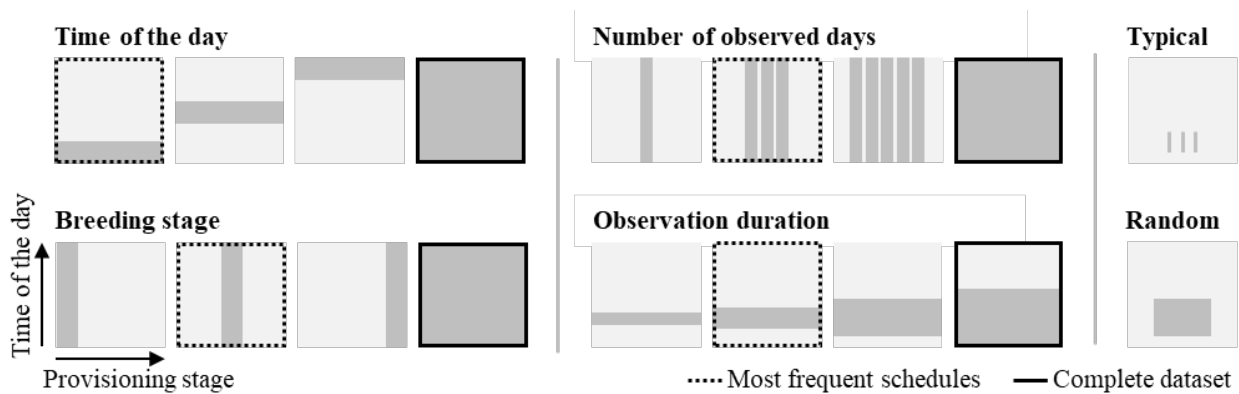


Figure 4.1 Visualisation of the simulated partial monitoring subsets (dark grey) for each dimension of sampling schedules compared to the complete dataset (black squares). Each square represents the provisioning period, with time of day (sunrise to sunset) on the vertical axis and days (first egg hatching date to 14-day chick age) on the horizontal axis. For observation duration, the full morning was used as the complete dataset to avoid time-of-day biases. The two final panels on the right show the strict typical design, which combines the most frequent schedules from all other dimensions (dotted squares), and a flexible pseudo-random version, in which observation periods like those in the typical design are randomly drawn within commonly reported ranges.

Analytical approach to detect sources of noise and bias

For each simulated monitoring strategy, we calculated the nest visitation rate and nest attendance for each jackdaw pair and compared them against values derived from the complete dataset. Differences between metrics were evaluated in three complementary ways: (i) mean estimates across all pairs, (ii) variance among individuals, and (iii) consistency in pair ranking. Differences in mean estimates were tested using general linear mixed-effects models, with pair ID as a random effect, while differences in variance were tested with a Levene's test. To assess rank consistency, we used Spearman's rank correlations and quantified the percentage of pairs that truly changed rank position rather than through chain effects caused by other shifts (e.g., two pairs increasing a rank simply because one pair dropped two ranks).

To evaluate the combined impact of all common dimensions of sampling schedules, we created 1,000 pseudo-random bootstrap subsets. Specifically, for each bird pair, we randomly picked one time of day and one day during the period when parents feed their chicks, ensuring that the total amount of observation stayed the same in terms of observation duration and number of monitored days (we used three 2.5-hour sessions over three days, which represents the most common design; see Chapter 2). For each run, we calculated visitation rate and nest attendance per pair, producing a distribution of mean values across all replicates. We then examined whether the mean of the complete dataset fell within the 95% confidence interval (CI) of bootstrapped means and compared this distribution with the fixed-schedule typical design to determine whether randomised sampling reduces deviations from the complete data. Statistical analyses were performed in R (version 4.3.1; R Core Team, 2023). Linear mixed-effects models were fitted with the lme4 package (Bates et al., 2015) and Levene's test implemented in the car package (Fox et al., 2024).

4.3 Results

Effects of partial monitoring on parental care estimations

Our simulations on single dimensions of sampling schedules showed that the impact of restricted monitoring on parental care estimates depend on both the behavioural metric considered and the methodological dimension modified (full details in Table 4.1 and Appendix C; Figs. C.1–C.4). First, subsetting the complete dataset by time of day, mean visitation estimates were significantly lower during midday or afternoon compared to full-day monitoring, while subsetting to the

morning, the most common sampling approach, yielded comparable estimates (Fig. C.1). Second, the number of days monitored had a big impact on the estimates, with single-day monitoring being clearly insufficient as reflected by strongly biased visitation rate estimations (Fig. C.2). This bias was considerably reduced when extending the sampling to three or five days. Third, while subsetting per breeding stage did not affect the mean visitation rate, it had an effect on nest attendance, with estimates for both early and late provisioning stages differing significantly from the full period (Fig. C.3). Finally, restricting the observation duration to three-hour morning sessions altered mean nest attendance estimates but not visitation rate compared to full morning data (Fig. C.4).

Noise and biases in individual-level estimates of parental investment

Table 4.1 Differences in mean estimates, variance, and rank correlation of visitation rate (Vis.) and nest attendance (Att.) between the simulated partial sampling schedules and the complete dataset. Significant differences in mean estimates, differences in variance and low rank correlations, and subsets causing more than 1/3rd of pairs to change in rank position are underlined and bold.

Dimension	Data subset	Mean		Variation		Rank correlation			
		Diff. mean estimates		Levene p-value		Spearman's rho		% rank changers	
		Vis.	Att.	Vis.	Att.	Vis.	Att.	Vis.	Att.
Time of day	Morning	-0.09	0.60	0.7639	0.5622	0.86	0.85	<u>36</u>	<u>36</u>
	Midday	<u>-1.41</u>	-1.92	0.8679	0.4206	0.90	0.97	<u>36</u>	<u>36</u>
	Afternoon	<u>-0.38</u>	-3.63	0.4661	0.5237	0.92	0.95	29	<u>36</u>
Observation duration	One hour	-0.09	-0.90	0.3399	0.9906	0.89	0.86	<u>36</u>	29
	Three hours	-0.05	<u>-1.61</u>	0.6921	0.9607	0.93	0.91	14	29
	Five hours	-0.09	0.27	0.9727	0.9946	0.98	0.93	14	29
Number of observations	One day	<u>-0.89</u>	-1.70	0.8174	0.3884	<u>0.54</u>	0.91	<u>57</u>	<u>43</u>
	Three days	-0.41	-0.71	0.9562	0.7568	0.77	0.97	<u>50</u>	21
	Five days	-0.21	-0.43	0.9559	0.7550	0.99	0.98	14	21
Breeding stage	Early prov.	0.18	<u>14.60</u>	0.9965	0.8877	0.71	0.78	<u>43</u>	<u>57</u>
	Mid prov.	-0.48	-4.24	0.5600	0.3665	0.79	0.90	<u>43</u>	29
	Late prov.	0.16	-8.34	0.3626	0.9704	0.95	0.94	<u>21</u>	29
Combined	Typical design	0.48	<u>-29.72</u>	<u>0.0029</u>	0.3116	<u>0.55</u>	0.83	<u>57</u>	<u>50</u>

Our simulations revealed both noise (i.e. greater variability among pairs) and biases (i.e. systematic error of behavioural estimates) in some of the dimensions of sampling, but rank correlations between subsets and the complete dataset were high overall (Table 4.1), indicating that relative differences among pairs remained largely consistent across sampling schemes. However, accuracy decreased when examining investment during a reduced number of monitored days. When sampling was limited to a single day, this resulted in a large number of rank changes among pairs (35% of pairs), with a mean rank-shift distance of 30%. Increasing the number or duration of observation sessions reduced these deviations but did not eliminate them, suggesting that partial sampling can be inadequate for estimating differences in parental investment at the level of individuals or pairs.

Combined dimensions: Typical and pseudo-random schedules

Applying the most frequent monitoring design identified in the literature (i.e. three hours in the morning, during three days in the mid-provisioning stage), we examined how typical combinations of the different sampling dimensions influence estimates of parental behaviour (Fig. 4.2). With visitation rate as the behavioural metric, mean values across pairs were similar to those from the complete dataset, but both variance and rank correlation differed significantly. In contrast, for nest attendance, the same monitoring design produced means less than half those of the full dataset, while variance and overall rank structure remained stable (Table 4.1). These opposing results show that visitation rate is less affected by restricted sampling, whereas nest attendance is highly sensitive to observation schedule. Notably, even when rank correlations were high, half of the pairs changed markedly in rank position, showing that short, fixed observation windows can alter individual-level comparisons.

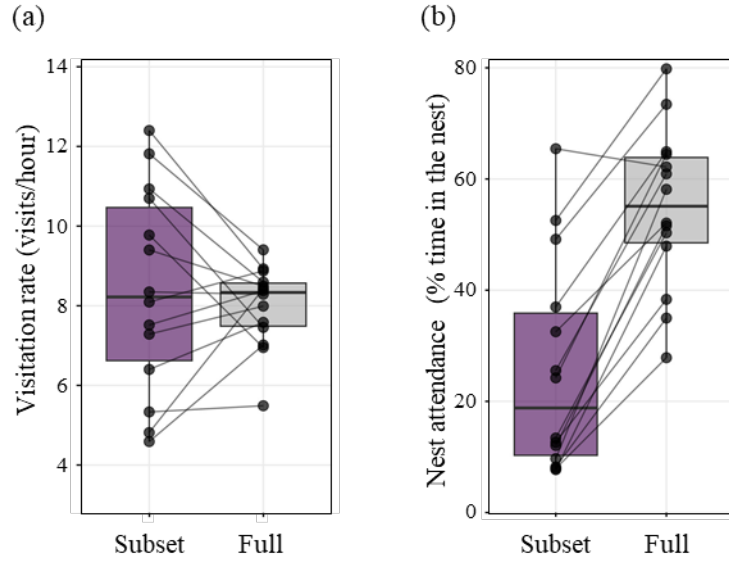


Figure 4.2 Comparison of full dataset with most frequent monitoring design for (a) visitation rate and (b) nest attendance. The typical monitoring design detected in the literature is shown in purple and the full continuous data in grey. Black lines link pairs.

Finally, we tested whether distributing observation effort more evenly over time could reduce the biases detected in fixed sampling designs. To do this, we simulated pseudo-random monitoring schedules that used the same total effort as the strict typical design but now spread across the observation period (Fig. 4.3). For visitation rate, the mean of bootstrapped pseudo-random subsets (8.51 visits/hour) closely matched the complete dataset (8.31 visits/hour) as well as the strict typical design (8.39 visits/hour). All three estimates laid well within the bootstrapped 95% confidence interval (7.54–9.51), and variation among replicates was low ($CV = 0.06$), indicating minimal bias. Results were different, however, for nest attendance. Here, variability among pseudo-random replicates was higher ($CV = 0.12$), with deviations of up to $\pm 36\%$ from the complete dataset mean. The strict typical design produced a much lower mean value (25.6%), well outside the 95% bootstrap confidence interval of the pseudo-random subsets (39.8–64.6). This confirms that fixed sampling tended to capture periods of low attendance, whereas pseudo-random schedules covered the full temporal range and recovered the true mean ($\approx 51\%$).

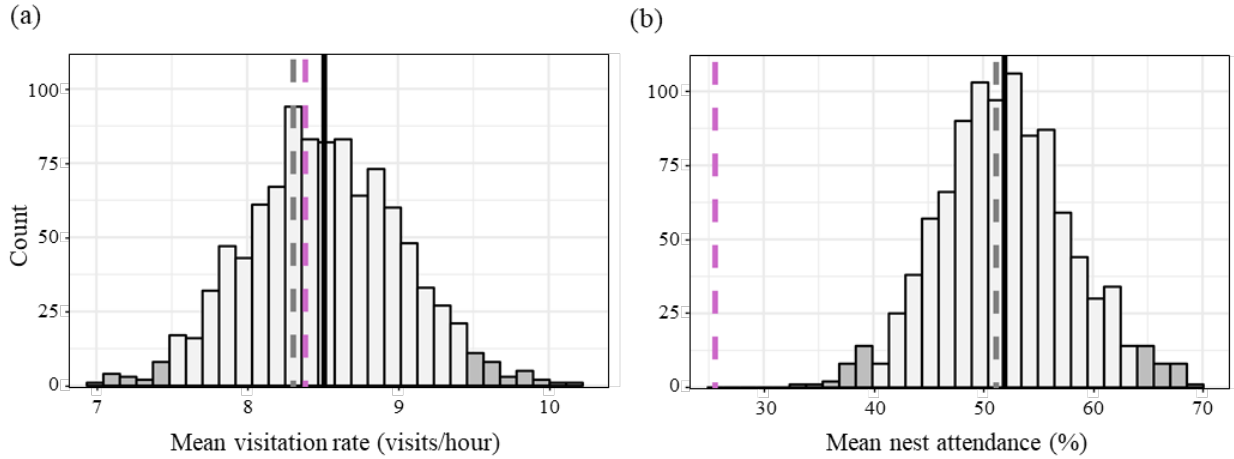


Figure 4.3 *Bootstrapped mean estimates under pseudo-random monitoring schedules for (a) visitation rate and (b) nest attendance. Dashed lines indicate the mean of the complete dataset (grey) and the mean of the strict typical design subset (purple); the solid black line marks the mean of the bootstrapped pseudo-random subsets. Darker bars denote the 2.5th and 97.5th percentiles.*

4.4 Discussion

Our simulations provide a detailed assessment of how methodological practices influence estimates of parental care. By comparing partial monitoring schedules with the complete dataset as a reference, we were able to separate the consequences of limited temporal coverage into increased imprecision through noise and bias arising from non-representative observation windows. Overall, methodological choices affect both the magnitude of behavioural estimates and the inference drawn about among-pair differences in parental investment. However, these effects were behaviour-specific: nest attendance, which follows predictable daily rhythms (Bambini et al., 2019; Setash et al., 2021), was particularly sensitive to observation timing and duration, whereas visitation rate was comparatively robust. Importantly, reliability depended more on how sampling effort was distributed across the breeding period than on the total amount of data collected.

Ultimately, the key issue is not whether parental care can be measured without error, which is unlikely without continuous, high-resolution data, but how such errors influence the inferences we draw. From this perspective, the value of comparing continuous and partial data is not to argue that all studies should monitor the full breeding cycle or abandon targeted observation designs. Rather, it is to evaluate the conditions under which partial sampling provides robust estimates and the circumstances in which it may misrepresent broader parental investment patterns. Our

simulations indicate that existing sampling protocols generally suffice for detecting broad-scale differences (e.g., between colonies or populations) but that they might be unreliable for quantifying variation among individuals or pairs, which is crucial to address many evolutionary questions. This is particularly relevant for studies aiming to quantify individual variation, repeatability, or selection on parental traits. This highlights that methodological choices regarding which behaviours to monitor, when to observe them, and how frequently to do so can strongly shape biological interpretations.

Recent advances in automated monitoring techniques provide opportunities to overcome many of the constraints that have historically limited continuous data collection. Automated video-surveillance systems in combination with computer-vision pipelines or RFID systems can now collect long-term continuous datasets with minimal observer presence and reduced disturbance, often at high-temporal resolutions (Hentati-Sundberg et al., 2023; Iserbyt et al., 2018; Jolles, 2021; Pou-Rossell et al., 2025; Chapter 3). When continuous sampling is not feasible, and one must rely on partial sampling, our simulations show that a practical way to minimise bias is to better distribute observations across the day and pseudo-randomly across the breeding stage, rather than concentrating effort within specific parts of stages. Overall, our results highlight that careful scheduling and study design can yield reliable estimates even when continuous monitoring is unfeasible, though the reliability of such approaches should be validated on a case-by-case basis.

These findings show that partial monitoring can introduce both stochastic noise and systematic bias in behavioural estimates of parental care. The magnitude and direction of these effects depend on the temporal dynamics of the behaviour quantified and on how sampling effort is distributed. Taken together, these findings underscore the importance of considering study design and the temporal structure of behaviour, and of balancing logistical constraints with optimal observation timing (Altmann, 1974; Martin & Bateson, 2007; Naguib et al., 2023). Continuous, high-resolution datasets provide a benchmark for quantifying these biases and offer a robust foundation for designing monitoring regimes that better capture temporal variation in parental activity. More broadly, these results emphasise that how parental care is measured can strongly influence conclusions about individual variation and its links to fitness, and support ongoing efforts to improve parental care quantification, facilitating comparability across studies and strengthening inference about parental investment and its consequences for fitness.

Chapter 5

Temporal dynamics of biparental
care across the full breeding cycle
in wild jackdaws

Abstract

In altricial animals, offspring are born underdeveloped and rely heavily on adults for feeding, protection, and thermoregulation, making parental care crucial for their survival. Although the central role of parental care as major determinant of fitness is widely recognised and backed by ample evidence, most empirical studies rely on short, stage-specific observations that provide only snapshots of parental investment. Hence, it remains unclear how parental behaviour unfolds across the full breeding cycle. In addition, parental care is often quantified as the additive effort of both parents, which can obscure how care is organised, such as the extent of joint versus alternated feeding trips. Here, we use an image-based autonomous monitoring system to acquire continuous parental care data of wild jackdaws (*Corvus monedula*) across two full breeding seasons, from 21 days before egg laying until 14 days after hatching. The system recorded nest attendance at 1-second resolution throughout daylight hours, yielding a large dataset of continuous observations from which we derived daily measures of total attendance (at least an adult present) and joint attendance (both adults present). Our results show that nest attendance is strongly restructured across the breeding cycle, and that total and joint attendance follow distinct temporal trajectories. During nest building, pairs differed widely in both metrics. During incubation, total attendance converged near its upper bound across pairs, while joint attendance still showed among-pair variation. After hatching, joint attendance declined to near zero for most pairs, whereas variation among pairs was expressed primarily in total attendance. Across stages, pair rankings were overall consistent, indicating that some pairs consistently invested more in attendance than others. This consistency appeared stronger within pre-hatching and post-hatching periods than across the transition between them, reflecting reduced among-pair variation at certain stages. Overall, our results show that nest attendance is highly dynamic across the breeding cycle and highlight joint attendance as an additional axis of parental behaviour that is largely missed by additive metrics.

5.1 Introduction

Parental care, where parents provide protection, nourishment, and guidance to their offspring, often entails substantial energetic costs and risks to parents. In birds, however, parental care is widespread and plays a crucial role in enhancing offspring survival, especially in species with altricial young, whose chicks hatch in an undeveloped state and depend entirely on parental provisioning and protection (Kendeigh, 1952; Mock, 2022). The importance of parental care is evident in species with bi-parental care, where the loss of one parent often results in breeding failure because the remaining individual cannot meet the energetic and temporal demands of raising the brood alone (Iserbyt et al., 2019; Mariette & Griffith, 2015; Sanz et al., 2000; Soler, 2014). Given this importance, it is not surprising that birds have played a central role in developing parental investment theory (Trivers, 1972), and empirical work has provided extensive insights into how parents allocate care, how parental effort is divided between the sexes, and how parental investment shapes reproductive success (Baldan & van Loon, 2022; Hinde, 2006; Lessells & McNamara, 2012; Mariette & Griffith, 2012; Royle et al., 2002). However, despite this long tradition of studying parental care, most empirical studies quantify parental effort using relatively short observation periods, often restricted to particular times of day, a limited number of days, or single breeding stages (Pou-Rossell et al. under revision.; Chapter 2). Such snapshots can only provide partial insights into how parental behaviour unfolds across the complete reproductive cycle, from nest construction through incubation and provisioning to fledging. We still know little about how parental care is structured across the full breeding cycle and how pairs change their behaviour between stages.

Understanding stage-to-stage parental care dynamics is important because the functions and constraints of care differ markedly across the breeding cycle (Mock, 2022) and are influenced by shifting physiological and environmental conditions (Kulaszewicz et al., 2018; Mota-Rojas et al., 2023; Simmonds et al., 2017). For example, nest attendance during incubation is closely tied to thermoregulation and embryo development, whereas during provisioning it may reflect brooding, guarding, and time allocation relative to foraging (Higgott et al., 2020; Johnstone & Hinde, 2006; Martin et al., 2007). More broadly, nest construction, incubation, and chick provisioning differ fundamentally in their functional demands, meaning that the same pair may need to reorganise both the amount and form of care it provides as breeding progresses. Different stages may also contribute unevenly to reproductive success (Mueller et al., 2019), raising the possibility that similar overall breeding outcomes could arise through different stage-specific pathways of

parental investment. At the same time, it remains unclear how pairs change relative to each other across these stages, that is, whether differences among pairs are maintained, amplified, or reduced as breeding progresses, or whether stage-specific patterns reflect stable investment tactics or flexible responses to changing conditions.

Understanding how parental care changes across breeding stages is only part of the picture. In species with biparental care, variation can also arise in how care is organised between partners. This is particularly relevant in birds, in which approximately 90–95% of species exhibit biparental care, with both parents contributing to different tasks throughout the breeding season (Cockburn, 2006). Classic theory emphasises that parents must balance current offspring needs against self-maintenance and future reproduction, with the scope for conflict, compensation or coordination changing across time and context (Trivers, 1972; Williams, 1966). The existence of such sexual conflict between partners is well established (Griffith, 2019; Harrison et al., 2009; Royle et al., 2002), and increasing evidence shows that parents often coordinate their parental efforts (Baldan & van Loon, 2022; Wojczulanis-Jakubas et al., 2023) and adjust their investment in response to their partner's behaviour and offspring demands (Hinde & Kilner, 2007; Johnstone & Hinde, 2006; Lessells & McNamara, 2012). Despite the well-documented importance of bi-parental care for reproductive success (Iserbyt et al., 2019; Mariette & Griffith, 2015; Sanz et al., 2000; Soler, 2014), many studies still quantify parental care using additive measures of total effort, such as feeding rates or overall nest attendance, effectively collapsing biparental behaviour into a single dimension. While informative, such measures can obscure how care is organised between partners, although the temporal organisation of care, not just its total amount, can be critical for reproductive success (Johnstone & Hinde, 2006; Royle et al., 2012; Trapote, 2023).

The way care is organised between partners may itself differ across breeding stages, because the extent to which simultaneous presence versus staggered attendance is advantageous is likely to depend on the task demands and constraints of the breeding cycle, for example during nest construction, incubation, or provisioning (Hahn et al., 2021; Iserbyt et al., 2017; Mariette & Griffith, 2015). Conversely, poor pair coordination can result in increased parental fatigue and reduced offspring survival, ultimately lowering fitness (Leniowski & Węgrzyn, 2018; Royle et al., 2002). Natural selection may therefore act not only on total care, but also on how care is organised within pairs across time, potentially making the breeding pair an important unit of variation (Björklund & Gustafsson, 2013). More generally, understanding behavioural variation among pairs within the same population is important because it reveals how much parental effort can diverge even under broadly similar ecological and social conditions. However, we still know

little about how such variation is expressed across the breeding cycle, particularly in terms of how joint versus solo attendance is structured and changes over time.

Here we use continuous monitoring of wild jackdaws (*Corvus monedula*), a hole-nesting bird with altricial development, to quantify the temporal structure of nest attendance across the complete breeding cycle, from nest construction through incubation and chick provisioning to fledging. Parental nest attendance was continuously monitored at 1-s resolution using a solar-powered, automated Raspberry Pi camera system deployed at a breeding colony throughout two entire breeding seasons (Pou-Rossell et al., 2025; Chapter 3). Using nest attendance states (0, 1, or 2 birds present), we characterise both total attendance, defined as the presence of any parent, and joint attendance, defined as the simultaneous presence of both parents, across the breeding stages. This allows us to address two linked questions: first, how total and joint attendance patterns change across the breeding cycle, and second, whether pair differences in these forms of attendance are consistent over time or reorganised as parental tasks shift. Because the functional demands of reproduction change markedly across stages, we predict that both attendance metrics will vary across the breeding cycle, but not in the same way, with total attendance necessarily increasing during incubation but joint attendance being less restricted across stages. We also predict that joint attendance captures a distinct dimension of biparental behaviour that is not fully reflected in additive measures of total attendance, and that pair differences will be more consistent within broad reproductive phases but less consistent across transitions between them.

5.2 Methods

Study system and species

Our study was conducted using a long-term monitored population of wild jackdaws that breed colonially in artificial nest box towers across Lleida, north-eastern Spain (see Chapter 1 for general study-system background). We focused on one of these towers where our automated monitoring system was deployed at 14 nests during 2023 and 12 nests during 2024. Jackdaws provide bi-parental care, with both sexes contributing to nest building, incubation-related activities, and chick provisioning, with females often investing more in material transport and incubation and males more in vigilance/guarding, and considerable variation among pairs and individuals (Hahn et al., 2021; Lockie, 1955; Röell, 1978).

Behavioural and phenology data collection

Parental nest attendance was monitored continuously using a solar-powered automated Raspberry Pi camera system, described in detail in Chapter 3 (Pou-Rossell et al., 2025). The system captured synchronised images from inside each nest box at a rate of one frame per second, from sunrise to sunset, every day throughout the breeding season (15 March to 15 July). We installed all electronics before nest construction began to minimise disturbance, and the system operated autonomously with minimal intervention until after fledging, when it was removed once jackdaws had left the breeding site. In total, we collected approximately 25 million frames each year. To determine breeding phenology for each pair, nest boxes were visited four days per week, typically for less than 30 min per visit. These checks were used to record occupancy, laying date (date of first egg), clutch size, and hatching date (date of first chick hatching) as precisely as possible.

Data processing

Images collected by the monitoring system were processed using a custom YOLOv8 computer-vision model trained to detect adult jackdaws in nest-box images (Jocher et al., 2023), as described in detail in Chapter 3 and Appendix B.4. Because jackdaws are monomorphic and our computer-vision model could not reliably distinguish individuals, we did not quantify individual-specific attendance. Instead, for each frame, detections were converted into an attendance state based on the number of adults present in the nest box (0, 1, or 2 individuals). Even though our computer vision model was highly accurate overall, it increasingly confounded adults with fledglings from the day 16 after hatching onwards. We therefore restricted all post-hatching analyses to the first 14 days after hatching. To reduce the influence of short false positives and false negatives, we applied a conservative interpolation step: when the detected number of birds differed from the surrounding frames for short sequences of fewer than 5 s, those values were replaced using the adjacent states. Longer changes were retained as true state changes, given the high overall model accuracy (Pou-Rossell et al., 2025; see Appendix B.5). From these corrected frame-by-frame attendance states, we summarised daily attendance as the number of seconds spent in the nest by 0, 1, or 2 adults. For each pair and day, we then derived two attendance metrics: (i) *total attendance*, defined as the proportion of monitored time in which at least one parent was present, and (ii) *joint attendance*, defined as the proportion of attended time in which both parents were simultaneously present.

In our population, females typically lay three to seven eggs from late April to mid-May, incubation lasts ~18–22 days, and chicks fledge ~32–35 days after hatching. Using the laying and hatching dates obtained from nest-box checks, we assigned each daily record to one of four breeding stages: nest building, incubation, first week after hatching and second week after hatching. The nest-building stage was defined as the 3-week period preceding laying of the first egg. Although pairs likely differ in the exact onset and duration of nest construction, this standardised window allowed consistent comparisons among pairs. Incubation was defined from clutch completion to the day the first egg hatched. Jackdaws typically lay one egg per day until clutch completion and females may delay full incubation until the clutch is complete (Cooper & Voss, 2013; Wang & Beissinger, 2009; Wiebe et al., 1998). Consistent with this, exploratory analyses showed a progressive increase in nest attendance during clutch completion, after which attendance patterns more clearly reflected full incubation (see Appendix D; Fig. D.1). We therefore used clutch completion as the start of the incubation phase. The post-hatching period was divided into days 0–6 and days 7–13 days after first hatching. This distinction was biologically relevant because some pairs continued incubating unhatched eggs during the first week, whereas by the second week, all viable eggs had hatched.

Data analysis

All analyses were conducted on daily attendance proportions. Because only one full pair was observed breeding in both years, each pair-year combination was treated as a unique breeding attempt. The final dataset comprised 1,102 daily records from 26 breeding attempts spanning nest building to 14 days post-hatching.

To estimate population-level stage differences while simultaneously quantifying stage-specific among-pair variation and cross-stage consistency, we fitted linear mixed-effects models (LMMs) separately for total and joint attendance using *lme4* (Bates et al., 2015). We used Gaussian models on the proportion scale because they provided a single, interpretable framework from which we could estimate stage means, stage-specific among-pair variances, cross-stage correlations, and repeatability. Each model included breeding stage and year as fixed effects, and stage-specific random effects for pair identity. We specified the random-effect structure as $(0 + \text{stage} | \text{pair identity})$, which allowed the variance-covariance matrix to directly estimate among-pair variation separately for each stage, as well as the correlations among pair effects across stages. For ease of interpretation, we report among-pair variation as standard deviations rather than variances. Models were fitted using REML.

We obtained estimated marginal means and 95% confidence intervals for each stage using *emmeans* (Searle et al., 1980), and report these on the proportion scale. To test sequential changes across the breeding cycle, we performed planned contrasts between adjacent stage: nest building versus incubation, incubation versus first week post-hatching, and first week post-hatching versus second week post-hatching. To assess whether breeding attempts with higher total attendance also showed higher joint attendance, we modelled joint attendance as a function of total attendance, controlling for year and including a random intercept for pair identity.

To quantify how consistently pairs maintained their relative attendance across days within each stage, we calculated stage-specific repeatability as the intraclass correlation between among-pair variance and total variance from the Gaussian models. Cross-stage consistency in pair strategies was quantified directly from the estimated correlation matrix of the stage-specific random effects, that is, from the model-estimated correlations among pair effects across stages. Confidence intervals for repeatability and cross-stage correlations were obtained by parametric bootstrapping with 1,000 simulations. For descriptive purposes, we also estimated an overall repeatability across all stages from a simpler model including a pair random intercept. To summarise pair-level attendance structure across the four stages, we conducted principal component analyses (PCA) on stage-specific pair means for each attendance metric, excluding three pairs with missing stage-specific means.

While Gaussian and variance assumptions, including normality of residuals and homoscedasticity were reasonably met (see Appendix D), we conducted sensitivity analyses to assess whether alternative modelling choices influenced our conclusions (Appendix D). Specifically, we compared the Gaussian models on the raw proportion scale with models fitted to logit-transformed proportions, and with weighted Gaussian models using weights proportional to the number of available frames, to account for daily recording time among days and pairs. These alternative models yielded qualitatively similar stage patterns (see Appendix D.1; Table D.1), supporting the robustness of the main results. We report the unweighted Gaussian models because they offered the most straightforward framework for variance partitioning, repeatability estimation, and cross-stage comparison. All analyses were performed in R version 4.5.2 (R Core Team, 2023).

5.3 Results

Mean attendance patterns across the breeding cycle

The jackdaw pairs differed considerably in the average time devoted to care during each breeding stage, and in different ways for total and joint attendance (Fig. 5.1). Total attendance rose strongly from nest building to incubation ($\beta = 0.48 \pm 0.02$ SE, $p < 0.0001$), then declined across the two post-hatching stages (incubation to first week post-hatching: $\beta = -0.16 \pm 0.02$ SE, $p < 0.0001$; first to second week post-hatching: $\beta = -0.29 \pm 0.03$ SE, $p < 0.0001$; Fig. 5.1a). On average, pairs spent 43% of the monitored time in the nest during nest building (mean [95% CI]: 0.43 [0.39–0.47]), 91% during incubation (0.91 [0.90–0.92]), 76% in the first week after hatching (0.76 [0.71–0.80]), and 46% in the second week post-hatching (0.46 [0.38–0.55]). By contrast, joint attendance dropped sharply from nest building to incubation ($\beta = -0.34 \pm 0.02$ SE, $p < 0.0001$) and remaining close to zero throughout the provisioning period (incubation to first week post-hatching: $\beta = -0.06 \pm 0.02$ SE, $p < 0.001$; first to second week post-hatching: $\beta < 0.01 \pm 0.01$ SE, $p = 0.952$; Fig. 5.1b). Pairs spent 43% of attended time together during nest building (0.43 [0.39–0.48]) but only 10% during incubation (0.10 [0.07–0.12]), after which joint attendance remained very low, at around 3% of the attended time in both post-hatching stages.

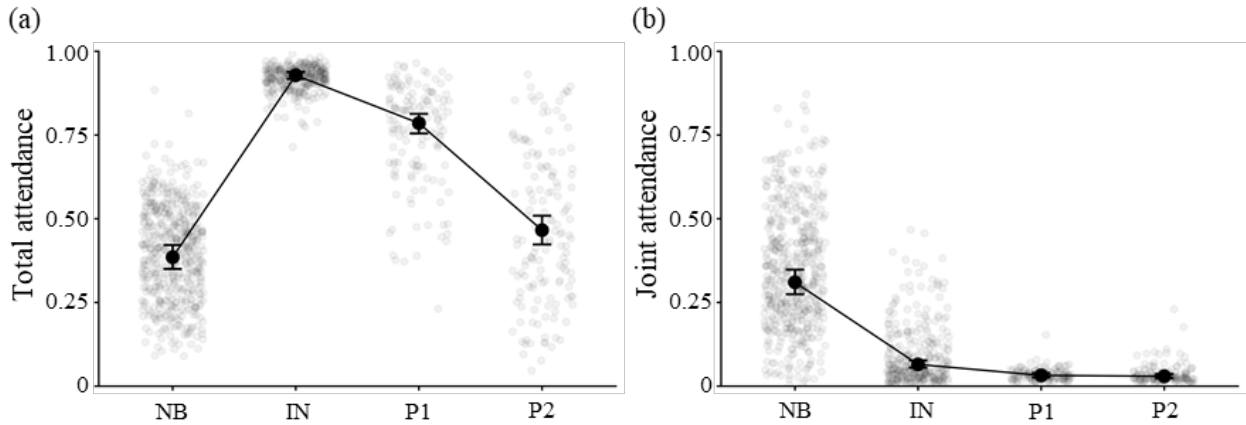


Figure 5.1 Stage-specific population-level means of (a) total attendance and (b) joint attendance. NB = nest building, IN = incubation, P1 = first provisioning week, and P2 = second provisioning week. Grey dots show raw daily observations for all pairs within each stage. Black points show population-level estimated marginal means $\pm$ SE from the Gaussian model, controlling for year.

Pair-level differences within stages

Among-pair variation within breeding stages varied strongly across the breeding cycle (Fig. 5.1). For total attendance, among-pair variation was moderate during nest building ($SD \approx 0.11$), almost absent during incubation ($SD \approx 0.01$), and increased again after hatching ($SD \approx 0.10$), reaching its highest level during the second week post-hatching (first week: $SD \approx 0.10$; $SD \approx 0.20$). For joint attendance, among-pair variation was greatest during nest building ($SD \approx 0.10$), lower during incubation ($SD \approx 0.05$), and almost absent during both provisioning stages ($SD < 0.004$). Thus, the stages in which among-pair variation was higher differed between both attendance metrics.

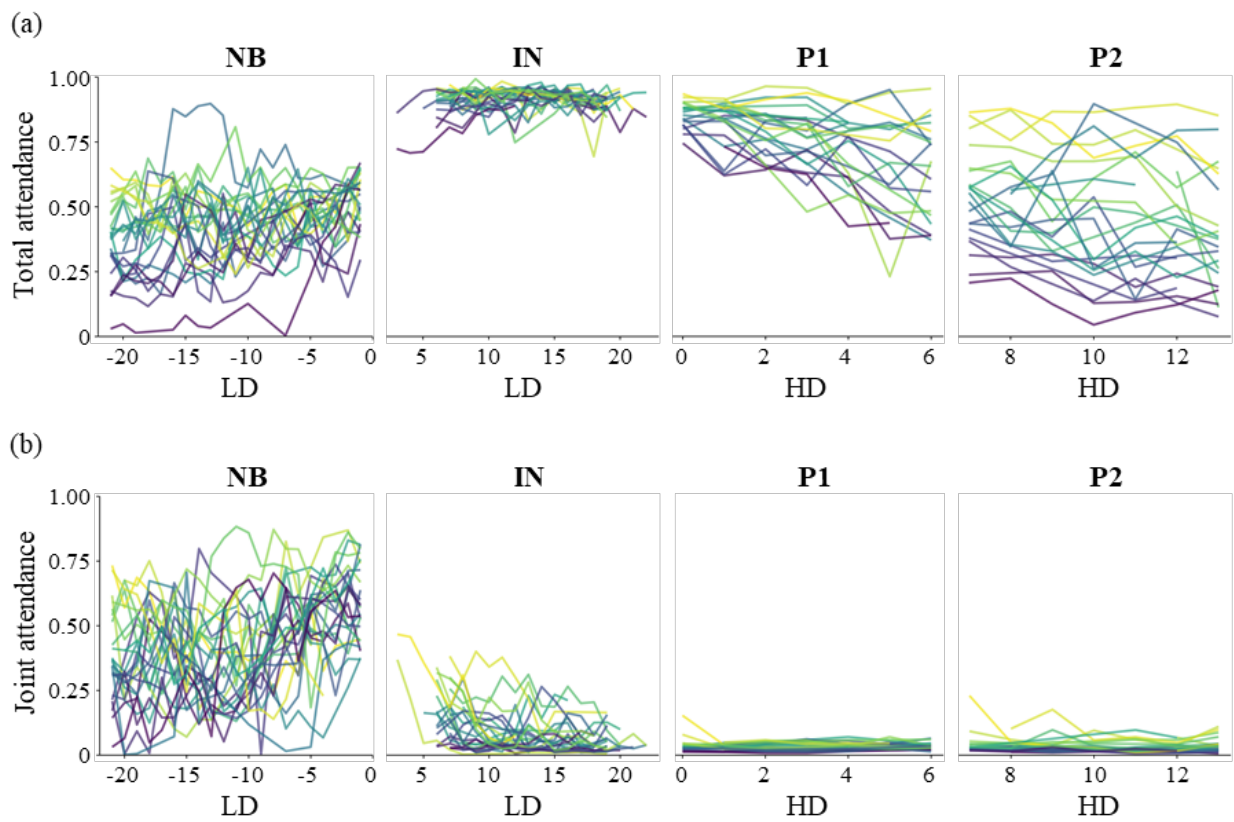


Figure 5.2 *Pair-level day-to-day attendance patterns within breeding stages.* Total attendance (a) and joint attendance (b) are plotted against time, measured relative to laying date (LD) or hatching date (HD). Colours indicate pair identity. Within each stage, pairs are ordered by their value on the first day shown to facilitate visual comparison of relative pair rankings across subsequent days. NB = nest building, IN = incubation, P1 = first provisioning week, and P2 = second provisioning week.

These patterns of variation were reflected in day-to-day trajectories and repeatability estimates within stages (Fig. 5.2). For total attendance, repeatability was highest during the second week of provisioning ($R = 0.782$ [0.69–0.88]), intermediate during nest building (0.57 [0.41–0.68]) and the

first week of provisioning (0.52 [0.31–0.66]), and close to zero during incubation (0.01 [0.001–0.06]). The very low repeatability during incubation reflects the fact that nearly all pairs attended the nest almost continuously at this stage, leaving little scope for among-pair variation. Joint attendance showed a different within-stage pattern: repeatability was highest during nest building ($R = 0.44$ [0.28–0.55]), lower during incubation ($R = 0.18$ [0.07–0.28]), and effectively absent during provisioning (week 1: $R = 0.00$ [0.00–0.11]; week 2: $R = 0.00$ [0.00–0.08]). Overall, pair differences were most clearly maintained in stages where there was sufficient among-pair variation and least informative when attendance values were compressed near their floor or ceiling.

Consistency of pair differences across stages

Overall repeatability of total attendance across stages was moderate ($R = 0.28$ [0.16–0.40]), indicating that some pair differences persisted across the breeding cycle. Pairwise cross-stage correlations showed that this consistency was strongest between the post-hatching stages, with attendance during the first week after hatching positively correlated with attendance during the second week post-hatching ($r = 0.88$ [0.71–0.99]; Fig. 5.3a). There was also weaker evidence that pairs with relatively high total attendance during nest building tended to remain relatively high during the first post-hatching week ($r = 0.42$ [0.01–0.75]). By contrast, correlations involving incubation were imprecisely estimated and did not provide clear evidence for consistency across stages (nest building to incubation: $r = 0.61$ [–0.78–1.00]; incubation to first week post-hatching: $r = 0.58$ [–0.53–0.98]), likely because among-pair variation during incubation was strongly reduced.

Overall repeatability of joint attendance across stages was lower, but still non-zero ($R = 0.18$ [0.10–0.26]), again indicating limited persistence of pair differences across the breeding cycle. However, pairwise cross-stage correlations provided limited clear evidence that pairs maintained their relative rankings in joint attendance across successive stages, as all confidence intervals overlapped zero after bootstrapping (nest building and incubation: $r = 0.33$ [–0.18–0.75], incubation and first week post-hatching: $r = 0.98$ [–0.99–0.99]; first and second week post-hatching $r = 0.41$ [–1.00–0.99]; Fig. 5.3b). Thus, unlike total attendance, joint attendance showed little clear carryover of pair differences across stages because all pairs showed very little joint attendance in the later stages.

Principal component analyses broadly supported these patterns. For total attendance, the first two components explained 85.4% of the variation among pairs (PC1 = 60.7%, PC2 = 24.7%). PC1

loaded similarly across all four stages, consistent with an overall tendency for some pairs to attend more than others across the breeding cycle, whereas PC2 contrasted the early breeding stages with the post-hatching stages, indicating a redistribution of attendance effort across reproduction. For joint attendance the first two components explained 67.5% of the variation (PC1 = 38.9%, PC2 = 28.6%) and mainly separated pre-hatching from post-hatching joint attendance, further suggesting that pair differences in joint attendance were structured differently before and after hatching.

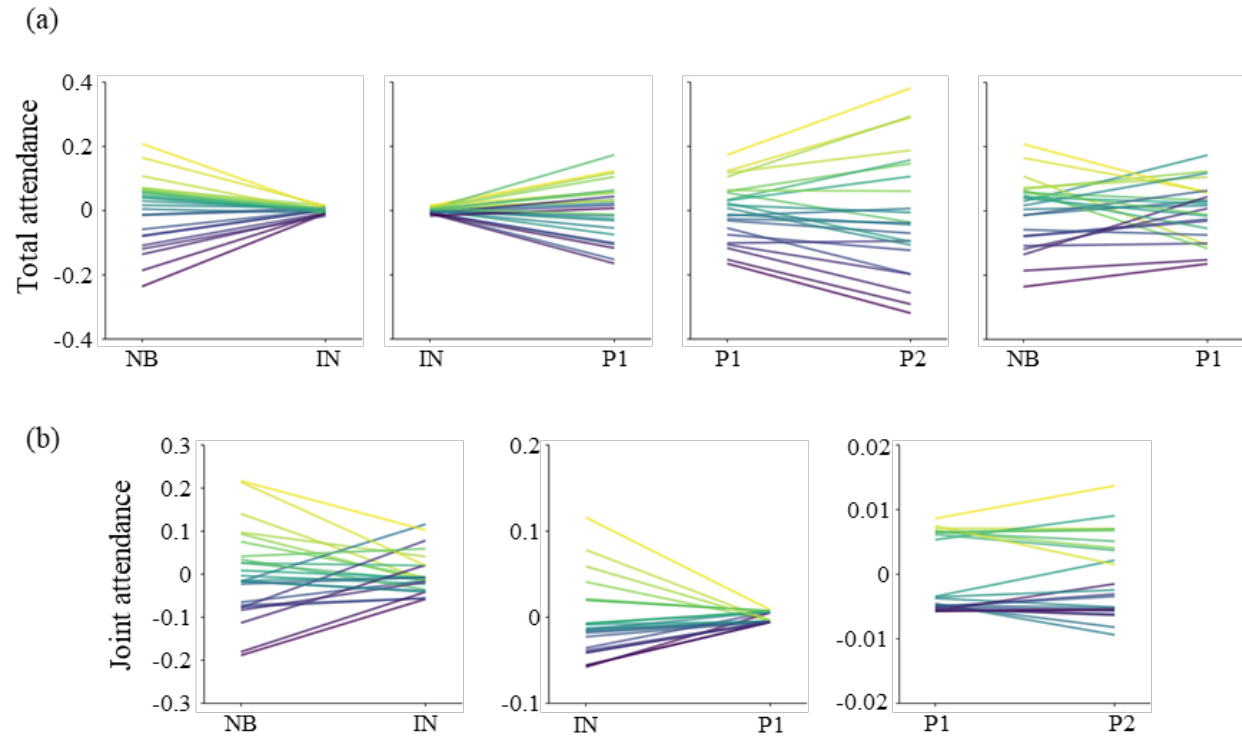


Figure 5.3 Cross-stage correlation of pair-level mean behavioural estimates. (a) Correlations of mean-centred total attendance and (b) mean-centred joint attendance between pairs of breeding stages. Colours indicate pair identity. Within each paired-stage comparison, pairs are ordered by their value in the first stage to facilitate visual assessment of whether pair rankings are maintained in the subsequent stage. NB = nest building, IN = incubation, P1 = first provisioning week, and P2 = second provisioning week.

Relationship between total and joint attendance

The relationship between total and joint attendance differed across the breeding stages (Fig. 5.4). During nest building, when both metrics showed substantial among-pair variation, pairs with higher total attendance also tended to show higher joint attendance ($\beta = 0.75 \pm 0.06$ SE, $p < 0.0001$; Fig. 5.4a). In other words, pairs that spent a higher proportion of their time together than alone in the nest also spent more time in the nest overall. During incubation, the association was negative ($\beta = -0.24 \pm 0.10$ SE, $p = 0.018$; Fig. 5.4b), although interpretation is limited because

total attendance was strongly constrained near its upper bound. After hatching, no clear relationship was detected between the two metrics, with total and joint attendance not correlated for both the first week post-hatching ($\beta = -0.003 \pm 0.01$ SE, $p = 0.722$; Fig. 5.4c) and the second week post-hatching ($\beta = 0.01 \pm 0.01$ SE, $p = 0.501$; Fig. 5.4d), when joint attendance remained near zero for almost all pairs.

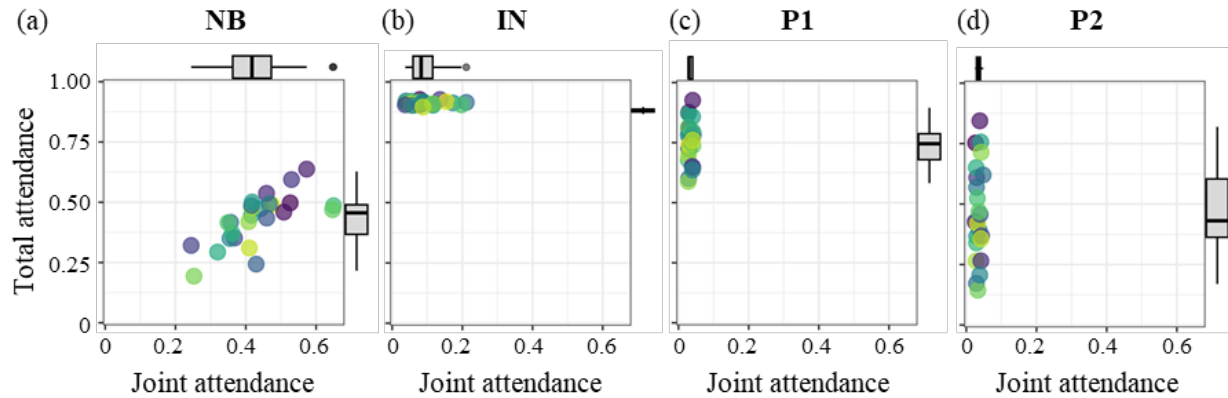


Figure 5.4 Relationship between total and joint attendance within each breeding stage. (a) nest building, (b) incubation, (c) first week post-hatching, and (d) second week post-hatching. Each point represents the predicted mean within-stage value for a pair; colours indicate pair identity. Marginal boxplots summarise the distribution of pair means within each stage.

5.4 Discussion

In this study, we used continuous monitoring of wild jackdaws to quantify how nest attendance is organised across the breeding cycle. We show that attendance is strongly restructured across the breeding stages, not only in mean levels but also in how variation among pairs is expressed and how care is distributed between solitary and joint presence. Total and joint attendance followed distinct temporal trajectories, with each metric revealing different aspects of parental behaviour at different stages. While previous work has suggested that these dimensions of attendance can differ (Grissot et al., 2024; Wang et al., 2023), our continuous high-resolution data reveal how these differences unfold across the full breeding cycle and how they shape the expression of pair-level variation. These results indicate that additive measures of parental effort alone can miss important aspects of how care is organised, and that inferences about conflict or cooperation based on from a single stage may not generalise across the breeding cycle.

During the nest-building stage, both population-level means and among-pair variation was high for total as well as joint attendance. This pattern suggests that pairs differ substantially in how

much time they allocate to behaviours happening in the nest during this period (e.g., resting in the nest, nest construction, or nest-site defence), which may reflect variation in pair-bond strength (Hahn et al., 2021, 2025). In contrast, during incubation, among-pair variation in total attendance was minimal and total attendance approached its upper bound for all pairs. This likely reflects strong functional constraints, as successful incubation requires that at least one parent maintains appropriate conditions for embryo development, thereby limiting the scope for behavioural divergence among pairs in the proportion of time the nest is attended (Carey, 1980; Hepp & Kennamer, 2018). However, this convergence in total attendance during incubation does not deny the existence of different roles among sexes. Although we could not distinguish individuals in our dataset, jackdaw incubation is known to be performed primarily by females, whereas males provide most food to their incubating partners (Henderson et al., 2000). This means that the limited variation observed in total pair-level attendance during incubation may largely reflect the fact that females are almost continuously constrained to remain in the nest, while differences among pairs may arise more from variation in male behaviour. Male presence during incubation may therefore form part of a broader coordination system that includes courtship feeding and, depending on context, vigilance, nest defence or mate guarding (Hahn et al., 2021; Kokko & Morrell, 2005; Møller & Birkhead, 1991). Thus, even when total attendance converged across pairs, meaningful variation persisted in how attendance is organised between partners, particularly in the extent to which they attend jointly.

After hatching, joint attendance was close to zero for all pairs, indicating that simultaneous nest attendance is not a common strategy during the provisioning stages. In contrast, total attendance declined progressively, with some pairs spending only around 10% of the day in the nest and others remaining there for close to 80%. During the first post-hatching week, total attendance remained relatively high, with relatively high among-pair variation. One possible explanation is that some clutches could still be completing hatching if eggs hatch asynchronously, and such broods may require continued brooding or incubation shortly after first hatching (Wang & Beissinger, 2009; Węgrzyn et al., 2023). By the second week, total attendance dropped further while among-pair variation increased markedly. At this stage, all viable eggs should have hatched already, and larger chicks were probably better able to thermoregulate (Andreasson et al., 2016), reducing the need for prolonged nest attendance. However, asynchronously hatched broods may still require extended brooding of younger chicks, potentially constraining pairs differently and thereby contributing to the observed increase in variation. These stage-specific differences in brood demands may therefore help explain both the marked among-pair variation in total

attendance during the post-hatching period and the high within-stage repeatability observed across the two provisioning stages. This possibility will be explored further in follow-up work.

At the same time, lower nest attendance during provisioning does not necessarily imply reduced parental care, as pairs may differ in brood size, prey type, visit duration, or provisioning frequency. For example, some pairs may deliver food through frequent short visits, whereas others may spend longer periods inside the nest without providing more food overall. In addition, under warm conditions, parents may reduce time spent in the nest to avoid overheating chicks, especially in larger broods, thereby lowering nest attendance without necessarily reducing care (Johnson & Best, 1982), which will be the focus of future work.

Additionally, because joint attendance was minimal for all pairs during the provisioning period, reduced total attendance in the post-hatching stages can have different interpretations. It may reflect a coordinated reduction in nest attendance by both parents, without necessarily implying a proportional reduction in overall care if care is being delivered mainly through brief provisioning visits. Alternatively, it may reflect a decline in overall care if one parent reduces or ceases its contribution, forcing the other to compensate with a higher workload (Hinde, 2006; Johnstone & Hinde, 2006). Thus, low joint attendance after hatching does not imply an absence of cooperation, as cooperation may instead be expressed through temporal coordination, such as visit alternation or through complementary division of tasks between partners (Baldan et al., 2019; Pilakouta et al., 2018). Because individuals could not be identified in our dataset, we could not directly test for alternation, sex-specific roles or responsiveness to partner behaviour. Even so, our continuous dataset provides detailed insights on the temporal organisation of attendance across multiple scales, allowing us to compare pair-level attendance and the degree of overlap between partners throughout the breeding cycle.

Within stages, pairs often retained similar rank positions relative to one another from day to day, but this pattern differed between attendance metrics and breeding stages. For total attendance, day-to-day consistency in pair rank was highest during the provisioning stages, suggesting stable pair-specific differences under broadly similar post-hatching constraints. By contrast, day-to-day consistency in total attendance was lower during nest building even though among-pair variation was high, which may indicate that behaviour at this stage is more flexible, perhaps because it is less constrained by immediate brood demands. Ceiling effects in total attendance during incubation, likely reduced day-to-day repeatability by compressing variation among pairs. For joint attendance, day-to-day consistency was high only during nest building, but low during

incubation and absent during the provisioning stages. Again, compressed variation among pairs in joint attendance during post-hatching stages likely reduced day-to-day repeatability.

Across stages, pairs also showed some consistency in their relative differences.

Cross-stage repeatability was relatively high within the two post-hatching weeks for total attendance, and stronger within the pre-hatching period for joint attendance, whereas it was weaker across the hatching transition for both attendance metrics. This discontinuity should not necessarily be interpreted as inconsistency in pair behaviour across the breeding cycle, but rather as evidence that attendance strategies are reorganised in response to changing reproductive demands across stages, especially around the hatching transition.

Future work should build on these findings by linking continuous pair-level monitoring with information on individual identity and additional components of care. Identifying individuals would allow to determine whether the stage-specific patterns described here arise from stable sex-specific roles, from differences in how much each parent contributes and how both parents coordinate their care (i.e. visit alternation or synchronisation), or from how partners adjust their behaviour to one another through time. More broadly, combining attendance data with more detailed measures such as material delivery during nest building, incubation schedules, provisioning rate, prey type, and off-nest activity would help clarify which components of care are most closely associated with reproductive performance across stages such as nest structure, hatching success, or offspring body condition. Such approaches would provide a more complete understanding of how parental care is organised, how flexible it is under different constraints, and how pair-level strategies translate into fitness outcomes.

Our results show that parental attentiveness cannot be adequately captured by a single attendance metric applied uniformly across the breeding cycle. Both the amount of attendance and the way care is organised vary across stages, and the expression of pair differences depended strongly on the functional demands of each breeding stage. These findings indicate that parental care is not a fixed trait expressed uniformly through time, but a dynamic and continuously reorganised process, in which both the level and temporal organisation of care shift in response to changing reproductive demands across the breeding cycle. This highlights the importance of explicitly accounting for stage-specific variation in studies of parental care.

Chapter 6

General discussion

Parental care has been a central topic in behavioural ecology for more than a century and has generated a rich and well-developed body of work, particularly in birds (Clutton-Brock, 1991; Cockburn, 2006; Royle et al., 2012). This research has clarified how parental investment varies across individuals and environments (Santos & Nakagawa, 2012; Schneider & Griesser, 2015; Tieleman et al., 2008), how partners negotiate their contributions (Hinde, 2006; Johnstone & Hinde, 2006; Wang et al., 2023), and how care strategies both reflect and influence life-history trade-offs and reproductive success (Stearns, 1976; Williams, 1966). Parental behaviour is therefore not only considered a major determinant of fitness, but also as a clear manifestation of how reproductive decisions shape the ecology and evolution of natural populations.

Despite these advances, important aspects of parental care remain poorly resolved. In particular, we still have limited understanding of how care unfolds continuously across the full breeding cycle, how parental contributions change at fine temporal scales, and how different dimensions of care vary among pairs over time. A major reason is that monitoring parental care in the wild remains logistically difficult and data collection has often been restricted to short or selective observation windows. As a result, many studies still rely on snapshots of behaviour that may not properly reflect its full temporal structure.

In this thesis, I aimed to help address this gap by developing and applying a novel monitoring approach that combines open electronics with computer vision to enable continuous, scalable, and standardised behavioural measurement. First, I showed that methods used to quantify parental behaviour are highly heterogeneous across the literature and frequently rely on selective monitoring schedules that capture only snapshots of parental investment across the breeding season (Chapter 2). Next, I described the development of a centralised, multi-unit monitoring system designed to collect continuous data throughout the breeding period of wild jackdaws, integrating Raspberry Pi single-board computers with YOLO-based computer vision pipelines (Chapter 3). Using the continuous dataset collected by this system, I then demonstrated how simulated partial monitoring schedules can introduce noise and bias in behavioural estimates when compared with the full monitoring dataset (Chapter 4). Finally, leveraging these complete observations, I showed that nest attendance patterns change markedly across the breeding season and highlighted the value of distinguishing additive parental care from joint parental care as a complementary axis of variation among pairs (Chapter 5). In this final chapter, I summarise the main findings, integrate them into the current knowledge, discuss key limitations, and outline future directions for the study of parental care.

6.1 Diversity of methods to quantify parental care

By definition, parental care encompasses all behaviours that are aimed at increasing offspring survival and development, including nest building, incubation routines, brooding, provisioning, and predator defence. Many of these behaviours occur intermittently, vary across stages, and are sensitive to environmental conditions (Clutton-Brock, 1991; Mock, 2022; Royle et al., 2012). Quantifying parental investment is therefore inherently challenging, particularly in wild systems where field access, weather, disturbance risk, and labour constraints limit observation time. The biological diversity of parental behaviour, together with logistical limitations in behavioural monitoring in the field, also leads to the use of highly heterogeneous approaches. Thus, parental care is frequently measured through proxies that are not directly comparable across studies, and even apparently similar metrics (such as nest attendance) may reflect different behaviours depending on how, when, and where observations are conducted. There is therefore an urgent need for more detailed, temporally comprehensive, and standardised data to better characterise how parental care is organised, how it changes over time, and how it responds to fluctuating ecological and social conditions. Chapters 2 and 4 directly addresses these problems.

In Chapter 2, I conducted a literature review that showed that parental care is commonly monitored only partially, with sampling concentrated in restricted temporal windows. Many studies rely on short observation sessions, often scheduled in the morning or around periods of expected activity, and monitoring is frequently limited to a subset of days within a stage, most likely during the offspring provisioning period. This approach is understandable given the practical costs of continuous monitoring, but it has two important caveats. First, partial schedules may systematically under-sample behavioural events that occur outside the chosen window (e.g., late-day provisioning peaks, compensatory behaviours after a disturbance, or stage-specific shifts in daily routines). Second, even when the same monitoring schedule is applied across pairs, the resulting estimates can be uneven in precision because individuals and pairs differ in when they express care. Thus, the combination of biological temporal structure and selective observation effort can generate both noise (reduced precision) and bias (systematic deviation), with the direction and magnitude depending on the behaviour quantified and the sampling design.

The parental care literature is extremely large, an inevitable reflection of the diversity of species, field conditions, and scientific goals, and hence some behaviours and approaches were not fully represented in our sample (including detailed measures of nest building, incubation behaviour, and post-fledging care). This review was not intended to provide a comprehensive survey of all

approaches, nor to critically evaluate or rank specific study designs. Instead, by randomly selecting a subset of studies, we seek to identify common patterns in how parental care is typically monitored and reported, and to highlight recurring challenges that could affect interpretation of behavioural estimates. Indeed, in Chapter 4, I used simulations based on continuous parental effort data (see Chapter 3) to demonstrate that restricting observation schedules can introduce both noise and bias in behavioural estimates, by simulating the partial monitoring schedules previously identified in the literature and comparing the resulting estimates with those obtained from continuous monitoring across the full observation period. Importantly, I found that behavioural estimates depend more on how sampling effort was distributed across the breeding period than on the total amount of data collected. These findings emphasise the importance of accounting for both study design and the temporal structure of behaviour, while balancing logistical constraints with strategically timed observations (Altmann, 1974; Martin & Bateson, 2007; Naguib et al., 2023).

Chapter 4 also showed that although pair-level estimates could change substantially under different sampling schedules, partial monitoring can still be informative for describing population patterns. However, even though the within-season temporal coverage was exceptionally high, we acknowledge that our simulations were based on a single breeding season and used a limited number of pairs. Expanding these analyses across additional years and more pairs will be an important next step, and we are now doing so to test how robust these findings are. At the same time, our results already indicate that changing the observation window can alter what is observed, even within a single pair. Therefore, continuous monitoring should be considered the gold standard for estimating parental investment because it maximises temporal coverage and reduces reliance on assumptions.

A key implication of Chapters 2 and 4 is that there is substantial room for standardisation in reporting, even though there may never be a single “standard” protocol suitable for all study systems. Across the literature, essential methodological details are often inconsistently described, including the exact timing of observations, the distribution of sampling effort across days and stages, the criteria used to define behavioural events, and the extent of missing data or unobserved periods. This lack of reporting consensus limits both comparability and replicability. Without clear documentation of when observations took place and what proportion of the relevant period they represent, it becomes difficult to assess whether differences among studies reflect biological variation or methodological effects on behavioural estimates (as highlighted in Chapter 4). In this context, this thesis outlines practical guidelines for reporting parental care methods, with the aim

of improving transparency, comparability, and the interpretability of behavioural estimates across studies.

6.2 The potential of Open Electronics and computer vision

Open Electronics provide a particularly effective pathway to improve the temporal coverage and continuity of behavioural monitoring in the wild. Compared to many commercial solutions, Open Electronics can lower barriers to tool development and deployment by making designs modular, customised to the constraints of a given study system and repairable and upgradable over time (Oellermann et al., 2022). When the design and code of open systems are accessible, researchers can evaluate methodological decisions, replicate pipelines, and build on existing solutions rather than reinventing systems in isolation, improving reproducibility. These attributes are especially valuable for long-term field studies, where data continuity can matter as much as the detail of the measurements (Altmann, 1974; Naguib et al., 2023). Automated monitoring systems can make data collection more practical especially in remote locations, reducing the need of repeated site visits and minimising disturbance in studies where human presence can alter behaviour (Jolles, 2021; Pou-Rossell et al., 2025). When continuous recording is combined with modern computer-vision tools, raw image-based data can be processed far more efficiently, enabling behavioural quantification at temporal and behavioural resolutions that were rarely feasible before (Chan et al., 2024; Ferreira et al., 2020). Although this thesis focuses on parental care of birds, the same logic applies more broadly. Many ecological processes are inherently temporally structured, and increased temporal resolution and continuity can reveal dynamics that would otherwise remain hidden, from diel and seasonal soundscape dynamics in acoustic communities (Yoh et al., 2024) to shifts in daily activity patterns of wild animals (Tan et al., 2013), and high-frequency hydro-chemical dynamics in rivers (Rozemeijer et al., 2025). This highlights the wider potential of continuous monitoring approaches to uncover fine-scale temporal structure across ecological systems.

In Chapter 3, I presented a centralised monitoring system I developed to autonomously record continuous parental effort throughout the breeding season under field conditions. The system was designed not simply to record a single nest, but to optimise the simultaneous monitoring of parental care across multiple breeding pairs. It is modular and scalable across multiple nest boxes, solar-powered, and connected to the internet to enable remote access, data transfer, and system performance monitoring. By combining multiple units in a centralised scheme, the system made

it possible to obtain synchronised long time series of nest-level behaviour with minimal disturbance. This provided the temporal coverage required to quantify temporally detailed attendance dynamics across the breeding stages and establishes a strong foundation that can now be extended to provide an even richer picture of parental care.

One natural next step is to improve the link between detections and individual identity. Because jackdaws are largely monomorphic in appearance, camera-based detections alone cannot always identify which individuals are present, and during nest building in particular, some detections may occasionally involve other colony members exploring nests or stealing material. Integrating individual identification, for example through RFID antennas with PIT tags or through visual marks that could be detected by computer vision, would therefore allow detections to be assigned to known individuals and would enable sex-specific and individual-based analyses. However, nest-based measures such as attendance or visits are widely used as proxies of parental effort, but they capture only one component of care. Being in the nest may reflect incubation, brooding, guarding, resting, or other forms of nest-associated investment, while some important parental activities occur outside the nest and remain less visible. This is not specific to our system, but rather reflects a broader challenge in parental care monitoring, where the biological meaning of commonly used metrics must always be interpreted in relation to the behaviours they represent.

A particularly promising direction for future work is therefore to build on this nest-level baseline by adding both behavioural and spatial resolution. Within the nest, continuous detections of presence and visitation already provide a robust starting point for quantifying parental care (Austin et al., 2019; Hinde, 2006; Iserbyt et al., 2018), but recent advances in computer vision make it increasingly feasible to move beyond presence alone towards the automated classification of behavioural states and events (Chan et al., 2025; Dell et al., 2014; Jocher et al., 2023; Nath et al., 2019). In fact, we have already trained a pose estimation model to detect the beak, head, neck, and tail of jackdaws, providing a basis for future analyses of posture, orientation, and social responsiveness between pair members. Extending this pipeline to classify behaviours such as incubation posture, feeding, nest-material delivery, or courtship feeding would substantially increase the biological richness of the dataset. Outside the nest, complementary tools such as external cameras or tracking devices could help connect nest attendance to guarding, foraging effort, off-nest coordination, and the wider ecological context in which parental decisions are made (Fijn et al., 2017). Together, such extensions would not replace the value of the current system, but would build on it to develop a more complete picture of how parental care is organised across time and space.

From a technical perspective, the current implementation also provides a baseline that can be improved as both Open Electronics and computer vision methods evolve rapidly (Jocher & Qiu, 2026). In this thesis, automated jackdaw detections were highly effective during much of the breeding season, although performance declined later in the nestling stage when older chicks were sometimes confused with adults. This is a common issue of computer vision pipelines rather than a fixed limitation of the monitoring approach itself, and accuracy is expected to improve with larger annotated datasets, updated model architectures, and expanded classification objectives separating adults from fledglings. The fact that raw recordings were retained is therefore especially valuable, because it allows the full dataset to be re-analysed retrospectively as models improve or research objectives change. Likewise, although post-season processing of a full breeding season remained computationally demanding, future versions could move towards automated daily or near-real-time processing pipelines, reducing bottlenecks after fieldwork and enabling earlier detection of technical problems during the season. In this sense, the system should not be viewed as a finished endpoint, but as a flexible platform that can continue to improve in parallel with ongoing advances in Open Electronics and computer vision.

More broadly, one of the main strengths of our approach is that it is adaptable beyond the specific case study presented in this thesis. Although it was developed to monitor parental care in jackdaws, the same general approach could be modified for other birds, colonial breeders, or any study system that requires repeated long-term monitoring of multiple sites in a synchronised way. Importantly, I had no experience with Open Electronics and computer vision algorithms when I started this thesis. In that sense, the contribution of Chapter 3 is not only our system itself, but also a demonstration that such a framework can be built, deployed, and iteratively improved by researchers without extensive prior engineering experience. By sharing the system design, code, and workflows openly via our GitHub repository, I hope this helps provide a practical route for others to adapt similar approaches to their own species, study questions, and logistical constraints, particularly where commercial solutions are too rigid or too costly (Jolles, 2021).

6.3 Temporal dynamics of parental care

This thesis focuses on understanding how parental care unfolds over time and highlights the importance of explicitly capturing its temporal dynamics across the breeding season. Using continuous observations of wild jackdaws, generated by the monitoring system described in Chapter 3, I show that nest attendance patterns differed markedly across breeding stages, with

clear differences before and after hatching in both population-level means and among-pair variation, while pairs showed relatively consistent repeatability in their attendance metrics across stages. In addition, parental care is not only characterised by how much care is provided, but also by how partners organise that care in time. Distinguishing between additive parental care, reflecting the overall amount of care provided by the pair, and joint parental care, reflecting how partners organise their care in time, therefore provides a more complete description of parental strategies and reveals dimensions of variation not captured by total care alone.

The stage-specific patterns we observed support the notion that parental care is not a unitary trait expressed uniformly over the reproductive cycle, but rather a sequence of behaviours shaped by shifting brood demands, constraints, and social interactions between carers. During nest-building stage, pairs differed substantially in how much time they allocate to behaviours happening in the nest (e.g., resting in the nest, nest construction, or nest-site defence). Because this stage is less tightly constrained by immediate offspring demands than later stages, the relatively high among-pair variation in both total and joint attendance may reflect differences in nest construction strategies, investment in establishing and securing the nest site, and the social context of pair formation and maintenance (Hahn et al., 2021, 2025). During incubation, by contrast, attendance becomes strongly constrained by the need to maintain suitable thermal conditions for embryo development (Carey, 1980; Hepp & Kennamer, 2018), which likely explains the near-maximal total attendance and the sharp reduction in among-pair variation. Nevertheless, pairs may still differ in how they allocate time between being together in the nest versus attending alone, potentially reflecting variation in behaviours such as courtship feeding, vigilance, or other forms of partner interaction (Hahn et al., 2021; Kokko & Morrell, 2005; Møller & Birkhead, 1991). After hatching, the functional role of nest attendance shifts again as parents must balance brooding, protection, and provisioning with increased activity outside the nest. Capturing these transitions requires data that span the full breeding season. Continuous monitoring made it possible to quantify not only how average attendance changes across stages, but also how the expression of among-pair differences expands or contracts through time and how consistent pairs are within and across stages.

Importantly, similar average levels of total attendance may conceal very different ways of organising care between pair members. For example, a relatively even division of nest presence between partners versus a more asymmetric situation in which one parent contributes disproportionately. Theory predicts that sexual conflict and cooperative dynamics can vary across contexts and stages (Johnstone & Hinde, 2006; McNamara & Wolf, 2015; Royle et al., 2002;

Trivers, 1972), and the pronounced shift in attendance patterns across the hatching boundary identified in Chapter 5 may reflect a broader reorganisation in how care is distributed and expressed by the pair across stages.

At the same time, this distinction also highlights the difference between patterns and mechanisms. Simultaneous nest presence may be associated with coordination, but it can also arise from independent responses to shared conditions (e.g. environmental constraints or brood demand), and it does not, by itself, demonstrate contingency between partners' actions (Hinde, 2006; Johnstone & Hinde, 2006; McNamara et al., 1999). Because individuals cannot be identified in the present dataset, we cannot test directly for alternation, sex-specific roles, or negotiation rules. Future work combining continuous monitoring with individual identification (e.g., RFID, marked individuals, or automated individual recognition) would enable explicit tests of how partners adjust to one another across breeding stages and would link the temporal patterns documented here to the behavioural mechanisms that generate them. Even without this resolution, the continuous data presented in this thesis reveal robust temporal structure in attendance at multiple scales, allowing a comparative assessment of pair-level effort and partner overlap across the breeding cycle. Further improvements in computer vision models to distinguish specific behaviours, such as carrying nest material, courtship feeding, incubation, vigilance, or resting, would allow continuous monitoring systems to move beyond presence-absence measures and provide more biologically informative proxies of parental effort, even if the individual-level mechanisms remain unresolved.

6.4 Concluding remarks

This thesis highlights how parental care is structured over time across the breeding cycle and how sensitive our inferences are to how behaviour is measured and quantified. A central message is that what we infer about parental investment depends strongly on how behaviour is defined and quantified, as well as how it is reported in research papers. By synthesising the diversity of monitoring approaches in the parental care literature and proposing practical guidelines for methodological reporting, I hope this thesis contributes to more transparent, comparable, and reproducible research. Clearer reporting will not eliminate the unavoidable heterogeneity of study systems, but it should make results easier to interpret, compare, and build upon.

Alongside these conceptual and methodological contributions, this thesis reflects a practical effort to make continuous monitoring more achievable in the field. By developing a centralised,

automated monitoring system based on Open Electronics and computer vision, this work provides a flexible DIY framework for long-term, automated behavioural monitoring. By making hardware lists, system designs, and software workflows openly available, this thesis lowers the barrier to adopting automated, continuous monitoring of parental care. I aim to provide a starting point that can be adapted by researchers facing similar monitoring challenges allowing researchers to build on existing designs rather than starting from scratch.

Finally, continuous monitoring also has clear potential beyond basic behavioural ecology, with clear applications in conservation and management. Many conservation problems depend on understanding when and why reproduction fails, how animals respond to disturbance, and how environmental conditions influence breeding decisions and parental effort. By improving our ability to measure behaviour continuously in natural settings, such approaches can contribute to a more mechanistic understanding of ecological processes and support more informed conservation and management decisions.

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Appendix A

Supplementary material

Chapter 2

Table A.1 Information extracted from the 51 selected studies after in-depth reading. References are assigned a numeric ID to facilitate cross-referencing across tables on different pages. Year diff. = difference from year of data collection to year of publication, obs. = observation, jus. = justification; dur. = duration. NB = nest building; IN = incubation; PR = nestling provisioning; FL = post-fledging. Prov. rate = provisioning rate.

Ref. ID	Citation	Year publication	Species	Family	Captivity
Ref1	Adams et al., 2015	2015	<i>Aegithalos caudatus</i>	Tits	no
Ref2	Andreasson et al., 2020	2020	<i>Cyanistes caeruleus</i>	Tits	no
Ref3	Balenger et al., 2007	2007	<i>Sialia currucoides</i>	Thrushes	no
Ref4	Bartsch et al., 2015	2015	<i>Luscinia megarhynchos</i>	Thrushes	no
Ref5	Bründl et al., 2019	2019	<i>Cyanistes caeruleus</i>	Tits	no
Ref6	Burtka & Grindstaff, 2015	2015	<i>Sialia sialis</i>	Thrushes	no
Ref7	Chin et al., 2017	2017	<i>Taeniopygia guttata</i>	Finches	yes
Ref8	Czyż et al., 2024	2024	<i>Remiz pendulinus</i>	Tits	no
Ref9	Diniz et al., 2015	2015	<i>Volatinia jacarina</i>	Seed eaters	no
Ref10	Engelbrecht & Mathonsi, 2012	2012	<i>Spizocorys conirostris</i>	Larks	no
Ref11	English & Montgomerie, 2011	2011	<i>Turdus migratorius</i>	Thrushes	no
Ref12	Evans & Stutchbury, 2012	2012	<i>Hylocichla mustelina</i>	Thrushes	no
Ref13	Evans et al., 2015	2015	<i>Sialia currucoides</i>	Thrushes	no
Ref14	Ewen et al., 2008	2008	<i>Notiomystis cincta</i>	Honeyeater-like	no
Ref15	Ferretti et al., 2005	2005	<i>Turdus rufiventris</i>	Thrushes	no
Ref16	Franz & Fontana, 2013	2013	<i>Sporophila hypoxantha</i>	Seed eaters	no
Ref17	Gilby et al., 2011	2011	<i>Taeniopygia guttata</i>	Finches	yes & no
Ref18	Gill & Stutchbury, 2005	2005	<i>Thryothorus leucotis</i>	Wrens	no
Ref19	Grüebler & Naef-Daenzer, 2008 (an. behav.)	2008	<i>Hirundo rustica</i>	Swallows and Martins	no
Ref20	Harrod & Mumme, 2021	2021	<i>Setophaga citrina</i>	Warblers	no
Ref21	Horton et al., 2014	2014	<i>Zonotrichia albicollis</i>	Sparrows	no
Ref22	Iserbyt et al., 2018	2018	<i>Cyanistes caeruleus</i>	Tits	no
Ref23	Kingma et al., 2010	2010	<i>Malurus coronatus</i>	Wrens	no
Ref24	Maguire & Safran, 2010	2010	<i>Hirundo rustica erythrogaster</i>	Swallows and Martins	no
Ref25	Mock et al., 2005	2005	<i>Passer domesticus</i>	Sparrows	no
Ref26	Nakagawa, Gillespie, et al., 2007	2007	<i>Passer domesticus</i>	Sparrows	no
Ref27	Pagani-Núñez & Senar, 2014	2014	<i>Parus major</i>	Tits	no
Ref28	Pagani-Núñez & Senar, 2016	2016	<i>Parus major</i>	Tits	no
Ref29	Pike et al., 2023	2023	<i>Certhidia olivacea</i>	Warblers	no
Ref30	Porras-Reyes et al., 2021	2021	<i>Sialia mexicana</i>	Thrushes	no
Ref31	Préault et al., 2005	2005	<i>Turdus merula</i>	Thrushes	no
Ref32	Pretelli et al., 2016	2016	<i>Hymenops perspicillatus</i>	Tyrants	no
Ref33	Raihani et al., 2010	2010	<i>Turdoides bicolor</i>	Thrushes	no
Ref34	Santema, Schlicht, Beck, & Kempnaers, 2021	2021	<i>Cyanistes caeruleus</i>	Tits	no
Ref35	Sanz & García-Navas, 2009	2009	<i>Cyanistes caeruleus</i>	Tits	no
Ref36	Schwagmeyer et al., 2008	2008	<i>Passer domesticus</i>	Sparrows	no
Ref37	Serrano Davies et al., 2024	2024	<i>Parus major</i>	Tits	no
Ref38	Siefferman & Hill, 2007	2007	<i>Sialia sialis</i>	Thrushes	no
Ref39	Styrsky et al., 2005	2005	<i>Hylophylax naevioides</i>	Warblers	no
Ref40	Thorogood et al., 2011	2011	<i>Notiomystis cincta</i>	Honeyeater-like	no
Ref41	Tieleman et al., 2008	2008	<i>Troglodytes aedon</i>	Wrens	no
Ref42	Tomás et al., 2013	2013	<i>Cyanistes caeruleus</i>	Tits	no
Ref43	Van Dijk et al., 2012	2012	<i>Remiz pendulinus</i>	Tits	no
Ref44	Vargas-Soriano et al., 2010	2010	<i>Campylorhynchus yucatanicus</i>	Wrens	no
Ref45	Vitousek et al., 2018	2018	<i>Tachycineta bicolor</i>	Swallows and Martins	no
Ref46	Voss et al., 2008	2008	<i>Hirundo rustica</i>	Swallows and Martins	no
Ref47	Wegmann et al., 2015	2015	<i>Parus major</i>	Tits	no
Ref48	Wiebe & Slagsvold, 2014	2014	<i>Cyanistes caeruleus</i> & <i>Ficedula hypoleuca</i>	Tits & Flycatchers	no
Ref49	Wilcoxon et al., 2010	2010	<i>Aphelocoma coerulescens</i>	Corvids	no
Ref50	Williams & DeLeon, 2020	2020	<i>Progne subis</i>	Swallows and Martins	no
Ref51	Wright et al., 2010	2010	<i>Manorina melanophrys</i>	Honeyeater-like	no

Ref. ID	N pairs clarity	N pairs	N years	Year diff.	Method primary	Methods secondary
Ref1	yes	172	18	21	Direct observation	no
Ref2	yes	28	1	3	RFID	Body temperature sensor
Ref3	yes	64	2	3	Video & Manual annotation	no
Ref4	yes	4	5	7	Video & Manual annotation	RFID
Ref5	yes	50	2	6	Video & Manual annotation	no
Ref6	yes	152	2	6	Video & Manual annotation	no
Ref7	no	87	1	3	Video & Manual annotation	no
Ref8	yes	49	4	13	Video & Manual annotation	Nest temperature logger
Ref9	yes	81	2	5	Video & Manual annotation	no
Ref10	yes	5	3	4	Direct observation	no
Ref11	yes	98	1	3	Video & Manual annotation	no
Ref12	yes	18	2	9	Direct observation	Radio-tagging
Ref13	yes	56	2	4	Video & Manual annotation	Video & semi-automated annotation
Ref14	yes	39	1	4	Direct observation	no
Ref15	no	NA	4	8	Video & Manual annotation	no
Ref16	no	NA	3	6	Video & Manual annotation	Direct observation
Ref17	yes	40	1	2	Video & Manual annotation	no
Ref18	yes	19	3	8	Direct observation	no
Ref19	yes	114	4	8	Direct observation	Radio-tagging
Ref20	yes	37	3	3	Direct observation	Video & Manual annotation
Ref21	yes	25	2	4	Video & Manual annotation	Direct observation
Ref22	yes	38	2	2	RFID	Video & Manual annotation
Ref23	yes	73	3	4	Direct observation	no
Ref24	yes	58	2	8	Direct observation	no
Ref25	yes	50	5	10	Direct observation	no
Ref26	yes	60	2	3	Video & Manual annotation	no
Ref27	yes	29	1	3	Video & Manual annotation	no
Ref28	yes	32	1	5	Video & Manual annotation	no
Ref29	yes	26	1	2	Direct observation	no
Ref30	yes	31	1	4	Video & Manual annotation	no
Ref31	yes	32	2	3	Direct observation	no
Ref32	yes	31	1	4	Video & Manual annotation	no
Ref33	yes	44	4	5	Direct observation	no
Ref34	yes	105	1	2	RFID	no
Ref35	yes	59	2	3	Video & Manual annotation	RFID
Ref36	yes	47	3	7	Direct observation	no
Ref37	no	NA	1	5	Video & Manual annotation	no
Ref38	yes	40	2	6	Video & Manual annotation	no
Ref39	yes	125	3	6	Direct observation	no
Ref40	no	75	1	5	Video & Manual annotation	no
Ref41	yes	22	1	4	Direct observation	no
Ref42	no	NA	1	7	RFID	Video & Manual annotation
Ref43	yes	20	2	6	Video & Manual annotation	no
Ref44	yes	45	1	3	Video & Manual annotation	Direct observation
Ref45	yes	63	1	3	RFID	Nest temperature logger
Ref46	yes	38	3	9	Direct observation	Nest temperature logger
Ref47	yes	62	1	3	Video & Manual annotation	no
Ref48	yes	70	2	8	Video & Manual annotation	no
Ref49	yes	80	3	4	Direct observation	no
Ref50	yes	8	2	3	Video & deep-learning annotation	no
Ref51	yes	27	3	6	Direct observation	Video & Manual annotation & Audio recorder

Ref. ID	Method jus.	Weather jus.	Breeding stage clarity	Schedule clarity	Schedule as range	Schedule from	Schedule to	Obs. dur.
Ref1	yes	yes	yes	yes	yes	0600	1600	1
Ref2	yes	no	yes	yes	no	0700	2100	14
Ref3	yes	yes	yes	yes	yes	0915	1215	4
Ref4	yes	no	yes	yes	no	0600	1000	4
Ref5	yes	no	yes	no	NA	no	no	no
Ref6	yes	no	yes	yes	yes	0630	1030	1
Ref7	yes	no	yes	yes	yes	0700	1100	3
Ref8	no	no	yes	yes	yes	0700	1230	1.5
Ref9	yes	yes	yes	yes	yes	0600	1000	2.2
Ref10	yes	yes	yes	yes	yes	0800	1200	no
Ref11	no	no	yes	no	yes	0900	1300	no
Ref12	yes	no	no	yes	yes	0600	1700	1
Ref13	yes	no	yes	yes	yes	0620	1115	2
Ref14	yes	no	yes	no	NA	no	no	2
Ref15	yes	yes	yes	yes	no	0530	1130	6
Ref16	no	no	no	no	yes	0800	2000	6
Ref17	yes	no	yes	no	NA	no	no	8
Ref18	yes	no	yes	yes	yes	0600	1400	1
Ref19	no	yes	yes	no	NA	no	no	1
Ref20	yes	yes	yes	yes	yes	0700	1100	1.5
Ref21	yes	yes	yes	yes	yes	0530	1130	3
Ref22	yes	no	yes	yes	yes	0700	1700	2
Ref23	no	no	yes	yes	yes	0530	1100	1
Ref24	yes	no	yes	yes	yes	0700	1830	1
Ref25	yes	no	yes	no	yes	0700	1300	1
Ref26	yes	yes	yes	yes	yes	0500	1200	1.5
Ref27	yes	no	yes	yes	no	0700	1400	7
Ref28	yes	no	yes	yes	no	0700	1400	7
Ref29	yes	yes	yes	yes	yes	0630	1000	1
Ref30	no	no	yes	yes	yes	0700	2000	0.9
Ref31	no	no	yes	yes	yes	1000	1800	1
Ref32	yes	yes	yes	yes	yes	0800	1300	4
Ref33	no	no	yes	no	NA	no	no	1.5
Ref34	yes	yes	yes	yes	no	no	no	no
Ref35	no	yes	yes	no	NA	no	no	1
Ref36	yes	yes	yes	yes	no	1000	1100	1
Ref37	yes	no	yes	yes	yes	0800	1200	1
Ref38	no	no	yes	yes	yes	0600	1100	4
Ref39	no	no	yes	yes	yes	0645	0915	1
Ref40	yes	no	yes	yes	no	0900	1200	3
Ref41	no	no	yes	yes	no	0600	1200	6
Ref42	yes	no	yes	no	NA	no	no	2
Ref43	no	no	no	no	yes	0700	2100	3
Ref44	yes	yes	no	no	NA	no	no	no
Ref45	yes	no	no	no	NA	no	no	24
Ref46	yes	no	no	yes	yes	0500	1100	4
Ref47	yes	no	yes	no	NA	no	no	1
Ref48	yes	yes	yes	yes	yes	0700	1830	1.5
Ref49	yes	no	yes	yes	yes	0700	1000	1
Ref50	yes	yes	yes	yes	no	0600	2100	15
Ref51	yes	no	no	no	NA	no	no	no

Ref. ID	N Obs. clarity	N Obs. NB	N Obs. IN	N Obs. PR	N Obs. FL	IN dur.	PR dur.	Prov. rate	Visit rate	Nest attendance
Ref1	yes	no	no	8	no	13	18	no	yes	no
Ref2	yes	no	no	1	no	16	22	no	yes	no
Ref3	yes	no	no	2	no	14	21	yes	no	no
Ref4	yes	no	no	4	no	14	12	no	yes	no
Ref5	no	no	no	NA	no	16	22	yes	yes	no
Ref6	yes	no	no	2	no	14	20	no	yes	yes
Ref7	yes	1	1	1	no	14	18	yes	yes	yes
Ref8	yes	no	1	1	no	14	20	yes	no	no
Ref9	yes	no	no	2	no	13	13	yes	no	no
Ref10	no	no	no	NA	no	13	13	yes	no	no
Ref11	yes	no	no	3	no	14	13	yes	no	yes
Ref12	yes	no	4	2	no	14	15	no	yes	yes
Ref13	yes	no	no	2	no	14	21	yes	no	yes
Ref14	yes	no	no	2	no	14	21	yes	no	no
Ref15	yes	no	5	1	no	14	16	yes	no	yes
Ref16	no	NA	NA	NA	no	18	14	yes	yes	yes
Ref17	no	no	no	NA	no	14	18	yes	yes	yes
Ref18	yes	no	no	6	no	16	14	yes	no	no
Ref19	yes	no	no	no	10	17	27	yes	no	no
Ref20	yes	no	no	1	no	13	12	no	yes	no
Ref21	yes	no	no	2	no	14	12	no	yes	yes
Ref22	yes	no	no	16	no	16	22	no	yes	no
Ref23	yes	no	no	4	no	15	12	yes	no	no
Ref24	yes	no	no	3	no	17	27	yes	no	no
Ref25	yes	no	no	8	no	11	14	no	yes	no
Ref26	yes	no	2	2	no	12	14	yes	no	yes
Ref27	no	no	no	NA	no	15	22	yes	no	no
Ref28	no	no	no	1	no	15	22	yes	no	no
Ref29	no	no	no	1	no	14	15	yes	no	yes
Ref30	yes	no	no	4	no	14	21	yes	no	yes
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Ref32	yes	no	1	2	no	16	15	yes	no	no
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Ref34	yes	no	no	3	no	16	22	no	yes	yes
Ref35	yes	no	1	1	no	16	22	yes	yes	yes
Ref36	yes	no	3	no	no	11	14	yes	yes	yes
Ref37	yes	no	no	1	no	15	22	yes	no	no
Ref38	yes	no	no	1	no	14	18	yes	no	no
Ref39	yes	no	no	3	no	17	15	no	yes	no
Ref40	yes	no	no	1	no	14	21	yes	yes	no
Ref41	yes	no	no	3	no	15	17	yes	no	no
Ref42	yes	no	no	2	no	16	22	no	yes	no
Ref43	yes	NA	1	1	no	14	21	no	no	yes
Ref44	no	no	no	NA	no	15	16	yes	no	no
Ref45	no	no	10	NA	no	14	19	no	yes	no
Ref46	no	no	NA	NA	no	17	27	no	yes	yes
Ref47	yes	no	no	2	no	15	22	yes	no	no
Ref48	yes	no	no	4	no	14	15	no	no	no
Ref49	yes	no	no	1	no	18	21	yes	no	no
Ref50	yes	no	16	no	no	16	28	no	no	yes
Ref51	no	no	no	NA	no	16	13	no	yes	no

Ref. ID	Monitoring NB	Monitoring IN	Monitoring PR	Monitoring FL
Ref1	no	NA	1-17	no
Ref2	no	NA	10	no
Ref3	no	NA	2-3, 14-16	no
Ref4	no	NA	5-11	no
Ref5	no	NA	9-17	no
Ref6	no	NA	6-8	no
Ref7	1	2, 4, 6	8	no
Ref8	no	7	12	no
Ref9	no	NA	1-8	no
Ref10	no	NA	3-6	no
Ref11	no	NA	3, 6, 9	no
Ref12	no	NA	NA	no
Ref13	no	NA	3-5, 13-15	no
Ref14	no	NA	16-21	no
Ref15	no	4-8	10	no
Ref16	NA	NA	1-14	no
Ref17	no	NA	5-10	no
Ref18	no	NA	1-15	no
Ref19	no	NA	NA	1to10
Ref20	no	NA	1-7	no
Ref21	no	NA	5-6	no
Ref22	no	NA	6-22	no
Ref23	no	NA	4-10	no
Ref24	no	NA	4-5, 9-15	no
Ref25	no	NA	3-10	no
Ref26	no	9, 11-12	7, 11	no
Ref27	no	NA	10-16	no
Ref28	no	NA	10-14	no
Ref29	no	NA	5-6	no
Ref30	no	NA	1-21	no
Ref31	no	NA	6-9	no
Ref32	no	10-15	2-4, 8-11	no
Ref33	no	NA	4-10	no
Ref34	no	no	19-21	no
Ref35	no	7	11	no
Ref36	no	4-5, 9-10	NA	no
Ref37	no	NA	11	no
Ref38	no	no	7	no
Ref39	no	NA	2-10	no
Ref40	no	NA	13	no
Ref41	no	NA	4, 7, 11	no
Ref42	no	NA	6, 11	no
Ref43	NA	8	10	no
Ref44	no	NA	NA	no
Ref45	no	4-14	1-19	no
Ref46	no	NA	NA	no
Ref47	no	NA	4, 11	no
Ref48	no	NA	2-12	no
Ref49	no	NA	3-5	no
Ref50	no	3-16	NA	no
Ref51	no	NA	6-13	no

*Appendix **B***

Supplementary material Chapter 3

B.1 Centralised multi-unit monitoring system: hardware

Core unit hardware

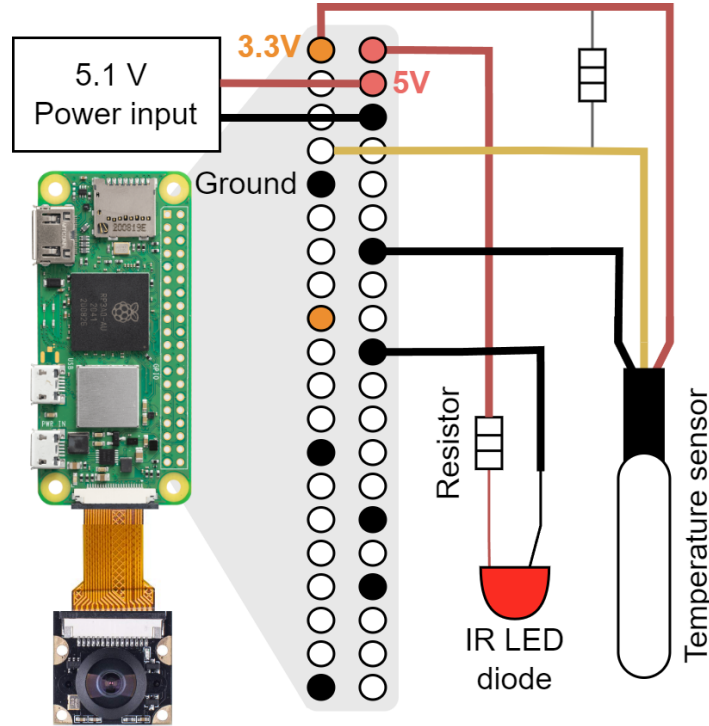


Figure B.1 Schematics of the connections of a single unit of our proof-of-concept implementation, with powering to the Raspberry Pi using the GPIO pins. Red pins provide 5V but can also be used as a power input, orange pins provide 3.3V and black pins ground. A 4.7 kΩ pull-up resistor is used for the temperature sensor and a 120 Ω resistor for the IR LED diode.

All the nest-boxes were employed with a Raspberry Pi (RPi) Zero 2W (Raspberry Pi Foundation, Cambridge, UK) with heat sinks for dissipation, a 128 GB SD card (SanDisk LLC, USA), a wide-angle 130° IR camera (Keyestudio, China), a 940 nm IR LED diode (ams-OSRAM, Austria) and a DS18B20 temperature sensor (AZ-Delivery, Germany). For the master RPi, though, we used a more powerful model RPi 4B+ 8GB RAM with a PiJuice HAT (Pi-Supply, Bells Yew Green, UK) with its built-in 1820 mAh battery. Datetime can be synchronised using internet connection, or by being periodically calibrated from the parent unit, using a wireless or wired Local Area Network (LAN). However, Real Time Clocks (RTC) are an effective solution when no internet connection is available (note that humidity could significantly affect the operation of precision equipment in outdoor settings, leading to subtle timing discrepancies between units. To mitigate this, it is crucial to protect the electronics from weather conditions, and periodic recalibration of the RTCs may be

required depending on the level of accuracy needed. Still, even with minor RTC inaccuracies, parent and child units could still synchronise to maintain precise coordination). A HUAWEI E8372h-320 Dongle LTE/4G (Huawei Technologies Co., Ltd., China) with a SIM card was used to provide internet connection to up to 16 devices. These are the peripherals we used for our study case, but other extra peripherals might be implemented in this system. When adding sensors to this system, consider the extra power consumption, the extra usage of CPU resources from the RPi and the storage use of the extra collected data.

Multi-unit system: hardware

Our centralised multi-unit system consists of a single parent unit controlling the power input of the other child units using a 16-channel relay board (AZ-Delivery, Germany) through its GPIO pins. Each relay channel functions as a switch that the parent RPi can activate or deactivate. The positive wire supplying power to each child RPi is routed through one of these relay channels, allowing the parent RPi to control the power input to each child unit by bridging or cutting the connection as needed. This setup ensures that, once the parent RPi is powered on, it can activate all relay channels, supplying power to the child RPi's and synchronising their startup. Besides, only the parent unit used a PiJuice HAT, as once this unit is on it can already power on the child units.

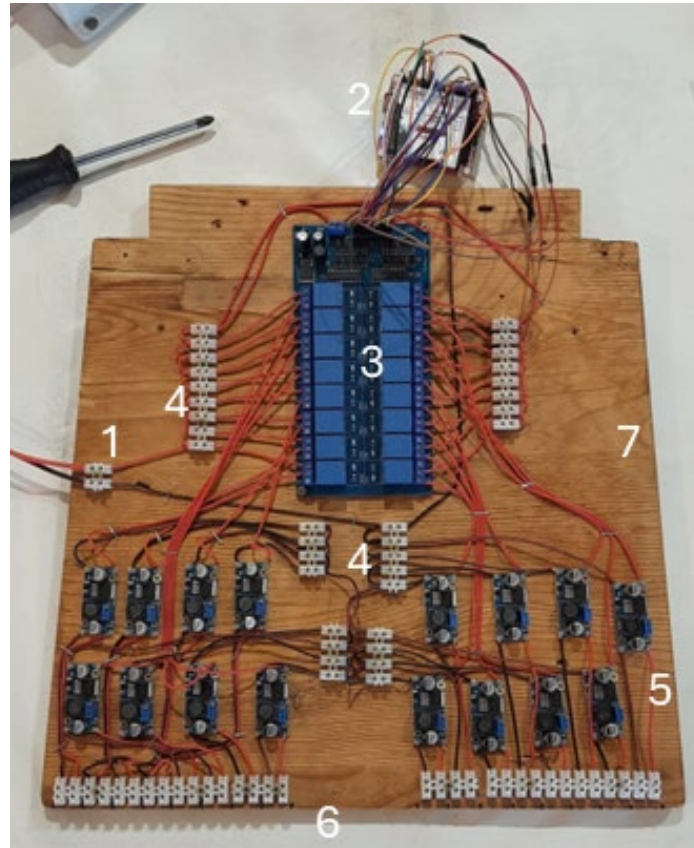


Figure B.2 *Connection board of our proof of concept, used to control (1) the power input from the battery to the children RPi with (2) a 16-channel Relay board (AZ-Delivery, Germany) controlled by (3) the Parent unit. (4) Input wires are split into 16 and each positive is routed through the relay board. (5) Buck converters are used to provide the convenient 5V to the (6) output where the RPi's are powered from. (7) We used a wooden board as an insulator to prevent short-circuits in the electronics.*

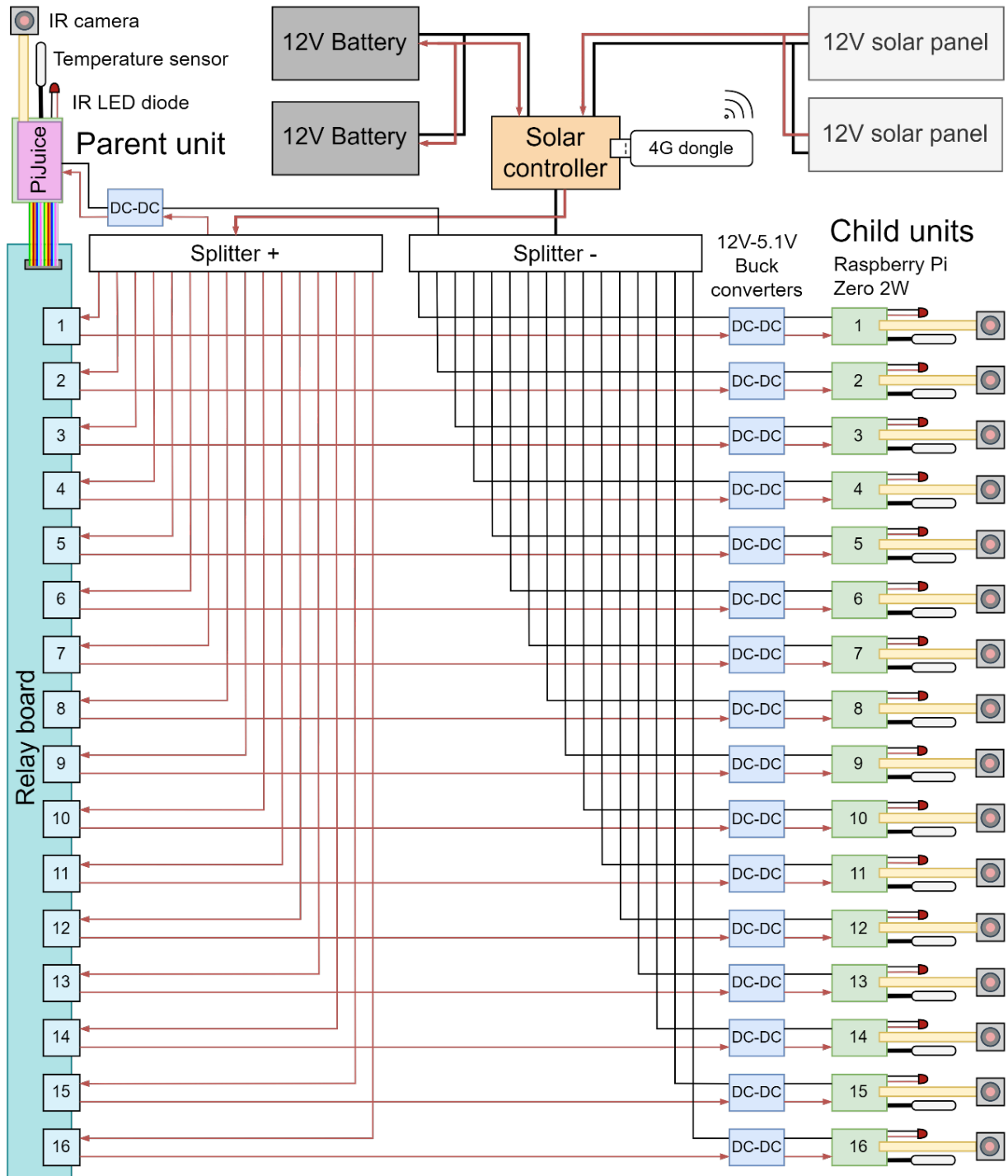


Figure B.3 Connections schematics for our proof-of-concept implementation, using multiple RPi's in a parent-child system powered through a relay board. Each relay channel is controlled by one single GPIO pin from the parent RPi. Providing power to the GPIO pin closes the relay channel, allowing the power flow from the battery to the child unit. When cutting power to the GPIO pin the relay channel cuts the current to the child unit, thereby turning it off.

Solar power system: hardware

There are several categories of lead-acid batteries, including flooded, gel, and absorbent glass mat (AGM). AGM is the newest of the three and the best suited for solar applications because of its zero-to-low maintenance and deep discharge cycle. Alternatively, Lithium-ion (Li-ion) and Lithium Iron Phosphate (LiFePO₄) batteries are increasingly popular for solar applications due to their higher energy density, longer lifespan, lighter weight, and efficiency compared to lead-acid types. They also handle deep discharge better and require less maintenance. However, they typically come at a higher upfront cost. Various types of solar panels exist, including monocrystalline, polycrystalline, and thin-film panels. Among these, monocrystalline panels typically offer the highest efficiency and space efficiency due to their ability to capture sunlight more effectively. Polycrystalline panels are generally less expensive but slightly less efficient, while thin-film panels are lightweight and flexible, though they have lower efficiency. The choice of panel depends on the system's power requirements, budget, and installation environment. Regarding the solar charge controller, there are two primary types: Pulse Width Modulation (PWM) and Maximum Power Point Tracking (MPPT) controllers. MPPT is a newer technology that harvests more energy, but the advantages of MPPT over PWM controllers come at a cost. Specially in smaller systems and in warmer climates where MPPT's energy boost is not as significant, a less expensive PWM controller can be the right choice.

Our proof-of-concept implementation contains a 100Ah and 80Ah 12V AGM battery wired in parallel, thereby having a capacity of 2.16kWh. The batteries are charged by a 190W and 100W 12V monocrystalline solar panel wired in parallel and controlled by a EPEVER PWM VS3024AU 30A solar charge controller. The load of the solar controller was split in sixteen to route the positive wire through each of the relay channels. Every output of the relay was then connected to a LM2596 buck converter to provide the correct 5.1V input for the RPi's instead of the 12V coming from the battery. We used 12 AWG wires for the solar system (for the solar panels, solar controller and batteries) and 22 AWG wires for all the connections coming from the solar controller load to the RPi.

Power requirements calculations

The daily power consumption of our system was calculated using the formula $((Wh_a * n_a + Wh_b * n_b) * t) / V * 1.2$, where Wh refers to the power consumption of the RPi computer (Jolles, 2021; Proppe et al., 2020). If there are different models of RPi in the system, multiply the consumption for the number of RPi's of each kind (n). t is the number of hours in a day that the

system should be working with that power consumption and V is the voltage of the system. It's a good practice to add the 20% to this calculation (multiply by 1.2) to consider power loss due to buck conversion and long wire length use, besides power dissipation during overheating periods. For example, with a system composed by one RPi 4B+ with a maximum power consumption of 6.4Wh and 13 RPi Zero 2W with a maximum power consumption of 2.2Wh working for 17h per day (from dawn to dusk) we would need a 12V battery with a size of at least 67Ah.

The size of the solar system to power the electronics while charging the battery was calculated using the formula $Ah * 2 * V / (h * e)$, where e refers to the solar panel efficiency and the daily power consumption (Ah) is multiplied by 2 to power the system while charging the battery during the sunny hours (h). Hence, for a system consuming 67Ah and the solar panels receiving 8h of sunlight a day with an efficiency of 70% we would need a 287W solar panel system. It's also a good practice to increase the battery size to at least the double to keep the system working under continuous cloudy days (i.e. battery of at least 134Ah). The minimum amperage of the solar controller is calculated dividing the power of the solar panels by their voltage (i.e. 23.92A). Consider connecting extra batteries and/or solar panels in parallel to increase the size of the power supply if the system requires higher power consumption after the first installation. Solar power system size calculations are provided in an excel file in the GitHub page associated with this paper (<https://github.com/mpourossell/Centralised-Multi-RPi-Recording-System>), together with storage capacity calculations and budget details for the materials needed for our proof of concept.

B.2 Software details

Custom scripts for the replication of our system can be accessed at the GitHub repository accompanying this paper. Scripts are divided into 3 main groups:

- (i) **System centralisation scripts:** Control of parent unit working schedules with PiJuice HAT configuration and control of the child units using the relay board. This group of scripts are run to schedule the system's powering on and off according to sunlight and to synchronise the performance of all units.
- (ii) **Data collection, conversion and transfer:** Individual units run these scripts to collect sensor data at desired schedules with desired configuration. For example, when collecting image data, some units might receive direct sunlight during the morning and might require different camera configuration from the other units. Hence, it's advisable to do some piloting in-site to assure setting the correct recording parameters to each

unit. Some other scripts are run to convert raw collected data into a preferable format to save it more efficiently. For example, image sequences can be converted to compressed videos for storage saving, while allowing a faster upload to cloud storage services. Data can be transferred to a cloud storage at scheduled times and automatically cleaned from the unit for a more efficient storage space use in the SD card.

- (iii) **Real-time system performance monitoring:** This group of scripts create a local network across multiple units, centralised by the parent unit, and collects specific information from each unit in real-time. The parent unit creates a local web server and continuously updates the incoming information. This local web server can be published online so it can be accessed from elsewhere for a real-time remote system performance monitoring.

Raspberry Pi Status - Roca Guilla, Lleida

2024-02-12 12:53:48

Hostname	Datetime	CPU Temperature	Nest Temperature	Storage use	Google Drive	Camera Status	Last Recording
jackdaw00	2024-02-12 12:53:48	46.2°C (28.6%)	2024-02-12 12:53:01,10.69	109.2GB / 116.9GB (3.6%)	Connected	Recording	RG_jackdaw00_240212_125347.jpg
jackdaw01	2024-02-12 12:53:44	44.0°C (33.3%)	2024-02-12 12:53:02,11.56	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw01_240212_125343.jpg
jackdaw02	2024-02-12 12:53:44	40.8°C (37.5%)	2024-02-12 12:53:02,11.44	108.2GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw02_240212_125344.jpg
jackdaw03	2024-02-12 12:53:44	42.9°C (20.0%)	2024-02-12 12:53:02,10.75	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw03_240212_125344.jpg
jackdaw04	2024-02-12 12:53:44	49.4°C (28.6%)	2024-02-12 12:53:03,9.75	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw04_240212_125344.jpg
jackdaw05	2024-02-12 12:53:44	43.5°C (28.6%)	2024-02-12 12:53:03,10.25	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw05_240212_125343.jpg
jackdaw06	2024-02-12 12:53:44	41.3°C (28.6%)	2024-02-12 12:53:02,10.81	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw06_240212_125343.jpg
jackdaw07	2024-02-12 12:53:44	46.7°C (28.6%)	2024-02-12 12:53:02,10.81	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw07_240212_125343.jpg
jackdaw08	2024-02-12 12:53:44	37.6°C (50.0%)	2024-02-12 12:53:02,10.12	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw08_240212_125344.jpg
jackdaw09	2024-02-12 12:53:44	48.3°C (10.5%)	2024-02-12 12:53:03,12.06	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw09_240212_125344.jpg
jackdaw11	2024-02-12 12:53:44	45.1°C (37.5%)	2024-02-12 12:53:03,10.62	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw11_240212_125344.jpg
jackdaw12	2024-02-12 12:53:44	44.5°C (25.0%)	2024-02-12 12:53:02,11.94	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw12_240212_125344.jpg
jackdaw13	2024-02-12 12:53:44	45.6°C (12.5%)	2024-02-12 12:53:02,12.5	109.3GB / 116.9GB (3.5%)	Connected	Recording	RG_jackdaw13_240212_125343.jpg

Figure B.4 Screenshot of the custom website generated by the parent unit, showing real-time information with the status of all the units from our proof of concept installed in Roca Guilla bird nesting tower (Lleida, Catalonia, NE Spain).

B.3 Overall performance

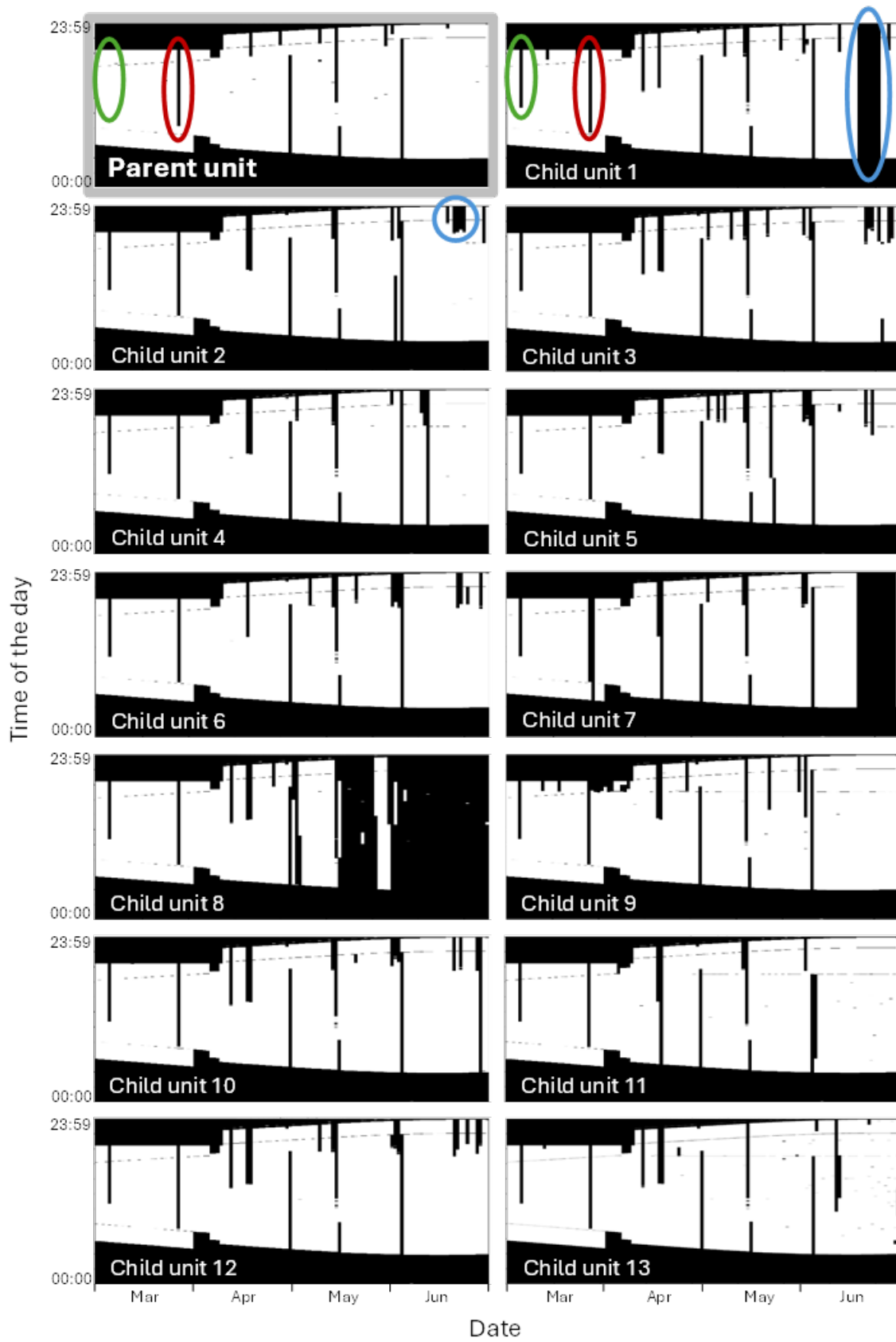


Figure B.5 Data availability plots showing unit performance during the four-month monitoring period in 2024, from 1 March until 30 June. Where units recorded data, this is shown in white and where no data was recorded, even when the unit was powered on, is shown in black. Data is shown at a second resolution but due to small scale only differences larger than a minute will be visible. Note that, when units occasionally shut down, this tended to happen on a few individual days scattered across the period rather than for consecutive days. Therefore, these small gaps do not represent significant data loss, as data were still collected during the surrounding time periods. Non-recording periods consistent across all units (example highlighted with red circles) primarily reflect general power shortages, typically caused by prolonged cloudy weather resulting in insufficient solar input. Instances where the parent unit recorded during these periods while the child units did not (example highlighted with green circle) likely indicate a failure in transmitting the power-on command, even though the parent unit remained operational. Isolated non-recording periods affecting only a single unit (example highlighted with blue circles) suggest erratic behaviour or spontaneous shutdowns, most likely due to intermittent power loss caused by poor contact in recycled jumper wires used to power the RPi's via the GPIO pins. Brief recording gaps around sunrise and sunset correspond to transitions between recordings with distinct camera settings optimised for changing light conditions. Finally, short, localised non-recording periods (thin black lines scattered across the plots) reflect unit reboots, after which recording automatically resumed.

B.4 Python pipeline for an automated image analysis using a custom yolov8 computer vision model

We trained a custom YOLOv8 model (specifically the YOLOv8m-pose model, chosen for its balance between speed and accuracy) to detect the presence of jackdaws in the nest-box and infer their body position throughout the millions of images recorded by the system. To build a representative training dataset, we selected a sample of 50 videos from each nest box, from which 200 frames were randomly extracted using a custom Python script. We focused on the period from nest construction until the third week after hatching, excluding chick ages greater than 16 days to avoid confusion with fully feathered juveniles.

From the extracted frames, 1,800 images containing at least one bird were selected, along with 200 images showing only the empty nest box (10% of the training set) to improve background differentiation. This dataset captured a broad range of bird postures, light conditions, and nest material variations. We manually annotated all images using the Computer Vision Annotation Tool (CVAT; <https://www.cvat.ai>), a free online tool for image and video annotation. Each bird was labelled with a bounding box (for object detection) and four key points for the tip of the beak,

head, neck, and tip of the tail (for pose estimation). When key points were not visible (e.g., the bird was facing away), they were assigned coordinates (0,0) for filtering purposes. Key points were consistently annotated in the same order (from beak to tail) and matched with their corresponding bounding boxes to ensure individual tracking.

A total of 3,257 birds were manually annotated across the 2,000 training images. CVAT annotations were initially saved in XML format and later converted to the YOLOv8 format using a custom Python script that accounted for key point visibility. YOLOv8m-pose was then trained for 300 epochs, striking an optimal balance between accuracy and computational efficiency compared to larger models like YOLOv8l and YOLOv8x. The training was conducted on a Lenovo IdeaPad Gaming 3 with an NVIDIA GeForce RTX 3060 GPU, taking approximately 6 hours and processing images at ~22 ms per frame. Higher-end GPUs or cloud-based services like Google Colab can further accelerate training.

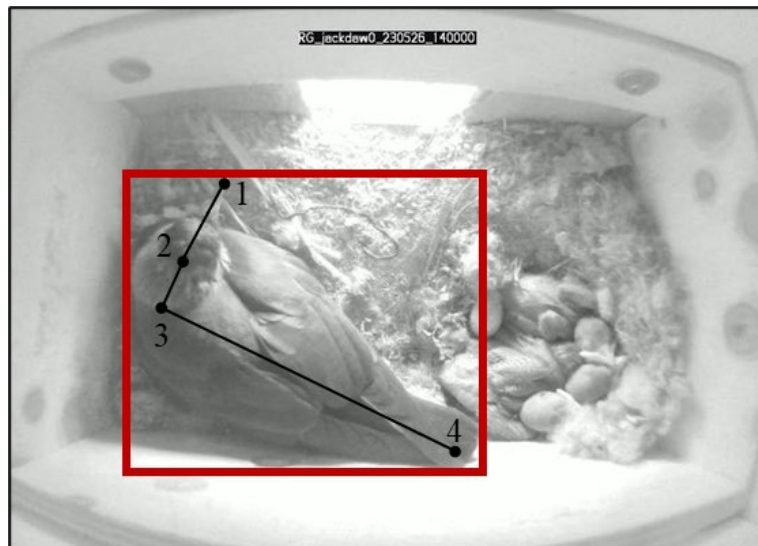


Figure B.6 Image annotation for object detection and pose estimation in a sample image. Red bounding box is used for object detection (a jackdaw) and points are used for pose estimation (1 for beak, 2 for head, 3 for neck and 4 for tail).

To apply the trained model, we developed a Python pipeline for automated inference on new videos. The pipeline processes frames individually, extracting bounding box coordinates, key point positions, detection confidence, timestamps, mean pixel values, and Raspberry Pi hostnames. Results are saved in CSV format for further analysis. Full documentation and the codebase are available in the GitHub repository accompanying this paper. Extended guidance on

YOLOv8 training and implementation can be found at <https://docs.ultralytics.com/models/yolov8>.

B.5 Model performance metrics validation

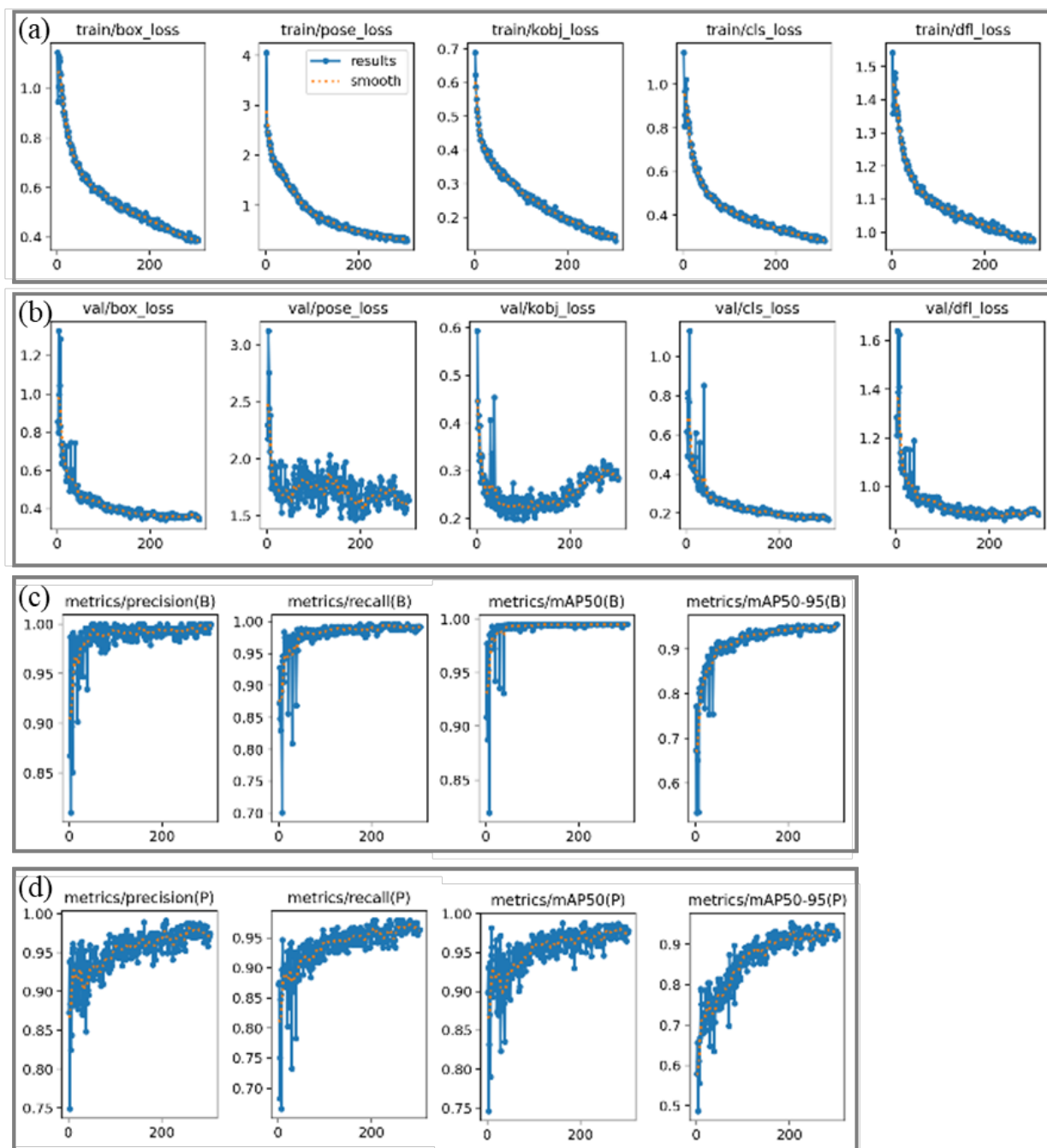


Figure B.7 Performance metrics of the custom YOLOv8 model (a) during the training and (b) validation. Metrics for (c) object detection and for (d) pose estimation show a high precision, especially for object detection.

Model performance metrics for object detection (B) and pose estimation (P) proof a high accuracy, even though a relatively small training sample was used compared to existing detection models for other purposes (e.g., detect moving vehicles in highways). For object detection, the average of the mean average precision calculated at varying intersection over union thresholds ($mAP50-95(B)$) was 0.956, $Precision(B)$ was 0.999 and $recall(B)$ was 0.992. For pose estimation, $mAP50-95(P)$ was 0.927, $Precision(P)$ was 0.975 and $recall(P)$ was 0.963.

Appendix C

Supplementary material

Chapter 4

C.1 Extended methods for sub-setting the complete dataset

As the provisioning stage was by far the most studied period according to our literature survey, we focused our simulations exclusively on this stage, using data from hatching until near fledging. To evaluate how different methodological choices influence behavioural estimates, we created subsets reflecting the main monitoring dimensions identified in the literature.

Time of the day

To assess the effect of monitoring at different times of the day, we selected 2.5-hour windows from the morning, midday, and afternoon. This duration (2.5 hours) reflects the most frequently used observation length in the literature. All subsets were compared against the complete dataset containing full-day recordings (sunrise to sunset) throughout the entire provisioning period.

Observation duration

Since the morning was the most frequently monitored time window (centred around 0945), we compared subsets of different durations (one, three, and five hours) during this period. These were compared to a full morning dataset (seven hours, from 0615–1315), to isolate the effect of observation length from time-of-day biases.

Breeding stage

We created three subsets focusing on specific provisioning stages: days 5–7 (early provisioning), 9–11 (mid provisioning), and 12–14 after hatching (late provisioning). Each subset included three days of observation (reflecting the typical number reported in the literature). The full dataset used for comparison comprised the complete day-by-day data from day five to 15 post-hatching to only include all data from the subsets.

Number of observed days

To examine the influence of the number of monitored days, we generated subsets centred on day ten post-hatching, with one (day ten), three (days 9–11), and five (days 8–12) observations. These were compared to a dataset covering seven days (7–13) to avoid early/late-stage effects.

Finally, we created two subsets simulating more realistic combinations of parameters commonly used in the literature:

Combined monitoring designs

Finally, we simulated two more realistic combinations of parameters: Typical design, 2.5-hour morning observations centred on 0945, for three days during the mid-provisioning stage (days 9–11), and pseudo-random design, 2.5-hour observations randomly distributed between 0800 and 1200 across three non-consecutive days between days 4–16 post-hatching, mimicking studies that used flexible monitoring ranges.

C.2 Supplementary figures from simulations

The following results present graphical comparisons of the simulated subset with the complete dataset across all dimensions of sampling schedules, both for visitation rate (Figs. C.1a–C.4a) and nest attendance (Figs. C.1b–C.4b).

Time of the day

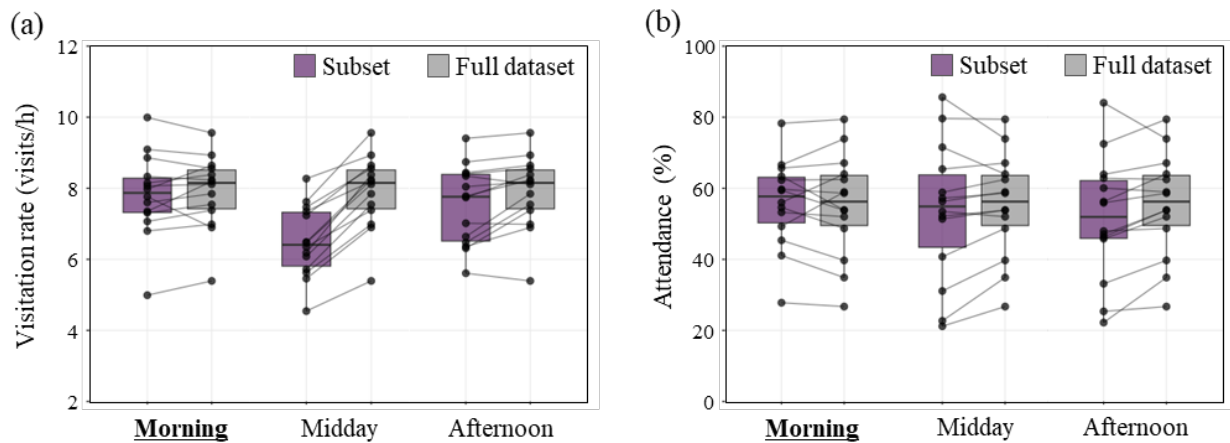


Figure C.1 Comparison of behavioural estimates between complete and simulated datasets across different times of the day. Quantification of visitation rate (a) and nest attendance (b) of jackdaw pairs using the full second week after hatching (in grey) compared to different monitoring schedules across the day (in purple), simulated by sub-setting the continuous dataset. Underlined and bold subsets indicate the most frequently used method as detected in the literature review. Each line connects the same pair across methods.

Number of observed days

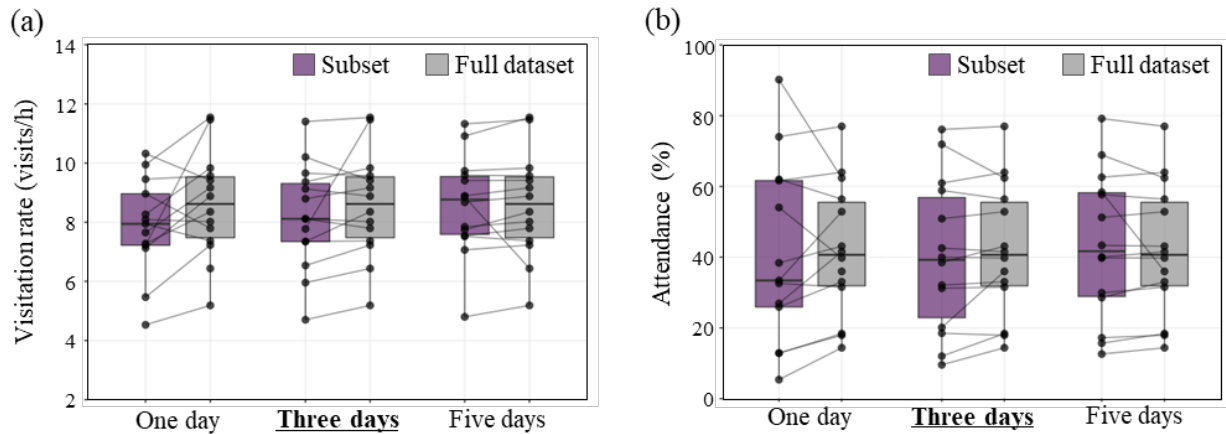


Figure C.2 Comparison of behavioural estimates between complete and simulated datasets across different number of observed days. Quantification of visitation rate (a) and nest attendance (b) of jackdaw pairs using the full second week after hatching (in grey) compared to different number of days monitored across that week (in purple), simulated by sub-setting the continuous dataset. Underlined and bold subsets indicate the most frequently used method as detected in the literature review. Each line connects the same pair across methods.

Breeding stage

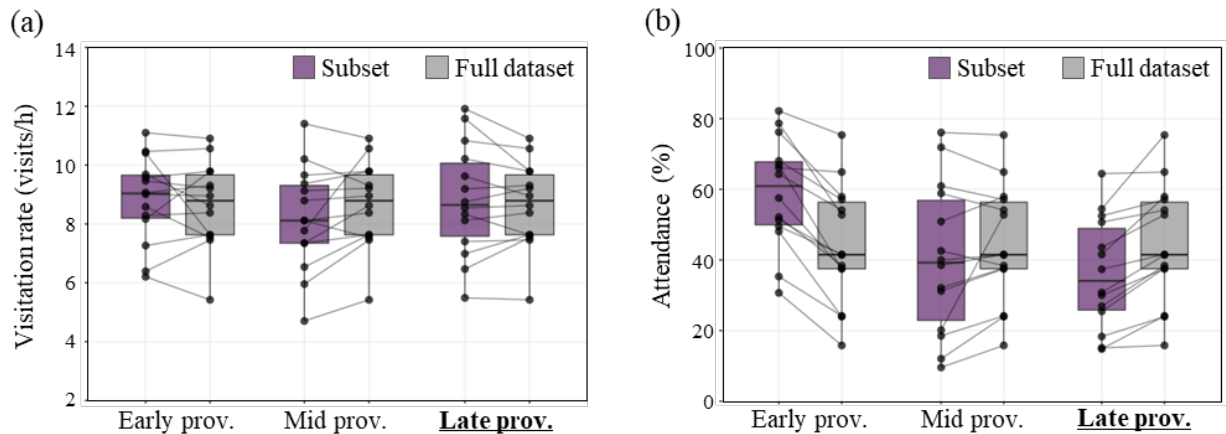


Figure C.3 Comparison of behavioural estimates between complete and simulated datasets across different parts of the provisioning stage. Quantification of visitation rate (a) and nest attendance (b) of jackdaw pairs using the full second week after hatching (in grey) compared to different monitoring schedules across the provisioning period (in purple), simulated by sub-setting the continuous dataset. Underlined and bold subsets indicate the most frequently used method as detected in the literature review. Each line connects the same pair across methods.

Observation duration

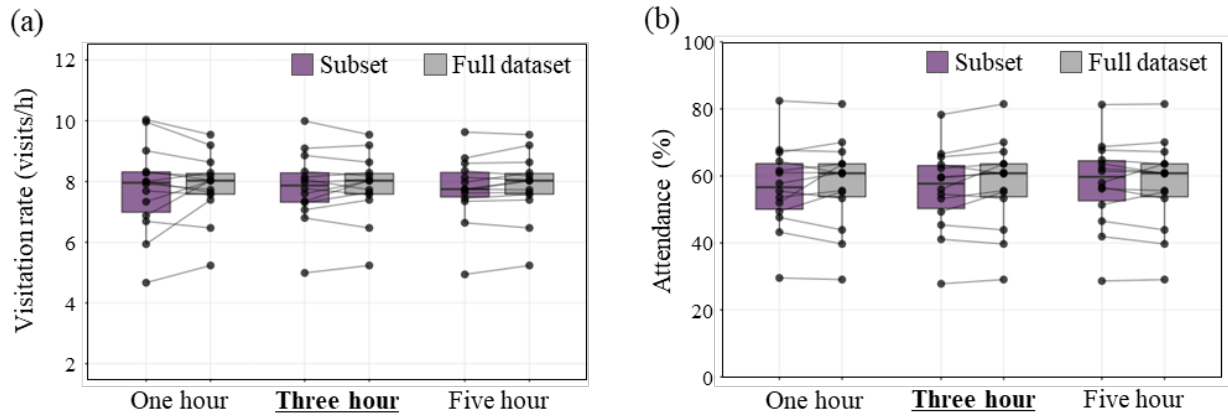


Figure C.4 Comparison of behavioural estimates between complete and simulated datasets across different observation durations. Quantification of visitation rate (a) and nest attendance (b) of jackdaw pairs using the full second week after hatching (in grey) compared to different observation durations across the morning (in purple), simulated by sub-setting the continuous dataset. Underlined and bold subsets indicate the most frequently used method as detected in the literature review. Each line connects the same pair across methods.

*Appendix **D***

Supplementary material

Chapter 5

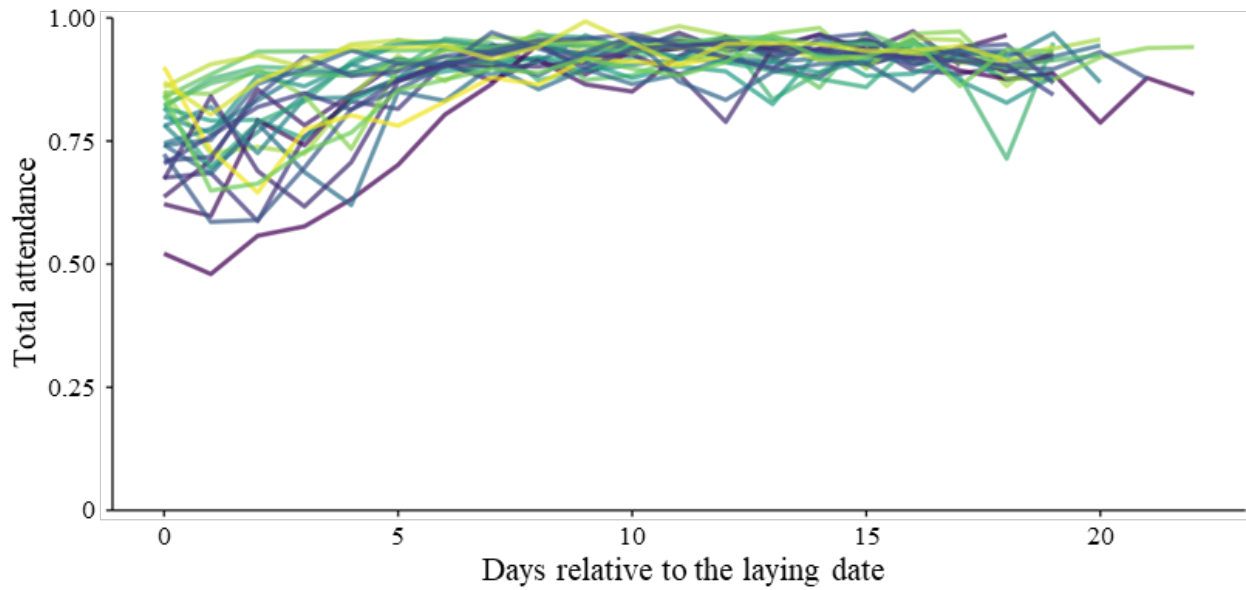


Figure D.1 Within-pair total attendance across days within the incubation stage, from first egg laying to first egg hatching. Colours indicate pair identity. Attendance increases markedly after clutch completion (approximately 4–5 days after the first egg is laid), with pairs spending most of the day at the nest, whereas total attendance is lower during the clutch completion period.

D.1 Sensitivity analyses

Table D.1 Stage-specific estimates for total and joint nest attendance under alternative modelling approaches. We fitted a linear mixed-effects model (LMM) on the proportion scale (LMM proportion) and compared its outputs with three sensitivity models: an LMM fitted to logit-transformed proportions (LMM logit) and a weighted LMM on the proportion scale with weights proportional to the number of available frames (scaled to mean 1; LMM proportion weighted). For models fitted on the logit scale, estimates were back-transformed to the proportion scale for comparison purposes. For each metric, model, and breeding stage, we report the estimated mean proportion and its lower and upper confidence limits. NB = nest building, IN = incubation, P1 = first provisioning week, and P2 = second provisioning week.

metric	method	stage	mean	lower	upper
total	LMM proportion	NB	0.429	0.386	0.473
total	LMM proportion	IN	0.912	0.9	0.923
total	LMM proportion	P1	0.756	0.713	0.799
total	LMM proportion	P2	0.463	0.379	0.547
total	LMM logit	NB	0.414	0.358	0.473
total	LMM logit	IN	0.92	0.911	0.928
total	LMM logit	P1	0.786	0.738	0.827
total	LMM logit	P2	0.456	0.359	0.555
total	LMM proportion weighted	NB	0.43	0.388	0.472
total	LMM proportion weighted	IN	0.913	0.902	0.924
total	LMM proportion weighted	P1	0.755	0.711	0.799
total	LMM proportion weighted	P2	0.463	0.378	0.547
joint	LMM proportion	NB	0.433	0.39	0.477
joint	LMM proportion	IN	0.096	0.069	0.122
joint	LMM proportion	P1	0.035	0.014	0.056
joint	LMM proportion	P2	0.036	0.015	0.056
joint	LMM logit	NB	0.411	0.356	0.468
joint	LMM logit	IN	0.065	0.047	0.088
joint	LMM logit	P1	0.032	0.027	0.039
joint	LMM logit	P2	0.029	0.024	0.037
joint	LMM proportion weighted	NB	0.435	0.392	0.478
joint	LMM proportion weighted	IN	0.094	0.067	0.12
joint	LMM proportion weighted	P1	0.034	0.015	0.053
joint	LMM proportion weighted	P2	0.036	0.017	0.055