Examining the role of trade-offs between current and future reproduction in shaping provisioning decisions in birds

by

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Abstract

Life-history theory and parental investment theory provide the theoretical framework for understanding the adaptive strategies employed by organisms to optimize reproductive success in dynamic environments. Avian species are a valuable model for testing these theories due to their diverse life-history strategies, readily observable behaviours, and amenability for manipulations of clutch/brood size. This thesis investigates the trade-offs associated with parental investment in current versus future reproduction, as well as the adaptive adjustments made by parents in response to changing environmental conditions, focusing specifically on Arctic-breeding Peregrine falcons (*Falco peregrinus tundrius*). The first objective of this thesis was to assess evidence for trade-offs between investment in current versus future reproduction in birds. To do this, we conducted a systematic review and meta-analysis of 52 studies, focusing on studies that included experimental manipulations of brood size and its impact on parental provisioning behaviours. The meta-analysis revealed strong support for the existence of trade-offs, with parents adjusting their provisioning efforts in response to changes in brood size. The systematic review also highlighted gaps in the published literature, including a lack of studies testing life-history trade-offs in longer-lived avian species, including raptors. The second major objective was to investigate evidence for adaptive adjustments in parental care in Peregrine falcons, which contributes to filling the gaps identified in the systematic review. This was achieved through two separate long-term studies; one observational and one experimental. The observational study relied on provisioning data collected over 7 breeding seasons and revealed that Peregrine falcons adaptively adjust their provisioning behaviour in response to natural variation in brood demand, with higher provisioning rates observed as nestling demand increases, both via increased nestling number and increased nestling age. We also show that variance in provisioning increases with increasing nestling demand, which is consistent with predictions from variance-sensitive provisioning theory. However, given the observational nature of the study, alternative explanations are also possible, and further work is required to allow stronger inference about the precise mechanism(s) underlying the observed shifts in variance. The experimental study involved providing food supplementation at Peregrine nests over 5 breeding seasons to evaluate how supplemental food would affect parental decisions with respect to allocation to current reproduction. We found no evidence that parents provided with supplemental food had higher provisioning rates to their offspring. However, despite the lack of effect on provisioning rates, there was strong support for a positive association between supplemental food and offspring survival probability and fledging body mass. Taken together, these results suggest that parents reallocated time/energy that was saved as a result of receiving supplemental food towards brooding or nest defence rather than towards provisioning. Overall, this research contributes to a better understanding of avian parental care strategies and their implications for reproductive success. The findings highlight the importance of adaptive adjustments in parental care behaviours in response to changing environmental conditions, particularly food availability. Future studies should continue to explore a broader range of parental care behaviours and incorporate detailed observations over multiple breeding seasons to further elucidate the mechanisms underlying parental investment decisions in birds, especially in longer-lived species like Peregrine falcons.

Preface

This thesis is an original work by Rebekah Alice McKinnon (RAM).

Chapter 2 of this thesis will soon, as of the time of writing, be submitted to *Biological Reviews* as McKinnon RA, Sridharan S, Lagisz M, Mathot KJ (upcoming 2024) 'Species longevity does not mediate the investment trade-off between current and future reproduction in birds.' RAM conceived of the study and revised the idea with help from KJM. Literature scoping searches were conducted by RAM. Initial screening of titles and abstracts was conducted by RAM and SS and was cross checked by KJM. RAM read all the full texts and conducted the data extraction. KJM provided assistance and cross checking of extracted data. Data analysis was conducted by RAM, with substantial guidance from ML, and aided by KJM. The manuscript was written by RAM with significant input from KJM. All co-authors contributed to revisions of the manuscript. All data and code required to reproduce analyses and figures presented in the manuscript (i.e., Chapter 2) will be archived, prior to submission, on the Open Science Framework (OSF) repository.

Chapter 3 of this thesis has been published in *Behavioral Ecology* as McKinnon RA, Hawkshaw K, Hedlin E, Nakagawa S and Mathot KJ (2023) 'Peregrine falcons shift mean and variance in provisioning in response to increasing brood demand.' DOI: https://doi.org/10.1093/beheco/arad103. RAM and KJM conceived of the study. RAM, KH, and EH contributed to data collection via fieldwork. RAM led camera trap data processing (4 years data) along with KH (3 years data). RAM processed and compiled the data for use in this study. Data analysis was conducted by RAM, with input from SN, KJM, and EH. The manuscript was written by RAM with support from KJM. All co-authors contributed to revisions of the manuscript. All data and code required to reproduce analyses and figures presented in the manuscript (i.e., Chapter 3) are archived on Dryad (https://doi.org/10.5061/dryad.6hdr7sr6q) and on the OSF repository. (https://osf.io/ep83x/?view_only=872641734b8342e391000f965623446d)

At the time of writing, Chapter 4 of this thesis has been accepted for publication at *Royal Society Open Science* as McKinnon RA*, Hedlin E*, Hawkshaw K and Mathot, KJ (2024) 'Food supplementing Peregrine falcon (*Falco peregrinus tundrius*) nests increases reproductive success without changes in parental provisioning rate.' (wherein * indicates joint first authors). The original experiment conducted as part of this study was conceived of by EH. RAM and KJM formulated model predictions and conceptualized research questions and data analysis. EH and KH conducted the field work. KH led camera trap data processing (3 years data) along with RAM (2 years data). RAM processed and compiled the data for use in this study. RAM led formal analysis and data visualizations, with support from KJM and EH. RAM wrote the initial manuscript draft with support from KJM. All co-authors contributed to revisions of the submitted manuscript. All data and code required to reproduce the analyses and figures presented in the manuscript (i.e., Chapter 4) are archived on Dryad (https://doi.org/10.5061/dryad.pnvx0k6wt) and on the OSF repository (https://osf.io/b8rka/?view_only=d4794a4f311241e89131b874a05a6bcc).

This research adhered to the stipulations of all required permits, including the University of Alberta Animal Use Protocol AUP00000042 (issued to Alastair Franke), Government of Nunavut Wildlife Research Permits (issued to Alastair Franke; # 2018-027 #2019-013), and the Environment and Climate Change Canada Bird Banding License (issued to Alastair Franke; Master Permit 10833).

Dedication

I dedicate this thesis to my grandmother, Elizabeth Esther Brisbane, to whom I credit my pursuit of education. In addition to being unwaveringly supportive and proud of my every accomplishment, big or small, she is responsible for the statement which changed the course of my life:

"Education is your escape."

Acknowledgements

I wholeheartedly thank my supervisor Kimberley Mathot for investing not only her time, energy, resources and effort into facilitating my research but also me as a person. Without Kim and her constant support through the many tests of my strength of will throughout the duration of this PhD I don't think I would ever have made it this far (at least not with my sanity still intact). Kim is a wonderful role model, an incredible scientist, and a beautiful person inside and out and I am forever grateful to have had the good fortune of being a student in her lab.

I am thankful for the dedicated individuals associated with the Government of Nunavut Department of Environment, the Kangiqliniq Hunters and Trappers Organization, Nunavut Arctic College, local Inuit guides, and the residents of Rankin Inlet who generously supported and embraced our research endeavours in the region. A special acknowledgment extends to Alastair Franke, for granting us permission to work within his study population, and for technical, logistical, and financial support, as well as providing access to long-term data. Logistical and technical support was also provided by the staff at Agnico Eagle Mines Ltd. I thank Alexandre Paiement and Nick Gullota for their contribution to data collection. Thank you to Inuit field technicians Andy Aliyak, Hugh Silu Oolooyuk, and Jaden Sigurdson for providing indispensable guidance and sharing their knowledge of the environment. Without their expertise, the field work would not have been possible. I thank Anna Jovtoulia for her contribution to data extraction from nest camera images.

Special thanks are owing to my PhD committee members Drs. Colleen Cassidy St. Clair and Andrew Derocher for all their help throughout the course of my PhD and for their investment of time and intellect in helping refine my research projects and the content of this thesis. I would also like to thank Dr. David Wesneat (University of Kentucky) for acting as an external examiner for my thesis, and Dr. Lien Luong for serving as an arm's length examiner. I am thankful also for the members of the

Mathot lab, past and present, namely: Josue Arteaga Torres, Nick Gulotta, Elene Haave Audet, Sheeraja Sridharan, Nathan Hobbs, Megan LaRocque, Ipshita Gayen, Deborah Hawkshaw and Jan Wijmenga, for contributing to refining the scope of the research contained in this thesis by providing regular feedback, especially during the planning stages. I would also like to thank the collaborators that I have had the pleasure to work with on various publications throughout the duration of my PhD, namely: Malgorzata (Losia) Lagisz, Shinichi Nakagawa, Erik Hedlin, Kevin Hawkshaw and Sheeraja Sridharan.

Without my grandmother, Elizabeth (Bissy) Brisbane, to whom I dedicate this thesis, I would never have accomplished this work. I owe not only my accomplishments to her, but my very life. I am also incredibly grateful for the support of my husband Nathan Macale who has constantly loved, comforted, and encouraged me throughout the duration of my PhD.

This research was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant (#RGPIN-2018-04358) and Northern Research Supplement (NRS-2018-517979) awarded to KJM. Additional financial support was provided by the University of Alberta Northern Research Award awarded to RAM. RAM also benefited from a Mitacs Accelerate Internship (grant #IT18033), sponsored by Arctic Raptors. Alastair Franke secured funding from the Government of Nunavut through grants SC180029, SC180030, SC190039, and SC190042, as well as from the Nunavut General Monitoring Program (EC73_2019-20). Alastair Franke further received in-kind funding from the Nunavut Arctic College and Agnico Eagle Mines (Meliadine Division).

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Chapter 1: Introduction

Thesis Overview

Life-history Theory

Life-history theory is a framework which explores the complex trade-offs influencing key aspects of the life cycles of diverse organisms (Stearns, 1976; Stearns, 1989). Over the last several decades, research has demonstrated the importance of life-history theory in understanding how organisms adapt to their environments to survive and reproduce, and it continues to be a significant field of study within evolutionary biology. Common questions within life-history theory include those related to age at first reproduction, frequency of reproduction, lifespan, and trade-offs between quantity and quality of offspring. For example, why do some birds, such as the House Sparrow (*Passer domesticus*), produce clutches with large numbers of small of eggs with a relatively low investment per offspring, compared to species like the Bald Eagle (*Haliaeetus leucocephalus*), which produces a small number of large eggs with a relatively large investment per offspring? (Verhulst & Nilsson, 2008; Winder & Watkins, 2020). Why do some species, such as the African elephant (*Loxodonta africana*), exhibit sexual size dimorphism? (Lee & Moss, 1986). Why do birds exhibit variations in lifespan, with some, like the Snowy Albatross (*Diomedea exulans*), living up to 80 years, while others, like the Ruby-throated Hummingbird (*Archilochus colubris*), typically live only a few years? (del Hoyo *et al.*, 2023; Carr & Golinski, 2020). Life-history theory explores the allocation of an organism’s limited resources to various life processes (i.e., growth, maintenance, reproduction), across its lifespan. The fundamental concept in all life-history research revolves around fitness and allocation trade-offs; allocating resources to one life process comes at the expense of another. Organisms face the challenge of optimizing resource allocation to maximise their fitness in the face of selective pressures and ecological constraints. Understanding how these trade-offs are resolved is essential for deciphering the adaptive strategies employed by organisms to maximise their evolutionary fitness.

Parental investment in offspring is one area of life-history theory that has received particularly significant attention, both for theoretical investigations (e.g., Trivers, 1972; Klug *et al.*, 2012; Lack, 1947; Smith & Fretwell, 1974; Einum & Fleming, 2004; Turbill, Bieber & Ruf, 2011; Wong, Meunier & Kölliker, 2013) and empirical investigations (e.g., Greig-Smith, 1980; James, 1981; Smith *et al.*, 1988; Hainstock *et al.*, 2010; Mims & Olden, 2012; Meister *et al.*, 2017; Cayuela *et al.*, 2019). Parental investment represents any parental expenditure (e.g., time, energy, resources) with the function of benefiting dependant offspring (Trivers, 1972; Robertson & Biermann, 1979). This investment may be made by both parents (i.e., biparental care), or be made exclusively by one parent (i.e., exclusive maternal or paternal care). Parental care can span various stages of offspring development from pre-natal phases such as incubation of eggs in birds, to post-natal care including food provisioning and nest defence. Any parental expenditure towards current offspring is ultimately unavailable for investment in self-maintenance and future offspring. The trade-off between parental investment in current versus anticipated future offspring is a key aspect of life-history theory (Stearns, 1976; Monaghan & Nager, 1997; Erikstad *et al.*, 1998; Milonoff *et al.*, 2004).

Parental Investment Theory

Trivers (1972) coined the term ‘parental investment theory’ which refers to a parent’s allocation of resources to enhance an offspring’s survival and reproductive success. This investment is categorised into mating investment (involving the sexual act and contribution of sex cells) and rearing investment, encompassing the time, energy, and resources dedicated to offspring care. All iteroparous species (i.e., species that experience multiple reproductive events in their lifetime) face a trade-off between immediate reproductive gains (via investing in their current offspring) and preservation of expendable energy and resources for future reproductive endeavours (Monaghan, Nager & Houston, 1998; Klemp, 2000; Milonoff *et al.*, 2004; Parejo & Danchin, 2006; Wang *et al.*, 2009). Parental investment theory aims to understand how parents mitigate these trade-offs (Stearns, 1989). As demand from current offspring increases, for example as offspring get older or more offspring are born, parents must increase their investment levels to meet the growing needs of their offspring. In doing so, however, they potentially jeopardize their own condition and, consequently, compromise their prospects for future reproductive success (Milonoff *et al.*, 2004; Leach *et al.*, 2019; Richardson, Stephens & Smiseth, 2020; Powers *et al.*, 2020). That such trade-offs should exist is intuitive, however, empirical evidence supporting these trade-offs has been mixed, with many studies reporting relationships that directly oppose those predicted by trade-offs (Metcalf, 2016).

A foundational model by van Noordwijk & de Jong (1986) highlights the impact of individual resource disparities. They use the simple example of human expenditure on homes versus vehicles; while a given individual who spends more money on a home will have less remaining to spend on a vehicle, individuals who have more money overall often purchase both expensive homes and expensive cars, while those with less money available will invest less in both their home and car. This results in a positive association between investment decisions at the phenotypic level, because this largely reflects the among-individual level relationship when variation among-individuals in access to resource is substantial. Similarly, empirical studies examining investment decisions in animals at the among-individual level often report positive correlations between certain life-history traits, but these may be concealing negative correlations at the within-individual level (Figure 1.1). Thus, van Noordwijk & de Jong's model emphasises the need for experimental studies which manipulate resource availability, or investment decisions, at the individual level to disentangle effects that occur at the among-individual versus within-individual levels. Understanding the resolution of within-individual trade-offs within the context of avian studies can provide valuable insights into the adaptive strategies employed by birds to optimize their lifetime reproductive fitness.

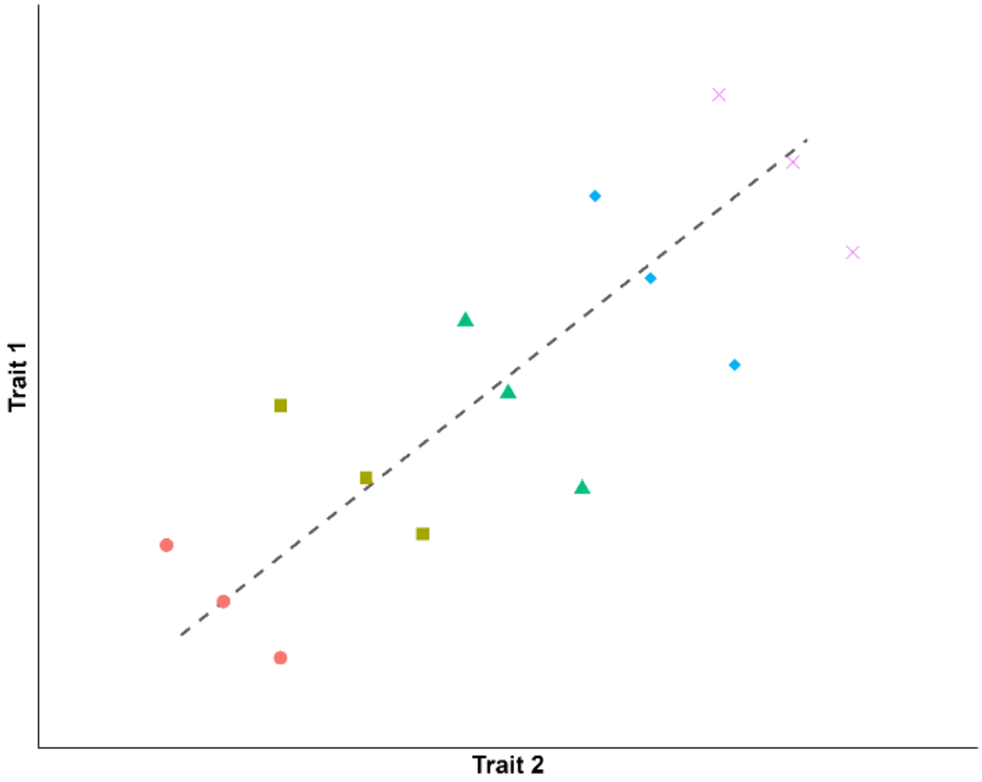

Figure 1.1: *an illustration of theory showing how within-individual trade-offs (e.g., between current and future reproduction) can be obscured at the population-level when individuals differ in access to resource. In this figure, each individual is represented by a different colour and shape. Within-individuals, there is a negative relationship between investment in trait 1 and investment at trait 2. However, individuals that have access to more resource can invest more in both trait 1 and trait 2. These among-individual differences result in an overall positive correlation between trait 1 and trait 2 at the population level.*

Birds are an important taxa in studies investigating life-history and parental investment theory as they are typically iteroparous, providing opportunity to study trade-offs between current and future reproduction; they have behaviours that are often easily observable in natural settings, facilitating the collection of detailed data on, for example, provisioning behaviours and parental care; they are amenable to experimental manipulations, facilitating the investigation of the impact of controlled variables on expression of life-history traits and parental investment decisions; their brood size can be manipulated bidirectionally, as birds accept young of others, unlike in mammals; and the avian class is highly diverse, with species exhibiting a wide range of life-history strategies, reproductive behaviours, and ecological adaptions.

Behavioural Plasticity & Optimal Foraging Theory

Understanding behavioural plasticity and its implications is crucial in the broader context of understanding organism adaptations, including optimal resource allocation strategies to enhance reproductive success and overall survival. Just as life-history and parental investment theories elucidate how organisms allocate resources across different life processes, behavioural plasticity encompasses the range of behaviours an individual can exhibit in different contexts or in the face of environmental variability (Mathot *et al.*, 2017; Brawn, 1991; Westneat *et al.*, 2011; Westneat, Schofield & Wright, 2012). By integrating insights from life-history theory, behavioural plasticity, and optimal foraging theory, it is possible to gain a more comprehensive understanding of the adaptive strategies employed by organisms to survive and reproduce in diverse and often unpredictable environments.

Behavioural plasticity is a crucial aspect of an organism's phenotypic expression, enabling it to navigate diverse ecological niches and respond to fluctuating resource availability (e.g., unreliable or inconsistent food availability) (Sofaer *et al.*, 2013; Trexler, 1997). The concept of reaction norms refers to the range of phenotypic expressions (i.e., different behavioural responses) a genotype can produce depending on the changing environmental conditions (Westneat *et al.*, 2011; Westneat *et al.*, 2012; Araya-Ajoy, Mathot & Dingemanse, 2015; Brawn, 1991). Animals exhibiting phenotypic plasticity can adjust their behaviour based on environmental stimuli, allowing for increased versatility in responding to ecological changes. For example, food availability is often unpredictable, and animals must therefore exhibit plasticity in their food-seeking behaviour to meet the energy demands of both themselves and their dependant offspring.

Optimal foraging theory facilitates predictions of an individual's food-seeking behaviour (Lemon & Barth Jr, 1992; Martins & Wright, 1993; Wright *et al.*, 1998; Wiebe & Slagsvold, 2015). While procuring food yields energy, the act of seeking and capturing food necessitates investment of both time and energy. To enhance fitness (i.e., lifetime reproductive success), animals should adopt a foraging strategy that optimises net energy gain while incurring the smallest possible cost (i.e., energy loss) (Wright *et al.*, 1998). Optimal foraging theory predicts that animals will adjust their foraging strategies to maximise energy intake while minimising energy expenditure, aligning with the fundamental principles of life-history theory which emphasize the allocation of limited resources to maximise fitness across an organism's lifespan. Animals must balance the energy invested in foraging with other essential activities, such as parental care and predator avoidance, to optimise their overall reproductive success. The ability to balance conflicting demands is fundamental in adaptive behavioural plasticity. Thus, behavioural plasticity often involves trade-offs, wherein animals must allocate limited energy to different behaviours based on the prevailing environmental conditions. For example, parents of altricial species must provision food to dependent offspring. If available food is abundant, parents may employ a strategy of higher delivery rates or expand their diet breadth (Emms & Verbeek, 1991; Rauter, Brodmann & Reyer, 2000; Magrath *et al.*, 2007; Garcia-Navas & Sanz, 2010; Mathot *et al.*, 2017; Westneat *et al.*, 2017; McKinnon *et al.*, 2023). However, in situations of low food availability and/or high demand from needy offspring, parents may make strategic use of food patches with more variable food supply (i.e., exhibit variance-sensitive provisioning behaviour) (McKinnon *et al.*, 2023; Westneat, Wright & Dingemanse, 2015).

Animals use a variety of environmental cues to modulate their behaviour. In birds, migratory patterns are responsive to seasonal variations (e.g., temperature) (Morton, 2002; Tindle *et al.*, 2014) and choice of nesting sites (Demeyrier *et al.*, 2016; Tolvanen *et al.*, 2020), and the timing of breeding activities (Ewald & Rohwer, 1982; Brawn, 1991; Fayt, 2003; Doligez *et al.*, 2008; Schoech, 2009) are linked to the availability of resources (e.g., food availability), for example. The degree of behavioural plasticity exhibited in response to environmental cues can vary among individuals in a population (Westneat *et al.*, 2012). Understanding these among-individual differences in behavioural responses is therefore essential for understanding the adaptability of populations to environmental uncertainty.

Thesis Objectives

Summary

In Chapter 2, using a meta-analysis of 52 studies, we examined plasticity in provisioning behaviour across birds in response to experimental manipulations of demand via brood enlargement and reduction to address the question, "Is there evidence for trade-offs between investment in current versus future offspring?". Although this is a key assumption in life-history theory, evidence from individual studies is often limited and/or contradictory. In Chapters 3 and 4 we examined plasticity in provisioning behaviour of Peregrine falcons in response to natural variation in offspring demand (i.e., offspring age and number) across 7 study years with varying environmental conditions (Chapter 3), and in response to experimental manipulations of food availability (via food supplementation of provisioning adults) across 5 study years (Chapter 4). With these chapters, we addressed the question, "Do Peregrine falcons exhibit evidence of adaptive plasticity in parental provisioning investment?"

Objective 1

This thesis begins with a systematic review and meta-analysis of 52 studies. The objective of this chapter (Chapter 2) was to evaluate evidence for trade-offs between investment in current versus future reproduction in birds. To effectively address this objective, we included only experimental studies on iteroparous birds, to avoid confounds with individual differences in access to resource (van Noordwijk & de Jong, 1986). The included experimental studies focused on the impact of manipulated demands from the current brood, via brood size manipulation experiments, on parental investment in provisioning behaviour. In addition to evaluating general support for trade-offs between current and future reproduction, we also evaluated whether the strength of response to brood size manipulations was shaped by expected future reproduction (residual reproductive value, RRV). To do this, we used species longevity as a proxy for RRV (i.e., the expected lifetime reproductive opportunities an individual has).

Objective 2

This thesis includes two chapters that present the results of long-term field studies in Arctic breeding Peregrine falcons. The objective of these chapters (Chapters 3 and 4) was to investigate evidence for adaptive adjustments in parental care in Peregrine falcons. We did so using two distinct investigations: first, an observational study looking at changes in provisioning in response to natural variations in brood demand (via brood size and age) (Chapter 3); and second, a field experiment in which we manipulated food availability by providing provisioning parents with supplemental food and examined the change in provisioning behaviour and offspring success (mass and survival) in response (Chapter 4).

Life-history theory extends to parental care dynamics more broadly, wherein adjusting levels of care provided to offspring in response to changing brood demands is crucial (Monaghan & Nager, 1997; Roulin, Ducrest & Dijkstra, 1999; Westneat *et al.*, 2017). As brood demand increases, parents are expected to adopt at least three (non-mutually exclusive) strategies to meet this increasing demand: increasing provisioning rates, reducing prey selectivity, and increasing variance-prone behaviour; it is theorised that they may do so in a hierarchical manner, first adopting increased provisioning rates, and only adopting variance-prone behaviour as a last resort in challenging conditions. We explored the hierarchical adoption of provisioning tactics in response to increasing brood demand in the first data chapter, exploring provisioning dynamics across seven study years in Chapter 3.

The aforementioned investment trade-off is influenced in large part by environmental conditions, particularly food availability. Low food availability leads to decreased investment in the current brood, as the likelihood of brood success is diminished relative to periods of more abundant food. Supplementing parents with additional food may therefore facilitate increased investment in the current brood. However, parents may use the more abundant food supply to instead shift their efforts towards other parental care activities such as nest defence or towards self-maintenance (resulting in increased likelihood of future reproductive success). Alternatively, caching species, such as Peregrines may use supplemental food to serve as an insurance against stochastic environmental variability and/or challenging provisioning conditions. We examined evidence for these potential parental responses to supplemental food supply in Peregrine falcons across 5 breeding seasons Chapter 4.

Conclusion

Overall, this research contributes to an understanding of the complex interplay of trade-offs in parental investment decisions, providing valuable insights into the mechanisms that shape reproductive strategies. The meta-analysis, which forms Chapter 2, covers a range of 26 bird species through 301 estimates extracted from 52 studies. This work provides a comprehensive assessment of trade-offs proposed by life-history and parental investment theories, an important fundamental concept in evolutionary biology as a whole. In Chapters 3 and 4 we conducted both observational and experimental studies in Arctic-breeding Peregrine falcons, a long-lived species understudied in the context of life-history trade-offs (as revealed in our systematic review, Chapter 2). This work highlights the nuanced adjustments in provisioning behaviour in response to varying brood demand and environmental conditions, through both observational and experimental studies.

In Chapter 5, I provide a broad overview of the key findings of this thesis and highlight key areas for future research. While this thesis provides valuable insights into reproductive strategies, there remains a need for further exploration across a broader range of species and the incorporation of more experimental work, particularly in longer-lived species, to enhance our understanding of these important trade-offs. This research fills important gaps in empirical research and highlights the importance of integrated approaches in unravelling the intricacies of parental care dynamics and points towards important avenues for future research.

Chapter 2: Meta-analysis of brood size manipulation experiments reveals trade-offs between current and future reproduction in birds

Abstract

Organisms must allocate resources among growth, survival and reproduction. Because resources are finite, this inevitably leads to trade-offs. Resource invested in growth cannot be invested in reproduction, and resource invested in current reproduction is no longer available for future reproduction. Life-history theory posits that trade-offs between current and future reproduction should be mediated by the relative costs and benefits associated with current versus future reproduction. When the value of the current brood is high (e.g., brood size is large), parents should invest more, but when the value of the current brood is low (e.g., brood size is small), parents should conserve investment for anticipated future reproductive opportunities to maximise lifetime reproductive success. The resolution of the trade-off between current and future reproduction is also expected to be shaped by expected future reproduction (called residual reproductive value, or RRV). Longer-lived species, which have more lifetime reproductive opportunities, pay greater costs when compromising future reproduction, and therefore, are expected to show smaller increased in current reproduction in response to increased value of current brood. Although trade-offs are fundamental to life-history theory, empirical studies have often failed to find support for these trade-offs. The lack of support for trade-offs has been suggested to be due in part to inappropriate study designs. Specifically, trade-offs should be investigated using experimental designs that allow within-individual changes in allocation to current versus future reproduction to be disentangled from among-individual differences in total resources available to allocate to reproduction. Here, we report the results of a systematic review and meta-analysis of experimental studies in birds in which brood size (and thus, brood value) was experimentally manipulated (i.e., enlarged, reduced) and parental investment decisions were recorded (e.g., provisioning rate). We extracted 301 estimates from 52 studies in 26 avian species. Consistent with the notion that trade-offs between current and future reproduction mediate parental investment decisions, we found that investment in the current brood increased when brood size was experimentally enlarged, and decreased when brood size was experimentally reduced. We also tested whether the response to brood manipulations was mediated by species longevity, based on the assumption that species longevity was a useful proxy for RRV. We found no support for the role of species longevity in mediating these responses, however, studies in long-lived species were under-represented in available studies, which may have limited our ability to detect effects of longevity. Our key finding, that parental provisioning was strongly affected by experimental brood size manipulations, is significant because it provides strong and general support for the role of trade-offs in shaping parental investment decisions.

Introduction

Trade-offs are central to life-history theory (Stearns, 1989; Stearns, 1992). For example, in iteroparous species (i.e., species where individuals have more than one reproductive bout during their lifetime), a trade-off may exist between current and future offspring such that higher investment in current reproduction comes at the cost of future reproduction (e.g., Fokkema, Ubels & Tinbergen, 2016; Hodges *et al.*, 2015; Ackerman & Eadie, 2003; Milonoff *et al.*, 2004). Understanding how such trade-offs are resolved is central to parental investment theory (Fisher, 1958; Trivers, 2017). As demand of current offspring increases, for example as offspring age, parents must increase their investment to minimise likelihood of energetic shortfall. However, this comes at the expense of resources available for investment in future offspring (e.g., Fokkema *et al.*, 2018; Richardson *et al.*, 2020). The extent to which parents increase their investment in the current brood with increasing demand should depend on the potential costs to future reproduction. If the costs to future reproduction are small, parents should increase investment in current offspring more than if the costs to future reproduction are large (Erikstad *et al.*, 1998; Sol *et al.*, 2016; Veronika Bókony *et al.*, 2009). In species where parents provision dependent offspring, this typically takes the form of increased provisioning rates, or greater size or biomass of delivered food items. In doing so, parents must balance their increased investment in offspring with decreased investment in their own condition (e.g., via self-feeding) thus reducing their capacity to invest in future reproductive efforts (e.g., Siefferman & Hill, 2008; Requena *et al.*, 2012). Parental investment theory strives to answer the question of how much parents should increase their investment in current offspring as demand from that offspring increases.

Although trade-offs are widely accepted as being a key mechanism shaping life-history decisions, empirical studies demonstrating such trade-offs are scarce (Metcalf, 2016). In fact, numerous studies find patterns that directly contradict the notion of trade-offs. Observational studies in birds often report a positive association between investment in current versus future offspring at the level of the population, as for example, parents which invest more in their current brood (e.g., by increased provisioning, nest defence) do not go on to have poorer body condition and/or survival (Reznick, Nunney & Tessier, 2000; Roff & Fairbairn, 2007; Santos & Nakagawa, 2012). This apparent contradiction has been eloquently explained in a simple model by van Noordwijk & de Jong (1986) showing that when individuals differ in how much resource they have available (e.g., due to differences in individual quality, or differences in territory quality), individuals with greater access to resource can invest more both in current and future reproduction (see also Reznick *et al.*, 2000; Xu *et al.*, 2023). As such, differences in the amount of resource available among-individuals can obscure trade-offs that are occurring at the within-individual level (see Figure 2.1). Thus, while a wealth of observational, population-level studies examining parental investment decisions exist, experimental studies are necessary to disentangle the effects of among-individual heterogeneity (e.g., differences in quality) from within-individual trade-offs in shaping these decisions (Santos & Nakagawa, 2012). Existing experimental studies additionally present conflicting results, across and even within studies. While some studies report consistently higher investment in enlarged broods relative to reduced brood (e.g., Baldan *et al.*, 2019; Berzins & Dawson, 2016), others find the opposite (e.g., Hall *et al.*, 2010; Maigret & Murphy, 1997), and some even report differences in strength and direction of response to experimental manipulations across study years and/or parental sex (e.g., Aho *et al.*, 2010; Mathot *et al.*, 2017).

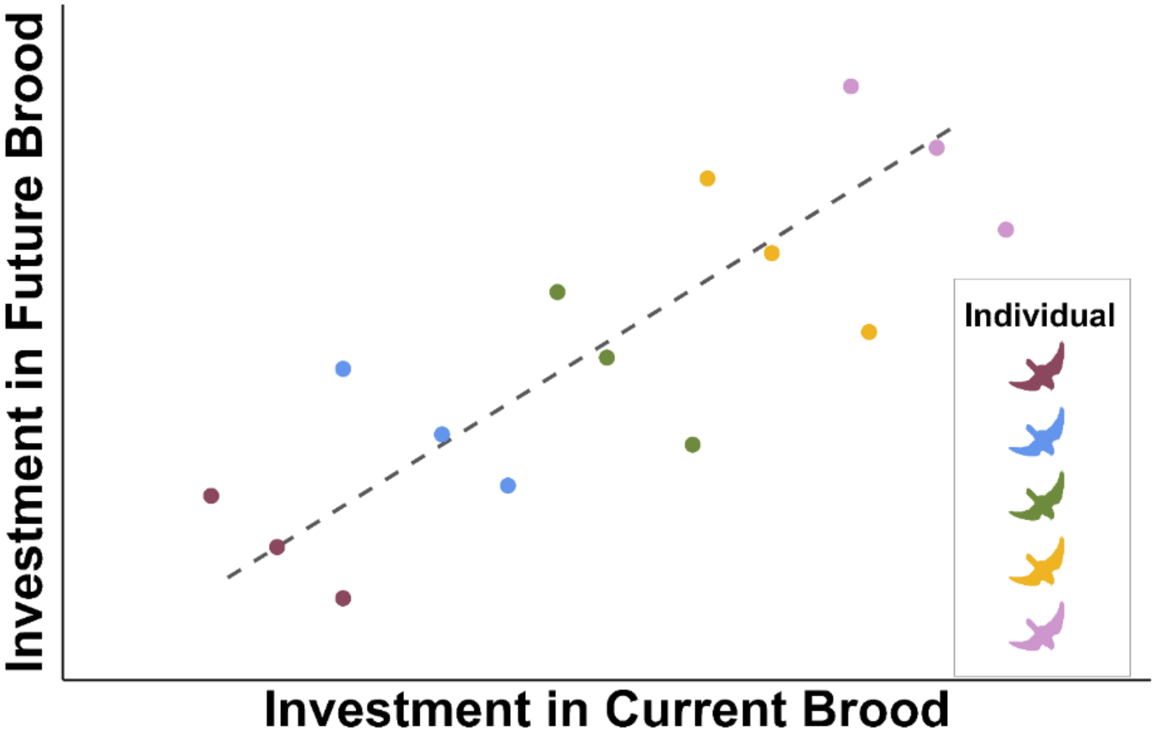

Figure 2.1: An illustration of how within-individual trade-offs can be obscured at the population-level if individuals differ in the amount of resource that they have available. When there is a positive relationship between two traits, e.g., investment in current versus future offspring, among-individuals this will result in a positive population level reaction norm (dashed black line), and the negative relationship between investment in current reproduction and investment in future reproduction at the within-individual level, as indicated by the negative within-individual reaction norm (different individuals indicated by different coloured dots), will be masked.

Here, we conducted a systematic review and meta-analysis of published experimental studies wherein demands of current reproduction were experimentally manipulated. We focused our review on birds because they are iteroparous, are amenable to manipulations of current reproduction via brood size manipulations, and parental investment can be quantified by provisioning effort. We used species longevity (specifically breeding longevity) as a proxy for residual reproductive value (RRV) because longevity influences expected future reproductive opportunities (Williams, 1966; Pianka & Parker, 1975); on average, during any given reproductive bout, long-lived species have more future reproductive opportunities (i.e., higher RRV) compared to short-lived species. The trade-off between investment in current versus future offspring is therefore expected to be mediated by species-specific RRV. Short-lived species (RRV ~ 0) should invest maximally in current reproduction regardless of the current brood value, while longer-lived species trade-off investment in current versus future reproduction. However, brood enlargement and brood reduction may have asymmetric effects on the trade-off between current versus future reproduction. This is because, all else being equal, higher RRV means increasing current investment in response to brood enlargement will have greater opportunity to impose costs on future reproduction, while reducing current investment in response to brood reductions will have greater opportunity to yield benefits for future reproduction. Thus, higher RRV may favour relatively smaller responses to brood size enlargements (due to high costs for future reproduction) compared to the magnitude of response to brood size reductions (due to high benefits for future reproduction).

Our primary objective was to assess support for proposed life-history trade-offs in reproductive investment in response to value of the current brood. Our secondary objective was to evaluate how species-specific differences in residual reproductive value (RRV) mediate this trade-off. Specifically, we predicted that: (1) provisioning parents would adjust their provisioning response according to the value of their current brood resulting in an increase in provisioning investment in enlarged broods and a reduction in provisioning investment in reduced broods; (2) longer-lived species would exhibit greater changes in provisioning investment than shorter-lived species in response to both enlarged broods and reduced broods (Figure 2.2a); (3) the magnitude of increase in investment in current brood in response to brood enlargement will decrease with increasing longevity (excluding semelparous species) (Figure 2.2b); and (4) the magnitude of decrease in investment in current brood in response to brood reductions will increase with species longevity (Figure 2.2b).

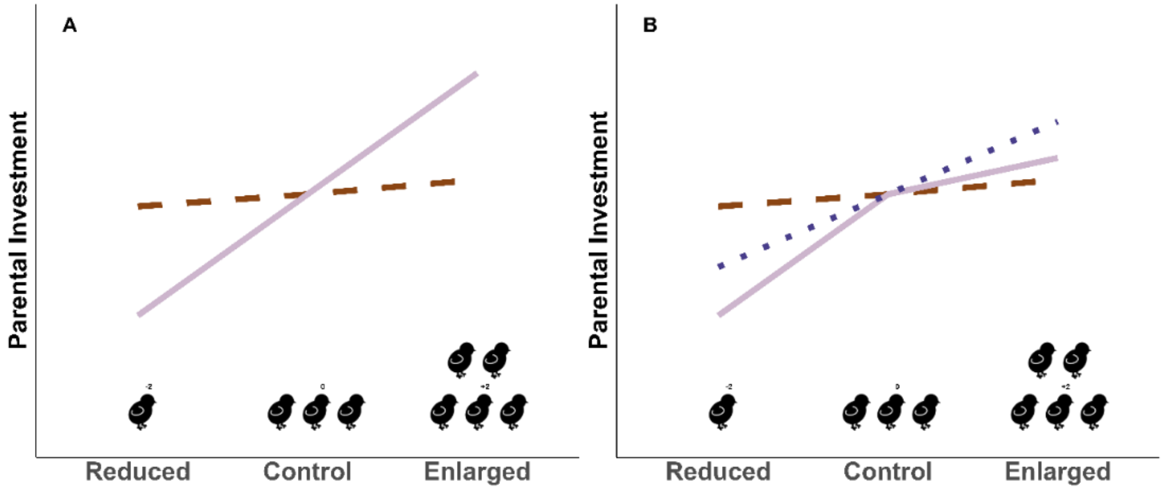

Figure 2.2: *An illustration of the predicted effect of experimentally manipulating the value of the current brood on parental effort as a function of species longevity (a proxy for expected RRV). Panel a) shows a contrast between a long-lived species (solid black line) with high RRV, and a short-lived species (dashed line) with negligible RRV. As RRV approaches zero, parents should invest maximally in current reproduction regardless of the current brood value, as indicated by the flat line. In contrast, long-lived species trade-off investment in current versus future reproduction, and therefore, are expected to respond to variation in current brood value; investing less if the current brood is of low value (reduced) but investing more if it is of high value (enlarged). Panel b) illustrates a scenario in which the trade-off between current versus future reproduction varies with increasing RRV. Specifically, as RRV increases, the costs of investment in current brood in terms of reduction in future reproduction are greater compared with species with intermediate RRV (dotted line). Therefore, species with high RRV they are not expected to increase investment as much with increasing brood value compared to species with intermediate RRV (dotted line). On the other hand, the anticipated benefit for future reproduction from reducing investment in the current brood are greater for species with high RRV compared to species with intermediate RRV, and therefore, we predict that species with the highest RRV would show the largest reduction in care with decreasing brood value.*

Methods

Systematic literature search

We conducted a literature search following the PRISMA protocol (Page *et al.*, 2021). Initial searches were carried out in both 'Web of Science' and 'Scopus' databases under the licence to the University of Alberta. All available publication years were included (1927-2022), but results were limited to articles written in English. Searches targeting non-English language sources are described below. The search was conducted using two search strings. The first search string contained provisioning terms: provision* OR "parental effort" OR "parental investment" OR "visit rate" OR "prey delivery" OR "energy delivery" OR "parental provision*" OR "feeding visit$" OR "feeding rate" OR "feeding effort". The second search string contained) terms related to brood demand: "brood size" OR "nestling number" OR "number of nestlings" OR "reduced brood" OR "enlarged brood" OR "clutch size" OR "brood reduction" OR "brood enlargement" OR "number of chicks" OR "chick number" OR "brood demand" The two strings of search terms were combined using the "AND" Boolean operator (see ESM for final search string in full, for ease of reproducibility). Database searches were conducted on March 30th, 2022. These search terms returned 2,001 results in 'Web of Science' and 1,207 in 'Scopus' (total from both databases: 3,208).

To ascertain which articles should be included in this review, results of both database searches were imported into Endnote and duplicates removed, leaving 2,268 unique references. Next, titles and abstracts were screened independently by two observers (RAM and SS) using Rayyan (Mourad Ouzzani, 2016) to evaluate suitability for inclusion in the study. Where the two observers did not reach the same conclusion about inclusion or exclusion of an article, the title and abstract were discussed jointly with KJM to reach a consensus. We selected studies for inclusion based on the following criteria. The study had to:

(i) Be conducted in a non-cooperatively breeding bird species. We excluded cooperative breeding systems or systems with helpers at the nest because in such systems, costs (and/or benefits) of reproduction are spread across more individuals, influencing the trade-off between current and future offspring.

(ii) Include an experimental manipulation of brood size (i.e., increase and/or decrease number of eggs or nestlings). Brood size manipulations must have been conducted using a random subset of nests in the population. Studies which conducted manipulations only on nests of a certain brood size were excluded. For example, if only the smallest clutches received additional eggs and the largest clutches had eggs removed, we excluded the study from our review.

(iii) Include a control category in which the nests were either unmanipulated, or which experienced swapping of eggs or nestlings, but no net change in number of eggs or nestlings.

(iv) Provide one of the following measures of parental investment: prey delivery rate (sometimes called feeding rate; usually approximated by nest visit rate), inter-visit interval, rate of prey biomass delivery, and/or prey size delivered. Although other measures of provisioning behaviour are commonly reported by existing literature (e.g., changes to diet breadth or prey type delivered) these were not included as they could not be quantified for the purpose of a meta-analysis or compared in a standardised way across different species. We did not consider other forms of parental investment that were unrelated to provisioning (e.g., nest defence, faecal sac removal, or incubation). We also excluded studies that only reported daily energy expenditure, since this did not allow parental investment in provisioning to be disentangled from other forms of parental investment or from investment in self-care.

(v) Not include any additional manipulation other than those described in point ii (above) that would change the cost of parental care. For example, estimates that included manipulation of offspring demand by food supplementing or by starving provisioning adults or nestlings, applying weights, or handicapping adults were excluded from the meta-analysis as these manipulations add an additional constraint on provisioning behaviour.

(vi) Provide extractable information that allowed us to calculate an effect size (Hedges' *g*) from either descriptive or inferential statistics, sample size, and a measure of uncertainty. This information could be extractable from the article, supplementary material, accompanying datasets, extracted from figures, or obtained directly from the authors.

From initial screening of title and abstracts, we retained 118 articles to be screened by reading the full text. We were unable to retrieve 1 article (either in print or online version) (Slagsvold & Rohwer, 2000) meaning the full tests of 117 articles were screened assessed for inclusion based on the above criteria. After reading the full text, a further 66 articles were excluded, leaving 51 for inclusion in this quantitative review (Appendix A: ESM for Chapter 2; Table S2.1). Articles which were excluded, after reading the full text, based on the above defined criteria are listed in Table S2.2 (Appendix A: ESM for Chapter 2) along with reasons for their exclusion.

We also conducted searches for articles written in other languages and from grey literature (e.g., unpublished theses) using the same search term strings outlined above. Searches were conducted using both 'Worldwidescience' (https://worldwidescience.org/) and 'Bielefeld Academic Search Engine, BASE' (https://www.base-search.net/). 'Worldwidescience' is a search engine maintained by the U.S. Department of Energy's Office of Scientific Information and enables searches of national and international scientific databases to increase global representation in literature searches. BASE is a search engine maintained by the University of Bielefeld Library that enables multilingual searches, including databases for grey literature (e.g., government reports, theses). Searches of Worldwidescience and BASE were conducted on July 12th, 2023. These searches returned 161 results from Worldwidescience and 82 from BASE (totalling 243). A total of 76 duplicate records were then removed. The remaining 167 records were screened based on title and abstract independently by 2 observers

(RAM and KJM) to evaluate suitability for inclusion in the study. Where the two observers did not reach the same conclusion about inclusion or exclusion of an article, the title and abstract were discussed until consensus was reached. A further 158 records were excluded through this process, leaving 9 to be sought for retrieval. A further 6 of these records were found to have already been published as articles (e.g., theses chapters published as independent articles) that had already been captured through our initial database search (primarily using Web of Science). The remaining 3 reports were then assessed for eligibility according to the criteria outlined above, resulting in the exclusion of another 2 reports. Finally, 1 report was retained resulting in a total of 52 studies from which data was extracted (see Appendix A: ESM for Chapter 2; Table S2.1). The full PRISMA flow chart is provided in Figure 2.3.

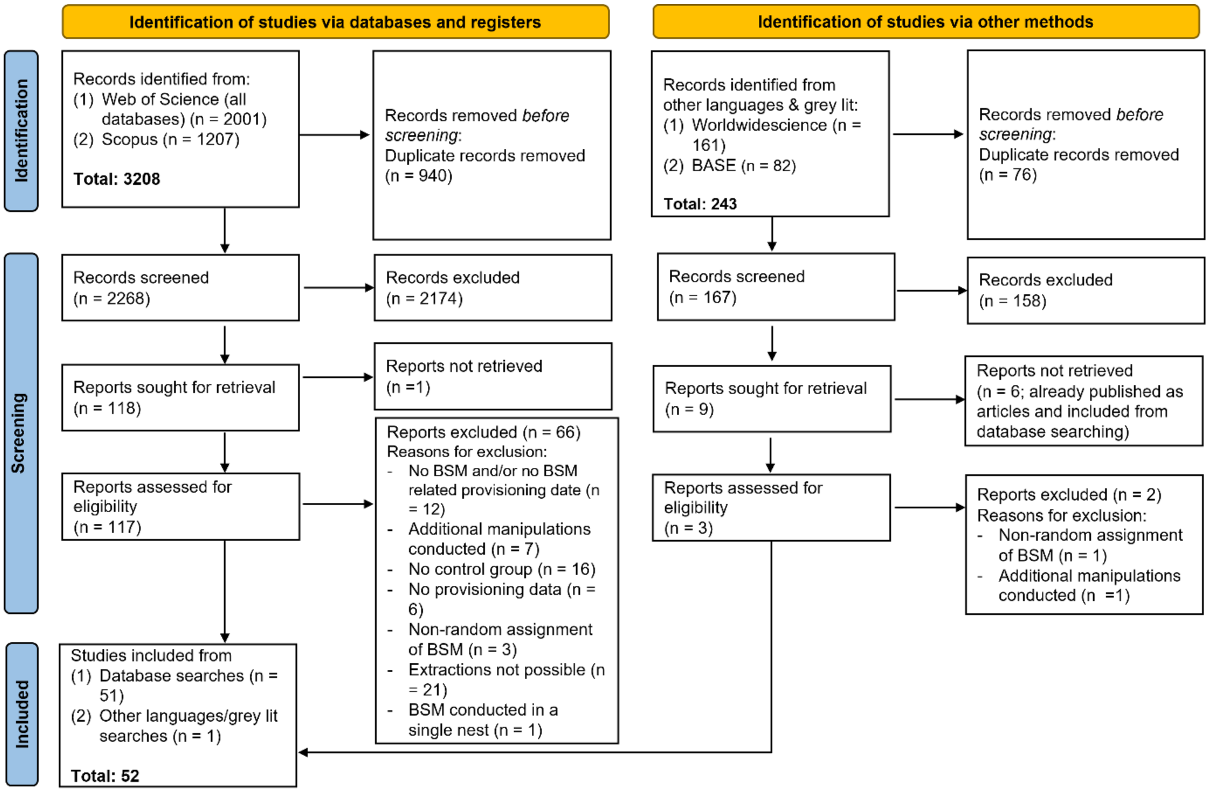

***Figure 2.3:** The PRISMA flow-chat showing the number of retained articles at each stage of refinement in the systematic review process. A list of included studies is provided in table S2.1 and a list of rejected studies (with exclusion reasons) is provided in table S2.2.*

Data extraction & effect size calculation

From the 52 articles that met the criteria for inclusion in our meta-analysis, we extracted a total of 301 estimates. Estimates were extracted by RAM and a subset of extractions (from 15/52 articles) were reviewed by KJM to ensure consistency and accuracy. Quality and methods of data collection within studies were not assessed (e.g., whether behavioural observations were made using nest cameras, or by observers from blinds).

Detailed descriptions and definitions of all information extracted from each study are provided in Appendix A: ESM for Chapter 2; Table S2.3, but in brief these included: the stage at which the treatment was applied (eggs or nestlings added/removed); the duration of the manipulation treatment, which was later categorised as either long (> 1 day) or short duration (< 1 day); and effort level (whether the provisioning metric measured provisioning behaviour at the level of the nest or the level of the nestling). We additionally noted several other details from each study, as outlined in Appendix A: ESM for Chapter 2, Table S2.3.

Since we were interested in the influence of species longevity on provisioning response to brood size manipulation, we also obtained the average lifespan of each species. We extracted this information from 'Birds of the World' by Cornell (accessible at https://birdsoftheworld.org/bow/home), and if not available there, we searched other reliable sources for this information (i.e., primarily published peer-reviewed literature) (see Appendix A: ESM for Chapter 2; Table S2.4 for details on sources of data). We similarly extracted average age at first breeding, fledging period (i.e., number of days of parental care provided to offspring before fledging), and the maximum lifespan recorded for that species. Finally, we calculated 'average breeding years' by subtracting the age at first breeding from average lifespan.

If an effect size was not directly provided within the study results, we extracted descriptive statistics over inferential statistics. If it was necessary to extract data from provided figures, we did so by using WebPlotDigitizer version 4.5 (accessible at https://automeris.io/WebPlotDigitizer.html). We also recorded the mean, SD (Standard Deviation) and SE (Standard Error) for all estimates, as reported. Where only one of SE or SD was provided, we calculated the other using the equation: $SE = SD/\sqrt{N}$, where N = number of nests. We then used this to calculate Hedges' *g* effect sizes using the 'escalc' function from the 'metafor' package in R (version 4.2.3). We calculated Hedges' *g* as it is suited to deal with small study sample sizes (Hedges & Olkin, 1985), of which there were several in our meta-analysis.

Data cleaning & data coding

We predicted that, at the level of the nest, parental effort would increase in brood enlargement treatments and decrease in brood reduction treatments. However, depending on the response variable, increased parental effort could lead to an increase in the measured response variable (e.g., provisioning rate, such as deliveries per hour), or decrease in the response variable (e.g., the time between consecutive provisioning visits, inter-visit intervals, or IVIs). Consequently, we introduced an additional column ('ES_flip') to our datasheet, which was used to adjust the sign of Hedges' *g* values in each corresponding row. The resultant column ensured that a positive effect size in the "adjusted effect size" column indicated a change in the predicted direction based on theory. For example, an increase in provisioning rate or decrease in inter-visit intervals (IVIs) for enlarged broods would be coded as positive, while a decrease in provisioning rate or increase in IVI for reduced broods would be coded as positive. This adjusted effect size was used in subsequent analyses. In the interpretation of our findings, a higher positive value denotes a more pronounced behavioural change in the predicted direction.

We centred and scaled both species average lifespan and average breeding years to ensure units were consistent across provisioning metrics and that data was expressed in a standardised form to facilitate comparisons across variables. Doing so means that our estimates reflect the effect of an increase in SD rather than years.

We linked our dataset to two different phylogenetic trees: Open Tree of Life (available at https://tree.opentreeoflife.org/opentree/argus/opentree14.9@ott93302) and Jetz *et al.* (2012) to determine if the phylogenetic effect of species relatedness levels should be included in our meta-analytic models. Separate meta-analytic models each using the phylogenetic information generated by the different trees were created and compared to ensure there were no differences generated according to the choice of tree used, which there were not.

Meta-analyses

We conducted all statistical analysis in the program R (version 4.2.3) and RStudio Version 1.2.1335 (Team, 2020). We created our models using the ‘rma.mv’ function from the ‘metafor’ package as this is suitable for fitting multivariate random-effects meta-analysis models. For all models, we included the Hedges’ *g* value as our response variable (observed effect size) and the inverse of sampling variances of the response variable as weights. We subsequently calculated the multi-level equivalent of heterogeneity (I^2), which quantifies variance not attributable to sampling error, for both total heterogeneity ($I^2_{[total]}$) and for each random effect (Nakagawa & Santos, 2012; Higgins & Thompson, 2002). I^2 is reported in place of *Q* here, due to the reliability and significance of *Q* being dependent largely on the number of studies (N) included (Nakagawa & Santos, 2012). I^2 is presented as a percentage (%) and can be used to determine if heterogeneity is high (I^2 = 75%), moderate (I^2 = 50%), or low (I^2 = 25%) (Nakagawa & Santos, 2012).

We created meta-analytic models in two steps. First, we assessed which random effects to include in the models. To do this, we ran null meta-regression models with no predictor variables but considering each of the following random effects: the phylogenetic and non-phylogenetic effect of species, the study ID, and the observation-level ID. From these models, we determined that heterogeneity explained by phylogenetic effect of species and non-phylogenetic effect of species was negligible ($I^2_{[phylogeny]}$ <0.01 for both) so these were dropped from subsequent models. However, study ID ($I^2_{[studyID]}$ = 40.39) and observation-level ID ($I^2_{[ObservationID]}$ = 11.77) were retained in future models. Total heterogeneity was moderate ($I^2_{[total]}$ = 52.16) justifying analyses of moderators via meta-regression.

In the second step, we assessed the importance of five potential moderators that were *a priori* expected to shape responses to brood size manipulations. We tested: 1) the effect of treatment (enlarged or reduced brood), with the expectation that brood enlargement would result in increased provisioning investment, and brood reduction in decreased provisioning investment; 2) Residual reproductive value (RRV) measured as (a) average lifespan (years) and (b) number of breeding years (average lifespan minus average age at first breeding) with the prediction that longer lived species and/or species with more breeding years would be more responsive to brood size manipulations (Figure 2.2); 3) Treatment stage (whether researchers moved eggs or nestlings to create enlarged or reduced broods), to test if this methodological decision influenced brood size manipulation response; 4) Treatment duration (whether the study was short term (≤ 1 day) or long term (> 1 day)) with the prediction that long term studies are more likely to reveal differences in provisioning response; and 5) Effort level (per brood or per nestling effect) with the prediction that changes in provisioning response would be more noticeable at the level of the whole brood. Surprisingly, none of the moderators by themselves appeared to be significant in explaining the variation in provisioning (see below), apart from treatment. Therefore, in a final multi-moderator model we decided to include only the moderators most pertinent to our research questions in further analysis: treatment, breeding years, and their interaction. As per Figure 2.2, we predicted that brood size manipulations would reveal either an effect of both treatment and longevity, but without an interaction effect (panel a), or an effect of treatment and longevity with an interaction between them wherein longer-lived species respond more strongly to brood reductions than brood enlargements (panel b).

We conducted additional analyses to examine the differences in response to brood size manipulations attributed to parental sex. To do so, we created a new datasheet in R which included only estimates for one parental sex (i.e., we excluded rows where ‘Sex’ was recorded as ‘both;’ see Appendix A: ESM for Chapter 2; Table S2.3). This contained 166 estimates (of 301 from the total dataset) from 12 (of 26) unique species providing us with sufficient statistical power to conduct sex-specific analyses. We again constructed meta-analytic models using the ‘rma.va’ function from the ‘metafor’ package which included the Hedges’ *g* value as the response variable and our random effect model structure. We included moderators for parental sex and the interaction between treatment and parental sex. We have reported results as ‘additional analyses’ as we did not generate *a priori* predictions about the effect of parental sex before conducting our initial analyses. To visualise meta-analytic results, we primarily used the R packages ‘ggplot2’ (Wilkinson, 2011), ‘orchaRd’ (Nakagawa *et al.*, 2023), ‘ggaluvial’ (Brunson, 2020) and ‘metafor’ (Viechtbauer & Viechtbauer, 2015).

Sensitivity analysis & analysis of publication bias

To evaluate the sensitivity of our model to more extreme estimates, we screened our extracted data for outliers. We identified 3 outliers which had Hedges’ *g* values (see *Data manipulation and data coding*) notably higher than our other estimates (i.e., Hedges’ *g* values of >5 where the 4th highest value was 3.2; see Appendix A: ESM for Chapter 2; Table S2.5). Notably, these estimates were all extracted from the same paper (Study ID 60; Ardia, 2007). We therefore performed sensitivity analysis by removing this study from our dataset and comparing the results of our final models (outlined in *Meta-analysis* section above). Results from analyses which excluded this paper were qualitatively and quantitatively similar to results from our main analyses that included them (see Appendix A: ESM for Chapter 2; Table S2.6 and Figure S2.1 for details of differences in model results), and therefore, we present results using the full data set in the main text.

Finally, we evaluated evidence for publication bias using funnel plot asymmetry in addition to testing the significance of the asymmetry using a multilevel version of Egger’s regression (Walters *et al.*, 2017; Lagisz *et al.*, 2021). We calculated the harmonic mean of sample sizes for each study (‘effectN’) and from this included effective *N*, i.e., the square root of effectN, as a fixed effect in our Egger’s regression model as well as random effects for study ID and observation-level ID. Calculating the harmonic mean of sample sizes is a strategy to address potential bias introduced by studies with very small or very large sample sizes. We also assessed the presence of a time lag effect by regressing our standardised effect sizes against publication year (i.e., ‘decline effect’; Yang, Lagisz & Nakagawa (2023)) again including random effects for study ID and observation-level ID.

Results

Overview

We extracted a total of 301 effect size estimates from 52 studies which conducted brood enlargement (*k* = 149) and/or brood reduction (*k* = 152) experiments. Estimates included 26 bird species (Figure 4), with Great tits (*Parus major*) and Pied flycatchers (*Ficedula hypoleuca*) contributing the most estimates to our meta-analysis (84 estimates from 12 studies, and 52 estimates from 8 studies, respectively). The most frequently reported response variables were feeding rate (158 estimates) and nest visit rate (as a proxy for feeding rate; 53 estimates). The least commonly reported response variables were load size (37 estimates) and visit rates per nestling (12 estimates). The average lifespan of included species ranged from 2 years for the Pied flycatcher to 20 years for the Brown pelican (*Pelecanus occidentalis*) and the resulting average breeding years ranged from < 1 year for the Red-winged blackbird (*Agelaius phoeniceus*) to 17 years for the Brown pelican (Figure 2.4).

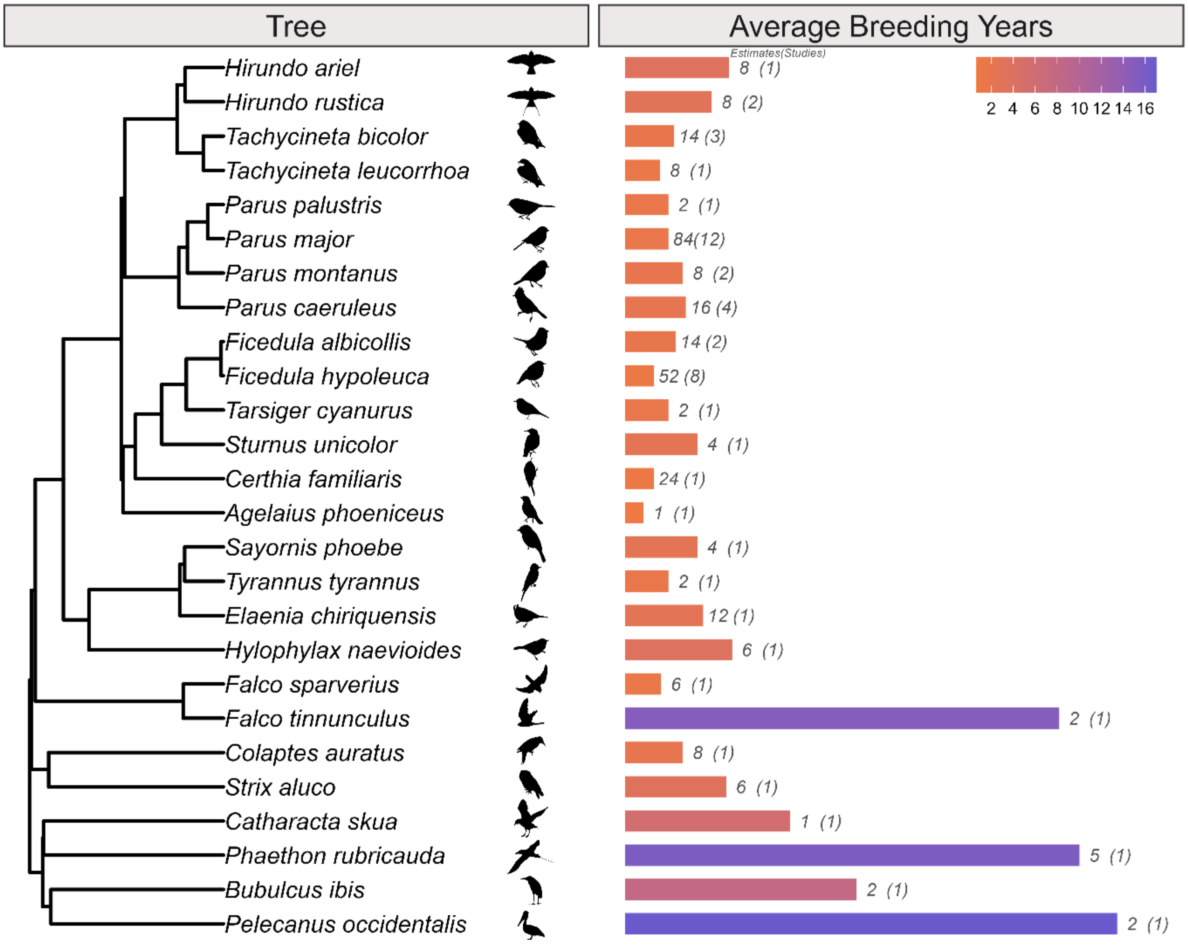

Figure 2.4: *An illustration of the phylogenetic relationships used in the meta-regression, and the associated reproductive longevity (calculated as average number of breeding years) for each species. Average breeding years are coloured on a gradient from orange to purple, with the scale representing (average) number of years from low (<1 year) to high (17 years). Shown in italics are the number of estimates for each species and the number of studies from which those estimates were taken; estimates(studies). Silhouettes of species were from PhyloPic.org (https://www.phylopic.org/permalinks/4d2aebec1e2f2da818396c344eb377c61d6ce0d70ddb15d09d7671defdf00ed2)*

Random effects only meta-analytical models

The overall effect estimate for the model containing all random effects was 0.43 (95% CI = 0.32, 0.55). We found that total heterogeneity was moderate ($I^2_{[total]}$ = 52.16). Of this, only a small percentage was explained by either the phylogenetic effect of species ($I^2_{[phylogeny]}$ <0.01) or non-phylogenetic effect of species ($I^2_{[species]}$ <0.01). Variance within phylogeny was also negligible ($\sigma^2_{[phylogeny]}$ = 0.00). Study ID accounted for the greatest proportion of the total heterogeneity ($I^2_{[studyID]}$ = 40.39) and had the greatest within-group variance ($\sigma^2_{[studyID]}$ = 0.13). Observation level ID also accounted for a substantial amount of total heterogeneity ($I^2_{[ObservationID]}$ = 11.77) but had comparatively little within-group variability ($\sigma^2_{[observationID]}$= 0.04). Therefore, study ID and observation level ID were retained in models testing moderator effects.

Meta-regression models with moderators

From our uni-moderator model including treatment (i.e., brood reduction or enlargement) we found that intercepts for both reduced and enlarged treatments differed significantly from 0 (reduction: β = 0.469; 95% CI = 0.340, 0.598; *p* = <0.0001; enlargement: β = 0.400; 95% CI = 0.271, 0.528; *p* = <0.0001). Although brood reduction tended to result in a greater change in provisioning behaviour than brood enlargement, the difference was not statistically significant (β = 0.070; -0.037, 0.176; *p* = 0.20; Figure 2.5).

Figure 2.5: *An orchaRd bubble plot (Nakagawa et al., 2023) of meta-analytic mean effect sizes, standardised mean difference (SMD, Hedges' g) by treatment group (enlarged, blue or reduced, red). Circles denote meta-analytic means and whiskers 95% confidence intervals (narrower) and 95% prediction intervals. Total number of estimates (k) is presented on the right, with number of studies contributing estimates in parentheses. Note that the number of studies in parentheses appears higher than the total number of studies included in the meta-analysis (52) as most studies conducted both brood enlargements and brood reductions. Total heterogeneity is included on the middle left ($I^2_{[Total]}$) Effect sizes are weighted by their precision (1/standard error, SE).*

Our other uni-moderator models also revealed a lack of support for a moderating effect of species longevity (average lifespan) (β = 0.0727; 95% CI = -0.0325, 0.1779; *p* = 0.1748), (scaled) average breeding years (β = 0.073; 95% CI = -0.036, 0.178; *p* = 0.178), treatment stage (estimated difference between egg and nestling: β = -0.047; 95% CI = -0.346, 0.252; *p* = 0.757), treatment duration (estimated difference between short and long duration manipulations: β = 0.065; 95% CI = -0.2428, 0.3733; *p* = 0.677), or effort level (estimated difference between per brood and per nestling effect): β = -0.011; 95% CI = -0.178, 0.157, *p* = 0.901).

Our multivariate model, directly testing our research question by evaluating support both for an effect of treatment (brood reduction or brood enlargement) and the interaction between treatment and breeding years (scaled), again revealed moderate heterogeneity ($I^2_{[total]}$ = 52.15) and that estimated effects for both the enlarged treatment (β = 0.3969; 95% CI = 0.268, 0.526; *p* = <0.0001) and reduced treatment (β = 0.4611; 95% CI = 0.331, 0.591; *p* = <0.0001) were significantly different from 0, but not different from each other (Figure 6; β = 0.064; 95% CI = -0.044, 0.173; *p* = 0.246). Although treatment effects tended to increase with breeding years, as predicted (enlarged:years: β = 0.063; 95% CI = -0.040, 0.166; *p* = 0.228 and reduced:years: β = 0.018; 95% CI = -0.094, 0.130; *p* = 0.751), neither were significantly different from either zero, nor from each other (Figure 2.6).

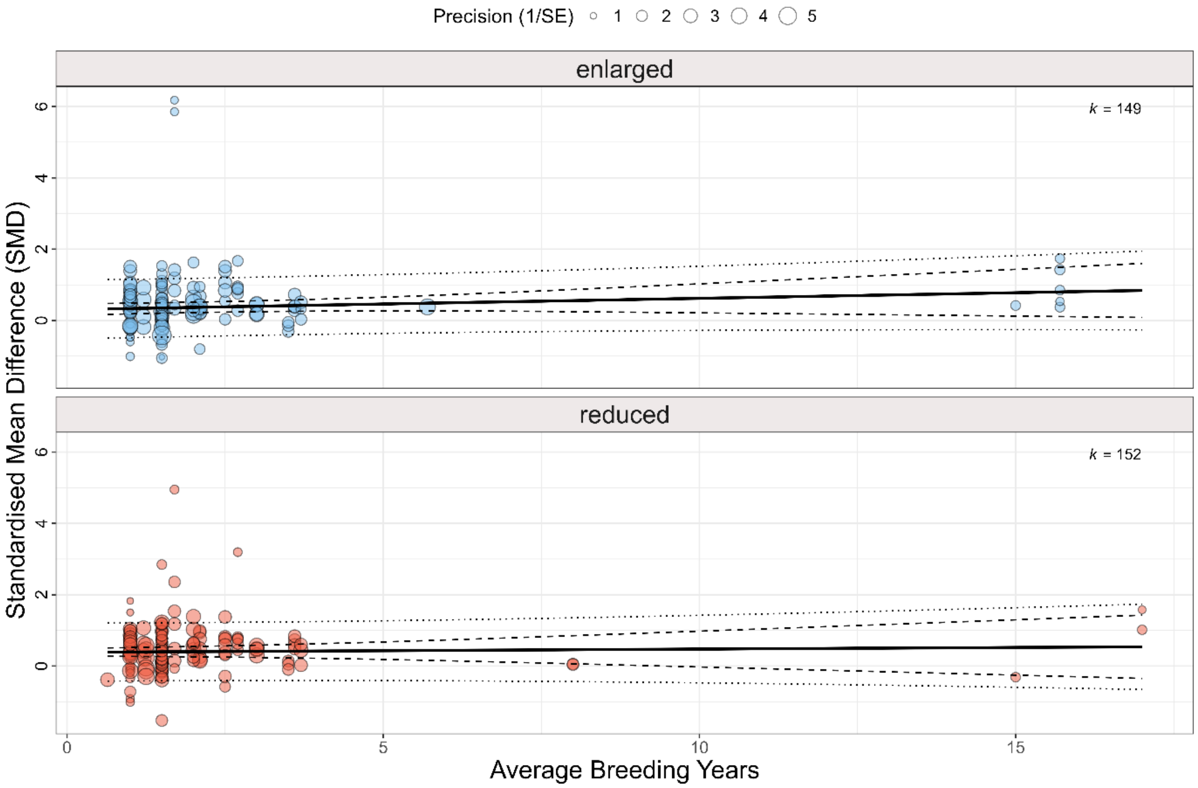

Figure 2.6: *An orchaRd bubble plot (Nakagawa et al., 2023) of meta-analytic mean effect sizes, standardised mean difference (SMD, Hedges' g) across average number of breeding years (raw, unscaled), separated by treatment group (enlarged = blue or reduced = red). Regression is presented as a solid black line. Inner dotted lines depict 95% confidence intervals and outer dotted lines 95% prediction intervals. Total number of estimates (k) is presented on the left of each plot panel. Effect sizes are weighted by their precision (1/standard error, SE).*

Our multivariate model testing the influence of parental sex on provisioning response revealed that both sexes of provisioning parent significantly adjusted their provisioning behaviour in response to brood size manipulations in the direction predicted by theory. Although the adjustment (irrespective of treatment) in males (β = 0.529; 95% CI = 0.344, 0.714; *p* = < 0.0001) tended to be more pronounced relative to females (β = 0.463; 95% CI = 0.284, 0.641; *p* = <0.0001), the difference was not significant (difference: β = 0.047; 95% CI = -0.055, 0.149, *p* = 0.363). Males adjusted their provisioning response to reduced broods (β = 0.563; 95% CI = 0.353, 0.773; *p* = <0.0001) more than females (β = 0.475; 95% CI = 0.273, 0.677), however, again, this difference was not significant (difference: β = -0.088; 95% CI = -0.284, 0.108; *p* = 0.378) (Figure 2.7). The difference between parents was smaller in response to brood enlargements, with males (β = 0.492; 95% CI = 0.277, 0.707; *p* = <0.0001) increasing their provisioning investment in enlarged broods only marginally more than females (β = 0.449; 95% CI = 0.241, 0.656; *p* = <0.0001) (Figure 2.7). Again, this difference was not significant (difference: β = -0.043, 95% CI = -0.251, 0.165; *p* = 0.682).

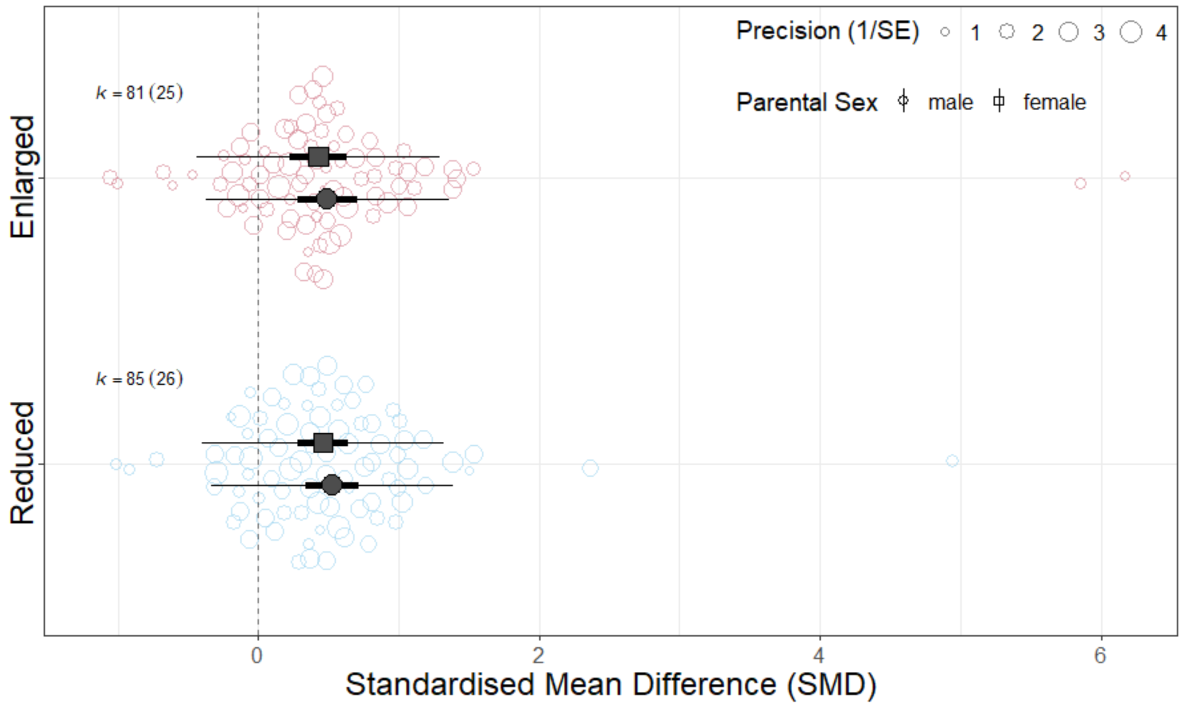

Figure 2.7: *An orchaRd plot (Nakagawa et al., 2023) of meta-analytic mean effect sizes, standardised mean difference (SMD, Hedges' g) by treatment group (enlarged, blue or reduced, red) overlaid by parental sex specific values (female, circle or male, square). Shapes (circle, square) denote meta-analytic means for each sex and whiskers 95% confidence intervals (narrower) and 95% prediction intervals. Total number of estimates (k) is presented on the left of each plot panel. Note that the number of studies in parentheses appears higher than the total number of studies included in sex-specific analyses (12) as most of these studies reported independent values for both male and female parents. Effect sizes are weighted by their precision (1/standard error, SE).*

Publication bias

Visual assessment of the funnel plots did not indicate evidence of publication bias (Figure 2.8). Further, Egger's test results showed a non-significant regression (β = -0.040; 95% CI = -0.171, 0.090; *p* = 0.543; Figure 2.9a) and we found no evidence of a time lag effect (β = 0.002, 95% CI = -0.012, 0.016; *p* = 0.806;

Figure 2.9b); both of which are consistent with a lack of evidence for publication bias. Additionally, we created an alluvial plot to check for patterns in connections between categorical variables related to study design (Figure 2.10) but did not find covariances of concern indicating that any heterogeneity across studies is unlikely to be due to variations in study design elements.

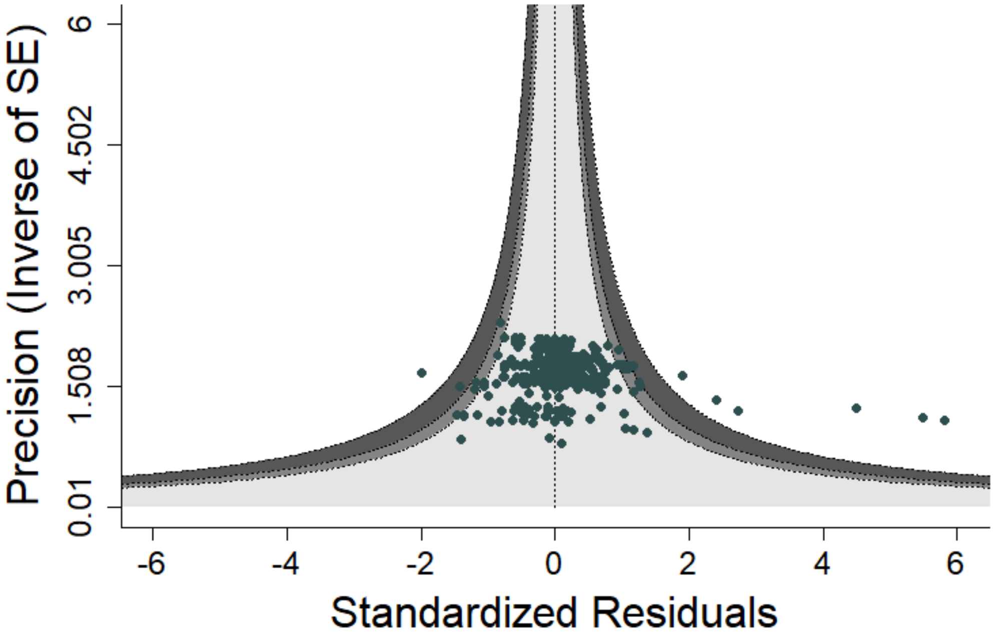

Figure 2.8: *A funnel plot of the precision (inverse of standard error, SE) of effect estimates against their standardized residuals. Confidence regions are represented in shades of grey (90%, 95% and 99% confidence).*

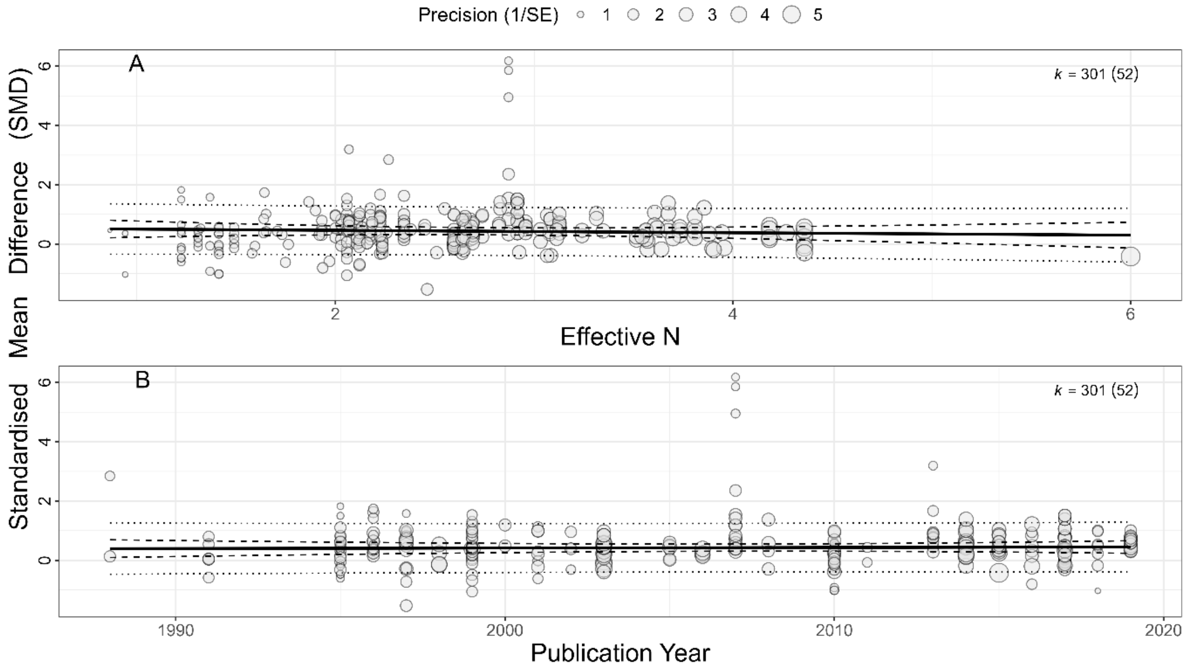

Figure 2.9: *Egger's regressions (A) to assess funnel asymmetry by plotting standardised mean difference (SMD) against effective N and (B) to assess evidence of a time lag effect of published effect sizes by plotting SMD against study publication year. Regressions are presented as solid black lines. Inner dotted lines depict 95% confidence intervals while outer dotted lines depict 95% prediction intervals. Total number of estimates (k) are presented on the right of each panel, with number of studies contributing estimates in parentheses. Effect sizes are weighted by their precision (1/standard error, SE).*

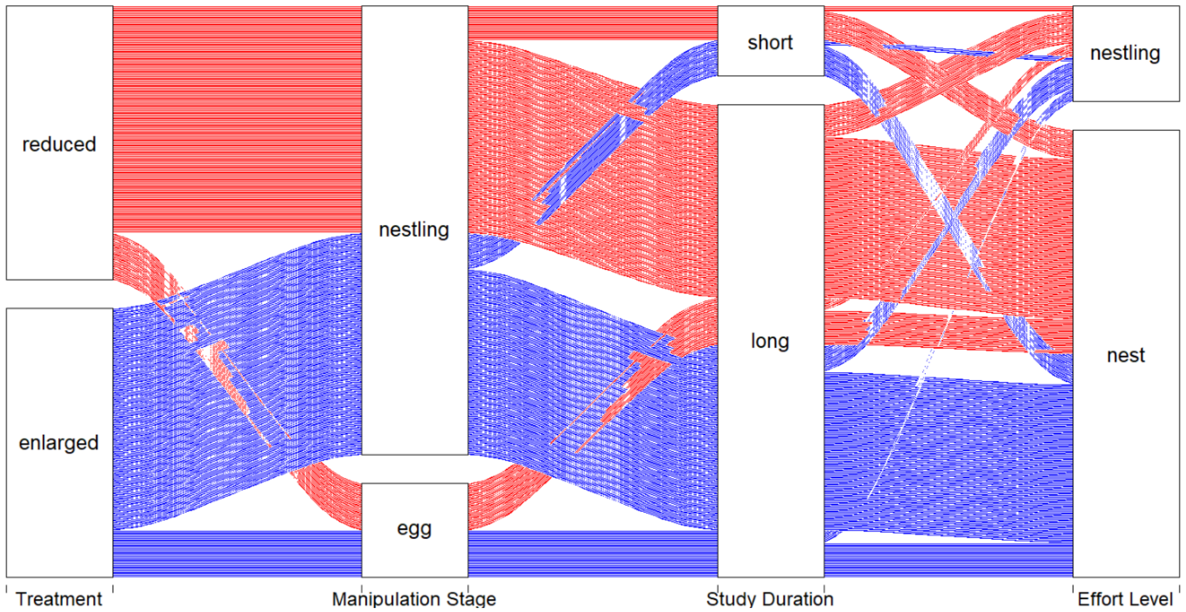

Figure 2.10: *An alluvial plot showing the relationship between categorical variables for: treatment (reduced = red or enlarged = blue), manipulation stage (nestling or egg), study duration (short- or long-term manipulation), and effort level (nest or nestling level). Categorical variables are represented as white rectangles. Connecting ribbons indicate transitions between categories and depict how categories are related to each other, most importantly with treatment. Wider ribbons between two categories indicate a larger number of studies fit into both of those categories.*

Discussion

Our analysis provides support for changes in parental investment consistent with predictions from life-history theory. We also tested the prediction that longer-lived species, with higher residual reproductive value (RRV), would exhibit more pronounced responses to manipulations of the size (i.e., value) of their current brood (Figure 2.2). However, we found only weak support for an effect of species longevity on responses to brood size manipulations, and no support for an interaction effect between experimental manipulation and species longevity. We also tested the role of several putative moderators of the relationship between brood demand and parental investments, and found moderate support that males adjust provisioning in response to brood size manipulations more strongly compared with females. We discuss the implications of these findings in the context of life history strategies and parental investment decisions.

Our finding that experimental manipulation of brood size resulted in significant changes in provisioning behaviour across bird species provides strong support for trade-offs proposed by life-history theory (Stearns, 1989; Monaghan *et al.*, 1998). We found that as the value of the current brood increased (via brood enlargement) parents increased their investment in provisioning to the current brood. As the value of the current brood decreased (via brood reduction), however, parents reduced their level of investment in provisioning to the current brood (Figure 2.5). Therefore, this meta-analysis provides strong and generalized support of proposed life-history trade-offs (Stearns, 1976; Stearns, 1989; Stearns, 1992). Additionally, our analyses included 26 species, yet we found no evidence that extent of behavioural change in response to brood size manipulations was linked to species relatedness i.e., no phylogenetic signal (Blomberg, Garland & Ives, 2003; Blomberg & Garland, 2002). This finding is significant, because it demonstrates that when among-individual differences in access to resource are accounted for by the experimental design, such as by random treatment assignment, there is evidence in support of the existence of trade-offs between current and future reproduction across birds.

We also tested whether the response to brood enlargements was consistently lower than responses to brood reductions. We had predicted an asymmetrical effect of brood size enlargement versus reductions because as brood reduction decreases the value of the current brood, parents should decrease their level of investment in a reduced brood in favour of investment in self-maintenance, and in turn, future broods. In contrast, brood enlargement increases the value of the current brood and so should result in increased investment but within the confines of available resources, both intrinsically (e.g., parental quality) and extrinsically (e.g., food availability) (e.g., Klemp, 2000; Strohm & Linsenmair, 2000; Parejo & Danchin, 2006; Bueno & López-Urrutia, 2012; Sousa & Marini, 2013; Leach *et al.*, 2019;

Booth & McQuaid, 2013). Although our results trended in the predicted direction, the difference was not statistically significant (Figure 2.6). However, given the high heterogeneity in effect sizes, we may have lacked the statistical power required to detect this effect.

Theory predicts that parents from longer-lived species should display greater responses (as measured by provisioning effort) to changes in the value of their current brood compared to shorter-lived species, considering their greater opportunity for future reproduction (Stearns, 1992), also called residual reproductive value or RRV (Stearns, 1976; Stearns, 1989; Reid *et al.*, 2010). We further predicted that an interaction effect would exist between brood size manipulations and species longevity wherein longer-lived species would exhibit a greater response to both brood reductions and brood enlargements than short-lived species (Figure 2.2). However, we found only weak evidence that the change in provisioning response increased with longevity, and no support for an interaction between longevity and treatment (Figure 2.6). We propose three possible (non-exclusive) explanations for these findings: (1) breeding longevity is a poor proxy for RRV; (2) lack of statistical power due to poor representation of long-lived species; and (3) lack of statistical power due to heterogeneity across species and studies (e.g., due to unaccounted for stochastic variation in environmental conditions, current age of parents, mechanism of trade-off).

Firstly, we used average breeding years (calculated as average lifespan – average age at first reproduction) as our proxy for RRV in analyses. Age at first reproduction varies across species, with longer lived species delaying age at first reproduction (Mourocq *et al.*, 2016). Additionally, there is likely to be less variation in age at first reproduction within short-lived species, as unnecessary delay would increase the risk of death before reproduction. However, longer lived species may exhibit greater variation in age at first reproduction, even within populations (Pyle *et al.*, 1997; Tettamanti, Witvliet & Bize, 2012), especially across sexes (Tettamanti *et al.*, 2012). Instances of individuals from longer-lived species delaying age at first reproduction until further beyond sexual maturity have also been more commonly reported (Mourocq *et al.*, 2016). Additionally, our calculation assumes birds reproduce each year until death, however reproducing after a certain age in many species is no longer beneficial to lifetime fitness (e.g., due to senescence) (Charmantier *et al.*, 2006; Mourocq *et al.*, 2016). For example, a long-term study by Tettamanti *et al.* (2012) found that in the Alpine Swift (*Apus melba*), a species which can live up to 26 years, age at both first and last reproduction can vary markedly. Across 120 male and 127 female Alpine swifts, first reproduction occurred between age 1 and 6 (years) and last reproduction between age 1 and 14 (years). Notably, they also found that reproducing after the age of 7 had minimal effect on lifetime fitness. Therefore, our use of an average value for both age at first reproduction and average lifespan when calculating average breeding years for use in our analyses as a proxy may not be an accurate representation of true RRV, particularly for longer-lived species. We had minimal diversity in average breeding years across the species in our meta-analysis with estimates being clustered between 1 to 4 years, yet the true range is likely even less than this if some individuals from longer-lived species delayed age at first reproduction beyond the average and/or ceased reproduction before death.

We cannot rule out that the predicted effect of longevity on parental response to experimental brood manipulation may exist, but that we did not have the statistical power required to detect it, particularly if the true range of breeding years is less than assumed here. Despite finding results generally in the predicted direction i.e., trending towards an increase in response with species longevity, our analysis included only a few studies on long-lived species. In our dataset comprising over 300 estimates, only 12 estimates came from species with more than 5 breeding years. This lack of representation of long-lived species potentially limits our ability to draw robust conclusions regarding the relationship between species longevity and adjustment in provisioning behaviour in response to brood size manipulations. This highlights the necessity for future brood size manipulation studies to intentionally focus on longer-lived species, to increase the available knowledge base of their response.

By addressing the current data imbalance, subsequent studies can contribute to a more representative exploration of how species longevity influences the adjustment in provisioning behaviour.

Environmental conditions act as critical external constraints shaping the extent to which parents can adjust their provisioning behaviour (e.g., Lu, Yu & Ke, 2011b; Sisask *et al.*, 2010; Berlincourt & Arnould, 2015), even when faced with experimental manipulations of their current brood. In particular, numerous studies report that food limitation significantly affects the level of investment parents are both willing and able to provide to their current brood (see meta-analysis by Ruffino *et al.*, 2014). In situations of limited food availability, parents may be constrained in their capacity to increase provisioning investment, even if they belong to longer-lived species with greater reproductive potential (Grüebler *et al.*, 2018). Similarly, if parents are themselves lower quality (e.g., have lower body mass, lower social ranking), even if they are long-lived, they may not have the energy available to increase investment with brood enlargement (Moreno *et al.*, 2002; Pagani-Núñez & Senar, 2014). Thus, the response of parents to brood size manipulations is not solely determined by species-specific characteristics (i.e., longevity, RRV) but is also tied to the prevailing ecological context. We did not include consideration of the ecological context in which the brood size manipulations occurred in the present systematic review and meta-analysis, largely because this information is not often presented in experimental brood size manipulation studies. While intrinsic factors, like species longevity, provide a theoretical framework for predicting responses to brood size manipulations, the reality is contingent on the stochastic nature of environmental conditions such as predator abundance, food availability, weather conditions. The incorporation of moderators related to both species longevity and environmental conditions in future studies may improve our understanding of the adaptive nature of parental investment strategies.

Temporal dynamics, specifically the current age of parents (i.e., at the time of the manipulation experiment), also likely plays a crucial role in mediating the trade-off between investment in current versus anticipated future offspring. For example, studies by Angelier *et al.* (2006) and Pugesek (1995) highlight age-related variations in parental investment and subsequent offspring quality. Younger and less experienced parents may exhibit differences in their ability to invest resources effectively in their offspring compared to older, more experienced parents (Tettamanti *et al.*, 2012). Experienced parents may have greater resource availability and/or exhibit more efficient resource allocation, resulting in improved offspring quality and enhanced reproductive success (Pugesek, 1995; van Noordwijk & de Jong, 1986; Xu *et al.*, 2023). The role of parental age in mediating the response to brood size manipulation is particularly pertinent in the context of the study of the influence of species longevity on provisioning response. For instance, even within species that are longer lived and therefore have a higher RRV on average, if the sample includes older individuals with low remaining reproductive opportunities, this will contribute to heterogeneity in estimates. Studies typically do not report or account for the age of parents in their population. It is unlikely that studies have age biased populations of breeding adults (i.e., that relatively young or relatively old individuals are sampled disproportionately) and we attempted to control for potential age-related biases by excluding studies which applied brood size manipulations in a non-random subset of nests (see exclusion criteria). Thus, we suggest that incomplete consideration of current parental age is an unlikely explanation for our lack of observed interaction between parental investment in response to brood size manipulations and longevity, but that this may be contributing to heterogeneity in our estimates. Future studies may benefit from consideration of how the timing of the manipulation experiment within the reproductive lifespan of parents could impact their response.

Our analysis revealed moderate heterogeneity in our dataset ($I^2_{[total]}$ = 52.15), primarily attributable to study ID ($I^2_{[studyID]}$ = 40.39). Addressing the potential heterogeneity across studies is crucial in meta-analyses to ensure the robustness and generalizability of findings. The presence of across-study heterogeneity can stem from various sources, including differences in experimental protocols, ecological contexts, or species-specific responses. To address this, we conducted thorough analyses examining the effects of various differences in experimental design across studies. Specifically, we investigated treatment stage (whether the manipulation occurred pre- or post-hatch), treatment duration, and effort level (whether investment was measured at the level the nest or level of the nestling) using uni-moderator mixed-effect meta-analytic models. These analyses did not uncover significant differences in results attributed to these specific study design elements. Additionally, we created an alluvial plot to check for patterns in connections between categorical variables related to study design (Figure 10) but did not find covariances of concern. This suggests that heterogeneity across studies is unlikely the result of differences in these commonly examined study design elements. Future studies aiming to assess this may consider exploring additional moderators through subgroup analyses.

Finally, we evaluated support for the role of several putative moderators on responses to brood size manipulations. There was no support for an interaction effect of RRV (measured as both average lifespan and average breeding years) on response to brood size manipulation. However, analysis of a subset of our estimates (166 of 305) which represented the response of only male or only female parents revealed moderate support for sex-specific responses to brood size manipulations, with males exhibiting slightly more pronounced responses compared to females (Figure 2.7). Qualitatively at least, this result aligns with previous research indicating that males may exhibit greater responsiveness to changes in brood value (Bowers *et al.*, 2014; Harrison *et al.*, 2009; Mock, Schwagmeyer & Parker, 2005). Specifically, the observed differences in provisioning responses between males and females may also stem from underlying mechanisms related to sex-specific investment strategies. Existing literature suggests that females may be less likely to substantially reduce investment as the value of the brood decreases (with brood reductions) due to their greater initial investment in the brood (i.e., via egg laying) than males, which also increases their certainty of relatedness to offspring (e.g., see Westneat & Sherman, 1993 for more on this). Further, females may already be provisioning at maximal capacity, limiting their ability to adjust provisioning behaviours in response to increased demands (imposed by an enlarged brood) compared to males who typically provision at lower rates (MacGregor & Cockburn, 2002; Sejberg, Staffan & Dennis, 2000; Trivers, 1972). Interestingly, this is the same reason we predicted that longer-lived species may exhibit greater responsiveness to brood size manipulations than shorter-lived species (Figure 2.2), and thus may reflect an expectation of greater future reproductive opportunities in males relative to females (Bateman, 1948; Louder *et al.*, 2019). Despite the proposed life-history trade-off between parental survival and investment in offspring, a meta-analysis by Santos & Nakagawa (2012) found that female birds did not suffer a survival cost of increased investment when the value of their current brood was experimentally increased. Our findings provide qualitative support for the idea that this may be due to lower female responsiveness to such increases, and that potentially negative consequences for offspring may be offset by increased male investment (Santos & Nakagawa, 2012); larger sample sizes would be required to more draw firm conclusions regarding sex-specific differences in response to current brood value.

Although empirical studies have often failed to find support for key life-history trade-offs, our meta-analysis reveals that when restricting analyses to studies that appropriately control for individual differences in access to resource, there is strong support that parental provisioning decisions in birds are shaped by the trade-off between investment in current versus future reproduction. Although response to experimental manipulations tended to increase with increasing species longevity, as predicted, the trend was not significant. We suggest this may be in part due to the relative paucity of studies in long-lived birds, reducing our power to detect effects of longevity. Future work that aims to test predictions derived from life-history theory that focuses on longer-lived avian species is needed to begin to fill this important gap in existing literature.

Chapter 3: Peregrine falcons shift mean and variance in provisioning in response to increasing brood demand

Abstract

The hierarchical model of provisioning posits that parents employ a strategic, sequential use of three provisioning tactics as offspring demand increases (e.g., due to increasing brood size and age). Namely, increasing delivery rate (reducing intervals between provisioning visits), expanding provisioned diet breadth, and adopting variance-sensitive provisioning. We evaluated this model in an Arctic breeding population of Peregrine falcons (*Falco peregrinus tundrius*) by analysing changes in inter-visit-intervals (IVIs) and residual variance in IVIs across 7 study years, over which environmental conditions varied. Data were collected using motion-sensitive nest camera images and data from 99 nests was analysed using Bayesian mixed effect models. We found strong support for a decrease in IVIs (i.e., increase in delivery rates) between provisioning visits and an increase in residual variance in IVIs with increasing nestling age, consistent with the notion that peregrines shift to variance-prone provisioning strategies with increasing nestling demand. However, support for predictions made based on the hierarchical model of tactics for coping with increased brood demand was equivocal as we did not find evidence in support of expected covariances between random effects (i.e., between IVI to an average sized brood (intercept), change in IVI with brood demand (slope) or variance in IVI). Overall, our study provides important biological insights into how parents cope with increased brood demand.

Introduction

Life-history theory predicts that parents should adjust the level of care they provide to offspring in response to changes in brood demand (Stearns, 1976; Trivers, 1972; Wright & Cuthill, 1990; Mathot *et al.*, 2012). For example, parents are expected to increase prey delivery rates as brood demand increases (Brodin, Jonsson & Holmgren, 2003; Bryant, 1988; Budden & Beissinger, 2009). This increase in delivery rates can come about by parents devoting additional energy to increase prey delivery, such as by flying faster, or limiting self-care behaviours (Moreno, 1987; Simmons, 1986; Cairns, 1987). Additionally, parents may broaden the range of delivered prey by shifting the type of prey delivered away from exclusively preferred prey types or reducing selectivity for larger prey items (Wright *et al.*, 1998; Schrimpf, Parrish & Pearson, 2012). In doing so, parents may decrease overall nutritional quality of delivered prey in favour of increasing overall energy delivered per unit time (Wiebe & Slagsvold, 2014; Chiu *et al.*, 2009).

A less commonly appreciated mechanism by which parents can cope with increased brood demand is to exhibit a shift in their preference or aversion for variable foraging options, a behavioural response referred to as variance-sensitivity. Preference for, or aversion to, variable foraging options is influenced by the probability that offspring will experience energetic deficit (Mathot *et al.*, 2017; Ydenberg, Brown & Stephens, 2007). When offspring are faced with an average expected intake that is lower than their energy requirements, more variable provisioning options provide a higher probability of starvation avoidance (i.e., survival) compared to less variable options (Figure 3.1a). Conversely, when there is a low probability of offspring experiencing energetic shortfall and, therefore, a high probability of survival, higher variance comes at a net cost i.e., an increased likelihood of starvation (Figure 3.1b). When offspring fitness is influenced asymmetrically by deviations above and below the mean delivery rate (Figure 3.1) (Stephens, Brown & Ydenberg, 2007), parents can use variance as a cue when making provisioning decisions to meet increases in brood demand by strategically shifting their use of provisioning options, termed “variance-sensitive provisioning” (Westneat *et al.*, 2012; Westneat *et al.*, 2017; Ydenberg *et al.*, 2007; Ydenberg, 1994)

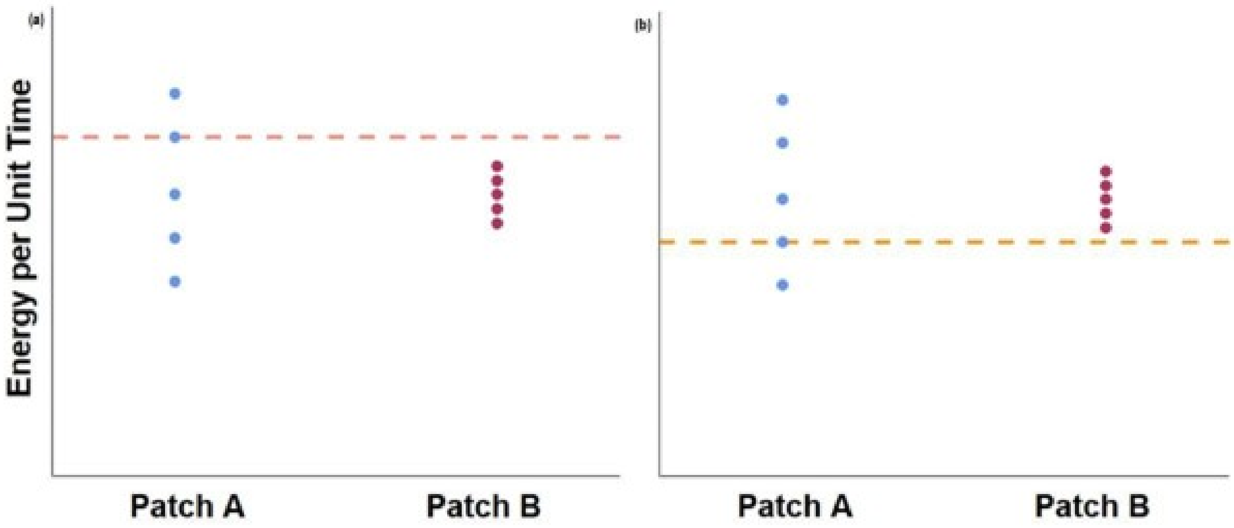

Figure 3.1: *An illustration representing two hypothetical foraging decisions i.e., two patches (A and B) which have the same mean reward but different variance around the mean. (a) Variance-prone: when a forager cannot meet their energetic demands at the less variable patch, they should forage at Patch A. However, (b) Variance-averse: when it is possible for a forager to consistently meet their energetic demands, represented by the dotted line, by foraging at a less variable patch, they should forage at Patch B.*

Studies assessing variance-sensitive provisioning behaviour are limited, and the few studies that have explicitly evaluated support for variance-sensitive provisioning have generated mixed support (Mathot *et al.*, 2017; Moore, 2002; Westneat *et al.*, 2012; Westneat *et al.*, 2017). Further, within studies, support for variance-sensitive provisioning often differs across study years. For example, Mathot *et al.* (2017) observed patterns in residual variance in inter-visit intervals (i.e., the interval between two successive provisioning visits, or IVIs) which were consistent with variance-sensitive provisioning in a year with lower temperatures and more frequent rainfall (a so-called ‘bad year’) but not in a warmer, drier (‘good’) year. Two other studies also found year-specific support for variance sensitive provisioning (Moore, 2002; Westneat *et al.*, 2017). Based on these observations, it has been suggested that adoption of tactics to cope with increased brood demand is hierarchical wherein variance-sensitive provisioning is adopted as a last-resort, after increasing provisioning rate and altering prey selectivity have been exhausted as options in years with unfavourable provisioning conditions (Moore, 2002; Mathot *et al.*, 2017).

Parents should demonstrate plasticity in provisioning behaviour within the constraints of year-specific conditions. Parents experiencing favourable foraging conditions are not expected to be working at their maximum level. Therefore, as brood demand increases (e.g., with increasing nestling age), parents should have *scope* to increase provisioning rate with increasing nestling demand either by allocating additional energy to provisioning behaviour or by expanding diet breadth before switching to variance prone provisioning strategies. However, in years with unfavourable conditions, for example years with inclement weather and/or low prey availability, parents may already be provisioning near their maximum limits while including non-preferred prey in the diet. Thus, in unfavourable years, parents may have little scope to increase delivery rates to their young to satisfy increasing demand as nestlings age and may be expected to adopt variance sensitive provisioning tactics sooner. Thus, while it is expected that the use of variance-sensitive provisioning tactics should increase with increasing demand in all years, the point where this tactic is adopted is expected to come earlier with respect to nestling age (a proxy of brood demand) when conditions are unfavourable (Figure 3.2). To test this idea, assessment of individual reaction norms of provisioning behaviour is required across both the duration of the period of parental care and across a range of environmental conditions (i.e., across multiple years). In particular, the hierarchical model of parental response to increased brood demand predicts specific patterns of covariance between provisioning to an average sized brood (individual reaction norm intercept), change in provisioning (slope), and variance in provisioning across years. Specifically, lower year-specific intercepts (i.e., higher effort indicated by lower IVI) are predicted to be associated with lower year-specific reaction norm slopes and higher year-specific variance (Figure 3.2).

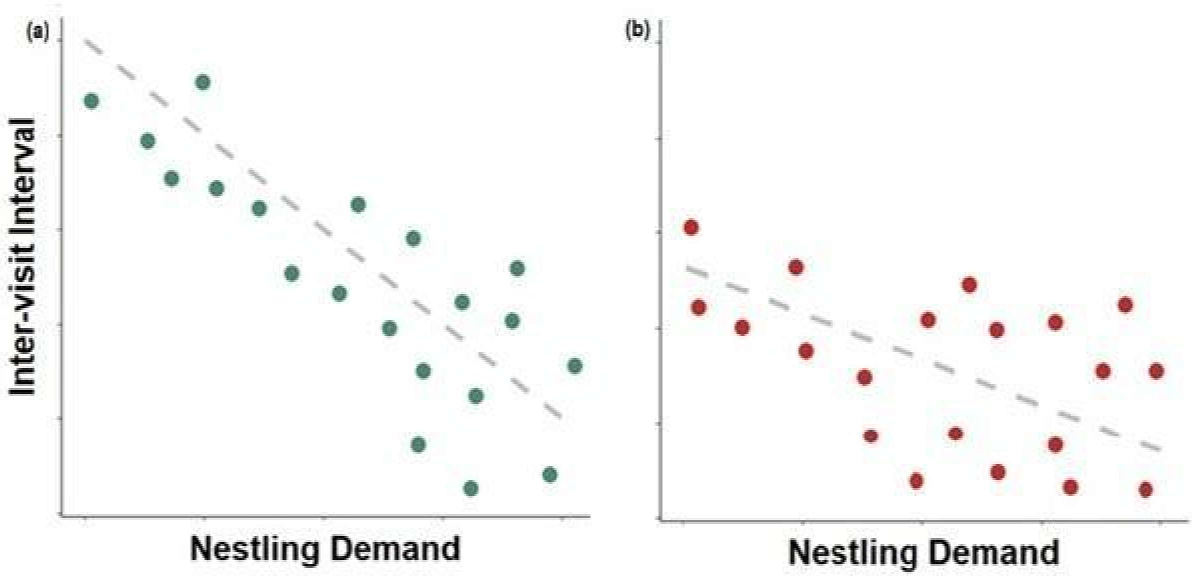

Figure 3.2*: A schematic representing the predictions from the hierarchical model of provisioning behaviour. While in all years it is expected that residual variance will increase with nestling demand (a) Years with high intercepts for inter-visit-interval (i.e., low parental effort) will also have steep reaction norm slopes in response to increasing nestling demand (increasing brood size or chick age) and low residual variance relative to (b) years with low intercepts (i.e., high parental effort) which will have shallow reaction norm slopes and high residual variance.*

There have only been four studies of variance-sensitive provisioning to date; three in passerines (Mathot *et al.*, 2017; Westneat *et al.*, 2011; Westneat *et al.*, 2017) one in terns (Sternidae) (Moore, 2002). However, raptors are also amenable to studies of variance-sensitive provisioning owing to their typically broad range of prey delivery options. Here, we studied provisioning behaviour in Arctic-breeding Peregrine falcons (*Falco peregrinus tundrius).* We investigated support for patterns of covariance predicted by the hierarchical model of parental provisioning. To do this, we collected provisioning data from 99 nests over a 7-year period encompassing a range of conditions including wide variation in average seasonal temperatures, precipitation, and prey availability (see Hawkshaw, Foote & Franke, 2021a). Our research addressed three questions. First, does variance in provisioning rate (which, all else being equal, implies differences in provisioning effort) increase with increasing nestling demand (primarily nestling age), which would be consistent with adoption of variance-sensitive provisioning with increasing brood demand? Second, do peregrines exhibit across-year differences in mean provisioning rates (i.e., intercept), adjustment in provisioning effort (i.e., plasticity or slope) with increasing nestling age, and variance in provisioning effort? Third, do intercept, slope, and variance in individual reaction norms covary as predicted by the hierarchical model of provisioning responses (Figure 3.2)? Specifically, we predicted that in years where parents are already provisioning at a high rate (low intercept for IVI) and have little scope to increase provisioning effort (shallow slope; small decrease in IVI), parents will adopt variance-sensitive provisioning behaviour sooner (high variance in IVI) compared to years where parents are not working as hard (i.e., high IVI). Adopting variance-sensitive provisioning would result in negative among-year covariance between intercept and slope, intercept and variance, and a positive covariance between slope and variance.

Methods

Study population & site

This study was conducted in a population of Peregrine falcons breeding close to Rankin Inlet, on the western shore of Hudson Bay, Nunavut (62.81, -92.09). The area is characterized primarily by tundra with numerous rocky outcrops, suitable for cliff nesting, across both coastal and inland areas. Further details on site specific geological information, and a description of vegetation cover can be found in Court *et al.* (1989). Peregrines are cliff-nesting and nests at this study location are distributed across mainland, coastal, and island sites. The number of active nests varies between years, ranging from 16-30. This resulted in a total of 160 historically active nests being routinely visited across the 7-year duration of this study. Peregrines in our study area lay clutches of 2-4 eggs (Ratcliffe, 1962) between early and late June, followed by incubation for approximately 32 days (with variability of 1-2 days e.g., due to delayed hatching) (Anctil, Franke & Bêty, 2014; Burnham & Cruz-Bernate, 1983). Asynchronous hatching occurs in July, resulting in 1-4 nestlings (Ratcliffe, 1962). The average hatch date for our study period was July 14th.

Peregrines are a generalist predator with a highly flexible prey range, including mammals, birds, and waterfowl. Our study population in Rankin Inlet has a particularly high contribution of mammalian prey in the diet (up to 1/3) compared to other peregrine populations that tend to be more specialized in birds (Bradley & Oliphant, 1991; Dawson, Mossop & Boukall, 2011). This dietary flexibility makes them a good study organism for assessing variability in provisioning decisions. Although raptors typically exhibit lower provisioning rates than passerines (i.e., visits where food is delivered to offspring), this can be offset by monitoring provisioning decisions for longer amounts of time (e.g., over days instead of over hours) (references). In addition, our study area in Rankin Inlet, Nunavut is located within the Canadian Arctic, an area which experiences large inter-annual fluctuations in environmental conditions, that are likely to generate significant differences in foraging conditions experienced by provisioning adults across years (references).

Data collection & processing

a. Life history data

Historical nest sites were surveyed by All-Terrain Vehicle (ATV) and snowmobile in May of each year, as peregrines began to arrive at the breeding site. Sites were surveyed until enough nests had full clutches that continuing to survey unoccupied sites became unfeasible given constraints generated by limited availability of researchers in the field (typically late-June). Catching and banding of adults occurred between May and June using toe-snare methods outlined in the Wildlife Animal Care Committee Class Protocol #001 – Raptor Collection for Falconry, provided by the Government of Alberta. Due to variation in catching effort, catching success, and logistical constraints, approximately 50% of adults in the breeding population each year are banded. This WHAT meant that we were unable to track individuals longitudinally across the study; either because they were unbanded in all years or were unbanded in some years before being banded.

We placed motion sensitive cameras (RECONXY models PC800, PC85, HC600, Ultrafire – company, location) attached to wooden stands within 1 m of all active nests, once located. All cameras were infrared enabled allowing images to be recorded during periods of low light. Cameras were set to record 3 images each time motion was detected, with 3 s between consecutive images, followed by a quiet period of 5-15 s during which the camera did not respond to motion triggers. In most years, cameras were also set to record time-lapse images. A single photo was taken at each time-lapse interval. A summary of camera settings for each year are provided in the electronic supplementary material (Appendix B: ESM for Chapter 3; Table S3.1).

We visited occupied nests every 5-8 days (environmental conditions permitting). Once hatched, nestlings were marked on their upper right legs using non-toxic markers to identify individuals throughout the season. Using an electronic scale, we weighed individually marked nestlings at each visit and replaced camera batteries and memory cards as required. We also conducted 2-min focal observations of adults while at the nest site, as part of a separate study. Hatch dates were determined from nest camera images, from which nestling age was calculated for the first hatched nestling.

b. Provisioning data

We extracted provisioning data from time-stamped nest camera images from a total of 146 nests. In 2013, the hard drive on which the photos from 14 nests were stored was lost in the field, and we were only able to obtain provisioning data for 12 of 26 nests monitored that year. Since we could only reliably score provisioning events that occurred within the camera frame, we restricted our data set to the period before the earliest age at which nestlings could move out of the nest scrape which we determined to be at nestling age 13 based on observation of next camera images (RAM personal observation). Thus, our analyses of provisioning data were restricted to the first 12 d after hatching.

We recorded the start and end time for each provisioning event. From this we calculated the interval between successive provisioning events calculated as the period between the start time of consecutive feeding visits, termed inter-visit interval, or IVI. We chose to use inter-visit intervals rather than the number of deliveries per day, as this provided multiple data points per day, improving our power to model variance. Although we were usually able to identify the sex of the parent that delivered the prey items to the nest (parental sex identified in 3915 of 5005 nest visits), we considered provisioning at the level of the pair of parents when calculating IVIs (in minutes). The time between two successive prey deliveries was used to calculate IVI regardless of whether the prey items were delivered by the male parent or the female parent, or a combination of the two. We felt this approach was justified because peregrines exhibit a division of labour, with males doing most of the hunting, and females doing most of the delivery to young (Olsen, Doyle & Boulet, 1998 and references therein). In the first 12 days post hatch, nestlings were fed almost exclusively by the female (N = 3873 visits out of 3915 visits where the parental sex could be identified). Thus, prey deliveries by females reflect the combined effects of male hunting effort and female allocation decisions. Given that we did not have the resolution of data to determine what percentage of prey items were hunted by males versus female parents, we limit our analysis to the level of the provisioning pair to match the resolution of our data with respect to provisioning effort. On average, 50% of birds were unbanded in any given study year. We assumed that the identity of unbanded males or females at a given nest site did not change within years, such that the identity of the provisioning pair was captured by the unique combination of nest site and year. However, our use of the combination of nest-site and year as a proxy for provisioning pair identity means that the same combination of male and female may be regarded as a different pair in a different year. However, this would tend to make our estimates of the importance of “provisioning pair” conservative, and our model comparisons none-the-less revealed “provisioning pair” to be important (see Results).

We determined camera failures, meaning periods in which the cameras should have been capturing images but were not (e.g., due to dead batteries, full memory cards) for years with time-lapse settings based on intervals of time between images which were larger than the preset time-lapse setting. These were recorded as ‘fail’ in the datasheet. There was a total error rate of < 0.5%, based on 5 years of data where time-lapse settings were used (2013-2014; 2017-2019). For the 2 years without time-lapse intervals (2015 and 2016), we excluded outliers in IVI (i.e., intervals between feeding events which were too long to be biologically possible) based on the distribution of datapoints from all 7 years (Appendix B: ESM for Chapter 3; Figure S3.1). This corresponded to 9 datapoints in total. The excluded datapoints were those above 4000 minutes (i.e., almost 67 hours, or 2.8 days); at this cut off there was a clear gap in points, with the next longest (included) datapoint being 2671 minutes (1.9 days) (see Appendix B: ESM for Chapter 3; Figure S3.1). Periods of camera failure were accounted for in IVI calculations wherein if the previous or current row was a recorded as ‘fail’ then the IVI was recorded as ‘NA’. As part of a separate study, a total of 47 nests across the 7 years were food supplemented (see Chapter 4). We excluded these nests from the current study, leaving a total of 99 nests for inclusion in analysis (2013, n=11; 2014, n=14; 2015, n=10; 2016, n=11; 2017, n=19; 2018, n=16; 2019, n=18).

We recognized IVI is an integrated measure that can reflect changes in various aspects of parental behaviour. For example, parents can alter their allocation of time to provisioning relative to other activities, work harder while provisioning, and/or change the selectivity of prey items hunted/delivered. Using IVIs as our measure of parental effort does not allow us to tease apart the contributions of different aspects of parental behaviour on provisioning rates. However, IVI is most appropriate for understanding the consequences of parental provisioning decisions on offspring, as it is the combined effect of parental behaviours on IVIs that ultimately determine offspring intake rates.

Originally, we intended to extract additional provisioning-related information, including prey type, biomass delivered, and biomass remaining after consumption by offspring. However, we were unable to accurately determine this information at 30% (4,637 out of 15,395) of the provisioning visits made across the 7-year study duration (e.g., due to poor image quality, prey being partially obstructed from view). Therefore, there is a substantial fraction of missing data, and more importantly, missing data is likely to be non-random with respect to prey characteristics (e.g., small prey more difficult to score than large prey). Furthermore, our nest cameras collected images only of the scrape, and did not include images of the surrounding areas, for example, where prey may have been cached or processed prior to delivery. Thus, prey type and size data, which we were able to score from camera trap images, were incomplete and likely biased, and we therefore did not use it for further analysis. We did, however, note that peregrines in our study provided at least 7683 small birds (passerines, shorebirds), 3430 mammals (ground squirrels, lemmings), and 1438 waterfowl (ducklings/goslings of various sizes) to offspring. Note, the total visits where prey type was scored (N = 12,551) exceed the number for which we had complete data (type + biomass: N = 10,758, see above) because we were able to score prey type but not biomass for N = 1793 visits.

Statistical analysis

All models were run using the brms package (Bürkner, 2017) in R (version 4.2.0). We followed the hierarchical approach of Nussey, Wilson & Brommer (2007) to assess support for random effects of increasing complexity. In each model, IVI was modelled as a function of brood size and nestling age (fixed effects) and sigma (i.e., variance) was modelled as a function of nestling age and brood size. Year was included as a random effect. Starting from the described basic model, we then increased model complexity by adding random effects for nest site, provisioning pair (i.e., the specific combination of year and site), year specific random slopes, as well as covariances between random effects.

Table 3.1 provides an overview of the models that were tested. We compared these models using leave one out cross validation with the ‘loo_compare’ function from the ‘loo’ package (Vehtari, Gelman & Gabry, 2017) (see Table 3.1 for output). The ‘elpd_diff’ and ‘se_diff’ values obtained provide an estimate of the difference in the expected log pointwise predictive density (elpd) and its standard error between models. A larger ‘elpd_diff’ and smaller ‘se_diff’ indicate that one model performs better than another, and a difference in ‘elpd’ of 2 or more units is generally considered to be strong evidence in favour of one model over another (Vehtari *et al.*, 2017).

Model	**Nest site**	**Pair**	**Year**	**Year (NestlingAge)**	**Year (BroodSize)**	**Sigma**	**Covariance**	**Elpd_diff (se_diff)**	**Rank**
m1a						x		-134.8(17.0)	8
m1b	x					x		-40.4(10.1)	7
m1c		x				x		-3.7 (3.9)	6
m1d	x	x				x		-3.7(3.7)	5
m1e	x	x	x			x		-2.5(3.0)	4
m1f	x	x	x	x		x		0.0 (0.0)	1
m1g	x	x	x			x	x	-0.6(3.1)	5
m1h	x	x	x	x		x	x	-0.2(0.4)	2
m1i	x	x	x	x	x	x	x	-0.7(0.5)	3

Table 3.1: *A table containing details of across-year models run for comparative purposes to first verify evidence for the existence of random effects for nest site, provisioning pair, year, year specific random slopes and second to assess evidence of covariance between random effects. All models additionally contained a sigma model with nestling age and brood size as fixed effects, and year as a random effect. Differences between models in terms of 'elpd' (and se) indicate that while the model which contained all random effects but did not estimate covariances performed slightly better than that which estimated covariance, there are negligible differences between the top three competing models.*

While we were interested in year-specific differences in constraints on provisioning behaviour, we anticipated that the analyses described above, which analyse year-specific provisioning responses, could generate patterns consistent with our predictions, not necessarily because of within-individual responses (the hypothesized mechanism). For example, year-specific differences in the types of individuals which are successful within a given year could also result in the patterns of covariance outlined in Figure 3.2. To address this, we ran an additional model for comparative purposes, which was the same as the top-performing model from the previously described model set with two exceptions: i) nestling age was nested within pair id, and ii) sigma (i.e., residual variance) was estimated across pairs (hereafter the ‘across pairs model’) rather than across years (hereafter the ‘across years model’). By running both models, we could evaluate whether patterns at the within-pair level were qualitatively similar to patterns at the among-year level, which would provide support for the interpretation that year-specific patterns arose via within-individual plasticity. Unless otherwise specified, results presented are those generated by the (top performing) across years model.

For all models, IVI was log-transformed before analysis to ensure that model residuals were normally distributed. On Day 0, the day the first nestling hatches (brood hatching) provisioning rates cannot be compared for a nestling that hatched in the morning versus in the evening, for example, and so nestling age 0 was excluded from the analysis. Further, nestling age was left zeroed (1 was subtracted for each row of nestling age so that nestling Day 1 was coded as zero) so that model intercepts were estimated for day 1 post-hatching, the first day when provisioning behaviour was analysed. Additionally, brood size was centred so that the model intercept was estimated at the average number of nestlings. Further, to facilitate comparison between influence of fixed effects on IVI, we scaled (standardized) both nestling age and brood size by dividing values by 1 standard deviation.

We used the mode of estimated effects (β, σ or ρ) and 95% credible intervals (CI) to evaluate support for each effect. Strong support for an effect is defined here as an effect with CI which did not overlap zero. Moderate support is defined as a CI that overlapped zero by less than 15%. Posterior distribution which overlaps zero by 15% or less equates to over five times greater support for interpretation of an effect in the estimated direction relative to an effect in the opposite direction (Marsman & Wagenmakers, 2017). If the estimated effect was approximately zero and a CI centred around zero, we interpret this as providing no support for the effect (also referred to as 'strong support for no effect’). When discussing the potential biological importance of a given observed effect, we use the estimated effect size on the observed scale for fixed effects (e.g., the effect of increasing nestling age in days on IVI in seconds). However, as variance estimates are unitless, we interpret the biological importance of random effects based on their relative contributions to total variance (i.e., proportion contribution). All results presented are from the top performing across-year model, unless otherwise specified.

Results

At the population-level, peregrines responded to increased brood demand (as indicated by nestling age and brood size) by reducing their provisioning inter-visit intervals (IVIs, i.e., provisioning at a higher rate) across all study years. There was some support that parents decreased IVI to a greater extent with increasing nestling age ($\beta_{\log(IVI)} = -0.18$, 95% CI = -0.25, -0.11; Figure 3.3a) compared to increasing brood size ($\beta_{\log(IVI)} = -0.12$, 95% CI = -0.16, -0.07; Figure 3.3b), though the difference was not significant.

As predicted, we found strong support (based on CI that did not overlap 0) that variance in logIVI increased with increasing nestling age ($\beta_{\log(\sigma)} = 0.08$, 95% CI = 0.06, 0.11; Figure 3.3c). Further, the increase in variance across ages is >2 fold greater than the variance within ages (see Figure 3.3c). However, contrary to our predictions, there was no evidence that variance in log(IVI) increases with increasing brood size ($\beta_{\log(\sigma)} = -0.01$, 95% CI = -0.03, 0.01; Figure 3.3d). This indicates that as nestling demand generated by increasing nestling age (but not number of nestlings) increased, parents demonstrated greater variability in provisioning effort (measured by IVI).

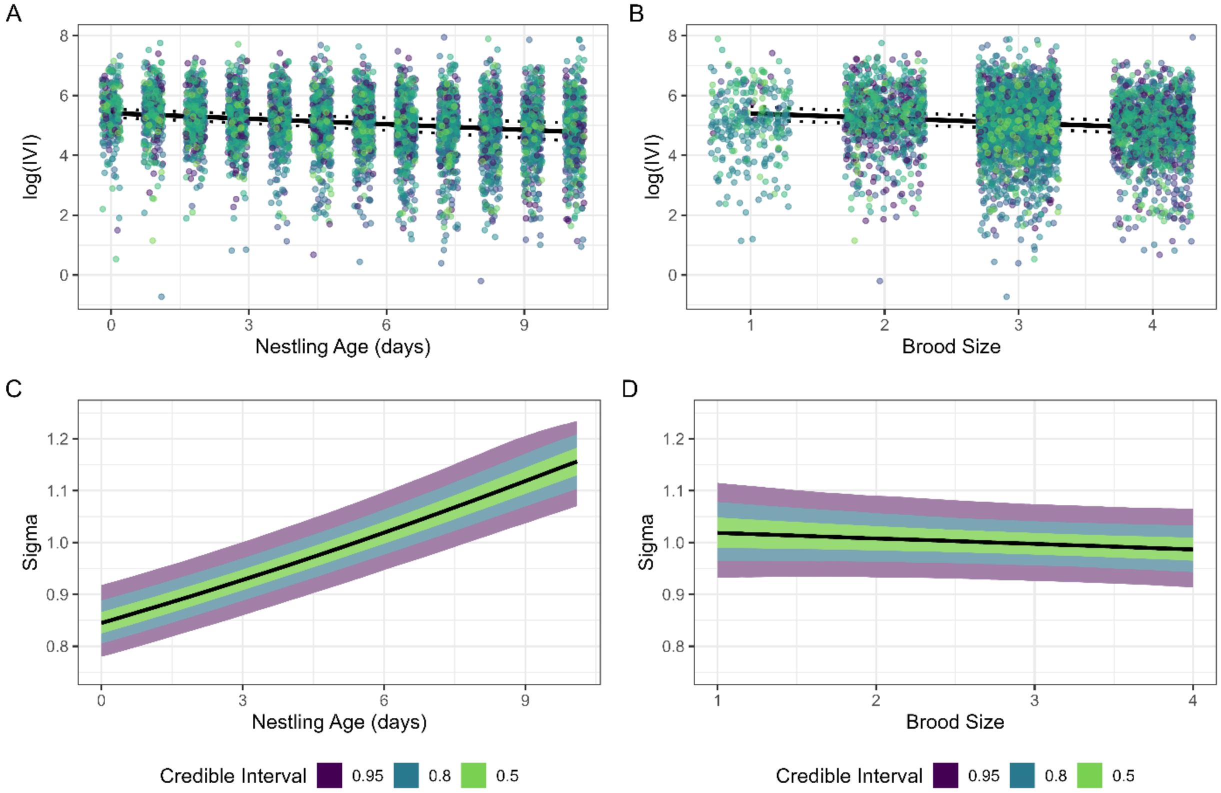

Figure 3.3: *Observations and model posterior predictions for (a) IVI across nestling age, (b) IVI across brood size, (c) standard deviation, σ (sigma: the root-square of variance) in IVI across nestling age, and (d) variance in IVI across brood size. Credible intervals are displayed for 0.95, 0.8 and 0.5. Plots were made using R packages 'gghalves' and 'ggplot2.'*

Our model comparisons revealed strong support for the presence of all the random effects considered: among-pair, among-site, and among-year differences in IVI intercept, among-year differences in reaction norm slope (plasticity), and among-year differences in residual variance (sigma) in IVI in response to increasing nestling age (Table 3.1). The variation in each of these random effects were of magnitudes that were likely to be biologically important. For example, the intercept in log-transformed inter-visit-interval (logIVI) was lowest in 2016 ($\beta_{\log(IVI)}$ = 5.31, 95% CI = 4.97, 5.59) and highest in 2013 ($\beta_{\log(IVI)}$ = 5.48, 95% CI = 5.22, 5.84). This corresponded to time between the start of consecutive provisioning visits to an average-sized brood of approximately 3.4 hours in 2016 compared with approximately 4 h in 2013. The relative change in IVI with increasing brood demand generated by increasing nestling age was greatest (steepest slope) in 2017 (β = -0.52, 95% CI = -0.88, -0.18) and smallest (shallowest) in 2013 ($\beta_{\log(\text{IVI})}$ = -0.26, 95% CI = -0.61, 0.13). This corresponds to a decrease in IVI of around 20 minutes from nestling age 1 to day 12 post-hatch in 2017, versus a decrease in IVI of 15 minutes in 2013. Variance in logIVI was greatest in 2016 ($\sigma_{(\exp)}$ = 0.85, 95% CI = 0.62, 1.17) and smallest in 2014 ($\sigma_{(\exp)}$ = 0.63, 95% CI = 0.45, 0.89). Even though pairs often used the same site across multiple years, among site differences in logIVI ($\beta_{\log(\text{IVI})}$ = 0.14, 95% CI = 0.02, 0.25) were lower than among pair differences ($\beta_{\log(\text{IVI})}$ = 0.19, 95% CI = 0.12, 0.26).

Our model comparison revealed that the top three models are within 2 units of difference in 'elpd' (Table 3.1) and are, therefore, indiscernible (Vehtari *et al.*, 2017). Specifically, models which additionally estimated covariances between random effects performed similarly to the model which estimated all random effects, but not their covariances. Thus, support for covariances is equivocal. Nonetheless, we report the estimated covariances to allow us to evaluate whether they are in qualitative agreement with the predictions outlined based on the hierarchical adoption of provisioning tactics (Figure 3.2).

We found weak evidence for a moderate negative correlation between intercept and variance in logIVI across the 7 study years (ρ = -0.25, 95% CI = -0.91, 0.67; Figure S3.2b) meaning that in years with a higher intercept (i.e., a longer time between consecutive provisioning visits to an average sized brood) there was less variance in logIVI relative to years with a lower intercept. There was no support for a correlation between slope and variance (ρ = 0.04, 95% CIs= -0.71, 0.76; Figure S3.2c) meaning that, contrary to our prediction, year specific responses to increased brood demand were unrelated to year-specific variation in IVIs. We found a weak, positive correlation between intercept and slope (ρ = 0.22, 95% CIs= = -0.71, 0.92; Figure S3.2a) such that higher intercepts (longer time between consecutive provisioning visits to an average sized brood) resulted in shallower slopes (smaller reduction in time between consecutive provisioning visits), and vice versa.

Results regarding correlations between intercept and variance, and slope and variance were qualitatively similar for both the across years and across pairs model (for across pair model, intercept v variance: ρ = -0.52, 95% CI -0.90, -0.07, slope v variance: ρ = 0.19, 95% CI = -0.22, 0.58). However, we found weak support for a moderately negative correlation between intercept and slope in the across pairs model (ρ = -0.25, 95% CI = -0.64, 0.38, unlike in the across years model). Thus, the results from the across-pair model suggest that higher intercepts result in steeper slopes, i.e., a longer time between consecutive provisioning visits to an average-sized brood results in comparatively larger reductions in IVIs as nestling age increases.

Discussion

The hierarchical model of provisioning proposes that parents should make strategic, sequential, use of three provisioning tactics as offspring demand increases. Initially, parents may increase their own energy expenditure to meet additional offspring needs, typically leading to an increased provisioning rate (Bowers *et al.*, 2014; Laczi *et al.*, 2017; Magrath *et al.*, 2007; Sanz & Tinbergen, 1999; Steen, Sonerud & Slagsvold, 2012). In response to further increase in demand, parents may expand the provisioned diet breadth (e.g., Grundel & Dahlsten, 1991; Radford, 2008; Wiebe & Slagsvold, 2015; Wright *et al.*, 1998; Małgorzata, 2004). Finally, parents may adopt variance-sensitive provisioning once these two other options have been exhausted (Mathot *et al.*, 2017; Westneat *et al.*, 2011; Westneat *et al.*, 2017). If parents adopt different strategies for managing increased brood demand hierarchically, as outlined above, then we predicted that parents should increase their provisioning rate with increasing brood demand (i.e., reduce IVI) and demonstrate increased variance in IVI with increasing nestling demand. More specifically, we predicted that parents provisioning at a higher rate (lower IVI) to an average sized brood should have reduced scope to increase provisioning (reduce IVI) as demand increases, and therefore, adopt variance-sensitive provisioning strategies sooner, resulting in higher residual variance in provisioning. We evaluated support for these predicted patterns of residual variance and covariance in an Arctic breeding population of Peregrine falcons. We found strong support that peregrines decrease provisioning IVIs with increased nestling age and increasing brood size. We also found strong support for an increase in residual variance in IVI with increasing brood demand generated by increasing nestling age, but not increasing brood size. However, we did not find strong support for predictions based on the hierarchical adoption of tactics for coping with increased brood demand. Support for covariances between year-specific provisioning effort, provisioning reaction norms, and residual variance in provisioning were equivocal, and not always in the predicted direction. We discuss the biological insights revealed by our approach, as well as the limitations of the current study, including the challenge of modelling heterogeneous residual variance, particularly using observational field data. Finally, we suggest how researchers aiming to address similar questions may overcome these challenges.

As predicted based on parental investment theory (Trivers, 1972; Emlen, 1966; MacArthur & Pianka, 1966), across years, provisioning adult peregrines consistently responded to increased nestling demand, as inferred by nestling age and nestling number, by reducing IVI. At least one earlier study in peregrines reported that parental response to increasing brood demand via increased nestling age was greater compared with parental response to increased brood demand via increased brood sizes (Olsen *et al.*, 1998). Although our results are qualitatively in agreement, the difference in parental reaction norm to increased nestling age versus increased brood size was not statistically significant. However, an important distinction between our study and that of Olsen *et al.* (1998) is that they distinguished between prey deliveries by male versus female parents and found a different response to nestling age versus brood size in males only. In our study, we were unable to differentiate male and female provisioning effort and used a pair-level measure of provisioning.

We found that provisioning pairs (i.e., the specific combination of year and nest site) had a greater influence on plasticity in IVI than territory (i.e., nest site), which is consistent with both existing theory and empirical results. At our research site, for example, earlier empirical work by Bradley & Oliphant (1991) found that peregrines hunt not only small birds but around a third of their total consumed biomass is mammalian (microtines, primarily Arctic Ground Squirrels (*Urocitellus parryii)* and Lemmings (various *Dicrostonyx* species)); a proportion markedly higher even than for other studied peregrine populations (Bradley & Oliphant, 1991 and references therein). Thus, while peregrines are highly territorial and differences in prey availability across territories can be significant (e.g., Sokolov *et al.*, 2014), we suggest that across nest sites in our study population, differences in territory quality may be less important as parents may have access to comparable total prey availabilities due to the large diet breadth reported previously in our population (Bradley & Oliphant, 1991). In contrast, the impact of pair quality on parental care (e.g., provisioning behaviour) is widely reported in the literature. For example, older and more experienced parents typically raise more offspring and/or offspring in better condition (Angelier *et al.*, 2006; Curio, 1983; Pittet *et al.*, 2012; Pugesek, 1995), as least up to a certain point, where age effects may either plateau or even reverse in the case of senescence (Zabala & Zuberogoitia, 2015).

Based on Mathot *et al.* (2017), we predicted an increase in residual variance in IVI with increasing brood demand because provisioning adults should be increasingly variance prone as offspring demand increases beyond what they can satisfy by expending more energy and/or reducing prey selectivity. We found strong support that parent IVIs became more variable as nestlings aged. This result is notable because mean and variance are normally positively correlated (Cohen & Xu, 2015). Thus, the null expectation would be that the decrease in mean IVI with increasing nestling age would coincide with a decrease in variance in IVI. We interpret the observed increase in the residual variance in IVI with increasing nestling age as a strategic shift towards more variable foraging options in response to increased nestling demand. However, at least three alternative explanations are possible. First, higher residual IVI with increasing nestling age may result from depletion of local food as the season progresses (Lima & Dill, 1990), making food discoveries less predictable. We suggest this is unlikely because the increased variance in IVI was coincident with a decrease in mean IVI, indicating that parents were returning with food more quickly with increasing nestling age.

Alternatively, the decrease in IVI and coincident increase in residual variance in IVI with increasing nestling age may reflect an increased availability of prey (both quantity and type) as the potential prey increase in abundance on the landscape (e.g., due to production of young by breeding animals). Indeed, a study monitoring changes in avian abundance and distribution in our study area reported increases in the abundance of on shorebirds and Sandhill cranes (but decreases or no change in other groups) (Hawkshaw *et al.*, 2021a). However, these changes in avian abundance were modest over the circa 120-day monitoring period and may have been confounded by changes in detectability (Hawkshaw *et al.*, 2021a). The changes in IVI (mean and variance) reported here occurred within 12-day periods (at each nest), which is unlikely to be sufficient for large-scale changes in prey availability across the landscape due to production of young.

A third possibility is that as nestlings age, the type and size of prey they can consume expands, for example, due to larger bill gape or reduced digestive constraints. Cade (1982) found the proportion of mammals in the diet of peregrine nestlings decreased as nestling age increased, while the proportion of small birds increased from around 10% to 90% over the first four weeks post-hatch. However, the study did not report on how much of this change occurred in the first 12 days post-hatch, which is the period over which decreasing mean IVI and increasing variance in IVI were observed in our study. found that The gape size of several bird species increased rapidly during the first few weeks of life, allowing consumption of larger prey during each provisioning visit Drent & Daan (1980). Although gape size increases in peregrine nestlings, they are exclusively fed by parents until beyond 12 days post hatch (i.e., the period examined in this study). Thus, parents can provision large prey items to nestlings with small gape sizes by tearing off appropriately sized pieces and consuming the remainder of prey themselves or caching it. Therefore, it is unclear whether age-related changes in gape size should change the type or size of prey provisioned by parents. We cannot rule out that shifting target prey type or increasing diet breath (type and/or size) with increasing nestling age contributed to the finding that mean IVI decreased while variance in IVI increased across nestling age. We suggest that studies that directly investigate age-related changes in prey type and size provisioned to nestling peregrines are warranted.

We did not find any support for parents increasing variance in IVI with increasing brood size. There are at least two potential explanations for this result. First, brood size might vary with parental quality such that better quality parents are more likely to have larger broods. In this case, larger brood sizes would not be expected to be associated with higher variance in provisioning because high quality parents are better equipped to cope with increased brood demand, and therefore, all else being equal, would be expected to resort to variance sensitive provisioning at higher levels of brood demand, including brood size. To properly evaluate this possibility would require experimental manipulations of brood size. Alternatively, if the observed pattern of decreasing mean IVI and increasing variance in IVI across nestling age is the result of an increase in the breadth of suitable prey, we would not expect to see a change in variance in IVI with larger brood sizes. This is because, unlike nestling age, larger brood sizes would not correlate with increased availability of suitable prey.

We found strong support for the inclusion of random effects for among-pair and among-site differences in IVI, and among-year differences in intercept (IVI to an average-sized brood), reaction norm slope (plasticity), and residual variance in IVI in response to increasing nestling age. We tested among-year correlations between intercept, slope and variance in IVI based on earlier studies that proposed that tactics for responding to increased brood demand might be adopted hierarchically (sequentially), with variance-sensitive responses adopted as a last resort. Although, the qualitative patterns of covariance did not always align with our predictions (Figure 3.2), the high degree of uncertainty in the covariance estimates (i.e., broad 95% CIs) means that we cannot draw strong conclusions with the current data.

Overall, our study provides mixed support for the notion that peregrines adopt variance-sensitive provisioning decisions to cope with increased brood demand. Although we found strong support for increased residual variance across nestling age, we likely lacked statistical power to estimate the covariances between random intercept, random slope and year-specific residual variance despite our large sample size. This highlights the challenge of modelling heterogeneous residual variances, which are known to be data-hungry analyses (Cleasby & Nakagawa, 2011). In recent years there has been a push in behavioural ecology to recognize the prevalence of heteroscedasticity in datasets (e.g., Nakagawa *et al.*, 2007; Westneat *et al.*, 2012), which has been under-reported despite being a source of important information about the biological processes being investigated (Cleasby & Nakagawa, 2011; Westneat *et al.*, 2015). Our results emphasize both challenges (data requirements) and opportunities (novel insights) that can be afforded by quantifying heterogeneous residual variance. The finding that residual variance in provisioning IVIs increases with increasing nestling age despite decreasing mean IVI hints at two (non-exclusive) mechanisms that may underlie age-related shifts in parental care decisions; variance sensitivity and/or age-related changes in diet.

In addition to the need for larger sample sizes, we suggest that across-year comparison of IVI alone may have been insufficient to fully assess patterns in provisioning in our study because it does not account for inter- or intra-annual variation in provisioned prey type or size, which may be substantial (Hawkshaw *et al.*, 2021a). All else being equal, parents exert more energy to reduce IVI. However, in years with an abundance of preferred prey, for example, it may be easier for parents to hunt successfully and thus exhibit lower IVIs without expending additional energy. Alternatively, parents may opt to bring larger prey per visit instead of reducing IVI as demand increases. For example, peregrines breeding near Canberra, Australia, maintained comparable nestling growth rates in both control and enlarged broods by increasing the size (and biomass) of delivered prey items to experimentally enlarged broods (Olsen & Tucker, 2003). Several other studies report peregrines increasing mass of delivered prey items instead of provisioning rate (Palmer, Nordmeyer & Roby, 2004; Dawson *et al.*, 2011; Olsen & Tucker, 2003; but see Zuberogoitia *et al.*, 2013). Provisioning larger prey items increases the likelihood of offspring survival (Dawson *et al.*, 2011). We suggest that future studies evaluating hierarchical models of provisioning either focus on systems in which there is little scope for inter-annual variation in prey type or quantify prey type and size in addition to IVI. We were unable to do this in our study as prey type and/or size could not be determined in approximately 30% of visits (4,637 out of 15,395 visits). As the success rate of prey identification varied across nests (due to camera placement), and likely due to prey type/size (e.g., larger prey easier to identify), we did not feel confident that our sampling of prey type/size was unbiased, and therefore, did not attempt to include analyses of prey type/size in the present study.

Additionally, the observed patterns of shifts in IVI may arise through any combination of tactics, for example, allocation of time to provisioning behaviour and/or hunting, quantity of prey consumed by the parents themselves versus delivered to offspring, selectivity of prey items hunted and delivered, and time spent processing hunted prey items before delivery. However, based on data collected in our study (nest camera images of exclusively the scrape) it was not possible to assess correlations between specific provisioning behaviours beyond IVI and the corresponding changes in IVI, to provide deeper insights into which tactics may be most prevalent and how they impact temporal patterns of provisioning as nestling demand increases. Future work is needed to ascertain the specific tactic(s) responsible for the patterns observed in this study.

Our study provides insights into the plasticity of parental investment decisions in peregrine falcons and raises new questions for future research. While we did not find strong support for the predicted covariances between provisioning intercept, plasticity and variance, modelling heterogeneous residual variance and covariances in intercept, slope, and variance are data-hungry analyses. Future work aimed at testing hierarchical provisioning decisions will require larger sample sizes. Nonetheless, our analyses did yield some novel insights. Consistent with a large body of work on parental investment theory, our results show that provisioning adult peregrines respond to increased nestling demand, both in terms of nestling age and nestling number, by reducing IVI. However, we also found that parents increase residual variance in IVI as a function of increasing nestling age, but not in response to increasing nestling number. This finding is consistent with a strategic shift in behaviour towards more variable foraging options with increased nestling demand as nestlings age.

Chapter 4: Food supplementing Peregrine falcons (*Falco peregrinus tundrius*) increases offspring mass and survival without changes in parental provisioning rate

Abstract

Parents are expected to exhibit intermediate levels of investment in parental care that reflect the trade-off between current versus future reproduction. Providing parents with supplemental food may allow for increased care to the current brood (additive model), re-allocation of parental effort to other behaviours such as self-maintenance (substitution model) or may provide parents with a buffer against provisioning shortfalls (insurance model). We investigated the impact of parental food supplementation on provisioning behaviour and breeding success in Arctic-breeding Peregrine falcons (*Falco peregrinus tundrius*) over five successive breeding seasons (2013-2017). We found that supplemental feeding had no impact on mean provisioning rates, yet resulted in increased offspring survival probability, increased fledgling body mass, and decreased variance in fledgling body mass and provisioning rates. These results are consistent with parents adopting a hybrid of the additive and substitution models. We suggest that food supplementation enables increased investment in other forms of parental care (e.g., nest defence, brooding) without altering mean provisioning rates. The lack of observed effects on mean provisioning rates, coupled with increased survival and body mass of offspring, suggests a potential reallocation of parental effort. The findings contribute to understanding the responses of Peregrine falcons to food supplementation, highlighting the need for future studies to explore broader environmental contexts and potential long-term effects on parental survival and future reproduction.

Introduction

Food is often a key factor limiting reproductive success in birds (reviewed in Martin (1987)). Greater food availability generally increases current reproductive success, though not always (Boutin, 1990; Ruffino *et al.*, 2014). While it seems intuitive that greater food availability should allow parents to provide a greater level of care to current offspring, thereby increasing reproductive success (Ruffino *et al.*, 2014; Asdell, 1946; Lack, 1966), studies that have manipulated food availability (i.e., food supplementation experiments) in breeding birds have yielded conflicting results. Some studies report no effect of food supplementation on parental provisioning, offspring growth, or offspring survival, some report positive effects, and others report negative effects (reviewed in Ruffino *et al.*, 2014; Ewald & Rohwer, 1982; Nilsson & Svensson, 1993; Clamens & Isenmann, 1989; Nilsson, 1994; Boutin, 1990).

In species that provide parental care to dependent young, parents must balance allocation of time and energy in care provided to their current offspring against time and energy invested in self-care and future reproduction (Trivers, 1972; Stearns, 1976). Optimal allocation is mediated by the relative costs and benefits of a given level of investment (Stearns, 1976; Stearns, 1989). Parents can increase the growth and survival of their current offspring by investing more in parental care behaviours, such as provisioning (Lifjeld & Slagsvold, 1989; Kacelnik & Cuthill, 1984; Wright, 1998; Wright *et al.*, 1998; Martins & Wright, 1993; Moreno *et al.*, 1995; Grüebler *et al.*, 2018). However, parents that invest more heavily in current offspring may reduce their capacity to invest in future offspring because increased investment in current offspring comes at the cost of self-care (Sanz & Tinbergen, 1999; Williams, 1966). Thus, when additional food is available (either naturally or via food supplementation), parents may not necessarily increase the rate at which they provide food to their current offspring, but may instead favour allocation towards self-care, which may account for some of the conflicting results previously reported (reviewed in Ruffino *et al.*, 2014; Ewald & Rohwer, 1982; Nilsson & Svensson, 1993; Clamens & Isenmann, 1989; Nilsson, 1994; Boutin, 1990; Mock *et al.*, 2005).

Specifically, we suggest that the effect of food supplementation on parental investment in the current brood may fit into one of three (non-exclusive) models that differ in how parents alter investment in current versus future reproduction with increasing food availability. We term these "additive", "substitution", or "insurance" models. First, food supplemented parents may take advantage of increased food availability to increase the level of care provided to young (Boutin, 1990; Ruffino *et al.*, 2014), which we call the “additive model”. Under this scenario, food supplementation of provisioning adults allows for an increase in the level of care provided to the current brood because, all else being equal (e.g., same level of brood demand, same environmentally imposed energetic costs), higher food availability allows for higher provisioning rates by parents without their spending additional time and/or energy searching for or delivering food. This may be particularly true in species where parents cache food items (e.g., Ruffino *et al.*, 2014), because supplemental food can be cached nearby, eliminating the need to search for prey until the cache is depleted. This could allow for higher provisioning rates without any negative effect on parental condition and/or future offspring. If parents adopt an additive strategy when provided with supplemental food, this should result in an increase in provisioning rate, fledging body mass and survival of offspring at supplemented nests relative to controls (Table 1).

Alternatively, food supplemented parents may take advantage of food supplementation to increase investment in self-care, which we term the “substitution model” (see also Boutin, 1990). The substitution model predicts that food supplementation enables breeding adults to maintain the same level of care to their young (e.g., rate of energy delivery) with less effort (e.g., less time spent searching for food), allowing them to reallocate time and/or energy towards self-maintenance. Thus, under the substitution model, we would predict comparable provisioning rates, fledging body masses and survival at supplemented nests relative to controls (Table 4.1). The increased investment in self-care also means that parents that adopt a substitution model when they are food supplemented would be predicted to experience increased survival and future reproductive success (Table 4.1).

Metric	**Additive**	**Substitution**	**Insurance**
Fledgling body mass	**Increase**	No change	**Increase in mean,** **Decrease in variance**
Survival probability of young	**Increase**	No change	**Increase in mean**
Provisioning rate	Increase	**No change**	Increase in mean, **Decrease in variance**
Parental survival	No change	Increase	No change
Future reproduction	No change	Increase	No change

***Table 4.1:** Summary of the key predictions of each proposed model of provisioning: additive, substitution, insurance. All predictions refer to supplemented nests relative to control nests. Although we did not have data available to test predictions related to parental survival and future reproduction, we have included them here for completeness (shaded light grey). Predictions that were supported by our analyses are in bold font.*

Finally, food supplementation may provide a buffer against variables that lead to yearly variation in reproductive success, such as years with low food availability and/or higher energetic costs, such that food supplementation allows breeding adults to mitigate the negative effects of such events on their offspring (Schoech *et al.*, 2008). We term this the “insurance model”. Under this model, the effects of supplementation should be most pronounced when background food availability is low (e.g., Schoech *et al.*, 2008; Boutin, 1990; Ruffino *et al.*, 2014). Provisioning rate may be either unchanged or increase if parents adopt the insurance model; if background prey availability is high, provisioning rates may be unaffected by food supplementation, while low background prey availability may result in increased mean provisioning rates for supplemented parents, relative to control parents. When looking across breeding attempts that include years with both high and low background prey availability, this would mean that supplemented nests should experience higher average provisioning rates, and lower variance in provisioning rates compared with control (non-supplemented) nests (Table 4.1). Previous work in the black sparrowhawk (*Accipiter melanoleucus*) has shown that for a given provisioning rate, greater consistently in prey deliveries (i.e., lower variance) leads to improved survival of offspring (Nebel *et al.*, 2020). Since the regular supply of supplemental food should provide a buffer against stochastic variability in background levels of food availability facilitating greater consistency in prey delivery, under the insurance model, food supplemented parents should have lower inter-annual variation in offspring production and be able to produce offspring with a higher body mass when background food availability is low compared to parents at non-supplemented nests. Finally, under the insurance model, because parents can successfully fledge young under a wider range of environmental conditions, we would expect to observe an overall increase in fledgling survival probability, and lower variance in success across differences in prey availability (such as across years).

In the present study, we conducted a food-supplementation experiment with Arctic breeding Peregrine falcons (*Falco peregrinus tundrius*) across 5 successive breeding seasons (2013-2017) to evaluate support for each of the three models described above. Specifically, we aimed to evaluate how parental food supplementation influences 1) mean and variance in provisioning behaviour, and 2) mean and variance in measures of reproductive success (fledging success and fledgling body mass) to test the predictions laid out in Table 4.1. Although the three models also generate predictions about parental survival and future reproduction (Table 4.1, shaded rows), we did not have a sufficient fraction of our study population marked to allow us to track individuals across years (see methods). Therefore, our analyses were restricted to the effects of food supplementation on current reproduction. Understanding the potential effects of food supplementation on parental investment will provide valuable insights into the trade-offs that provisioning peregrine’s face and the mechanisms they use to maximise their reproductive success.

Methods

Field methods

a. Study population & site

This study was conducted in Rankin Inlet, Nunavut (62.812, -92.094), an area comprised of large tundra stretches and rocky outcrops on which Peregrine falcons nest. Peregrines included in this study nested across coastal, island and mainland sites. A total of 127 nests were monitored across the 5-year study period (range 18-25 nests per year). However, sample sizes included in analyses varied for different response variables. An overview of sample sizes is provided in Table 4.2, and Appendix C: ESM for Chapter 4 provides detailed justification for removal of some nests from specific analyses. Although we did not collect data on natural prey availability as part of our study, previous work in the same population has shown that there is large inter-annual variation in peregrine prey densities (Hawkshaw *et al.*, 2021a; Hawkshaw, Foote & Franke, 2021b). We therefore assume that the 5-year study period included here was sufficiently long to capture both years of high and low relative prey abundance.

				Parental Care			**Reproductive success**					
	Total Nests studied			**Provisioning data**			**Fledgling body mass Nests (chicks)**			**Fledging Success Nests (chicks)**		
Year	**C**	**S**	**Total**	**C**	**S**	**Total**	**C**	**S**	**Total**	**C**	**S**	**Total**
2013	17	8	25	11	1	12	17 (33)	8 (24)	25 (57)	17 (55)	8 (28)	25 (83)
2014	13	10	23	11	8	19	13 (21)	10 (25)	23 (46)	13 (43)	10 (36)	23 (79)
2015	11	10	21	11	10	21	11 (16)	10 (28)	21 (44)	11 (35)	10 (30)	21 (65)
2016	17	12	29	16	12	28	15 (22)	12 (30)	27 (52)	15 (51)	12 (38)	27 (89)
2017	17	12	29	17	12	29	17 (25)	12 (25)	29 (50)	17 (46)	12 (43)	29 (89)
Overall	75	52	127	66	43	109	73 (117)	52 (132)	125 (249)	73 (230)	52 (175)	125 (405)

Table 4.2: *Overview of sample sizes as a function of treatment (C= control or S= supplemented) for each trait and each year, as well as overall sample sizes for the 5-year study. All sample sizes refer to number of nests, except for sample sizes provided in parentheses, which refer to number of nestlings.*

Egg laying took place between early and late June each year, with females each laying between 2-4 eggs (Ratcliffe, 1962). Eggs are incubated primarily by females for 33.5 days on average (Anctil *et al.*, 2014; Burnham & Cruz-Bernate, 1983) resulting in (asynchronous) hatching of between 1-4 nestlings in July (Ratcliffe, 1962). In this study, the average hatch date was July 13th (range: July 5th-26th). Peregrines are a caching species (Cameron & Olsen, 1993), meaning that they do not need to use supplemental food immediately, but may cache it for later use if and when required. Peregrines are generalist predators with a broad prey range including mammals, songbirds, shorebirds, and waterfowl. Our study population in particular has a high contribution of mammalian prey in the diet relative to other populations of peregrines, with mammalian prey comprising up to 1/3 of the total diet (Bradley & Oliphant, 1991; Dawson *et al.*, 2011).

c. Supplementation experiment

Within our study area, several nest sites are accessible only by helicopter, or have very limited accessibility depending on the weather. As these sites could not be visited regularly, they were excluded from the supplementation experiments (see Appendix C: ESM for Chapter 4). Of the nests that were accessible and therefore could be visited regularly, they were alternately assigned to supplemented or control treatments as the nests hatched. Treatments were assigned using a blocked spatial design such that there were 1-2 control nests in close proximity to each supplemented nest. Each year, 8-12 nests were food supplemented, which resulted in a total of 52 nests that were food supplemented (see Table 4.2 for sample sizes per treatment group and year) and 75 nests that were control nests. Both supplemented and control nests were visited at the same frequency; every 5 days, weather permitting, to control for rates of human disturbance at nests between supplemented and control nests.

Supplemented broods received commercially produced Common Quail (*Coturnix coturnix*) except in 2014 when there were 4 instances (out of 55 supplementations in that study year) where supplemented broods received commercially produced Rock pigeons (*Columba livia*) due to a lack of availability of quail. In these cases, pigeon was substituted 1:1 for quail according to the required supplementation treatment for the nests (see below and Appendix C: ESM for Chapter 4). Supplemental food was stored frozen and thawed to outside temperature prior to nest delivery. Supplemental quails or pigeons were provided whole (feathered) and placed within 1m of the scrape. Quail were selected as supplemental food based both on their commercial availability, and because they have similar nutritional profile to a number of other small birds and mammals (Dierenfeld, Alcorn & Jacobsen, 2002), suggesting they are likely of similar nutritional quality to naturally available prey in the study area.

Supplementation occurred between nestling age 5 to 25 days. We waited until nestlings were 5 days of age to begin supplementation to avoid disturbance immediately after hatch, and we stopped supplementation at age 25 days to avoid inducing early fledging. We also avoided visiting nests during inclement weather conditions such as during heavy rain, again to reduce unnecessary disturbance. When visits were missed, we compensated by providing supplemented nests with the missed quantity of quail in addition to the scheduled amount during the subsequently planned nest visit, or, where possible, by delivering the intended quantity of quail on the following day. The quantity of quail provided corresponded to approximately 50% of the brood's age specific energetic demand. Such demand was derived at the individual level from the observed amount of food necessary to suppress begging among captive bred falcon nestlings (Lynn Oliphant, personal communication, May 14, 2013). This resulted in increasing quantities of quail being provided to larger broods and as nestlings grew older (see Appendix C: ESM for Chapter 4 for detailed record of food supplementation quantities as a function of brood size and age). Although each visit resulted in deposits of large amounts of food, we expected that peregrines would exhibit normal caching behaviour (Booms & Fuller, 2003), and that supplemented quail could therefore be rationed over the following days. During our initial visits, we observed adults from a blind to confirm that they cached the quail in nearby locations and that supplemental food was being utilised only by adults at the supplemented nests. Although we were not able to subsequently monitor the caches to confirm that they were not used by other, non-target, pairs of peregrines, this is unlikely given that peregrines are highly territorial and aggressively defend their territory against intruders (White *et al.*, 2020). Across the study duration, there were only 2 instances where untouched quail remained at active nest scrapes upon our return 5 days later, once in 2014 and once in 2016.

d. Data collection & processing

A detailed description of routine nest visitations can be found in (McKinnon *et al.*, 2023). In brief, we began visiting historical nest sites in May of each study year, during the arrival of peregrines at the study site. We placed motion sensitive cameras within 1m of all active nests which collected images of all nest visits made by adults, including during periods of low light. Active nests were visited every 5 days, weather permitting (as previously discussed). Hatch date was determined from nest camera images. Hatched nestlings were marked on the right thigh with non-toxic markers as red, green, or blue, or left unmarked, to allow individuals to be monitored for the duration of the breeding season. We weighed nestlings at each visit to the nearest gram. We used the last body mass measurement taken in our analyses of nestling body mass at assumed fledging (see below).

Nestlings that were still alive on the final nest visit were presumed to have survived to fledging. Final nests visits occurred between nestling ages 21 and 35. We did not visit nests after day 35 to avoid inducing early fledging. Not all nests were visited at nestling age 35 days due to logistical constraints such as inclement weather limiting access to some nest sites. Nestlings that were alive on the final nest visit were leg banded for identification purposes. Avian leg gauges from Avinet Research Supplies were used to measure the nestlings' leg diameter, and appropriately sized leg bands were subsequently applied. Sex determination of nestlings followed the guidelines outlined in the banding guide provided by the United States Geological Survey (USGS) (available at https://www.pwrc.usgs.gov/BBL/Bander_Portal/login/speclist.php). Nestlings fitted with a band size of 6 (or smaller) were designated as male, while those with a band size of 7A (or larger) were identified as female. A total of 243 nestlings were sexed via this method: 114 female, 129 male. An additional 6 nestlings were not banded or sexed because it was deemed that banding these nestlings might induce early fledging based on the size and behaviour of the nestlings during the banding visit. These 6 fledglings were removed from analysis of body mass but were retained for all other analyses where sex was not included in the models (see below).

Provisioning data was extracted from time-stamped nest camera images and was analysed at the level of the pair because peregrines exhibit division of labour such that most hunting is done by the male, but most provisioning to young is done by the female (Palmer, Nordmeyer & Roby, 2001). Further details of extraction and processing of provisioning data can be found elsewhere (McKinnon *et al.*, 2023). We calculated inter-visit-intervals (IVIs) as the time (in minutes) between the beginning of successive provisioning visits. Between late-July and mid-August (the period in which we collected provisioning data), our study area does not experience full darkness. As such, provisioning visits could (and did) happen at any hour within the 24-hr day, and therefore, we did not treat successive provisioning visits any differently if they occurred within the same day, or across days. Hatch day (i.e., nestling age 0) was excluded from analysis, given the possibility for great variation in opportunity for feeding generated by time of hatching in the day (for example, the feeding opportunities of a nestling born in the morning versus late evening). Provisioning behaviour was only analysed between nestling day 5 (i.e., the start of nest supplementation experiments) up to a nestling age of 12 days. We did not include camera trap data collected after nestling age 12 days because we observed the first instance of a nestling moving out of frame of the nest camera at age 13 days meaning beyond this age, we could not be confident camera traps were capturing all parental provisioning visits. There were few nests at which cameras were placed but extraction of provisioning data was not possible due, for example, to camera and memory card problems; see ESM Table S3 for full details of which nests were excluded and why.

Although the three models laid out in Table 1 include predictions about parental survival and future reproduction, we were unable to obtain the data required to test these predictions. This is because logistical constraints and variation in catching success meant that approximately 50% of adults in the population in any given year are banded. Thus, we were unable to track individuals across years to evaluate the effect of supplementation in one year on survival and/or reproduction in the next.

Statistical methods

We first evaluated that the pseudo-randomized assignment of supplemented and control nests did not result in any significant differences in hatch date, clutch size or number hatched across treatments. To do this, we constructed three Bayesian regression models (i.e., one each for hatch date, clutch size, and number hatched) using Hamiltonian Monte Carlo (HMC) sampling conducted using the ‘brm’ function from the ‘brms’ package (Bürkner, 2017) in R (version 4.2.0). All three models included treatment as a fixed effect, with year and nest site ID included as random effects to account for inter-annual variation in breeding parameters, and non-independence of nests at the same sites across multiple years. Hatch date was modelled based on a Gaussian error distribution, while number hatched and clutch size were count data, and so modelled with a Poisson error distribution.

Next, we developed three models, again using the ‘brms’ package for Bayesian regression modelling, to test the predictions laid out in Table 1. All models included fixed and random effects. First, we modelled (log transformed) inter-visit-intervals (IVI) with a Gaussian error distribution and Markov chain Monte Carlo (MCMC) sampling using two different model structures. Both models included fixed effects for treatment (“food supplemented” or “control”), hatch date (centred and scaled at the level of the full dataset), and nestling age (centred and scaled at the level of the full dataset) and random effects for site, pair, and year. We also modelled heterogeneous residual variance (sigma) as a function of treatment within this model. However, we ran a second version of this model keeping all variables the same except including brood size on the day of observation (centred and scaled at the level of the full dataset) as an additional fixed effect. By including models both without and with brood size as a covariate, we were able to look at total parental effort as a function of treatment (regardless of any treatment-related differences in brood size), as well as treatment-related differences in parental effort experienced per nestling, respectively.

We modelled survival to fledging, a measure of reproductive success, using logistic regression with a Bernoulli distribution and MCMC sampling. The Bernoulli distribution models the probability of success (survival) as a function of the predictors. For this model, all individuals that hatched were included and coded as either 1 (survived to final nest visit) or 0 (did not survive to final nest visit). This model included fixed effects for treatment, number hatched (centred and scaled at the level of the full dataset), and hatch date (centred and scaled at the level of the full dataset) and random effects for site, pair, and year.

Finally, we modelled nestling final observed body mass (grams) with a Gaussian error distribution and MCMC sampling. This model included fixed effects for treatment, number of nestlings that survived to fledging (see above) (centred and scaled at the level of the full dataset), hatch date (centred and scaled at the level of the full dataset), nestling age (centred and scaled at the level of the full dataset), and nestling sex (male or female), and random effects for site, pair, and year. Nestling age was included because the final nestling body masses obtained range from day 21 post hatch to day 35 post hatch. During this period, growth is approximately linear until nestlings reach their asymptotic mass (Hedlin, 2016). Thus, we included nestling age as a covariate to account for the age gradient in final mass measurements. We included nestling sex as peregrines are sexually size dimorphic, with females being both larger and heavier than males (Mills, Taylor & Hemelrijk, 2019). Sex was coded as -1 or +1 such that the model intercept was estimated for the average nestling, irrespective of sex, as our predictions did not necessitate evaluation of the interaction between treatment and offspring sex.

For each model, the mode of estimated effects (β, σ or ρ) and 95% credible intervals (CrI) are presented and used to evaluate support for each effect. Estimates with CrIs which do not overlap zero are interpreted as providing strong support. Estimates with CrIs centred around zero are interpreted as providing no support for the effect. For estimates that were biased away from zero, but whose 95% CrI overlapped zero, we calculated the proportion of the posterior distribution which were in the opposite direction of the mean estimate value calculated from all model iterations. We present these, where appropriate, for the fixed effects in our models, within the results statement, as ‘pr’. When CrIs overlapped zero by less than 15%, we interpret this as providing moderate support for an effect in the estimated direction because this equates to over five times greater support for interpretation of an effect in the estimated direction relative to an effect in the opposite direction (Marsman & Wagenmakers, 2017).

Results

We first confirmed that the assignment of supplemental and control nests was random with respect to hatch date, clutch size or number hatched. Our analysis revealed no support for a difference between supplemented and control nests in hatch date (β = -0.42, 95% CrIs = -1.28, 0.45; pr = 0.168), clutch size (β = 0.00, 95% CrIs = -0.15, 0.14), or number hatched (β = 0.05, 95% CrIs = -0.10, 0.21; pr = 0.237).

Provisioning effort (inter-visit-intervals, IVIs)

We observed 5423 provisioning visits at 109 nests across our 5-year study period, from nestling ages 5 to 12, reflecting the period of supplementation. The average number of daily provisioning visits per nest was 6.81 (range 1 to 17). We did not observe a significant effect of food supplementation on mean IVI in either the IVI model excluding brood size (β = 0.01, 95% CrIs = -0.12, 0.14; pr = 0.41, Figure 4.1) or the IVI model including brood size (β = 0.05, 95% CrIs = -0.08, 0.17; pr = 0.24; Figure 4.1). However, supplemental feeding was associated with reduced variance in provisioning IVI both for the model without brood size covariate (σ = -0.04, 95% CrIs = -0.08, 0.00) and the model with brood size covariate (σ = -0.04, 95% CrI = -0.08, 0.00). Additionally, the log IVI of provisioning decreased with increasing brood size (β = -0.30, 95% CrIs = -0.44, -0.16) and with increasing nestling age (without brood size covariate: β = -0.11, 95% CrIs = -0.13, -0.09; with brood size covariate: β = -0.12, 95% CrIs = -0.14, -0.09). We also found strong support that logIVI varied across breeding pairs, territories, and years (see Table 4.3). However, we found no support for an effect of hatch date on IVI (see Table 4.3).

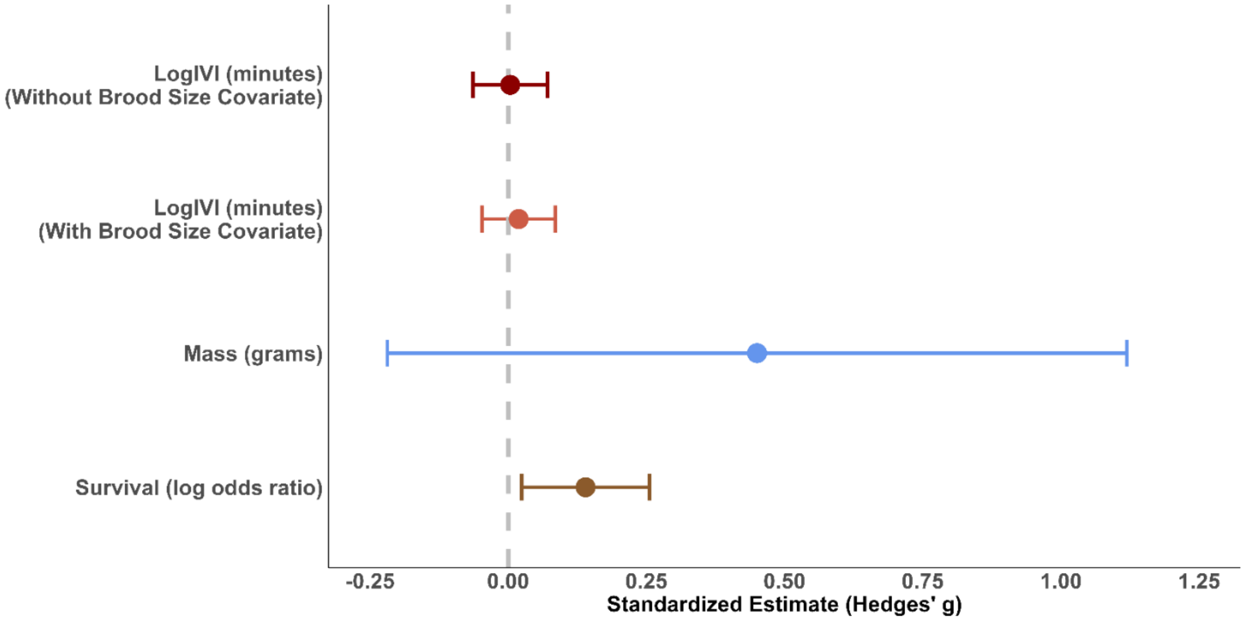

Figure 4.1: Estimated effect of food supplementation on parental provisioning rate (log IVI (minutes), nestling survival (log odds ratio), and nestling body mass at fledging (grams). Estimates and 95% CI have been standardized (using Hedges' *g* to facilitate comparison across response variables with different measurement units. Estimates are calculated from model outputs presented in table 4.3. Positive estimates indicate that providing supplemental food resulted in an increase in the response variable.

	Log IVI (minutes) (not controlling for brood size)	**Log IVI (minutes) (controlling for brood size)**	**Survival probability**	**Body mass at fledging (g)**
Fixed effects	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**	**β (95% CI)**
Intercept	**4.94 (4.66, 5.23)**	**4.91 (4.64, 5.19)**	**-0.06 (-1.31, 1.11)**	**636.43 (554.97, 713.31)**
Hatch date	β-0.01 (-0.05, 0.03)	-0.02 (-0.06, 0.02)	**-0.57 (-1.03, -0.22)**	-3.53 (-11.22, 4.18)
Number hatched	NA	NA	-1.44 (-3.23, 0.17)	NA
Brood size	NA	**-0.30 (-0.44, -0.16)**	NA	-14.09 (-44.22, 15.88)
Nestling age	**-0.11 (-0.13, -0.09)**	**-0.12(-0.14, -0.09)**	NA	**16.09 (-5.83, 26.17)**
Treatment	0.01 (-0.12, 0.14)	0.05 (-0.08, 0.17)	**2.39 (1.11, 3.93)**	*24.68 (-3.53, 53.22)*
Random effects	**σ (95% CI)**	**σ (95% CI)**	**σ (95% CI)**	**σ (95% CI)**
Site ID (i.e., territory)	0.09 (0.00, 0.20)	0.07 (0.00, 0.17)	0.71 (0.04, 1.75)	22.36 (1.92, 43.52
Pair ID	0.28 (0.22, 0.35)	0.27 (0.21, 0.33)	2.59 (1.70, 3.79)	33.45 (12.16, 52.27)
Year	0.25 (0.07, 0.71)	0.26 (0.07, 0.70)	0.90 (0.05, 2.63)	36.32 (9.23, 93.56)
Residual variance Intercept	0.05 (0.02, 0.08)	0.05 (0.02, 0.08)	1 (1, 1)[1]	4.84 (4.67, 5.01)
Residual variance (treatment)	**-0.04 (-0.08, 0.00)**	**-0.04 (-0.08, 0.00)**	NA	**-0.76 (-0.98, -0.54)**

Table 4.3: *Model results for provisioning behaviour (Log IVI in minutes), survival probability (survived = 1, died = 0), and body mass (grams) at fledging. Two models exploring sources of variation in provisioning behaviour are presented, one without brood size as a covariate and one with brood size as a covariate to differentiate between total provisioning effort independent of treatment related differences in brood size and provisioning effort per nestling, respectively. Provisioning behaviour and body mass were modelled with gaussian error distributions and as such, we were able to model treatment-related differences in residual variance. Survival probability was modelled with a Bernoulli error family, which assumes a residual variance of 1, and therefore, does not allow for modelling treatment-related differences in residual variance. Significant fixed effects and heterogeneous residual variances are indicated in bold.*

Offspring survival probability

Our analysis was based on the survival outcomes of 405 nestlings at 125 nests across the 5-year study duration. Overall, 156 nestlings died before the final nest check, and 249 survived. We found strong support for a negative association between survival probability and hatch date (β = -0.57, 95% CrIs = -1.03, -0.22) and strong support that supplemental feeding improved survival probability (β = 2.39, 95%

CrIs = 1.11, 3.93; Figure 4.1). We found moderate support that survival probability decreased with increasing number of young hatched in a given nest (β = -1.44, 95% CrIs = -3.23, 0.17; pr = 0.036). Additionally, we found strong support for variability in survival probability across breeding pairs (σ = 2.59, 95% CrIs = 1.70, 3.79), territories (σ = 0.71, 95% CrIs = 0.04, 1.75), and years (σ = 0.90, 95% CrIs = 0.05, 2.63) (see also Table 4.3).

Nestling body mass at fledging

We analysed nestling body mass for the 249 nestlings from 102 nests which survived to fledging. The average mass of a fledgling, irrespective of sex, was 618.96g (95% CrIs = 558.54, 676.41). Fledgling body mass was significantly higher for female fledglings relative to males (β = 104.40, 95% CrIs = 95.23, 113.33) irrespective of treatment group, as expected given that body size was used as a criterion to assign fledgling sex. We found moderate support that supplemental feeding increased mean fledgling body mass (β = 24.68, 95% CrIs = -3.53, 53.22; pr = 0.035; Figure 4.1) and strong support that supplementation reduced variability in fledgling body mass (σ = -0.76, 95% CrIs = -0.98, -0.54) relative to controls. Additionally, we found that age at fledgling significantly impacted body mass, with older nestlings having a higher mass on average (β = 16.09, 95% CrIs = 5.83, 26.17; pr = 0.001). Thus, lower fledgling body masses were also moderately associated with later hatch dates (β = -3.53, 95% CrIs = -11.22, 4.18; pr = 0.224). We found weak support that larger brood sizes (at fledging) resulted in lower fledgling body mass (β = -14.09, 95% CrIs = -44.22, 15.88; pr = 0.177). Finally, we found strong support for differences in fledging body mass across pairs (σ = 33.45, 95% CrIs = 12.16, 52.27), territories (σ = 22.36, 95% CrIs = 1.92, 43.52), and years (σ = 36.32, 95% CrIs = 9.23, 93.56).

Discussion

We evaluated the effect of parental food supplementation on provisioning behaviour and reproductive success in Arctic breeding Peregrine falcons. We assessed results in view of three potential non-exclusive strategies parents may adopt when provided with supplemental food: additive, substitution, or insurance (Table 4.1). We found partial support for all three mechanisms. Consistent with both the additive and insurance models, we found strong support that supplementation increased the probability of offspring survival and moderate support for an increase in fledging body mass. Consistent with the insurance model, we also observed decreased variance in fledgling body mass and decreased variance in provisioning IVIs under food supplementation. However, we found no support for a change in mean provisioning rate (provisioning inter-visit intervals, or IVIs) which is consistent with the substitution model, but inconsistent with either additive or insurance models. This study contributes to existing knowledge of the effects of food supplementation (i.e., an abundant and easily accessible food supply) on parental investment. Importantly, it also demonstrates that none of the models as laid out in Table 4.1, on their own, can fully account for the responses to food supplementation observed in the present study. Below, we discuss how our results might be explained by a combination of additive, substitution, and insurance models, and how future studies could test our suggested hybrid model.

If peregrines use food provided during supplementation experiments either in addition to their baseline parental investment ("additive model") (Boutin, 1990; Ruffino *et al.*, 2014), or specifically to meet offspring demand under more challenging conditions ("insurance model") (Schoech *et al.*, 2008), we predicted an increase in mean provisioning rates (i.e., decrease in provisioning inter-visit intervals, IVIs) for peregrines that received the supplementation treatment. While we found no evidence that mean IVIs differed as a function of treatment, we did find support for reduced variance in IVIs for food supplemented nests. There are several potential explanations for this finding. First, our findings may indicate that rather than reducing IVI, supplementation allowed parents to change prey selectivity to favour more nutritionally or energetically beneficial prey types and/or select for larger prey items. Shifts in prey type could explain the increase in nestling body mass and survival in the absence of an increase in provisioning rate (e.g., Durell, 2000), and could also be associated with reduced variance (Stephens &

Krebs, 1986). Initially, we aimed to collect prey type and biomass information from our camera trap images. However, around 30% of provisioning visits lacked accurate data due to issues such as poor image quality and partially obstructed views of prey. This is not only a large fraction of missing data, but missing data is likely to be non-random. For example, small prey items are likely to be more easily missed in camera trap images compared to larger prey. Moreover, our nest cameras only captured images of the scrape, missing details about surrounding areas where prey might have been processed. Consequently, incomplete and potentially biased prey type and size data were excluded from further analysis. However, we acknowledge that shifts in prey selectivity may have occurred and could account both for the higher survival and increased fledging body mass observed at supplemented nests in the absence of changes in provisioning rates. Accurate measures of prey type and quality provisioned to young would be required to test this directly.

Similarly, due to movement of nestlings out of the nest scrape from around day 13 post hatch, provisioning behaviour was only assessed for around half the brooding period. As nestlings age, their demand for food increases (McKinnon *et al.*, 2023). We found this to be true even within the 12-day period, thus the increase in demand and resultant increase in sibling competition later in the breeding season may result in more pronounced differences in mean IVIs across supplemented in control nests. However, previous research indicates that peregrine growth (and thus potential increases in demand) plateaus at around day 25 post-hatch (Hedlin, 2016). This, coupled with our finding of an effect size of almost 0 in the first 12 days ($\beta = 0.01$, 95% CI = -0.10, 0.13), suggests that it is unlikely that significant differences in provisioning rate at supplemented and control nests would emerge only in the latter half of the breeding season.

Another possibility is that we lacked power to detect effects of supplementation treatment on mean IVIs. This is unlikely given that our estimates of provisioning effort were based on 5423 observations at 109 nests over 5 years, suggesting that our dataset should have had sufficient power to detect an effect of supplementation treatment on provisioning IVI had it been there. Indeed, we were able to detect significant effects of nestling age and brood size, two proxies for brood demand, on provisioning IVI. Consistent with a large body of earlier empirical work in both peregrines (e.g., Olsen & Tucker, 2003; Olsen *et al.*, 1998; Jenkins, 2000; McKinnon *et al.*, 2023) and birds in general (e.g., Cauchard *et al.*, 2021; Mathot *et al.*, 2017; Rytkonen, Koivula & Orell, 1996; Grüebler *et al.*, 2018), peregrines decreased provisioning IVIs with increasing brood demand. Furthermore, we observed a significant decrease in the variance in IVI in supplemented nests (Table 4.3). Detecting heterogenous residual variances is notoriously data hungry (Cleasby & Nakagawa, 2011), thus, the fact that we had the power to detect this effect suggests that the lack of observed effect of treatment on mean IVIs reported here is likely to be biologically real, and not due to lack of statistical power.

The lack of observed effect of food supplementation treatment on mean IVI is consistent with the substitution model, however, the substitution model on its own does not predict that food supplementation will lead to an increase in offspring body mass or decrease in variance in either body mass or IVI (Table 4.1). Thus, our findings that food supplementation resulted in increased survival probability and increased fledgling body mass suggest that the substitution model, as we originally proposed it, cannot fully account for our results. Overall, our data are consistent with food supplemented peregrines adopting a combination of the three models. The decreased variance in IVI observed in food supplemented nests is at least partially consistent with the insurance model, and decreased variance may account for the increased survival and increased body mass of young of food supplemented nests. For example, previous work in another raptor, the black sparrowhawk, found that even when mean provisioning rates were identical, lower variance in provisioning was associated with increased survival (Nebel *et al.*, 2020).

Another possibility is that our view of expected changes under the substitution and additive models may have been unduly limited. In the substitution model, we initially only considered substitution within the same form of parental care (i.e., provisioning behaviour) however, substitution may be occurring across different forms of parental care, specifically from provisioning to brooding and/or nest defence. In this case, parents could facilitate an increase in offspring survival without a change in provisioning effort; this is consistent with our findings. For example, since peregrines are a caching species (Turner, Lawrence & Czechura, 1993; Cameron & Olsen, 1993), the provision of supplemental food allows them to increase their reserve food supply in caches located near the nest scrape meaning parents can more actively shelter and protect their offspring from both inclement weather and predation, both of which could have contributed to the increased survival likelihood at food supplemented nests. Increased nest attendance would be expected to be particularly important in our study population, as previous work has shown that inclement weather is a major contributor to nestling mortality, and furthermore, that sheltering young from rainfall leads to a significant increase in survival (Anctil *et al.*, 2014). We suggest that food supplemented broods may benefit from higher nest attendance by parents, which is a readily testable prediction in a variety of systems but would require data on non-provisioning nest visits in addition to provisioning nest visits. Thus, we suggest that our findings of increased offspring survival and body mass in supplemented nests, despite constant IVI, may indicate that parents are using food supplementation to add to their total level of care provided to offspring by substituting effort that would have otherwise been spent on searching for prey, towards effort spent on nest defence and protection of offspring. This equates to a hybrid of our originally proposed models.

Our study provides important insights into the response of provisioning Peregrine falcons to increases in food availability, and the resultant impact on offspring both in terms of body mass at fledging and survival probability. We found strong support for increased survival and moderate support for increased body mass of nestlings at food supplemented nests, with no evidence of changes in mean parental provisioning rates. Given the non-mutually exclusive nature of the three models we proposed, future studies would allow for stronger inference if they tested the full suite of predictions derived from these models (Table 4.1), including parental survival and future reproduction). For example, if well powered studies fail to detect any effect of food supplementation of parental survival and future reproduction, and also observe increased nest attendance, that would provide strong support for the model we propose whereby supplemented parents increase investment in other (non-provisioning) forms of parental care. Detailed observation of the type and size of prey, and well as provisioning decisions (e.g., evenness of provisioning among young) would also provide important insights into the mechanisms underlying the observed changes in nestling body mass and survival. Understanding the potential impacts of food supplementation on parental investment is crucial for gaining insights into the trade-offs and mechanisms employed by provisioning Peregrine falcons (and other species) to maximise reproductive success.

Chapter 5: Discussion

Life-history and parental investment theory provide the foundation for understanding the adaptive strategies employed by organisms to maximize reproductive success in dynamic and unpredictable environments (Stearns, 1989). Parental investment theory in particular highlights the trade-offs associated with allocating limited resources to current reproduction versus anticipated parental investment in future reproductive attempts (Trivers, 1972; Milonoff *et al.*, 2004; Wang *et al.*, 2009). This trade-off in turn shapes parental behaviours such as investment in provisioning and nest defence. Behavioural plasticity allows parents managing these trade-offs to adjust their investment strategies in response to changing environmental conditions and/or the demand of their current offspring (Westneat *et al.*, 2012; Mathot *et al.*, 2017; Westneat *et al.*, 2017). By investigating these theories through both a systematic review and meta-analysis of 26 bird species, and in the context of Arctic-breeding Peregrine falcons, this thesis contributes to our understanding of avian parental care strategies and their implications for reproductive success.

Fulfilment of thesis objectives

Objective 1: investigate the availability of evidence for trade-offs between investment in current versus future reproduction in birds.

In Chapter 2, I conducted a comprehensive systematic review and meta-analysis to investigate the effects of experimental brood size manipulations on parental investment in provisioning. I investigated this particularly in relation to species longevity, as longer-lived species need to more carefully balance the trade-off in investment due to the anticipation of greater opportunities for future reproduction, relative to short-lived species (Fokkema *et al.*, 2016; Richardson *et al.*, 2020; Milonoff *et al.*, 2004; Erikstad *et al.*, 1998). Through a series of meta-analytic models, I explored the responses of parents to experimental brood enlargements and reductions to investigate evidence for investment trade-offs proposed by life-history theory (Stearns, 1989). The results confirmed that there is strong and broad support for trade-offs between investment in current versus future reproduction in birds. Specifically, we found a statistically significant effect of brood size manipulations on parental provisioning effort, with parents increasing investment in enlarged broods and decreasing investment in reduced broods, illustrating that current investment decisions are mediated by current brood value (Erikstad *et al.*, 1998). Although intuitive, this is a significant finding because empirical studies investigating life-history trade-offs often report conflicting or equivocal results (Metcalf, 2016). However, we demonstrate that studies whose designs appropriately control for individual differences in quality by experimentally manipulating current brood value, show consistent and strong support for predicted allocation decisions if parental care decisions reflect a trade-off between current and future reproduction.

We additionally investigated whether the strength of trade-off was shaped by species longevity (i.e., average number of breeding years), assuming that species longevity was a valid proxy for residual reproductive value (RRV) (Williams, 1966). However, while theory suggests that longer-lived species should exhibit more pronounced responses to their higher residual reproductive value (RRV), evidence in support of this was weak. Our analysis did not find a significant interaction effect between experimental brood size manipulation and species longevity. We propose several possible explanations for this. First, there are a lack of available studies investigating provisioning response in longer-lived species, limiting our ability to draw robust conclusions about the relationship between longevity and responsiveness to brood manipulation. Second, longevity (average breeding years) may not be a good proxy for RRV given that it fails to account for variability across individuals in a population, particularly in longer-lived species (Tettamanti *et al.*, 2012; Mourocq *et al.*, 2016). Finally, both environmental factors (e.g., food availability, see meta-analysis by Ruffino *et al.*, 2014) and temporal dynamics (Lu *et al.*, 2011a; Berlincourt & Arnould, 2015) shape parental investment decisions, but could not be accounted for in our review, which may have reduced our power to detect effects.

Objective 2: investigate evidence for adaptive adjustments in parental care in Peregrine falcons.

In Chapters 3 and 4, we conducted field-based studies to explore the strategies of investment in parental care by Arctic-breeding Peregrine falcons. Chapter 3 presents findings from an observational study conducted across 7 study years (2013-2019) examining the provisioning response of parents to natural variation in brood demand as generated by changes in brood size and nestling age across the breeding season. Chapter 4 presents the outcomes of an experimental study conducted across 5 of those study years (2013-2017), investigating the impact of supplemental food on parental investment in parental care (provisioning) and offspring success (i.e., fledgling mass and survival). In doing so, we could evaluate evidence for adaptive adjustments in parental care, particularly via provisioning behaviour, in peregrines. For both of these studies, we deployed motion-sensitive camera and conducted regular nest visits to collect data on provisioning rates, nestling growth (body mass), and ultimately fledging success.

The results of the observational study (Chapter 3) reveal that parents adaptively adjust their provisioning behaviour in response to brood demand by reducing inter-visit intervals (IVIs) between provisioning visits, indicating higher provisioning rates. This pattern was consistent across all 7 study years, and the decrease in IVI was slightly more pronounced with increasing nestling age compared to increasing brood size. There was strong support for an increase in the variance of IVI with increasing nestling age, suggesting greater variability in provisioning effort as nestling demand increased. Although multiple distinct mechanisms could lead to increased variance in parental provisioning with increasing brood demand, we suggest this may arise via variance-sensitive provisioning decisions. This analysis also highlighted significant differences across pairs, sites, and years in the plasticity and variance in IVIs.

This study makes a notable contribution to the literature, as studies that explicitly consider variance in provisioning decisions are relatively rare (Mathot *et al.*, 2017; Westneat *et al.*, 2012;

Westneat *et al.*, 2017; Moore, 2002). It also serves to demonstrate the importance of considering variances in addition to means when investigating biological processes due to the prevalence of (under-reported) heteroscedasticity in ecological datasets (Westneat *et al.*, 2015). Overall, this study provided novel insights into the relationships between parental care via provisioning and brood demand across study years, generally emphasising the capacity of peregrines for adaptive adjustment in behaviour. Future studies aiming to evaluate support for variance-sensitive provisioning behaviour relative to alternative mechanisms for meeting increased demand should either focus on systems in which there is little scope for across-year differences in available prey types or quantify prey type and size in addition to IVIs. In doing so, this work could ascertain the specific tactic(s) responsible for the patterns observed in this study.

The results of the experimental study (Chapter 4) reveal a positive association between food supplementation of provisioning adults and both offspring survival probability and fledging body mass. However, there was no evidence of changes in mean or variance in provisioning effort (as measured by IVIs) between supplemented and control (non-supplemented) nests. To our knowledge, only one other study found increased offspring survival without increased provisioning in response to food supplementation (namely, Seress *et al.*, 2020). These results suggest that peregrine parents may be reallocating additional energy provided by supplemental food to increase their investment in other forms of parental care rather than provisioning, for example brooding and nest defence. Interestingly, Seress *et al.* (2020) found that while provisioning rates of Great tits (*Parus major*) remained consistent across supplemented and control nests irrespective of habitat, survival was higher in supplemented nests in urban but not forested habitats; they attribute this to lower background food availability in urban areas, aligning with the findings of this thesis chapter. This chapter highlights the need for further investigation of the complex mechanisms underlying adaptive parental adjustments in parental care in peregrines. To address this, future studies should conduct detailed behavioural observations to directly monitor parental care behaviours beyond provisioning, such as brooding and nest defence. Additionally, quantifying the energy budget of parents at supplemented and control nests by monitoring metabolic rates, energy expenditure and food intake of parents could determine support for reallocation of energy to other forms of parental care (Fort, Porter & Grémillet, 2011).

Study species

While empirical research investigating evidence for reproductive trade-offs on the appropriate scale (i.e., experimentally and/or at the within-individual level) is surprisingly limited across all species (Metcalf, 2016; Santos & Nakagawa, 2012), research in longer-lived species is even more rare (Clutton-Brock & Sheldon, 2010). For example, in Chapter 2, our meta-analysis revealed an almost complete absence of brood manipulation studies conducted in longer-lived species. Yet, longer-lived species are required to balance this trade-off between investment in current versus future offspring over more breeding years and are thus arguably more appropriate to study in this context than shorter-lived species. In fact, avian research on parental care and reproductive behaviour even more generally is conducted almost exclusively in short-lived species, particularly passerines. As noted by Williams (2018), passerines are central-place foragers, facilitating easy behavioural observations; typically feed at high rates, making larger sample sizes for parental care behaviours such as provisioning easier to obtain; and typically begin to reproduce in their first year, making monitoring of generational effects easier.

Chapters 3 and 4 of this thesis encompass both observational and experimental approaches to investigate parental care and reproductive success in Peregrine falcons, a long-lived cliff-nesting raptor species. Peregrines can live for up to 20 years in the wild (or up to 25 in captivity) (White *et al.*, 2020) and breed annually, with a minimum 81-85% annual survival for breeding adults in the Canadian Arctic (Court *et al.*, 1989). Thus, Peregrines are theoretically an ideal model species for studying questions relating to reproductive trade-offs and parental care. However, they are also logistically challenging to study (Court *et al.*, 1989). Cliff nest sites are difficult to locate and access, making data collection challenging, and feeding rates relatively low, meaning long-term studies are necessary to obtain sufficiently large sample sizes to conduct robust analyses (Westneat *et al.*, 2015; Cleasby & Nakagawa, 2011). Despite these challenges, we conducted research in an Artic-breeding population of peregrines over 7 consecutive breeding years, resulting in large sample sizes with which to investigate parental care behaviours, particularly related to provisioning, and reproductive success. In doing so, Chapters 3 and 4 effectively begin to fill a research gap identified in Chapter 2.

Conclusions & future directions

The research presented in this thesis contributes to our understanding of avian parental care strategies, particularly focusing on the trade-offs between investment in current versus future reproduction and the adaptive adjustments made by Peregrine falcons in response to variations in offspring demand, and food supply. The findings of studies included in this thesis underscore the multi-dimensional dynamics of parental investment decisions in birds and the importance of adaptive adjustments in response to varying environmental conditions (particularly food availability). By improving our understanding of the factors influencing parental care strategies and their implications for reproductive success, this research provides valuable insights into avian life-history trade-offs and adaptive behaviour.

Future studies building on this work should conduct detailed behavioural observations to monitor a broader suite of parental care behaviours, including brooding and nest defence and/or quantify parental energy budgets to determine resource allocation among different parental care behaviours. Additionally, collection of data on prey availability and type and size of prey items provisioned, not just rate of provisioning, are necessary to disentangle potential mechanisms of adjustments in parental care behaviours. Studies must do so over multiple breeding seasons, encompassing a range of environmental conditions, particularly food availability, to assess variability of parental responses to changes in the relative value of their current offspring. And finally, additional research is needed on longer-lived species, particularly raptors, where the need to balance the trade-off between investment in current versus future reproduction is more pronounced.

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Appendices: Electronic Supplementary Material (ESM)

Appendix A: ESM for Chapter 2

Search string details

a. Description of string formation and usage

Below is the final search string of terms relating to provisioning and brood demand. Terms within each category were separated by the Boolean operator ‘OR’ while categories were separated by ‘AND’ such that a study needed to have a term from both the first and second category (provisioning and brood demand, respectively) within its title, abstract or key words in order to be returned by the database searched. This search string was originally formed within ‘advanced search’ in Web of Science and can be copied and pasted directly to replicate our search.

Note: The same strings were used in each of our database searches (i.e., also for Scopus, worldwidescience, and BASE) with edits to reflect the database ‘wildcard’ characters. For example, in Web of Science the asterisk symbol (*) can be used to capture any group of characters, including no character i.e., “provision*” captures provision, provisioning, provisioned, provisions etc; and the dollar sign ($) can be used to capture any single character i.e., “feeding visit$” captures feeding visit and feeding visits.

Wildcard characters are used for precisely the same meaning across Web of Science and Scopus. In worldwidescience and BASE the use of ‘$’ is replaced by ‘?’. Descriptions of the wildcard usage for each of our searched databases can be found (linked) at: Web of Science, Scopus, worldwidescience and BASE.

b. Full search string

(TS=(provision* OR "parental effort" OR "parental investment" OR "visit rate" OR "prey delivery" OR "energy delivery" OR "parental provision*" OR "feeding visit$" OR "feeding rate" OR "feeding effort")) AND TS=("brood size" OR "nestling number" OR "number of nestlings" OR "reduced brood" OR "enlarged brood" OR "clutch size" OR "brood reduction" OR "brood enlargement" OR "number of chicks" OR "chick number" OR "brood demand")

Supplementary tables

Table S2.1: *A full list of studies (both peer-reviewed publications and theses) that contributed estimates to the meta-analysis. Studies are listed in alphabetical order by first author.*

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Table S2.2: A full list of studies (both peer-reviewed publications and theses) that were excluded after reading the full text. Studies are listed in alphabetical order by first author, along with reasons for their exclusion.

Reference	**Reason**
Arnold TW (1993). Fledging Success in Experimentally Manipulated Broods of House Wrens. *Wilson Bulletin*, 105(3):448-454.	No Provisioning Data
Arnold TW (2011). An Experimental Study of Fledging Success in American Coots (*Fulica americana*): Effects of Brood Size, Food Availability, and Hatching Asynchrony. *Auk*, 128(4):737-745.	Additional Manipulations Conducted
Beissinger SR (1990). Experimental Brood Manipulations and the Monoparental Threshold in Snail Kites. *American Naturalist*, 136(1):20-38.	Extractions Not Possible
Bowers EK, Nietz D, Thompson CF, Sakaluk SK (2014). Parental Provisioning in House Wrens: Effects of Varying Brood Size and Consequences for Offspring. *Behavioral Ecology*, 25(6):1485-1493.	No Control
Cauchard L, Angers B, Boogert NJ, Lenarth M, Bize P, Doligez B, et al. (2017). An Experimental Test of a Causal Link Between Problem-Solving Performance and Reproductive Success in Wild Great Tits. *Frontiers in Ecology and Evolution*, 5.	No Brood size manipulation Related Provisioning Data
Conrad KF, Robertson RJ (1993). Patterns of Parental Provisioning by Eastern Phoebes. *Condor*, 95(1):57-62.	Extractions Not Possible
Cucco M, Malacarne G (1995). Increase of Parental Effort in Experimentally Enlarged Broods of Pallid-Swifts. *Canadian Journal of Zoology*, 73(8):1387-1395.	Non-Random Brood size manipulation
Dykstra CR, Karasov WH (1993). Nesting Energetics of House Wrens (*Troglodytes aedon*) in Relation to Maximal Rates of Energy-Flow. *Auk*, 110(3):481-491.	Additional Manipulations Conducted

Edge KA, Jamieson IG, Darby JT (1999). Parental Investment and the Management of an Endangered Penguin. *Biological Conservation*, 88(3):367-378.	No Provisioning Data
Emaresi G, Bize P, Altwegg R, Henry I, Van Den Brink V, Gasparini J, Roulin A (2014). Melanin-Specific Life-History Strategies. *American Naturalist*, 183(2):269-280.	No Brood size manipulation Related Provisioning Data
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Fokkema RW, Ubels R, Tinbergen JM (2016). Great Tits Trade Off Future Competitive Advantage for Current Reproduction. *Behavioral Ecology*, 27(6):1656-1664.	Additional Manipulations Conducted
Galbraith H (1983). The Diet and Feeding Ecology of Breeding Kittiwakes (*Rissa tridactyla*). *Bird Study*, 30:109-120.	No Brood size manipulation Related Provisioning Data
Gebczynski A, Taylor JRE, Konarzewski M (1996). Growth of Dovekie (*Alle alle*) Chicks Under Conditions of Increased Food Demand at the Nest: Two Field Experiments. *Canadian Journal of Zoology*, 74(6):1076-1083.	No Provisioning Data
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Gori DF (1988). Adjustment of Parental Investment with Mate Quality by Male Yellow-Headed Blackbirds (*Xanthocephalus xanthocephalus*). *Auk*, 105(4):672-680.	No Control Group

Gow EA, Wiebe KL, Musgrove A (2015). Nest Sanitation in Response to Short- and Long-Term Changes of Brood Size: Males Clean More in a Sex-Role-Reversed Species. *Animal Behaviour*, 104:137-143.	No Brood size manipulation Related Provisioning Data
Green DJ, Ydenberg RC (1994). Energetic Expenditure of Male Ospreys Provisioning Natural and Manipulated Broods. *Ardea*, 82(2):249-262.	Extractions Not Possible
Gustafsson L, Qvarnstrom A, Sheldon BC (1995). Trade-Offs between Life-History Traits and a Secondary Sexual Character in Male Collared Flycatchers. *Nature*, 375(6529):311-313.	No Provisioning Data
Hainstock MH, Smith MC, Carr J, Shutler D (2010). Parental Investment and Brood Value in Tree Swallows, *Tachycineta bicolor*. *Behaviour*, 147(4):441-464.	Extractions Not Possible
Hario M (2001). Chick Growth and Nest Departure in Baltic Black Guillemots *Cepphus grylle*. *Ornis Fennica*, 78(3):97-108.	Non-Random Brood size manipulation
Heaney V, Monaghan P (1995). A Within-Clutch Trade-Off Between Egg-Production and Rearing in Birds. *Proceedings of the Royal Society B-Biological Sciences*, 261(1362):361-365.	No Control
Heaney VF (1997). Within Brood Trade-Offs in Reproductive Effort: An Experimental Study on the Common Tern *Sterna hirundo*. PhD thesis. Available: https://theses.gla.ac.uk/71774/	Non-Random Brood size manipulation / Additional Manipulations
Hebert PN, McNeil R (1999). Hatching Asynchrony and Food Stress in Ring-Billed Gulls: An Experimental Study. *Canadian Journal of Zoology*, 77(4):515-523.	No Brood size manipulation
Hegner RE, Wingfield JC (1987). Effects of Brood-Size Manipulations on Parental Investment, Breeding Success, and Reproductive Endocrinology of House Sparrows. *Auk*, 104(3):470-480.	Extractions Not Possible

Hinde CA, Kilner RM (2006). Negotiations within the Family over the Supply of Parental Care. *Proceedings of the Royal Society B-Biological Sciences*, 274(1606):53-60.	No Control
Ibáñez-Álamo JD, Arco L, Soler M (2012). Experimental Evidence for a Predation Cost of Begging Using Active Nests and Real Chicks. *Journal of Ornithology*, 153(3):801-807.	No Control Group
Jelinek V, Pozgayova M, Honza M, Prochazka P (2016). Nest as an Extended Phenotype Signal of Female Quality in the Great Reed Warbler. *Journal of Avian Biology*, 47(3):428-437.	No Brood size manipulation
Jones G (1987). Parent-Offspring Resource-Allocation in Swallows during Nestling Rearing - an Experimental-Study. *Ardea*, 75(2):145-168.	Extractions Not Possible
Klemp S (2000). Effects of Parental Effort on Second Brood, Moult and Survival in the Grey Wagtail *Motacilla cinerea*. *Ardea*, 88(1):91-98.	No Control Group
Komdeur J, Wiersma P, Magrath M (2002). Paternal Care and Male Mate-Attraction Effort in the European Starling is Adjusted to Clutch Size. *Proceedings of the Royal Society B-Biological Sciences*, 269(1497):1253-1261.	Non-Random Brood size manipulation
Leffelaar D, Robertson RJ (1986). Equality of Feeding Roles and the Maintenance of Monogamy in Tree Swallows. *Behavioral Ecology and Sociobiology*, 18(3):199-206.	Extractions Not Possible
Leonard ML, Horn AG, Gozna A, Ramen S (2000). Brood Size and Begging Intensity in Nestling Birds. *Behavioral Ecology*, 11(2):196-201.	Additional Manipulations Conducted
Lifjeld JT, Slagsvold T (1991). Sexual Conflict Among Polygynous Pied Flycatchers Feeding Young. *Behavioral Ecology*, 2(2):106-115.	Additional Manipulations Conducted

Lozano GA, Lemon RE (1998). Parental-Care Responses by Yellow Warblers (*Dendroica petechia*) to Simultaneous Manipulations of Food Abundance and Brood Size. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, 76(5):916-924.	No Control
Lucass C, Korsten P, Eens M, Muller W (2016). Within-Family Parent-Offspring Co-Adaptation in a Wild Bird: On Static Traits, Behavioural Reaction Norms, and Sex Differences. *Functional Ecology*, 30(2):274-282.	No Brood size manipulation
Mariette MM, Griffith SC (2015). The Adaptive Significance of Provisioning and Foraging Coordination Between Breeding Partners. *American Naturalist*, 185(2):270-280.	No Brood size manipulation Related Provisioning Data
Martins TLF (1997). Fledging in the Common Swift, *Apus apus*: Weight-Watching with a Difference. *Animal Behaviour*, 54:99-108.	No Provisioning Data
Martins TLF, Wright J (1996). Cost of Reproduction and Allocation of Food Between Parent and Young in the Swift (*Apus apus*). *Behavioral Ecology*, 4(3):213-223.	Extractions Not Possible
Martins TLF, Wright J (). Brood Reduction in Response to Manipulated Brood Sizes in the Common Swift (*Apus-Apus*). *Behavioral Ecology And Sociobiology,* 32(1):61-70.	Extractions Not Possible
Moreno J (1987). Parental Care in the Wheatear *Oenanthe oenanthe* - Effects of Nestling Age and Brood Size. *Ornis Scandinavica*, 18(4):291-301.	Extractions Not Possible
Murphy MT, Armbrecth B, Vlamis E, Pierce A (2000). Is Reproduction by Tree Swallows Cost Free? *Auk*, 117(4):902-912.	Extractions Not Possible

Musgrove AB, Wiebe KL (2014). Northern Flickers Increase Provisioning Rates to Raise More but Poorer Quality Offspring When Given Experimentally Enlarged Broods. *Auk,* 131(4):571-582.	Extractions Not Possible
Nur N (1984). Feeding Frequencies of Nestling Blue Tits (*Parus caeruleus*): Costs, Benefits and a Model of Optimal Feeding Frequency. *Oecologia*, 65(1):125-137.	Extractions Not Possible
Olsen J, Tucker AD (2003). A Brood-Size Manipulation Experiment with Peregrine Falcons, *Falco peregrinus*, near Canberra. *Emu*, 103(2):127-132.	Extractions Not Possible
Ostreiher R, Heifetz A (2015). The Blessing of Having Younger Nestmates: The Case of the Arabian Babbler. *Behavioral Ecology*, 27(2):393-400.	No Brood size manipulation
Patterson CB, Erckmann WJ, Orians GH (1980). An Experimental-Study of Parental Investment and Polygyny in Male Blackbirds. *American Naturalist*, 116(6):757-769.	Extractions Not Possible
Pryke SR, Griffith SC (2009). Socially Mediated Trade-Offs Between Aggression and Parental Effort in Competing Color Morphs. *American Naturalist*, 174(4):455-464.	Extractions Not Possible
Przybylo R, Merilä J (2000). Intersexual Niche Differentiation in the Blue Tit (*Parus caeruleus*). *Biological Journal of the Linnean Society*, 69(2):233-244.	No Control
Ridenour M (2020). Insulin-Like Growth Factor 1 and the Hormonal Mediation of Sibling Rivalry in Eastern Bluebirds (*Sialia sialis*).	Additional Manipulations Conducted
Roulin A, Ducrest AL, Dijkstra C (1999). Effect of Brood Size Manipulations on Parents and Offspring in The Barn Owl Tyto Alba. *Ardea*, 87(1):91-100.	No Control Group

Rytkonen S (1995). Parental Care in the Willow Tit (*Parus montanus*): Nest Defence and Nestling Provisioning in the Light of the Parental Investment Theory. *Acta Universitatis Ouluensis Series A Scientiae Rerum Naturalium*:1-37.	Extractions Not Possible
Saino N, Calza S, Moller AP (1997). Immunocompetence of Nestling Barn Swallows in Relation to Brood Size and Parental Effort. *Journal of Animal Ecology*, 66(6):827-836.	No Control
Saino N, Ninni P, Incagli M, Calza S, Sacchi R, Moller AP (2000). Begging and Parental Care in Relation to Offspring Need and Condition in the Barn Swallow (*Hirundo Rustica*). *American Naturalist*, 156(6):637-649.	Additional Manipulations Conducted
Sendecka J, Cichon M, Gustafsson L (2007). Age-Dependent Reproductive Costs and the Role of Breeding Skills in the Collared Flycatcher. *Acta Zoologica,* 88(2):95-100.	No Provisioning Data
Shutler D, Clark RG, Fehr C, Diamond AW (2006). Time and Recruitment Costs as Currencies in Manipulation Studies on the Costs of Reproduction. *Ecology*, 87(11):2938-2946.	Extractions Not Possible
Siefferman L, Hill GE (2005). Male Eastern Bluebirds Trade Future Ornamentation for Current Reproductive Investment. *Biology Letters*, 1(2):208-211.	No Control
Siefferman L, Hill GE (2007). The Effect of Rearing Environment on Blue Structural Coloration of Eastern Bluebirds (*Sialia sialis*). *Behavioral Ecology and Sociobiology*, 61(12):1839-1846.	No Control
Simmons R (1986). Food Provisioning, Nestling Growth and Experimental Manipulation of Brood Size in the African Redbreasted Sparrowhawk Accipiter-Rufiventris. *Ornis Scandinavica,* 17(1):31-40.	No Brood size manipulation
Slagsvold T, Rohwer S (2000). Sexual Conflict in Birds with Biparental Care: Should a Parent Desert a Brood with Low Reproductive Value? *Ornis Norvegica*, 23(1):38-49.	No Control

Tolonen P, Korpimäki E (1996). Do Kestrels Adjust Their Parental Effort to Current or Future Benefit in a Temporally Varying Environment? *Ecoscience*, 3(2):165-172.	No Control
Verhulst S, Tinbergen JM (1997). Clutch Size and Parental Effort in the Great Tit (*Parus Major)*. *Ardea,* 85(1):111-126.	N=1 Brood size manipulation
Westneat DF, Mutzel A, Bonner S, Wright J (2017). Experimental Manipulation of Brood Size Affects Several Levels of Phenotypic Variance in Offspring and Parent Pied Flycatchers. *Behavioral Ecology and Sociobiology*, 71(6).	No Control
Whittingham LA (1989). An Experimental-Study of Paternal Behavior in Red-Winged Blackbirds. *Behavioral Ecology and Sociobiology,* 25(1):73-80.	No Brood size manipulation Related Provisioning Data
Wiersma P, Tinbergen JM (1993). No Nocturnal Energetic Savings in Response to Hard Work in Free-Living Great Tits. *Netherlands Journal of Zoology*, 52(2):263-279.	No Control
Williams JB (1987). Field Metabolism and Food Consumption of Savannah Sparrows during the Breeding Season. *Auk*, 104(2):277-289.	Extractions Not Possible
Wright J, Both C, Cotton PA, Bryant D (1998). Quality vs. Quantity: Energetic and Nutritional Trade-Offs in Parental Provisioning Strategies. *Journal of Animal Ecology*, 67(4):620-634.	Extractions Not Possible
Wright J, Cuthill I (1989). Biparental Care: Short-Term Manipulation of Partner Contribution and Brood Size in the Starling, *Sturnus vulgaris*. *Behavioral Ecology*, 1(2):116-124.	Additional Manipulations Conducted
Wright J, Hinde C, Fazey I, Both C (2003). Begging Signals More Than Just Short-Term Need: Cryptic Effects of Brood Size in the Pied Flycatcher (*Ficedula hypoleuca*). *Behavioral Ecology and Sociobiology*, 52(1):74-83.	No Control

Table S2.3: An overview of the information extracted from each article included in this meta-analysis. See data available on OSF at the following link for the full dataset used: https://osf.io/cxhtw/?view_only=4a3356ecb94b432a96d9ff31ed592ddc

Column Heading	**Details**
StudyID	Represents the record number of that study in the EndNote library used for management of all studies included in this meta-analysis.
Author	Family name of author(s) for that study. We recorded the family names for up to 2 authors (e.g., Berzins&Dawson), but if the study had more than 2 authors, we recorded the family name of the first author followed by et al (e.g., Baldan et al).
Year	Year of study publication. Recorded as YYYY format.
FocalSpC	Common name of the species investigated in that study. Recorded in sentence case and as plurals e.g., Eastern phoebes not Eastern Pheobe.
FocalSpL	Latin name of the species investigated in that study. Recorded in sentence case e.g., Sayornis phoebe.
Treatment	Treatment conducted in that study i.e., experimental brood enlargement or experimental brood reduction. This was recorded as ‘enlarged’ for brood enlargements, or ‘reduced’ for brood reductions.
Treatment(details)	Number of eggs or nestlings added or removed as a short sentence/phrase. For example, “remove x eggs” or “add 2 nestlings” according to what was conducted in the study. This information is also reflected in other columns i.e., Treatment (for whether eggs/nestlings were added or removed), and Treatment_stage (for egg or nestling, see below)
Fixed_Variable_Manip	Whether the experimental manipulation conducted involved a fixed number of additions/removals at each nest, or a variable number of additions/removals depending on the natural characteristics of each nest. For example, many studies removed 2 nestlings from all nests and recorded the brood size created, but some removed either 1 or 2 nestlings to instead create broods of a specific size. In the latter case, even though the magnitude of manipulation was non-random, the selection of nests and assignment to enlargement or reduction treatments was random.
Treatment_CONT	The number of eggs/nestlings added/removed as a numerical value. If a variable number of eggs/nestlings were added/removed, the average value was recorded. For example, if Treatment(details) recorded “remove 2-3 nestlings” then 2.5 was recorded in this column.
ManipDay	Day (post-hatch) on which manipulations were conducted (recorded as integer value). Pre-hatch manipulations of clutch size were recorded as 0 e.g., studies which added/removed eggs instead of nestlings.
Control(details)	Recorded as TRUE (for a true control) or FALSE. A true control was one in which the control nests were handled in the same manner and at the same regularity as the treatment nests. For example, nestlings or eggs may have

	been swapped for control nests while keeping the brood/clutch size unchanged. FALSE indicates that unmanipulated nests served as controls.
Control_broodsize	Average control brood (or clutch) size recorded as a numerical value. This information was recorded from the study when available, otherwise, it was extracted from Cornell All About Birds (Ornithology, 2019).
SourceOfBS	Source of control_broodsize information i.e., 'study' for if this information was reported in the study itself, 'prev study' if this information was recorded based on what was presented in a different study on the same species, or cornell if this information was recorded from Cornell All About Birds.
Treatment_stage	Stage at which the manipulation was conducted i.e., 'egg' if eggs were added/removed, or 'nestling' if nestlings were added/removed.
Treat_dur_min	Minimum number of days between manipulation and behavioural observations.
Treat_dur_max	Maximum number of days between manipulation and behavioural observations. This was recorded as 'NA' when the Treat_dur_min was equal to Treat_dur_max.
TreatDurCat	Treatment duration categorised into either 'long' term or 'short' term. This was based on Treat_dur_min and Treat_dur_max; where behavioural observations occurred only on the same day as the manipulation the study duration category was recorded as 'short' but where observations were made repeatedly across the breeding period it was recorded as 'long.' *
SubjectID	Where the same individuals were used for multiple experimental treatments (e.g., the same control nests for enlarged and reduced treatments) the same subject ID was used to avoid pseudo replication. This was typical in studies which performed both experimental brood enlargements (at some nests) and brood reductions (at other nests) but had one common control group against which both treatment groups were compared i.e., 42/52 studies.
RespCat	Response variable investigated in that study categorised as either feeding rate (FeedingRate), visit rate (VisitRate) used by some studies as a proxy for feeding rate, or load size (LoadSize). Some were also at the nestling level i.e., FeedingRatePerNestling and VisitRatePerNestling.
ResponseVar	Details of the measured provisioning response of the parents, within each response category i.e., feeds/visits per unit time, IVI, prey size, load size
Effort_level	Whether the parental effort was at the level of the nest (recorded as 'parental') or at the level of the nestling ('nestlinglevel') e.g., a RespCat (above) of FeedingRate was recorded as 'parental' while FeedingRatePerNestling was recorded as 'nestlinglevel.'
StudyDesign	Whether the study was conducted within or among individuals. Some studies conducted within subject manipulations, for example measuring the feeding rate to the nest before adding/removing nestlings (as the control) and then again after adding/removing nestlings at the same nest; these were recorded as 'within.' Other (most) studies conducted among-subject manipulations with some nests acting as control nests and some as treatment nests throughout the study period (recorded as 'among').

Nind_control	Number of provisioning parents total across all control nests i.e., for biparental care species, 2 per nest; for uniparental care, 1 per nest. For species with uniparental care or in species where sex of provisioning parent cannot be teased apart (e.g., due to division of labour like in Peregrine falcons) Nind_control is equal to Nnests_control (below).
Nnests_control	Total number of control nests.
Nind_treat	Number of provisioning parents across all nests for that treatment group (see 'Treatment' above). As with Nind_control, nest. For species with uniparental care or in species where sex of provisioning parent cannot be teased apart Nind_treat is equal to Nnests_treat (below).
Nnests_treat	Total number of nests to which that treatment was applied i.e., in rows recorded as 'enlarged' in the Treatment column (see above) this is the number of nests at which brood enlargement occurred.
Sex	Sex of provisioning parent i.e., male, female or both (where the study reported total feeding rate irrespective of parental sex, for example)
ES_flip	We wanted positive effect sizes to reflect a change in the direction predicted by theory. We marked rows which needed to be 'flipped' (to make their effect positive if aligning with theory) with a -1, and those which didn't need to be flipped with a 1. For example, inter-visit intervals (IVIs) are predicted to decrease at the level of the nest (reflecting an increase in provisioning rate) as brood demand increases (via brood enlargement) so we flipped rows meeting this criterion so that a decrease in IVI at an enlarged brood would be presented as a positive effect size.
Direct	Whether information needed to calculate mean, SE and/or SD was available from raw data associated with the study (e.g., data from the study provided in an online repository) recorded as 'yes' or 'no.'
Control_Mean	Mean estimate for control group
Control_SD	Standard deviation (SD) and standard error (SE) for the control group. When it was only possible to extract one of these from the study (e.g., from a figure using WebPlotDigitizer, or from results text) so we calculated the other using the equation $SE = SD/\sqrt{N}$, where N = number of nests (i.e., Nnests_control, see above)
Control_SE	
Treatment_Mean	Mean estimate for the treatment group
Treatment_SD	Standard deviation (SD) and standard error (SE) for the relevant treatment group. When it was only possible to extract one of these from the study (e.g., from a figure using WebPlotDigitizer, or from results text) so we calculated the other using the equation $SE = SD/\sqrt{N}$, where N = number of nests (i.e., Nnests_treat, see above)
Treatment_SE	
Notes	Any additional notes relevant to data extraction e.g., which figures (and/or parts of figures) data was extracted from and exactly what data was extracted from that figure (i.e., mean and SE or mean and SD etc.)

*It should be noted that all ‘short’ term studies were also those conducted at the within-individual level (see ‘StudyDesign’) with complete overlap between the two (i.e., all within-individual studies were short-term and all short-term studies were at the within-individual level). Thus, ‘TreatDurCat’ is equivalent to ‘StudyDesign’ in this review.

Table S2.4: Data sources for life-history data (including references cited in Birds of the World, Cornell, when data was collected from there or alternative references where data was not available from Cornell). Column names match those used in R code used in analyses (available at: https://osf.io/cxhtw/?view_only=4a3356ecb94b432a96d9ff31ed592ddc). FocalSpC = common name of focal species; Latin_Name = Latin binomial of focal species; Age_at_first_repo(years) = average age at which focal species first reproduces (in years); Lifespan_ave(years) = average lifespan of focal species, from hatch to death (in years); AccordingToBirdsOfTheWorldByCornell = details relating to lifespan and/or reproductive behaviour for the focal species provided on Cornell Birds of the World (when this information was available from there); LifespanRef = source of information in previous columns (i.e., reproductive age, lifespan).

FocalSpC	**Latin_Name**	**Age_at_first_repo(years)**	**Lifespan_ave(years)**	**AccordingToBirdsOfTheWorldByCornell**	**LifespanRef**
Tree swallows	Tachycineta bicolor	1	2.7	Tree Swallows have a maximum lifespan of 8 to 12 years, with about 20% surviving their first year. Annual adult survival rates range from 13% to 51%, with most estimates falling between 40% and 50%. Aging and senescence affect reproductive output, with telomere length in one-year-old females correlating strongly with future survival probability, suggesting a genetic component to lifespan.	Winkler, D. W., K. K. Hallinger, D. R. Ardia, R. J. Robertson, B. J. Stutchbury, and R. R. Cohen (2020). Tree Swallow (Tachycineta bicolor), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.login.ezproxy.library.ualberta.ca/10.2173/bow.treswa.01
Eurasian Treecreepers	Certhia familiaris	1	2	Not available on Cornell Birds of the World	https://www.bto.org/understanding-birds/birdfacts/treecreeper
Great tits	Parus major	1	2.5	Not available on Cornell Birds of the World	https://www.worldlifeexpectancy.com/bird-life-expectancy-great-tit

Eastern phoebes	Sayornis phoebe	1	3.5	After their first year, birds typically exhibit an annual survival rate of at least 40%. It's not unusual to find adults aged 3-4 years (HPW), with the longest recorded lifespan being 10.3 years.	Weeks Jr., H. P. (2020). Eastern Phoebe (Sayornis phoebe), version 1.0. In Birds of the World (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.login.ezproxy.library.ualberta.ca/10.2173/bow.easpho.01
American kestrels	Falco sparverius	1	2.25	Assessing survival rates is complicated due to challenges in distinguishing mortality from other factors. Estimated first-year mortality of 62.9% for kestrels and an average annual adult mortality of 57.1%. Estimated annual mortality rates of 69% for juveniles and 45% for adults. The oldest wild American Kestrel lived to 11 years and 7 months, while captive individuals have survived up to 14 years on average.	Smallwood, J. A. and D. M. Bird (2020). American Kestrel (Falco sparverius), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.login.ezproxy.library.ualberta.ca/10.2173/bow.amekes.01
Eurasian Kestrels	Falco tinnunculus	1	16	First-year mortality ranges from approximately 50% to 70%, while mortality in subsequent years is about 30% to 40%. The oldest recorded bird lived to be 16 years old.	delHoyo, J., A. Elliot, and J. Sargatal, eds. 1992. Handbook of Birds of the World, Vol. 1. Barcelona: Lynx Edicions.
Blue tits	Cyanistes caeruleus	0.9	3	Juvenile mortality peaks at about 70% between fledging and November. Many breed in their first year. Around 75% of breeding pairs survive to the following season, with some remaining together for up to four successive years. Suburban pairs are generally less productive due to lower-quality available food. The maximum recorded lifespan is 12 years and 4 months.	https://app.bto.org/birdfacts/results/bob14620.htm

Northern flickers	Colaptes auratus	1	9.2	Survivorship in this woodpecker species tends to be lower compared to others. Banding and recovery data from a central British Columbia study revealed the oldest male was 10 years old, and the three oldest females were 9 years old. The maximum recorded longevity is 9 years and 2 months. Adult survivorship is estimated at 0.43, with an apparent survival rate of 0.47 from another study, although this estimate has limited reliability due to small sample size. Factors influencing survival include climatic patterns like the North Atlantic Oscillation, while survival rates for juveniles remain uncertain due to dispersal patterns and lack of recovery data in their first year.	http://www.biokids.umich.edu/critters/Colaptes_auratus/
Collared flycatchers	Ficedula albicollis	1	3.5	Not available on Cornell Birds of the World	http://uu.diva-portal.org/smash/get/diva2:170007/FULLTEXT01
Fairy martins	Hirundo ariel	0.9	4.5	Not available on Cornell Birds of the World	https://www.hww.ca/en/wildlife/birds/purple-martin.html#:~:text=Banding%20has%20also%20provided%20information,recaptured%20at%20its%20breeding%20colony.
White-rumped swallow?	Tachycineta leucorrhoa	1	2.21	Not available on Cornell Birds of the World	Built, F (2011). Apparent survival and return rate of breeders in the southern temperate White-rumped Swallow (*Tachycineta leucorrhoa)*. *The International Journal of Avian Science*, 153(1), 198-194. DOI: 10.1111/j.1474-919x.2010.01079.x

Eastern kingbirds	Tyrannus tyrannus	1	2.5	Survivorship studies in both central New York and eastern Oregon suggest that approximately two-thirds of Eastern Kingbirds survive annually. While detectability of these birds is high, around 90% for males and 84% for females, survival estimates remain consistent across different methods. Interestingly, blood sampling for parentage analyses does not negatively impact survival, and females bled for this purpose actually exhibit slightly better survival rates. In central New York, most individuals live for just 2 years, with females typically having slightly lower survival rates than males, possibly due to reproductive costs. However, those females that survive to a second breeding season tend to live longer, with a lifespan of around 4 to 5 years being common. Juvenile survival rates are challenging to measure due to low natal philopatry in some areas, but estimates in eastern Oregon suggest a minimum survival rate of around 29.1%.	Murphy, M. T. and P. Pyle (2020). Eastern Kingbird (Tyrannus tyrannus), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.login.ezproxy.library.ualberta.ca/10.2173/bow.easkin.01
European Pied flycatcher	Ficedula hypoleuca	1	2	Oldest ringed individual 15 years; annual mortality of first-years 73% (53% for older birds).	https://app.bto.org/birdfacts/results/bob13490.htm

Marsh tits	Parus palustris	1	5	Not available on Cornell Birds of the World	https://plantura.garden/uk/garden-birds/marsh-tit
Willow tits	Parus montanus	1	3	Not available on Cornell Birds of the World	https://app.bto.org/birdfacts/results/bob14420.htm
Barn swallows	Hirundo rustica	1	4	The Barn Swallow holds a longevity record of 15 years and 11 months. In Nebraska, annual adult survival estimates over a 15-year period averaged 35%, with no significant difference between male and female survival rates, while in Denmark, males exhibited slightly higher survival rates than females, with female survival showing more variability.	https://www.hww.ca/en/wildlife/birds/barn-swallow.html#:~:text=Although%20the%20average%20lifespan%20of,16%20years%20have%20been%20observed.
Brown pelicans	Pelecanus occidentalis	3	20	There are no reliable estimates for age-specific survival rates; however, based on band recoveries, it's indicated that approximately 30% of individuals survive their first year, and less than 2% survive beyond the age of 10, with a recorded maximum lifespan of 43 years.	https://seaworld.org/animals/facts/birds/brown-pelican/
Lesser elaenia	Elaenia chiriquensis	1.1	3.8	Not available on Cornell Birds of the World	Guaraldo AC, Bravo SP, Bridge E and Marini, MA (2021). Longitudinal and Cyclic Poleward Migration of a South American Intra-Tropical Migrant Flycatcher, The Lesser Alaenia (*Elaenia Chiriquensis*). *Ornitologia Neotropical*. 32:97-105
Spotted antbirds	Hylophylax naevioides	1.2	4.9	The maximum observed lifespan recorded was 14 years and 7 months in an adult male, while two other adult males lived for 13 years and 6 months and 13 years and 5 months.	https://doi.org/10.1093/beheco/11.6.648

Red-flanked bluetail	Tarsiger cyanurus	1	2.5	Not available on Cornell Birds of the World	https://birdfact.com/birds/red-flanked-bluetail
Collared flycatchers	Ficedula albicollis	1	2	About 90% of eggs hatch, with 85% of hatchlings successfully fledging, resulting in an overall success rate of 77%. Predation by forest dormice (Dryomys nitedula) is the primary cause of chick loss in Ukrainian nests. Typically, these birds breed at one year of age, with the oldest recorded individual being 7 years and 11 months old.	https://app.bto.org/birdfacts/results/bob13490.htm
Cattle egrets	Bubulcus ibis	2	10	The oldest recorded Cattle Egrets from band recoveries include individuals aged 23 years in South Africa, 17 years in North America, and 11.1 years in Australia. While the maximum lifespan remains unknown, only a small percentage of banded birds recovered are older than 7–8 years. Survivorship patterns indicate highest mortality among juveniles, followed by a gradual decrease in mortality with age. However, compared to other Ardeids, Cattle Egrets exhibit lower juvenile mortality rates. Despite variations in fledgling production and juvenile mortality across regions, Cattle Egrets demonstrate high adaptability and long-term survival.	https://birdfact.com/birds/cattle-egret#:~:text=The%20average%20lifespan%20of%20a,recorded%20as%20surviving%20substantially%20longer.

Great skuas	Catharacta skua	5.3	11	Sexual maturity on average at eight years (5–12); adult survival 90% (Shetland).	https://nora.nerc.ac.uk/id/eprint/526491/1/bulletin15_03.pdf
Tawny owls	Strix aluco	1.5	5	In a study in Belgium, out of 256 eggs laid, 24% failed to hatch, while 94% of the 195 hatched young fledged successfully. First-year mortality rates in Sweden were 71%, declining to 44% in the second year and 48% in the third. Switzerland reported a first-year mortality rate of 49%, decreasing to 25% in subsequent years. In the UK, productivity initially increased with age for males up to 3 years and females up to 9 years before declining. Denmark observed juvenile predation by mammals post-fledging and by raptors about two months later, with breeding typically starting between 1 to 2 years and the oldest recorded bird being 18 years and 10 months.	https://a-z-animals.com/animals/tawny-owl/
Red-tailed tropicbirds	Phaethon rubricauda	3.8	19.5	The oldest banded bird on record lived for 32 years and 8 months, but aluminum bands typically wear out after 13 to 15 years, leading to band loss issues. Among 719 band recoveries of adult birds reported to the US Fish and Wildlife Service Bird Banding Lab, 1% were 20 years or older, 5% were 10 years or older, and 9% were over 8 years old. Data from band recaptures on Johnston Atoll between 1984 and 2003 show that 45%	https://www.worldlifeexpectancy.com/bird-life-expectancy-red-tailed-tropicbird

				of the population is over 5 years old, with 9.5% being 10 years or older.	
Red-winged blackbirds	Agelaius phoeniceus	1.5	2.14	The oldest recorded Red-winged Blackbird lived to at least 15 years and 9 months, with another male reaching 14 years and 5 months. Annual adult survival rate remains consistent across ages, estimated between 42.1% to 62.0%, with a mean life expectancy of 2.14 years and no discernible differences between sexes.	Yasukawa, K. and W. A. Searcy (2020). Red-winged Blackbird (Agelaius phoeniceus), version 1.0. In Birds of the World (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi-org.login.ezproxy.library.ualberta.ca/10.2173/bow.rewbla.01
Spotless starlings	Sturnus unicolor	1	1.57	Not available on Cornell Birds of the World	Kauzálová, T., Tomášek, O., Mulder, E., Verhulst, S. and Albrecht, T., 2022. Telomere length is highly repeatable and shorter in individuals with more elaborate sexual ornamentation in a short-lived passerine. Molecular Ecology, 31(23), pp.6172-6183.

Table S2.5: The 10 highest sign-adjusted Hedges' g values (G_flip) and associated variance (vi) from our data set in order from highest to lowest (Order; 1 = highest, 10 = lowest of the 10), with Study ID (i.e., unique study identifier) and first author family name (Author).

Order	**Study ID**	**Author**	**G_flip**	**vi**
1	60	Ardia	6.178651	0.699744
2	60	Ardia	5.853459	0.64046
3	60	Ardia	4.948396	0.492333
4	1923	Sousa&Marini	3.1939	0.517127
5	1894	Smith et al	2.845341	0.387206
6	60	Ardia	2.357643	0.205543
7	1364	Moreno et al	1.825483	0.944366
8	1805	Schreiber	1.737018	0.420658
9	1923	Sousa&Marini	1.669731	0.27172
10	1731	Rythonen et al	1.626598	0.241951

Table S2.6: The comparison of model results with and without Ardia, 2007 (Study ID 60). Model estimates (estimate), associated standard error (se), 95% credible intervals (lower CI, upper CI), and p-values (p-value) for the model containing all estimates, and the model without Ardia, 2007 (Study ID 60).

Models		**estimate**	**se**	**lower CI**	**upper CI**	**p-value**
All estimates	Intercept (i.e., enlarged treatment)	0.3969	0.0656	0.2678	0.5261	<0.0001
	Reduced treatment	0.0641	0.0551	-0.0444	0.1726	0.2458
	(Interaction) Enlarged:Breeding Years (scaled)	0.0633	0.0524	-0.0398	0.1664	0.2279
	(Interaction) Reduced: Breeding Years (scaled)	0.0181	0.057	-0.0941	0.1303	0.7512
Without Study ID 60	Intercept (i.e., enlarged treatment)	0.3599	0.0526	0.2564	0.4634	<0.0001
	Reduced treatment	0.068	0.0533	-0.037	0.173	0.2033
	(Interaction) Enlarged:Breeding Years (scaled)	0.0716	0.0443	-0.0155	0.1587	0.1067
	(Interaction) Reduced: Breeding Years (scaled)	0.0231	0.0511	-0.0775	0.1236	0.6521

Supplementary figures

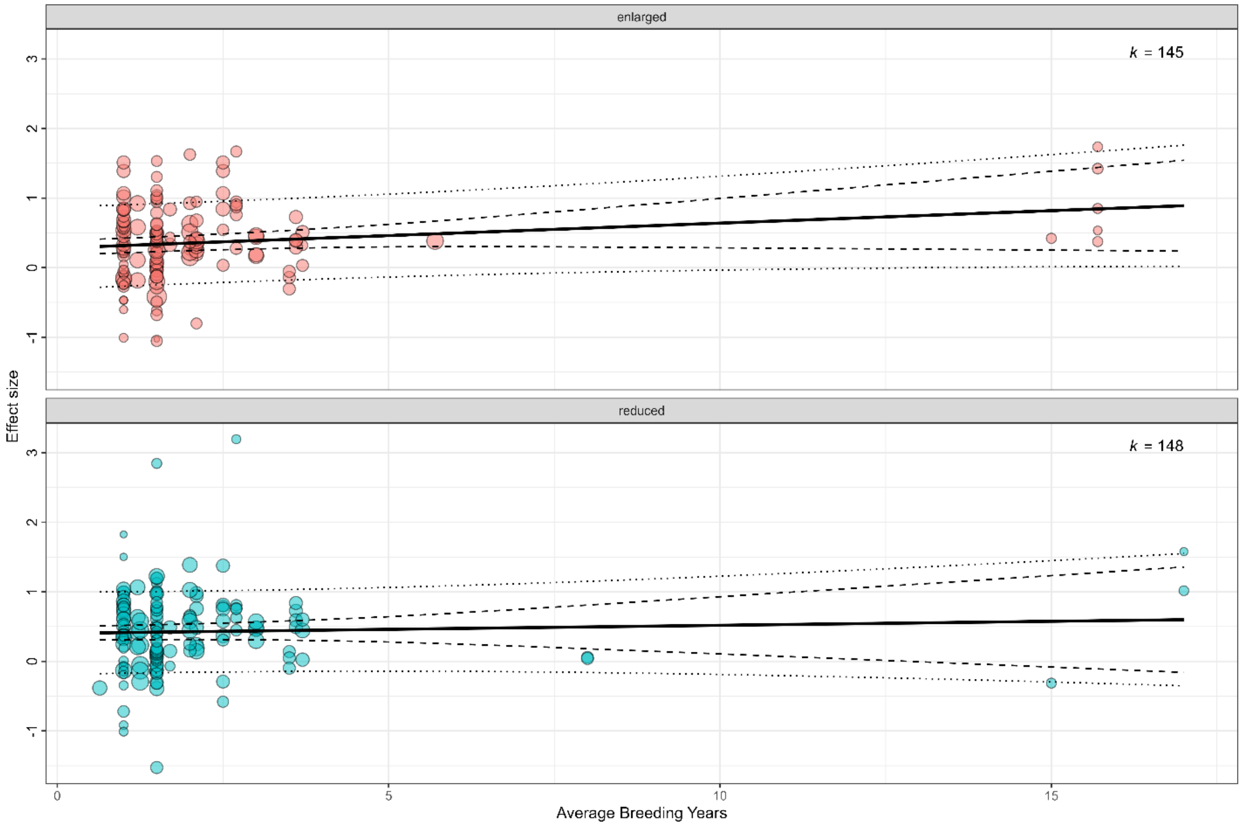

Figure S2.1: The recreation of Figure 5 from main manuscript without Ardia, 2007 (Study ID 60). An orchaRd bubble plot of meta-analytic mean effect sizes, standardised mean difference (SMD, Hedges' g) across average number of breeding years (raw, unscaled), separated by treatment group (enlarged, blue or reduced, red). Regression is presented as a solid black line. Inner dotted lines depict 95% confidence intervals and outer dotted lines 95% prediction intervals. Total number of estimates (k) is presented on the left of each plot panel. Effect sizes are weighted by their precision (1/standard error, SE).

Appendix B: ESM for Chapter 3

Supplementary figures

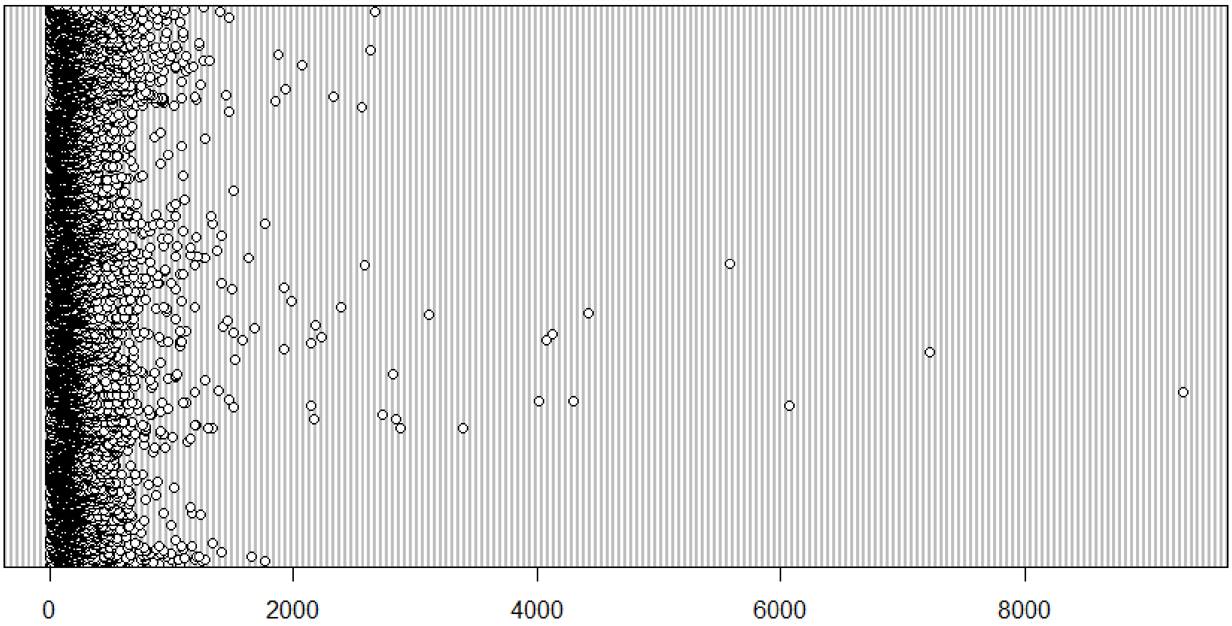

Figure S3.1: *A dotchart showing the distribution of IVI (untransformed) across all 7 study years. A cut-off of 4000 minutes was set when determining outliers, resulting in the exclusion of 9 datapoints.*

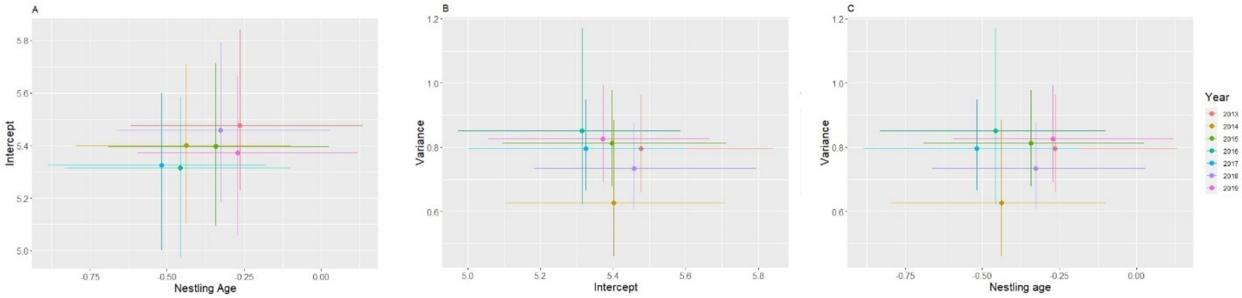

Figure S3.2: *Figures showing the covariances between intercept, slope and variance in logIVI across 7 study years (means and 95% credible intervals are reported). (a) There was a weak, positive covariance between intercept and slope generated by increasing nestling age, (b) a moderate, negative covariance between intercept and variance, and (c) no evidence of covariance between slope and variance.*

Appendix C: ESM for Chapter 4

Supplementary tables

Table S4.1: *2 nest sites in 2016 for which weight measurements were not recorded due to site locations being impossible to access at the necessary regularity for inclusion as controls in the supplementation experiment (i.e., only by helicopter) but at which nest cameras were placed allowing for collection of IVI data.*

Year	**Site**	**Comments**
2016	145	Clutch size, 4. Number hatched, 3. Number surviving to assumed fledging/camera removal (Aug 9), 2
2016	30	Clutch size, 4. Number hatched, 4. Number surviving to assumed fledging (Aug 30), 2

Table S4.2: *Number of quail provided to young depending on nestling age, brood size, and year.*

Year	Nestling Age	Brood Size	Number of Quail Provided (Range)
2013	1	1	5-6
2013	2	1	5-6
2013	2	2	5-6
2013	3	3	5-6
2013	4	3	5-6
2013	5	3	5-6
2013	6	4	5-6
2013	7	4	5-6
2013	8	4	5-6
2013	9	3	5-6
2013	10	3	5-6
2013	11	3	5-6
2013	12	3	5-6
2014	0	1	3-10
2014	0	2	3-13
2014	0	3	3-5
2014	1	1	3-10
2014	1	2	3-10
2014	1	3	3-13
2014	2	1	4-7
2014	2	2	3-8

2014	2	3	3-13
2014	2	4	5-13
2014	3	2	4-7
2014	3	3	3-10
2014	3	4	5-13
2014	4	3	3-10
2014	4	4	3-13
2014	5	2	3-5
2014	5	3	3-9
2014	5	4	3-13
2014	6	2	3-5
2014	6	3	3-8
2014	6	4	4-13
2014	7	2	3-5
2014	7	3	3-8
2014	7	4	4-13
2014	8	2	3-5
2014	8	3	3-8
2014	8	4	4-13
2014	9	2	3-5
2014	9	3	3-8
2014	9	4	4-13
2014	10	2	3-5

2014	10	3	3-8
2014	10	4	3-13
2014	11	2	3-5
2014	11	3	3-8
2014	11	4	3-13
2014	12	3	3-8
2014	12	4	3-10
2015	0	1	4-6
2015	0	2	4-6
2015	1	1	4-11
2015	1	2	2-11
2015	1	3	3-7
2015	2	2	3-11
2015	2	3	3-11
2015	3	2	3-5
2015	3	3	2-11
2015	3	4	5-7
2015	4	3	2-11
2015	4	4	5-7
2015	5	2	3-5
2015	5	3	2-7
2015	5	4	5-7
2015	6	2	3-5

2015	6	3	2-11
2015	6	4	5-7
2015	7	2	3-5
2015	7	3	2-11
2015	8	2	3-5
2015	8	3	2-11
2015	9	2	3-5
2015	9	3	2-11
2015	10	2	3-5
2015	10	3	2-11
2015	11	2	3-5
2015	11	3	3-11
2015	12	2	3-5
2015	12	3	3-11
2015	13	2	3-5
2015	13	3	3-11
2015	14	3	2-11
2015	15	2	3-5
2015	15	3	2-11
2015	16	2	3-5
2015	16	3	2-11
2015	17	2	3-5
2015	17	3	2-11

2015	18	3	2-11
2015	19	3	2-11
2015	20	2	5-6
2015	20	3	2-11
2015	21	2	3-6
2015	21	3	2-11
2015	22	2	5-6
2015	22	3	2-11
2015	23	2	3-6
2015	23	3	2-11
2015	24	2	3-6
2015	24	3	3-7
2015	25	2	3-6
2015	25	3	2-7
2015	26	2	3-6
2015	26	3	2-7
2015	27	2	3-6
2015	27	3	2-7
2015	28	2	3-6
2015	28	3	2-11
2015	29	2	3-6
2015	29	3	2-7
2015	30	2	3-5

2015	31	3	3-7
2015	32	3	3-7
2016	0	1	2-5
2016	0	2	3-8
2016	0	3	3-8
2016	1	1	2-5
2016	1	2	2-8
2016	1	3	3-8
2016	1	4	3-8
2016	2	1	2-5
2016	2	2	2-5
2016	2	3	3-8
2016	2	4	3-8
2016	3	2	2-5
2016	3	3	3-6
2016	3	4	3-8
2016	4	2	2-5
2016	4	3	2-7
2016	4	4	3-8
2016	5	2	2-5
2016	5	3	2-7
2016	5	4	3-8
2016	6	2	2-5

2016	6	3	2-7
2016	6	4	3-8
2016	7	2	2-5
2016	7	3	2-7
2016	7	4	3-8
2016	8	2	2-5
2016	8	3	2-7
2016	8	4	3-8
2016	9	2	2-5
2016	9	3	2-7
2016	9	4	3-8
2016	10	2	2-5
2016	10	3	2-7
2016	10	4	3-8
2016	11	2	2-5
2016	11	3	2-7
2016	11	4	3-8
2016	12	2	2-5
2016	12	3	2-7
2016	12	4	3-8
2016	13	2	2-5
2016	13	3	2-7
2016	13	4	3-8

2016	14	2	2-5
2016	14	3	2-7
2016	14	4	3-8
2016	15	2	2-5
2016	15	3	2-7
2016	15	4	3-8
2016	16	2	2-5
2016	16	3	2-6
2016	16	4	4-8
2016	17	2	2-5
2016	17	3	2-6
2016	17	4	4-8

Table S4.3: *18 sites across 3 study years for which it was not possible to extract IVI data from nest camera images, but for which we collected mass and survival data and the explanations for why it was not possible to extract IVI data.*

Year	**Site**	**Explanation**
2013	4	Hard drive containing nest camera images lost in the field
2013	7	Hard drive containing nest camera images lost in the field
2013	19	Hard drive containing nest camera images lost in the field
2013	23	Hard drive containing nest camera images lost in the field
2013	28	Hard drive containing nest camera images lost in the field
2013	31	Hard drive containing nest camera images lost in the field
2013	33	Hard drive containing nest camera images lost in the field
2013	35	Hard drive containing nest camera images lost in the field
2013	39	Hard drive containing nest camera images lost in the field
2013	67	Hard drive containing nest camera images lost in the field
2013	75	Hard drive containing nest camera images lost in the field
2013	85	Hard drive containing nest camera images lost in the field
2013	98	Hard drive containing nest camera images lost in the field
2014	28	Camera angle/position made it impossible to accurately score provisioning visits
2014	47	Memory card not storing images correctly and/or camera not correctly functioning (not triggering for motion)
2014	75	Camera angle/position made it impossible to accurately score provisioning visits
2014	97	Camera angle/position made it impossible to accurately score provisioning visits
2016	15	Camera angle/position made it impossible to accurately score provisioning visits