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Dynamics of species with complex life cycles in a warming world: a mechanistic perspective

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Dynamics of species with complex life cycles in a warming world: a mechanistic perspective

A dissertation submitted in partial satisfaction of the
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in Biology

by

Madeline Cowen

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ABSTRACT OF THE DISSERTATION

Dynamics of species with complex life cycles in a warming world: a mechanistic perspective

by

Madeline Cowen

Doctor of Philosophy in Biology

University of California, Los Angeles, 2024

Professor Priyanga A. Amarasekare, Co-Chair

Professor Pamela J. Yeh, Co-Chair

A central objective of ecology is to understand the factors, biotic and abiotic, that shape the survival and persistence of species. Developing such an understanding is particularly challenging for organisms with complex life cycles, whose behavioral and physiological responses to the environment during one life stage can carry over to affect future life stages and scale up to affect population dynamics. Building on this understanding to then make predictions about how populations might respond to ongoing and future climate change is an additional defining challenge for contemporary ecological research.

The goal of my dissertation is to uncover behavioral and physiological mechanisms that shape survival, and evaluate the consequences of these processes for populations. Working across diverse taxa, I use statistical approaches to identify the behavioral mechanisms that affect survival and growth rate at the level of individuals, and develop a novel theoretical framework of mathematical models that link behavior and physiology to demographic rates in order to quantify impacts at the population level. Chapter 1 introduces this novel theoretical framework, which incorporates temperature responses of the ectothermic (e.g. eggs, hatchlings) and endothermic (e.g. juveniles, adults) life stages that comprise the avian life cycle into a multi-season, stage-structured population model. I use this framework to compare the effects of different warming regimes, including deterministic increases to mean annual temperatures, seasonal differences in warming severity, and stochastic hot extremes. Using non-migratory arid-zone passerine birds as a case study, I find that stochastic hot extremes represent an immediate threat to population persistence and that realistic levels of warming over the next century may cause considerable – and in some cases, catastrophic – declines in abundance.

In Chapter 2, I expand this framework to account for the empirical observation that extreme temperatures can have persistent effects on a bird's condition beyond the period of extreme temperature exposure. Focusing on temperature-induced condition changes for only the adult stage, I find that low levels of warming that are not enough to trigger acute increases in mortality rates can nevertheless cause adult condition to deteriorate and lead to declines in

abundance. The severity of impacts from such condition changes on bird populations depends on two factors: first, on the negative consequences of being in poor condition for vital rates, and second, on how quickly adults in poor condition can recover to good condition under favorable environments. This work shows that failing to account for temperature-induced condition changes could lead to underestimation of warming costs to birds.

For Chapter 3, I turn my attention to the underlying factors that affect demographic rates. I focus on the juvenile stage of a territorial reef fish, which exhibits a trade-off between body size at the time of settlement on the reef and growth rate after settling, such that juvenile fish are more likely to survive if they are large at settlement but grow slowly. I assess possible behavioral mechanisms that give rise to this trade-off, and find that larger juveniles undertake foraging strategies that increase survival, but also experience higher costs from conspecific chasing, which reduce growth rate. Since water temperature during the larval (pre-settlement) period has been previously shown to determine size-at-settlement in this system, my work reveals how temperature effects during early life stages can impact survival and growth in a future life stage through condition and behavior.

Together, the chapters of my dissertation reveal an important role of temperature and behavior interacting to affect vital rates that have downstream impacts on later life stages. My work underscores the value of integrating detailed empirical work on species with complex life histories with mechanistic models that scale individual-level mechanisms up to population dynamics.

The dissertation of Madeline Cowen is approved.

Peter Philip Marra

Van Maurice Savage

Pamela J. Yeh, Committee Co-Chair

Priyanga A. Amarasekare, Committee Co-Chair

University of California, Los Angeles

2024

To people who work to build and sustain a most precious thing:

a welcoming community

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Acknowledgments

A PhD is difficult under normal circumstances, but several exceptional obstacles made my graduate experience particularly challenging.[1] I have tremendous gratitude for all of the people who supported me through this period, encouraged me, and brought joy and laughter into my life.

First, I would like to thank my advisor, Priyanga Amarasekare. Words cannot convey how grateful I am to have joined her lab, even though the limited time I had to work with her was interrupted and overshadowed by unjust treatment from the university. Priyanga has been a wonderful mentor and a cheerleader for my ideas. I am grateful to have as an advisor someone so deeply committed to her students' success, and so confident in their abilities to achieve excellence. In her mentorship and her own practice of science, Priyanga exemplifies an approach to research that I greatly admire and aspire to. Her broad thinking and endless curiosity about connections between different systems and concepts has shown me how to resist the limitations we sometimes put on our science, how to be interdisciplinary, and how taking the time to pursue a deeper understanding always pays off. Taking her class at the end of my Master's program was a pivotal moment for me. Her approach to teaching and science inspired me to pursue a new line of training and a new topic of research, which has led to the dissertation work presented here. I am tremendously proud of the work I have

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[1] Obstacles include infection by a flesh-eating parasite, a global pandemic, the unjust suspension of my advisor and subsequent retaliatory treatment toward my labmates and me by my university. Unfortunately, these are not the only obstacles. Some of my experience is documented in a news article in the Chronicles of Higher Education.

accomplished as a student in her lab, and I thank her for believing in me, for trusting me, and for encouraging me.

I am also sincerely grateful for my co-advisor, Pamela Yeh. Especially amid the challenges I faced in the last few years of graduate school, Pam has been an incredible advocate. Her tireless advocacy has offered me much reprieve and has meant more to me than I can express. I am grateful for her thoughtful feedback on my research, her conviction in my abilities, and her encouraging words. I have also greatly appreciated her advice and guidance around navigating graduate school and preparing for next steps. Thank you for checking in on me frequently, and for reminding me about the fulfilling parts of an academic community.

I also want to thank Van Savage. I have learned so much from every conversation with Van, and always appreciate his insightful feedback and questions that push me to think more deeply about my work. My dissertation work represents my first foray into theoretical ecology, and the fascinating discussions from his Biomath course, the careful, rigorous approach he taught, and the welcoming environment he created were instrumental to me feeling like I could contribute in this field.

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I also want to thank staff in my department who helped me navigate the administrative side of graduate school, especially Tessa Villasenor who frequently lent a listening ear and offered words of encouragement.

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Next, I would like to thank members of the Amarasekare lab. I started attending Amarasekare lab meetings even before I joined the lab as a student, and during those I enjoyed learning from lab members like Guilherme Casas Gonçalves and Andrew Endo. After I joined Priyanga's lab, Rosa McGuire, Rachel Potter, and Tanner Dulay were wonderful lab mates. For an entire academic year, I was able to be part of a friendly lab where we exchanged ideas, laughed, and learned from each other. This year was one of the best out of my graduate experience. Unfortunately, this ended too soon when communication with our advisor was forcibly cut off. I was glad to have Rosa, Tanner, Pam Yeh, and Kurt Anderson as partners in countless frustrating meetings with UCLA administrators. The emails we had to write to advocate for ourselves could comprise a dissertation chapter in their own right. Thank you also to the undergraduates who stood with us during this time, especially Bucky Squier.

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Many graduate students participated in the development of the 2021 Departmental Climate Survey, as well as the subsequent analyzing of the data and preparation of the Report on the UCLA EEB 2021 Department Climate Survey. This represented a tremendous amount of time on a very precious and sensitive dataset that was emotionally challenging to work on, since we wanted to accurately represent the experiences, good and bad, of our peers. I thank every person who played a role in this project, and a special thanks to the core group that wrote the report with me and saw the project through to the end: Rachel Turba, Alayna Mead, and Marissa Ochoa.

One of the most important communities I was part of during my PhD was the Bruin Birding Club (BBC). I am incredibly grateful to Samuel Bressler, the founding president of the club, for doing the difficult work of establishing an organization, recruiting folks familiar with and new to birding, and making an inviting culture for club events. I grew tremendously as a leader of this club, explored and learned so much about Southern California (its ecological, political, and cultural histories, and connected with communities of people doing amazing engagement work across the area), developed my own core values and philosophies, and met countless wonderful people. I have been so inspired to see the dedication and commitment to this organization of so many students, despite the many demands on their time and the COVID-19 pandemic occurring shortly after the club's inception. Thank you to the BBC board members who put in so much of their energy into keeping this amazing club and community alive. I loved working with all of you, and want to give a special shout out to several people for their friendship and dedication: Rosa McGuire, Graham Montgomery, Fabiola Torres-Toledo, Samantha Snowden, Sylvia Zhang, Yuka Wu, Aslan Li, Russell Stottlemyer, Rujin Yu, Jeffrey Cheng, and Ellis Song.

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Curriculum Vitæ

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Education

M.S. in Ecology & Evolutionary Biology (2016-2018) UCLA

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Publications

7. Rankin, T.L.*, **Cowen, M.C.***, Kandlikar, G.S., Shulzitski, K., and S. Sponaugle. 2023. Behavioral mechanisms underlying trait-mediated survival in a coral reef fish. *Frontiers in Fish Science* 1, 1276343. **These authors share first authorship.*
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9. **Cowen, M.C.**, Drury, J.P., Grether, G. Ecological drivers and evolutionary consequences of interspecific territoriality in North American songbirds. North American Ornithological Conference 2020.
8. **Cowen, M.C.**, Drury, J.P., and Grether, G. The persistence of interspecific territoriality across evolutionary timescales. Southern California Behavior Meeting 2020.
7. **Cowen, M.C.**, Drury, J.P., and Grether, G. The ecological and evolutionary stability of interspecific territoriality in North American passerines. International Society for Behavioral Ecology 2018.

6. **Cowen, M.C.**, Drury, J.P., and Grether, G. Ecological correlates and evolutionary stability of interspecific territoriality in sister North American passerines. Poster Presentation. UCLA Ecology and Evolutionary Biology Annual Research Symposium 2018.
5. **Cowen, M.C.** Determining the ecological and evolutionary circumstances associated with interspecific territoriality in sister North American songbirds. UCLA EcoEvo Pub 2018.
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3. **Cowen, M.C.**, Levin, R., Tsai, W., and McCormack, J. Offspring dispersal and territory acquisition of Western scrub-jays (*Aphelocoma californica californica*) at the Bernard Field Station. Pomona College, 2016.
2. **Cowen, M.C.**, Levin, R. Distribution and dispersal of the Western scrub-jays at the Bernard Field Station. Pomona Valley Audubon Society, 2015.
1. **Cowen, M.C.**, Bellantuono, A., and Martínez, D. Macerate immunofluorescence to locate gamma-H2AX in hydra nuclei. Poster presentation. Pomona College Summer Undergraduate Research Program Conference, 2014.

Teaching

- *Teaching certificates:* Certified Instructor with the Software Carpentry Consortium; CIRTL (Center for the Integration of Research, Teaching, and Learning) Associate
- *Teaching Associate or Assistant for the following courses at UCLA:* Advanced Statistics in Ecology and Evolutionary Biology; Quantitative Concepts for Life Sciences; Field Biology Quarter in Cocha Cashu, Peru; Animal Behavior; Teaching Evolution at the Elementary Level; Quantitative Concepts for Life Sciences; Life: Concepts and Issues; Field Biology Quarter in Cameroon; Biology of Vertebrates
- *Workshops given:* Co-organizer & instructor for 3 Software Carpentry (SWC) workshops, teaching assistant for 2 SWC workshops on R, git, github, Shell, and Python

Service and Engagement

- *UCLA EEB Graduate Climate Survey Report*: Co-authored The 2022 UCLA Ecology and Evolutionary Biology Department Graduate Climate Survey Report; Organized, co-developed, and analyzed data from Department Graduate Climate Survey
- *Co-chair of Hacky Hours Committee*, which organizes and runs a weekly co-working space for graduate students and postdocs in the UCLA EEB Department.
- *Peer Reviewer* for PNAS, PeerJ, Behavioral Ecology, and Ecology
- *Bruin Birding Club:* Founding board member *(2019 - 2024)* and President *(2020 - 2023)* of UCLA's Audubon student chapter. Awarded ∼ $40,000 in funding across 11 grants from the National Audubon Society, the Hispanic Access Foundation, and UCLA's Green Initiative Fund, Arts Restoring Committee Fund, and GSA Discretionary Fund.

Introduction to the dissertation

Understanding the factors that shape biodiversity is a central goal of ecology. Widespread population declines and resulting loss of biodiversity (Bowler *et al.* 2019; Butchart *et al.* 2010; Rosenberg *et al.* 2019; Wagner 2020) emphasize a need to build on our basic understanding of biodiversity dynamics to make predictions of future population dynamics and identify species at risk of extinction. Fundamentally, declines in population abundance occur because of changes to demographic rates such as per capita survival and reproductive success. Variation between species (and between populations of the same species) in population-level responses to climate change must therefore be attributed to differences in these demographic rates. These demographic rates, in turn, are shaped by organisms' complex life histories, physiological responses, behavioral strategies, and morphological traits (Brown, Gillooly, *et al.* 2004; Griffith *et al.* 2016; Wong & Candolin 2015). The complex biological underpinnings of demographic rates can make responses of these rates to the environment non-linear, time-lagged, and variable across life stages (Kingsolver, Arthur Woods, *et al.* 2011). Developing a general understanding of global change effects on species persistence therefore requires unraveling the mechanisms shaping such effects, and addressing how such mechanisms scale from individuals to populations and communities.

Progress toward this general, predictive understanding can be made through at least two approaches of ecological research. The first approach builds on the longstanding tradition of collecting detailed information in the field regarding organismal traits and abundances, along with information about the abiotic and biotic environment. Statistical analyses of such data can reveal relationships between environmental conditions and population dynamics, which can then be used for generating predictions for the future and comparing across systems. Despite its ubiquity and utility, a persistent limit to this approach is that extrapolation beyond the conditions in which the data were collected is fraught with caveats, making it difficult to apply insights from one system to other species or populations with different life histories or environmental conditions (Elliott-Graves 2018). Similar caveats also apply when applying insights from past observations for projecting dynamics under the novel climate regimes (i.e. conditions beyond the range of observed environmental conditions) that organisms are likely to experience under global change (Fitzpatrick & Hargrove 2009; Urban 2019). Unfortunately, while empirical observations and detailed field studies provide a crucial foundation for our understanding of the processes governing population responses to global change, efforts to collect requisite empirical data and successfully develop interventions for species of concern are unlikely to keep pace with rapid, ongoing biodiversity loss (Butchart *et al.* 2010; Kindsvater *et al.* 2018).

A second approach for studying population-level responses to global change builds on the tradition of mechanistic modeling, which uses biological first principles of how the environment and other factors affect vital rates, and scales up to the level of population dynamics (Rastetter *et al.* 2003). Mechanistic models can be defined to capture varying degrees of biological detail, and can be used to investigate causal relationships between organismal traits and population responses (e.g. Can a particular mechanism of interest generate an observed pattern at the population level? Under what circumstances do particular life history traits affect population dynamics?). This tradition is especially well developed for evaluating variation in ectotherm population dynamics with respect to temperature (Bieg & Vasseur 2024; Ewing *et al.* 2016; Luhring & DeLong 2017; Savage *et al.* 2004). We have decades of theory on the physiological basis for ectotherm performance changes in response to temperature, and evidence that the temperature responses of vital rate functions are conserved across species (e.g. Dell *et al.* 2011; Gillooly, Brown, *et al.* 2001; Gillooly, Charnov, *et al.* 2002; Savage *et al.* 2004; Schoolfield *et al.* 1981; Sharpe & DeMichele 1977). While mechanistic modeling approaches can generate quantitative and robust insights, they too have limitations. For example, incorporating and integrating the complicated processes that are known to be important in nature requires detailed information regarding vital rate responses to the environment, which are often lacking for organisms that are not amenable to experimental study. Nevertheless, even when we lack precise measurements of all processes, such mechanistic models are vital for generating useful qualitative insights, whose scope (generality) is constrained by clearly defined model assumptions. Developing such models can also help identify gaps in our empirical understanding of natural systems and can foreground any implicit assumptions obstructing a more complete understanding of how global change affects population dynamics.

I find the interplay between these two approaches – empirical research and mechanistic modeling – to be most compelling, in part because observations of patterns in nature can inform the types of processes we model, and models can tell us which parameters are most important to measure. My dissertation reflects my efforts to advance through both avenues our understanding of how climate change affects populations. My three chapters are united in their goals of uncovering behavioral and physiological mechanisms that shape survival and other demographic rates, and evaluating the consequences of these processes for populations. Working across diverse taxa with complex life histories, I use statistical investigation of field data to identify the behavioral mechanisms that affect survival and growth rate at the level of individuals, and mechanistic modeling to characterize warming effects at the population level.

My first chapter develops a novel theoretical framework that links temperature responses of bird behavior and physiology to demographic rates and their population-level impacts. The mechanistic, mathematical model captures important aspects of avian life history and temperature responses, including both ectothermic and endothermic life stages (e.g. eggs, hatchlings, juveniles, adult birds) and incubation behavior. I use information about bird behavior and physiology to develop temperature response functions for life stage-specific vital rates (maturation, mortality, birth), and integrate these responses into a population model that accounts for both seasonal and diurnal variation in temperature.

As a first application of the model, I investigate consequences of warming for non-migratory, desert-dwelling passerine birds. I find that warming effects on population dynamics are likely to strongly depend on the specific warming pattern. Hot temperatures reached through dangerous levels of deterministic warming are predicted to cause large declines in abundance, especially if maximum summer temperatures increase faster than winter temperatures. Perhaps more alarming is the finding that stochastic hot extremes can devastate arid-zone bird populations even when these extreme events only result in modest increases in mean annual temperatures (e.g. 1.5°C).

In some cases, exposure to extreme temperatures can result in responses other than the acute responses captured by the model in Chapter 1. Recent empirical work has demonstrated that birds exposed to even brief periods of extreme temperatures can experience changes to their body condition that persist beyond the exposure to the temperature (Gardner, Amano, *et al.* 2016; Sharpe, Cale, *et al.* 2019). While such condition changes can affect survival (Gardner, Amano, *et al.* 2016), their implications for long-term bird population dynamics are unclear. My second chapter addresses this gap by extending the model in Chapter 1 to incorporate long-lasting (i.e. chronic) responses of birds to temperature variation. Specifically, I introduce temperature-response functions that capture transitions between good and poor condition states, and characterize poor condition birds as experiencing an increased mortality rate or decreased egg laying rate. I analyze the model with parameters that reflect the biology of arid-zone passerines and find that temperature-induced poor condition can have negative repercussions on bird populations even at low levels of warming that do not cause acute temperature responses.

My long-term vision for the framework introduced in Chapters 1 and 2 is to sequentially explore a broad array of important avian life history and climate change responses, with the goal of facilitating general, mechanism-based insights about relative susceptibility of different species and populations to climate change. In some cases, empirical data are available to support model extensions (e.g. investigating phenological shifts in breeding and migration in response to warming). Developing model extensions for other factors of interest will require sustained dialogue between theoretical and empirical approaches. This is particularly relevant for generating quantitative predictions of how climatic factors beyond temperature (e.g. precipitation) affect bird populations, for which a mechanistic understanding remains limited (Boyle *et al.* 2020).

Finally, Chapter 3 aims to uncover the mechanistic basis for a key life history trade-off between growth and survival in juvenile fish. Specifically, I investigate this trade-off in the bicolored damselfish *Stegastes partitus*, a common western Atlantic reef fish that defends benthic territories for sheltering, foraging (both on the territory and, primarily, in the water column), and mating (Emery 1973; Robertson *et al.* 1988). The early life stages of this damselfish consist of a pelagic larval stage, followed by an overnight metamorphosis into the juvenile stage after settling onto rubble or reef (D'Alessandro *et al.* 2007; Grorud-Colvert & Sponaugle 2009; Sponaugle & Cowen 1996). This metamorphosis can be clearly identified through examination of the fish's otoliths (ear stones), where daily deposition of materials in concentric increments provides a record of age (number of increments), daily growth rate (average width of increments), settlement date (a distinctly thick increment), and size-at-settlement (otolith radius at settlement) (Sponaugle 2010; Sponaugle & Cowen 1996). The early life stages experience high mortality rates, and a strong pattern of selective mortality emerges in just the first few days after settlement: larger size-at-settlement and slower juvenile growth rate are associated with higher survival (Johnson & Hixon 2010; Rankin & Sponaugle 2011, 2014). The mechanism(s) linking larger size with slower growth rate and enhanced survival are largely unknown, however, and the association between slower growth rate and higher survival seemingly contradicts the prevailing paradigm around early life selective mortality (Anderson 1988; Robert *et al.* 2023).

To address this gap, I investigated potential behavioral mechanisms that could give rise to these patterns. I analyzed a unique dataset that integrated detailed information about the size, growth, and survival of juvenile *S. partitus* with behavioral observations about foraging, movement, sheltering, and territorial activity. I used confirmatory path analysis (Lefcheck 2016), a recent statistical approach that tests the causal structure between variables, not simply correlation, to assess direct and indirect links between behavioral strategies and demographic rates. Interestingly, I found that size-at-settlement did not affect growth and survival directly, but rather indirectly via behavioral pathways: size-at-settlement explained differences in foraging behavior, such that larger fish traveled farther and spent less time sheltering than smaller fish, and this foraging strategy was then associated with higher survival. Furthermore, settlement size affected the outcome of conspecific chasing: larger fish chased by neighboring adults experienced slower growth.

As in Chapter 2, this work demonstrates how differences in condition (e.g. body condition or mass for birds, size-at-settlement for juvenile damselfish) can have consequences for demographic rates. Moreover, in both cases, condition can be temperature-dependent. In *Stegastes partitus*, water temperature strongly affects larval growth rate and the duration of the pelagic larval stage, which together determine size-at-settlement (Rankin & Sponaugle 2011). This is similar to the framework I analyze in Chapter 2, where variation in temperature can give rise to variation in bird condition. A key point of distinction between these two studies is the focal life stage, with Chapter 2 examining condition changes of adult birds and Chapter 3 focusing on the early life stages of fish. Condition changes that affect demographic rates in early life have the potential to cause downstream effects on future life stages, which could amplify corresponding population responses. The general modeling framework introduced in Chapter 2 is ideally suited to investigate the implications of such changes for avian populations, and is a key future extension.

Taken together, the chapters of my dissertation highlight how behavior and physiology can shape survival outcomes for diverse taxa in ways that carry over to affect future life stages, and which scale up to impact populations. Behavioral strategies can affect temperature responses of vital rates, and temperature variation can lead to differences in condition that affect behavioral strategies. Unraveling the complexity of population responses to temperature thus requires investigation into the specific mechanisms underlying temperature responses. In this way, my work underscores the value of detailed empirical work on the behavior and physiology of species with complex life histories, and of integrating such work with mechanistic models that scale individual-level mechanisms up to population dynamics.

Chapter 1

Population dynamics of endotherms with ectothermic life stages: birds in a warming world

1.1 Abstract

Climate change is causing severe and wide-ranging impacts on organisms worldwide, including population declines and extinctions. The unique biology of birds makes them vulnerable to climate warming in complex ways: birds are endothermic as juveniles and adults but also have ectothermic life stages (e.g. eggs) whose exposure to temperature variation depends on adult incubation behavior. A mechanistic framework for evaluating stage-specific effects of temperature variation is key to capturing this complexity and making reliable predictions about bird population responses to climate change. Here we present a stage-structured model of bird population dynamics that explicitly incorporates temperature effects on avian vital rates. We analyzed the model to examine the effects of seasonal temperature variation and climate warming on bird population dynamics, using parameters realistic for a desert-dwelling passerine bird and both deterministic and stochastic climate warming scenarios. We find that a deterministic increase in mean temperature by 1.5°C over 100 years will have few to no impacts on bird population dynamics, while 5°C of deterministic warming over 100 years could cause extinction. In contrast, stochastic hot extremes pose an acute threat that could devastate bird populations, even without substantial increases in mean temperature. Our work points to an important role of rising and extreme temperatures amid the complex impacts of climate change on avian population dynamics. This is a promising framework ripe for future development, and we outline research directions that would further integrate theory and data to provide mechanistic-based predictions of bird population responses to climate change.

1.2 Introduction

While numerous climatic factors will play an important role in shaping population dynamics in the next century (IPCC 2021), one of the most notable ways that climate change affects species is through rising and extreme temperatures (Johnston *et al.* 2013; Murali *et al.* 2023; Spooner *et al.* 2018). Temperature variation can have direct and indirect impacts on various dimensions of biodiversity, including behavior, physiology, and ultimately population dynamics (Bellard *et al.* 2012; Ceresa *et al.* 2021; Cunningham, Gardner, *et al.* 2021; McLean, Kruuk, *et al.* 2022; Parmesan 2006).

The direct effects are most obvious in ectotherms, whose performance and physiology immediately responds to temperature variation (Abarca & Spahn 2021; Kingsolver, Diamond, *et al.* 2013). These effects can cascade into indirect effects on endotherm population dynamics (e.g. Renner & Zohner 2018), but endotherms themselves are also directly impacted by temperature, in ways that are diverse (e.g.impacting different vital rates such as birth rate, maturation rate, and mortality rate), nonlinear, and variable by life stage (e.g. Dybala *et al.* 2013). This makes predicting the overall effect on population dynamics quite challenging.

Birds present a further complication with their unique life history as endotherms with ectothermic early life stages. As endotherms, birds can maintain relatively constant body temperatures within a wide range of ambient temperatures, allowing them to persist in diverse environments around the world (Buckley *et al.* 2012). Nevertheless, extreme temperatures due to global climate change are having drastic effects on many bird populations. These effects are especially well documented in desert-dwelling birds, which live in habitats with high environmental temperatures (Albright, Mutiibwa, *et al.* 2017; McKechnie & Wolf 2019). For example, behavioral thermoregulatory responses (reviewed in Bicego *et al.* 2007; Huey *et al.* 2012) can take time away from foraging and other activities (Cunningham, Gardner, *et al.* 2021; du Plessis *et al.* 2012), and high temperatures can have severe consequences, including lower reproductive output (Schou *et al.* 2021), dehydration (Albright, Mutiibwa, *et al.* 2017), and death (McKechnie, Rushworth, *et al.* 2021; Saunders *et al.* 2011). As average global temperatures rise and extreme heat waves become more common (IPCC 2021), this reality of avian sensitivity to hot extremes cannot be ignored.

Birds are also unique in that they have ectothermic early life stages that require buffering even from typical temperature variation (e.g. diurnal, seasonal). Adult birds generally incubate eggs and nestlings to maintain egg temperature within the optimal range for maturation (Turner 2002; Walsberg & Voss-Roberts 1983; White & Kinney 1974). When temperatures rise, adult birds cool eggs by spending more time incubating and attending the nest (Clauser & McRae 2017; Conway & Martin 2000; Nord & Williams 2015), but extreme temperatures can cause incubation to break down, exposing nests to lethal temperatures that cause hatching failure or sub-lethal temperatures that cause sub-optimal development (Belnap *et al.* 2019; Bourne, Ridley, Spottiswoode, *et al.* 2021; Clauser & McRae 2017). Mass egg and nestling mortality events due to high temperatures have already been observed (Holt & Boersma 2022; McCowan & Griffith 2021; Quintana *et al.* 2022; Salzman 1982; Sharpe, Bayter, *et al.* 2021).

While such mass mortality events are still somewhat rare, widespread population declines (Bowler *et al.* 2019; Iknayan & Beissinger 2018; Jiguet *et al.* 2010; Pollock *et al.* 2022; Rosenberg *et al.* 2019; Spooner *et al.* 2018) heighten the urgency of understanding warming effects on bird population persistence. Indeed, this pressing need has driven a wealth of research (e.g. Fink *et al.* 2020; Hostetler *et al.* 2015; Nater *et al.* 2023; Rushing *et al.* 2016; Wilson, LaDeau, *et al.* 2011) that has advanced and supported conservation efforts, yet several key gaps constrain our ability to make general predictions. First, much work has focused on warming responses of specific avian behaviors and vital rates, without also demonstrating whether or the extent to which such responses translate into effects on population dynamics (reviewed in Jenouvrier 2013; McLean, Lawson, *et al.* 2016). Second, many studies have focused on only one season or one life stage, thus identifying warming responses of potentially important underlying processes, but falling short of being able to predict net effects on population dynamics (reviewed in Jenouvrier 2013; McKechnie, Hockey, *et al.* 2012; Norris & Marra 2007). Third, many population models are species- or population-specific and based on statistical associations between trends in population abundances and temperature. While such models are highly useful for guiding conservation interventions, generalizing their predictions to novel thermal conditions or to other species or populations is often impractical (McKechnie, Hockey, *et al.* 2012; Urban *et al.* 2016; Urban 2019).

Developing a framework to address these limitations is a key research priority (Jenouvrier 2013; McKechnie, Hockey, *et al.* 2012). A promising approach for understanding overall impacts of warming on bird populations would be a mechanistic framework that starts with characterizing temperature effects on behavior and vital rates (e.g. birth, maturation, mortality) and scales up to translating these effects into population dynamics. While such an approach has been used successfully to predict warming effects on ectotherm fitness (Amarasekare & Savage 2012; Deutsch *et al.* 2008) and population dynamics (Bieg & Vasseur 2024; Ewing *et al.* 2016; Luhring & DeLong 2017; Savage *et al.* 2004), developing a similar mechanistic framework for birds is not straightforward due to the complex nature of avian life history and temperature responses.

Here, we take a first step toward this goal by presenting a mechanistic theoretical framework for predicting the effects of warming on avian population dynamics. The novelty of our framework is that it explicitly incorporates the ectothermic and endothermic stages of the avian life cycle, and projects population dynamics across the full annual cycle based on mechanistic descriptions of the temperature responses of avian vital rates. Using arid-zone passerine birds as a case study, we investigate the effects of different warming regimes on abundance. Specifically, we examine the consequences of deterministic warming scenarios with different seasonal patterns and different magnitudes of warming, as well as warming that arises due to stochastic hot extremes.

1.3 Methods

1.3.1 Mathematical framework

Model overview

We develop a stage-structured model of avian population dynamics that explicitly incorporates temperature effects on both the ectothermic and endothermic stages in the avian life cycle (Figure 1.1A). We capture this life history with two ectothermic stages (eggs and hatchlings) and two endothermic stages (non-breeding juveniles and breeding adults). We define the hatchling stage as the period during which recently hatched nestlings are unable to regulate their body temperature and rely on parental incubation (Dunn 1975; Price & Dzialowski 2018). The juvenile stage is defined as encompassing both the endothermic portion of nestling development (for altricial and semi-altricial species, when young rely on parental food provisioning but can thermoregulate) and endothermic young who have left the nest.

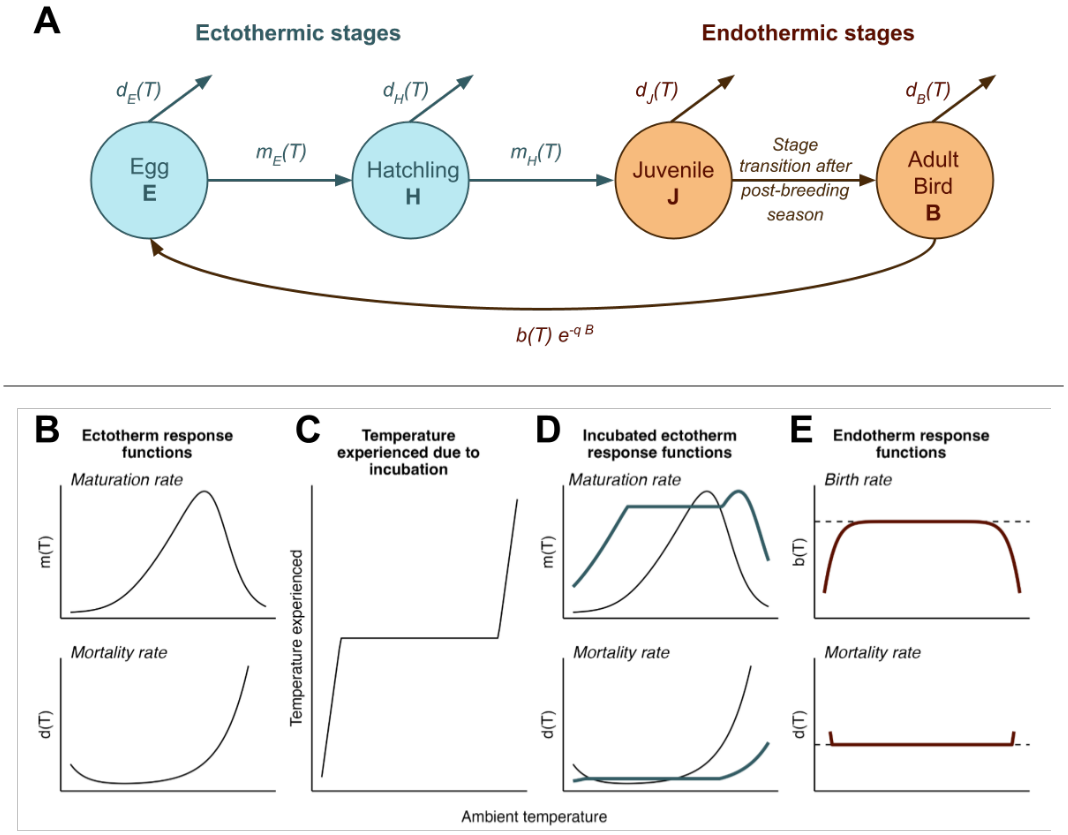

Figure 1.1: Schematic of the general stage-structured model of population dynamics with temperature-dependent vital rate functions. **A** depicts the transitions between developmental stages, with ectothermic stages in teal and endothermic stages in orange. **B-E** depict temperature-response functions for avian growth and survival. Panels in column **B** depict thermal reaction norms typically used to model ectotherm traits (maturation and mortality rates). Although bird eggs and hatchlings are ectothermic, they are buffered from ambient temperature through adult incubation behavior, and thus experience a different temperature than the ambient temperature (Panel **C**). At high temperatures, incubation breaks down and eggs/hatchlings are exposed to higher temperatures. Panels in column **D** show temperature responses of maturation and mortality for ectotherms that experience incubation (teal lines), contrasted with ectotherms that do not experience incubation (black lines). Panels in column **E** show endothermic trait temperature responses (brown lines), contrasted with how endothermic traits are typically modeled as temperature-independent (dashed black lines).

We consider the population dynamics of a seasonally breeding species. The annual cycle begins with the pre-breeding season, where only adults exist in the system. During the breeding season, adults lay eggs, which mature into hatchlings, and incubate both eggs and hatchlings until the latter mature into juveniles. Eggs laid late in the breeding season and hatchlings that remain at the end of the breeding season continue to mature during the post-breeding season, but there is no new reproduction. At the end of the post-breeding season, all juveniles transition into the adult stage, which serves as the input to the following year's pre-breeding season. We consider the duration of each season to be determined by photoperiod (i.e. calendar day). This is a reasonable assumption given that photoperiod is the primary cue for starting and ending breeding activities for most species, even if they fine-tune their breeding phenology with additional cues such as resource abundance (Dawson *et al.* 2001; Dawson 2008).

Stage-structured dynamics within each season are continuous and given by the following system of equations:

Pre-breeding season $(0 \leq t \leq t_{pre})$

$$\frac{dB_{pre}}{dt} = -d_B(T)B_{pre}$$

initial conditions:

$$B_{pre}(0,0) = B_0 \text{ for } y = 0$$

$$B_{pre}(0,y) = B_{post}(365, y-1) + J_{post}(365, y-1) \text{ for } y > 0$$

Breeding season $(t_{pre}+1 \leq t \leq t_{br})$

$$\begin{aligned}
\frac{dE_{br}}{dt} &= b(T)B_{br}e^{-qB_{br}} - m_E(T)E_{br} - d_E(T)E_{br}\\
\frac{dH_{br}}{dt} &= m_E(T)E_{br} - m_H(T)H_{br} - d_H(T)H_{br}\\
\frac{dJ_{br}}{dt} &= m_H(T)H_{br} - d_J(T)J_{br}\\
\frac{dB_{br}}{dt} &= -d_B(T)B_{br}
\end{aligned}$$

initial conditions:

$$X_{br}(t_{pre}+1,y) = 0 \text{ for } X = E, H, J$$

$$B_{br}(t_{pre}+1,y) = B_{pre}(t_{pre}+1,y))$$

Post-breeding season $(t_{br}+1 \leq t \leq 364)$

$$\begin{aligned}
\frac{dE_{post}}{dt} &= -m_E(T)E_{post} - d_E(T)E_{post}\\
\frac{dH_{post}}{dt} &= m_E(T)E_{post} - m_H(T)H_{post} - d_H(T)H_{post}\\
\frac{dJ_{post}}{dt} &= m_H(T)H_{post} - d_J(T)J_{post}\\
\frac{dB_{post}}{dt} &= -d_B(T)B_{post}
\end{aligned}$$

initial conditions:

$$X_{post}(t_{br}+1,y) = X_{br}(t_{br}+1,y) \text{ for } X = E, H, J, B \tag{1.1}$$

where the state variables, E, H, J, and B represent, respectively, the abundances of eggs, hatchlings, juveniles, and adult birds. The parameter q depicts the intraspecific competition coefficient, the index y the year of the simulation, and t_{pre} and t_{br} the last days of the pre-breeding and breeding seasons, respectively. The functions $b(T)$, $m_X(T)$ $(X = E, N)$, and

$d_Z(T)$ $(Z = E, N, J, A)$ depict, respectively, the temperature response of per capita birth, maturation, and mortality rates.

Functional forms of vital rate temperature responses

We derive mechanistic descriptions of the temperature responses of birth, maturation, and mortality rates from empirical evidence of adult bird sensitivity to extreme temperatures (Holt & Boersma 2022; McKechnie, Rushworth, *et al.* 2021; Whitfield *et al.* 2015) and from existing theory on such rate responses in ectotherms (Johnson & Lewin 1946; Ratkowsky *et al.* 2005; Schoolfield *et al.* 1981; Sharpe & DeMichele 1977) (Figure 1.1B-E). The equations and parameter definitions for the resulting functions can be found in Table 1 and are described in the following sections.

Endothermic life stages

While many theoretical approaches have typically focused on the invariance of endotherm performance across a wide range of ambient temperatures (Dell *et al.* 2011), investigating the effect of climate warming on bird population dynamics requires us to model the sensitivity of endothermic stages to temperature extremes (Jenouvrier 2013; McKechnie, Hockey, *et al.* 2012). We capture this sensitivity by using piecewise functions to describe the mortality rates of the endothermic life stages (juveniles and adults; Table 1.1; Figure 1.1E). We define lower and upper mortality inflection points between which the mortality rate remains constant. Below and above these inflection points, the mortality rate increases exponentially as temperatures become more extreme. Finally, we assume that birth rate is temperature-independent (but see Hurley *et al.* 2018; Schou *et al.* 2021; Sharpe, Bayter, *et al.* 2021).

Ectothermic life stages

In ectotherms, the maturation rate exhibits a left-skewed response with a faster decline at high temperature extremes (Figure 1.1B; Kingsolver 2009; Kingsolver, Diamond, *et al.* 2013; Schoolfield *et al.* 1981; Sharpe & DeMichele 1977; van der Have 2002; van der Have & Jong 1996), while the mortality rate increases exponentially with temperature above a temperature threshold, and increases with decreasing temperature below the threshold (Figure 1.1B, Gillooly, Brown, *et al.* 2001; Gillooly, Charnov, *et al.* 2002; Ratkowsky *et al.* 2005; Savage *et al.* 2004).

We begin by assuming that in the absence of incubation, the maturation and mortality rates of bird ectothermic life stages follow the same functional forms as those derived for ectothermic species. To account for incubation behavior that allows adults to maintain eggs and hatchlings at a constant temperature across a range of ambient temperatures, we define a function that relates the ambient temperature to the temperature experienced by the ectothermic stages (Figure 1.1C; Table 1.1). We use a piecewise function, such that adults buffer eggs from ambient temperature between upper and lower threshold temperatures, beyond which the efficacy of incubation breaks down. Accounting for incubation, the egg and nestling vital rates are constant during temperatures that favor incubation and generally follow ectothermic temperature responses at temperatures outside of the incubation thresholds (Figure 1.1D). Because the incubation function has two temperature thresholds and the ectothermic mortality temperature response has only a low temperature threshold, we approximated the underlying ectothermic mortality function with a piecewise function (Table 1.1). As a final step, we model the hatchling maturation rate (i.e. the rate at which ectothermic hatchlings mature into endothermic nestlings/juveniles) as being invariant with temperature, as evidence suggests that this rate is determined by factors such as food consumption and rate of biomass growth, rather than temperature per se (reviewed in Price & Dzialowski 2018).

Empirical support for parameter choices

To parameterize temperature response functions for ectothermic species, researchers typically measure average vital rates for populations exposed continuously to specific temperatures and use statistical approaches to fit functions to the data (Ardelan *et al.* 2023; Mordecai *et al.* 2019; Sinclair *et al.* 2016; Sunday *et al.* 2024). For the most part, such an approach is not feasible for birds due to logistical and ethical concerns. However, much empirical work on birds has investigated temperature impacts on various physiological rates and incubation behaviors. We leverage this by identifying relevant metrics that can serve as proxies for the parameters in the vital rate temperature response functions. We compiled a list of possible proxies for all parameters, along with ranges of values measured for these proxies in the literature, which we report in Appendix A.1 (Table A.1).

Table 1.1: Temperature-dependent vital rate functions.

Maturation rate for ectothermic stage i (i = E,H)

$$m_i(T) = \frac{m_{T_{R_i}} \left(\frac{T}{T_{R_{m_i}}} e^{A_{m_i}\left(\frac{1}{T_{R_{m_i}}} - \frac{1}{T}\right)} \right)}{1 + e^{A_{L_{m_i}}\left(\frac{1}{T_{L_{m_i}}} - \frac{1}{T}\right)} + e^{A_{H_{m_i}}\left(\frac{1}{T_{H_{m_i}}} - \frac{1}{T}\right)}}$$

$T_{R_{m_i}}$ = reference temperature for maturation
$T_{L_{m_i}}$ = lower temperature threshold
$T_{H_{m_i}}$ = upper temperature threshold
$m_{T_{R_i}}$ = per capita maturation at $T_{R_{m_i}}$
A_{m_i} = Arrhenius constant for temperature sensitivity of maturation at $T_{R_{m_i}}$
$A_{L_{m_i}}$ = Arrhenius constant for decrease in maturation rate with decreasing temperature below $T_{L_{m_i}}$
$A_{H_{m_i}}$ = Arrhenius constant for increase in maturation rate with increasing temperature above $T_{H_{m_i}}$

Mortality rate for stage i (i = E,H,J,B)

$$d_i(T) = \begin{cases} d_{T_{R_i}} * e^{a_{L_{d_i}}(T_{LI_{d_i}} - T)} & T < T_{LI_{d_i}} \\ d_{T_{R_i}} & T_{LI_{d_i}} \leq T \leq T_{UI_{d_i}} \\ d_{T_{R_i}} * e^{a_{H_{d_i}}(T - T_{UI_{d_i}})} & T > T_{UI_{d_i}} \end{cases}$$

$T_{LI_{d_i}}$ = lower mortality inflection point
$T_{UI_{d_i}}$ = upper mortality inflection point
$d_{T_{R_i}}$ = per capita mortality within thresholds
$a_{L_{d_i}}$ = rate of increase in mortality with decreasing temperature below $T_{LI_{d_i}}$
$a_{H_{d_i}}$ = rate of increase in mortality with increasing temperature above $T_{UI_{d_i}}$

Temperature experienced due to incubation

$$T_x(T_{amb}) = \begin{cases} T_{opt} - (I_L - T_{amb}) & T \leq I_L \\ T_{opt} & I_L < T < I_H \\ T_{opt} + (T_{amb} - I_H) & I_H \leq T \end{cases}$$

T_x = temperature experienced
T_{amb} = ambient temperature
I_L = lower incubation threshold
I_H = upper incubation threshold
T_{opt} = temperature experienced within thresholds

We present an example of this reasoning here by considering the response of the adult mortality rate to high temperatures. As described in the previous section, the adult mortality rate, like other piecewise equations in our modeling framework, requires two parameters to address the increase in mortality rate at high temperatures: an upper mortality inflection point $T_{UI_{d_B}}$, and the rate of increase above this inflection point $a_{H_{d_B}}$. For the upper mortality inflection point, we use the ambient temperature that first exceeds normothermic body temperature (Gerson *et al.* 2019; McKechnie 2022; McKechnie, Gerson, *et al.* 2021; McKechnie, Hockey, *et al.* 2012), as this measure is conservative relative to other plausible proxies (Appendix A.1: Table A.1), and because body temperature is fairly constrained across a wide range of bird species (McKechnie 2019; McKechnie, Gerson, *et al.* 2021; McKechnie & Wolf 2019), enabling generalization to species whose physiology has not been studied in depth.

Calculating a rate of increase in mortality rate requires measurements of the mortality rate at several temperatures above and below the upper mortality inflection point, which are very unlikely to be available and very hard to do for birds. However, there is substantial documentation in the empirical literature of temperatures that are likely to be lethal for birds. For example, several studies have reported mass avian mortality due to single-day extreme hot temperatures (e.g. Finlayson 1932; Holt & Boersma 2022; McKechnie, Rushworth, *et al.* 2021; Saunders *et al.* 2011). Moreover, the heat tolerance limit – the temperature associated with the onset of heat stress and inability to regulate body temperature after 10-30 minutes of exposure – has been measured for an even wider range of species (McKechnie, Gerson, *et al.* 2021; Whitfield *et al.* 2015). We thus define an upper total mortality point T_{UT}: the temperature where a single-day exposure will result in complete mortality for the population, i.e. the per capita mortality rate $d_B(T = T_{UT}) = 1$. This allows us to rearrange the adult mortality rate function (Table 1) using parameters that more closely align with empirically available data:

$$d_B(T) = d_{T_{R_B}} * e^{\frac{T_{UT_{dB}} - T}{T_{UT_{dB}} - T_{UI_{dB}}}} \text{ for } T > T_{UI_{dB}}$$

We follow a similar approach for all other parameters in our modeling framework (Appendix A.1: Table A.1).

Specific parameterization for model analysis

As a case study for investigating warming effects on bird population dynamics, we focused our analysis on passerine birds, the largest order of birds in the world ("Orders of Birds" 2020). Specifically, we focus on small, non-migratory passerines that inhabit temperate deserts, for several reasons. First, resident arid-zone species experience an environment in which water availability remains low throughout the year, allowing us to characterize the baseline case of how temperature variation alone influences population dynamics. Second, since arid-zone birds experience conditions close to their physiological limits, they are especially at risk from increasing global temperatures, a threat that is particularly severe for passerines with small body masses (Albright, Mutiibwa, *et al.* 2017; Conradie *et al.* 2020). Third, arid-zone species have been the focus of many physiological studies (reviewed in McKechnie, Rushworth, *et al.*

2021; McKechnie & Wolf 2019, Appendix A.1: Table A.1). We parameterized the model with realistic values for arid-zone passerines (Appendix A.1: Table A.1), and performed sensitivity analyses for all parameters (Appendix A.2). Though we focus our results on arid-zone passerines, the model is general and can accommodate a wide diversity of bird species, including non-passerines.

1.3.2 Model Analysis

All analyses were performed in R version 4.3.2 (R Core Team 2022).

Typical seasonal variation in temperature

We used the stage-structured, multi-season model (Equation 1) to investigate the effects of typical temperature variation (both diurnal and seasonal) as well as warming. We considered intra-annual variation in the average daily temperature to capture seasonal temperature variation, and diurnal variation in hourly temperatures to capture temperature extremes that could negatively impact vital rates within a single day (Appendix A.3: Figure A.4).

We used the following sinusoidal functions to depict seasonal and diurnal variation:

$$T_{daily}(t) = M_T - A_T \cos\left(\frac{2\pi t}{y}\right)$$

$$T_{hourly}(t) = T_{daily}(t) - a_T \cos\left(\frac{2\pi t}{y}\right)$$

where M_T is the mean annual temperature, A_T is the magnitude of seasonal fluctuations: $A_T = \frac{T_{max}-T_{min}}{2}$, and a_T is the magnitude of daily fluctuations.

To define a regime of seasonal temperature variation typical of temperate deserts, we obtained hourly temperature data from NOAA (`https://www.ncdc.noaa.gov/cdo-web/search`) for a weather station in the Sonoran Desert. For simplicity, we assume that the air temperature reflects temperatures experienced by the four life stages in our model (but see O'Connor *et al.* (2018), Wolf (2000), and Wolf & Walsberg (1996) for evidence of how operative temperature can vary due to behavioral thermoregulation and microsite selection). We used these data to calculate the average annual temperature and the amplitude of seasonal and diurnal fluctuations for 1961 to 1990 (the World Meteorological Society's reference period).

Using the temperature response functions above, we calculated average daily vital rates for each life history stage. We simulated dynamics using these average daily vital rates, and then characterized model behavior under typical temperature variation by examining within-year and across-year dynamics.

Climate warming: deterministic warming scenarios

We tested the Intergovernmental Panel on Climate Change (IPCC) predictions about increases in the mean annual temperature (IPCC 2021). We compared three magnitudes of warming: a 1.5°C, a 3°C, and a 5°C increase in the mean temperature across 100 years. Following previous studies (Amarasekare 2019; Endo & Amarasekare 2022), we considered three

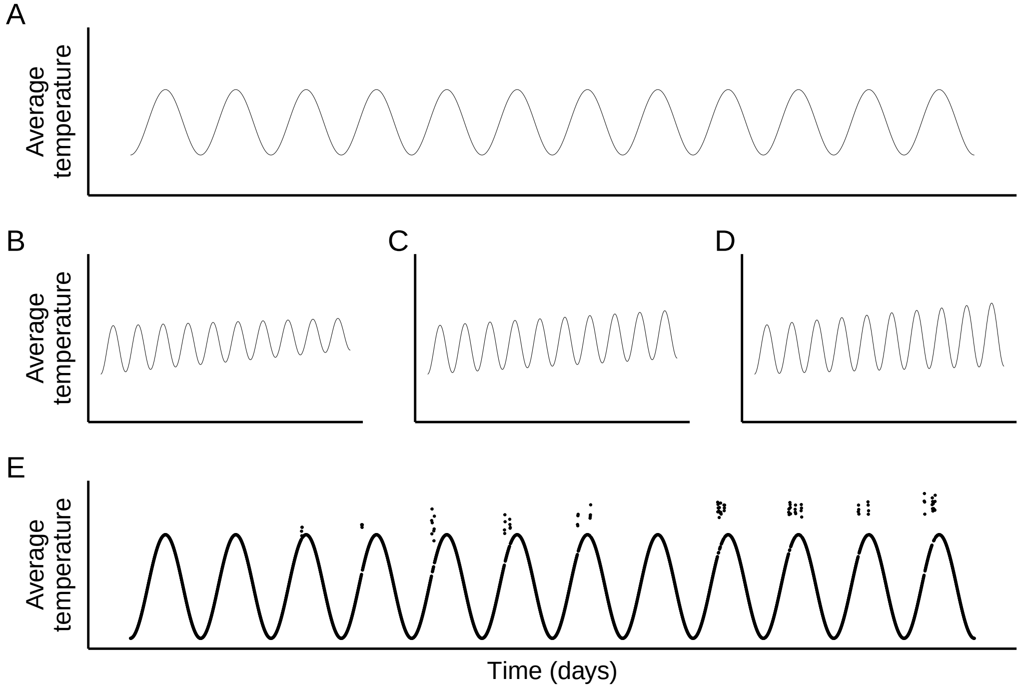

Figure 1.2: Non-stationarity as a signature of warming. Typical seasonal variation in temperature is stationary: the expected mean and variance of annual temperatures are constant with time. In contrast, climate warming is non-stationary: the expected mean and variance in temperature will change with time. We explore changes in mean and variance of annual temperatures with deterministic (**A-D**) and stochastic (**E**) regimes. **A** represents typical seasonal variation, where mean and variance are constant; **B-E** represent warming regimes with the same rate of change in mean annual temperature, but with differences in how the variance changes with time. In **B** ("warmer winters"), annual minimum temperatures increase faster than the annual maximum temperatures, resulting in a decrease in amplitude through time. In **C** ("baseline warming"), both the annual maximum and minimum temperatures increase at the same rate, resulting in no change to the amplitude. In **D** ("warmer summers"), the annual maximum increases faster than the minimum temperature, resulting in an increase in the amplitude. In **E**, warming occurs through a regime of stochastic hot extremes that increase in both intensity and frequency.

deterministic warming scenarios for each magnitude of warming. In each scenario, the mean annual temperature increases at the same constant rate, but the amplitude of the seasonal fluctuations are different. In the warmer-than-average winters scenario (hereafter "warmer winters"), annual minimum temperatures increase faster than annual maximum temperatures, resulting in a decrease in the amplitude of thermal oscillations (Figure 1.2B). In the warmer-than average summers scenario (hereafter "warmer summers"), annual maximum temperatures increase faster than annual minimum temperatures, resulting in an increase in amplitude of thermal oscillations (Figure 1.2D). Finally, in the baseline warming scenario, the maximum and minimum temperatures increase at the same rate, resulting in no change in amplitude (Figure 1.2C).

We depict deterministic warming scenarios using the sinusoidal function:

$$T_{daily}(t) = M_T + mt - (A_T + at)\cos\left(\frac{2\pi t}{y}\right)$$

where m and a represent the daily rate of increase in the average temperature and the amplitude, respectively. We calculated these rates as follows: $m = \frac{r_{max_T} + r_{min_T}}{2}$ and $a = \frac{r_{max_T} - r_{min_T}}{2}$, where r_{max_T} and r_{min_T} are the daily rates of increase in maximum and minimum annual temperatures. These daily rates of increase can in turn be calculated as $r_x = \frac{s_x}{100*365}$ where s_x is the degrees of increase over 100 years in the $x = max_T$ or min_T.

For each regime (degree of warming and warming scenario), we ran the model for 100 years and calculated the minimum adult abundance in the 101th year. We focused on the minimum rather than the mean abundance because the lower the minimum abundance the more susceptible populations are to extinction via demographic stochasticity. We also recorded the first year of each the simulation when temperatures were hot enough to affect mortality rates of the ectothermic and endothermic life stages (hereafter referred to as the ectothermic and endothermic mortality thresholds).

Climate warming: stochastic occurrence of hot extremes

In addition to increases in the mean annual temperature, the IPCC also predicts increases in the intensity, frequency, and duration of hot extremes (IPCC 2021). We examined the impact of hot extremes by simulating population dynamics for 100 years using a temperature regime of typical seasonal variation with stochastic hot extremes that increased in intensity, frequency, and duration over a period of 100 years.

We drew the number of hot extremes each year from a Poisson distribution. Both the duration of each hot extreme period and the average daily temperature of hot extremes were drawn from folded normal distributions (i.e. absolute value of draws from a Gaussian distribution). For each of these parameters, the expected value of the distribution increased each year. The start dates of each hot extreme period were sampled from a uniform distribution, restricting hot extremes to occur when eggs and hatchlings were present in the system (i.e. during the breeding season and the first month of the post-breeding season).

We investigated the impact of increasing intensity, frequency, or duration of hot extreme periods. We varied either the expected intensity, frequency, or duration in year 100 and kept the other two parameters constant. We used realistic values for expected intensity, frequency, and duration based on recent estimates about trends in heatwaves (Habeeb *et al.* 2015; Perkins-Kirkpatrick & Lewis 2020; Rohini *et al.* 2016; Russo *et al.* 2014): when the expected frequency was kept constant, it was set to five hot extreme periods. The expected intensity was set to 306 K, and the expected duration was set to four days.

We conducted 20 replicate simulation runs for each hot extreme parameter (intensity, frequency, or duration), and recorded the minimum adult abundance in the 101st year. We also recorded the first year of the simulation in which a hot extreme impacted the ectothermic and endothermic mortality rates. Finally, since hot extremes that increase in intensity, frequency, or duration over 100 years by definition increase the mean annual temperature over that period, we fit linear regression models to each simulation to calculate the degrees of warming that resulted from the hot extreme regime. This allowed us to compare the relative impact of the deterministic warming scenarios versus increasingly hotter, longer, and more frequent temperature extremes.

1.4 Results

1.4.1 Typical seasonal variation

Daily temperatures under typical seasonal variation fall entirely within the incubation and endothermic mortality thresholds (Figure 1.3A), resulting in maturation and mortality rates that are constant with respect to time (Figure 1.3B). Despite this invariance in trait responses, there is a clear intra-annual signature of seasonal variation in abundances (Figure 1.3C). This pattern arises from seasonal breeding and stage transitions throughout the lifecycle (e.g. hatchlings to juveniles, juveniles to adults). Since seasonal temperature variation exhibits a stationary distribution (i.e. mean temperature and amplitude of fluctuations remain approximately constant over time), the intra-annual variation in abundance also settles into a stationary distribution. As a result, mean annual abundance converges to a stable point equilibrium (Figure 1.3D), regardless of initial population abundance (Figure 1.3E), suggesting that population dynamics are stable under typical seasonal variation.

1.4.2 Climate warming: deterministic scenarios

Most of the deterministic warming regimes had moderate to no effects on bird population abundance (declines of 0-2.3% relative to no warming for 6 of 9 regimes; Figure 1.4A). This includes the magnitude of warming that corresponds to the optimistic IPCC projection: a 1.5°C increase in mean temperature over 100 years generated minor population declines (0-0.3%). In contrast, one warming regime resulted in severe declines: 5°C of warming with warmer-than-average summers led to a complete crash in abundance compared to typical seasonal variation.

The three warming scenarios (warmer winters, warmer summers, and baseline warming) varied substantially in their impact on population dynamics. Warmer summers had the most detrimental effect on abundance, while warmer winters with any amount of warming caused no declines in abundance. Baseline warming with 5°C of warming caused a 48.1% decline in population abundance, an effect similar to warmer summers with 3°C of warming (49.6% decline).

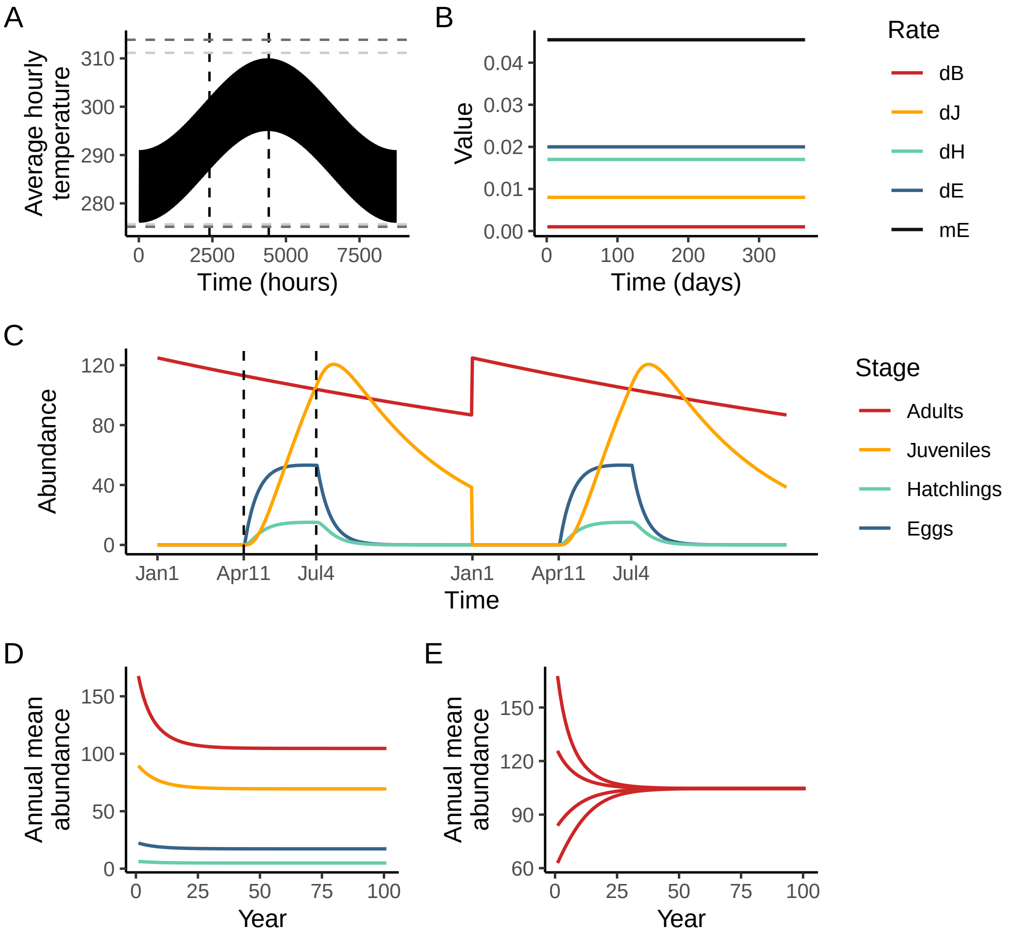

Figure 1.3: Population dynamics under typical seasonal variation in temperature. (**A**) Typical seasonal variation in temperature falls within the temperature thresholds where incubation becomes less efficient (light gray horizontal line) or adults experience a change in mortality rate (dark gray horizontal line). Vertical dashed lines indicate the beginning and end of the egg-laying period. (**B**) Since typical variation falls within these thresholds, vital rates do not vary in time. These rates are calculated for each hour and then averaged for each day. In the case of typical seasonal variation (no warming), these rates are invariable with time. (**C**) This results in populations dynamics that cycle during the year due to seasonal reproduction. Recall that after the egg-laying period, eggs and hatchlings mature into juveniles, and at the end of the year, the juveniles instantaneously become adults. When we consider population dynamics year-to-year, the dynamics appear to be stable: (**D**) annual mean abundances of each stage approach stable points, regardless of starting population size (**E**). Only adult dynamics represented in **E** for clarity.

Since maximum temperatures in warmer summers scenarios are always higher than in warmer winters or baseline warming for a given degree of warming, temperatures exceeded the ectothermic and endothermic mortality thresholds more quickly for warmer summers than for other warming scenarios (Figure 1.2B-C). For instance, when the mean temperature increased by 3°C, the ectothermic mortality threshold was reached within 42 years for warmer summers as opposed to 72 years for baseline warming and over 100 years for warmer winters; when the mean temperature increased by 5°C, the ectothermic mortality threshold was reached within 25 years under warmer summers, 43 years under baseline warming, and over 100 years under warmer winters (Figure 1.4B). The pattern was similar for the endothermic mortality threshold, which was reached within 45 years for warmer summers 5°C, 75 years for warmer summers 3°C, and 77 years for baseline warming 5°C (Figure 1.4C).

Two regimes with moderate increases in maximum annual temperatures (baseline warming with 1.5°C of warming and warmer winters with 5°C of warming) never exceeded the ectothermic mortality threshold, but did exceed the incubation threshold. This led to an increase in the egg maturation rate, without an accompanying increase in the egg mortality rate. As a result, more eggs matured into hatchlings, resulting in very minor increases in adult abundance (0.002-0.003% increase).

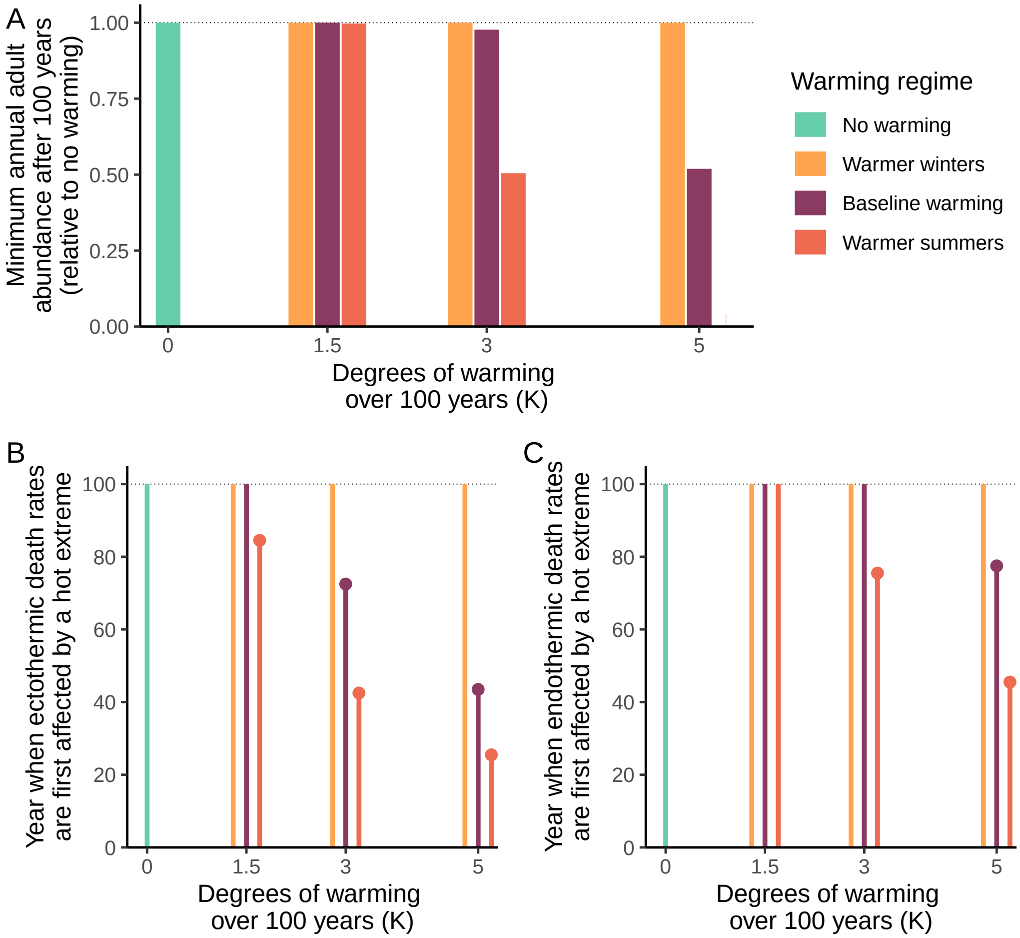

Figure 1.4: Warmer summers have a large impact on bird populations. In **A**, bars represent the minimum annual abundance of adults after 100 years with different warming regimes, relative to the minimum abundance expected after 100 years of no warming (dotted horizontal line). In **B** and **C**, points represent the first year of the simulation in which mortality rates for ecothermic (**B**) or endothermic (**C**) stages change because the temperature regime exceeds the ectothermic or endothermic mortality thresholds, respectively. For some regimes, these vital rates never changed during the course of the 100-year simulation.

1.4.3 Climate warming: stochastic hot extremes

In contrast to the deterministic warming scenarios, stochastic hot extremes generated severe population declines with only minimal increases in the annual mean temperature (Figure 1.5A). For instance, a 0.75°C increase in the mean temperature over 100 years due to stochastic hot extremes was sufficient for populations to crash. This is in stark contrast to the deterministic trend of 1.5°C of warming over 100 years, which caused no decline in abundance. In fact, our simulations suggest that a 0.75°C increase in the mean temperature over 100 years due to hot extremes alone can have as detrimental an effect on bird population dynamics as would a 5°C increase due to a steady deterministic trend.

In addition to causing population crashes, increasing intensity of hot extremes can cause temperatures that impact both ectothermic and endothermic stages within 20 years of warming (Figure 1.5B). Increases in the frequency and duration of hot extremes yielded similar results (Appendix A.3: Figure A.4, A.5).

Figure 1.6 illustrates the underlying dynamics through which stochastic hot extremes can generate such devastating effects (Figure 1.6; orange dot in Figure 1.5A). The extreme temperatures exceeded the ectothermic and endothermic mortality thresholds as early as year 38 and 47, respectively, leading to higher mortality rates across all stages (Figure 1.6B-C). The egg maturation stage first increased in year 5, but could not compensate for higher egg mortality rates later in the simulation (Figure 1.6B, 1.6D). By the end of 100 years, the compounding effects of hot extremes on vital rates resulted in large declines across all subsequent stages (hatchlings, juveniles, adults; Figure 1.6D, E).

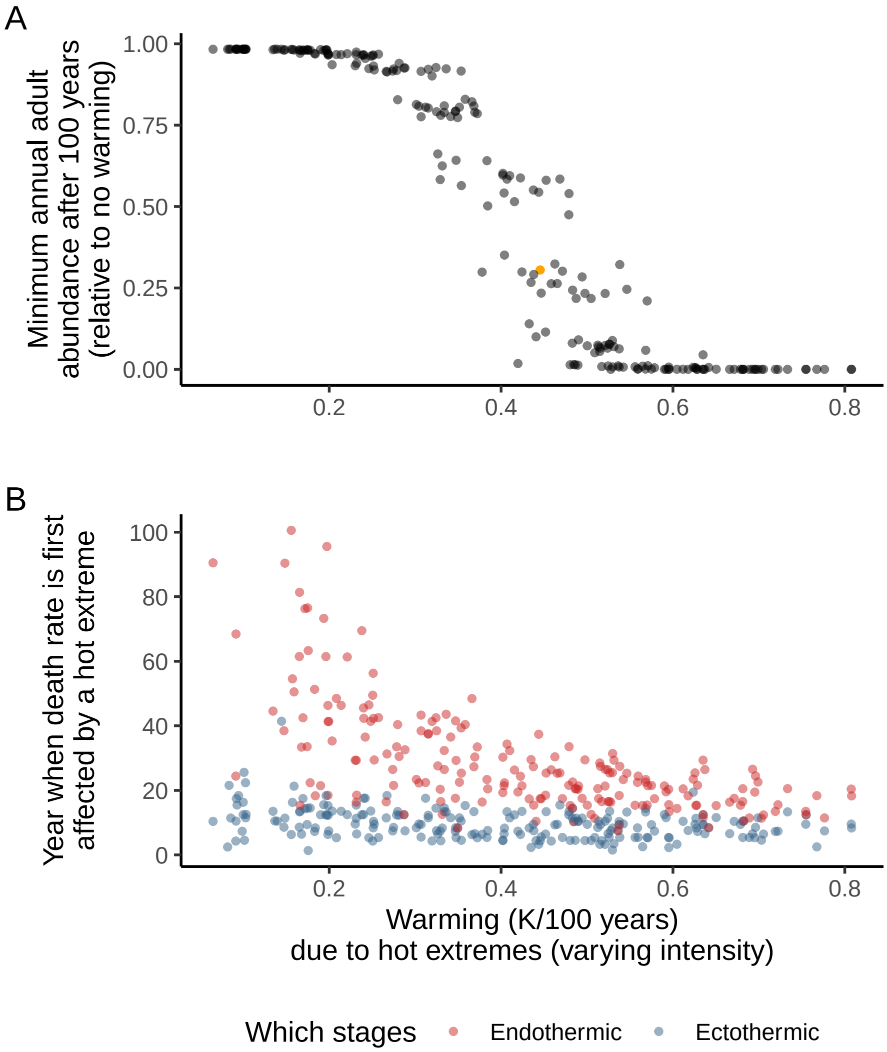

Figure 1.5: Stochastic hot extremes could have highly detrimental effects on bird populations. In **A**, points represent the minimum annual abundance of adults after 100 years with different warming regimes (relative to the minimum abundance expected after 100 years of no warming). Warming here is calculated as the increase in mean temperature over 100 years due to a regime of stochastic hot extremes that become increasingly hotter over the course of the simulation. Dynamics underlying the orange point are depicted in Figure 1.6. In **B**, points represent the first year of the simulation during which temperatures are high enough to affect the death rates of either ectothermic (blue) or endothermic stages (red).

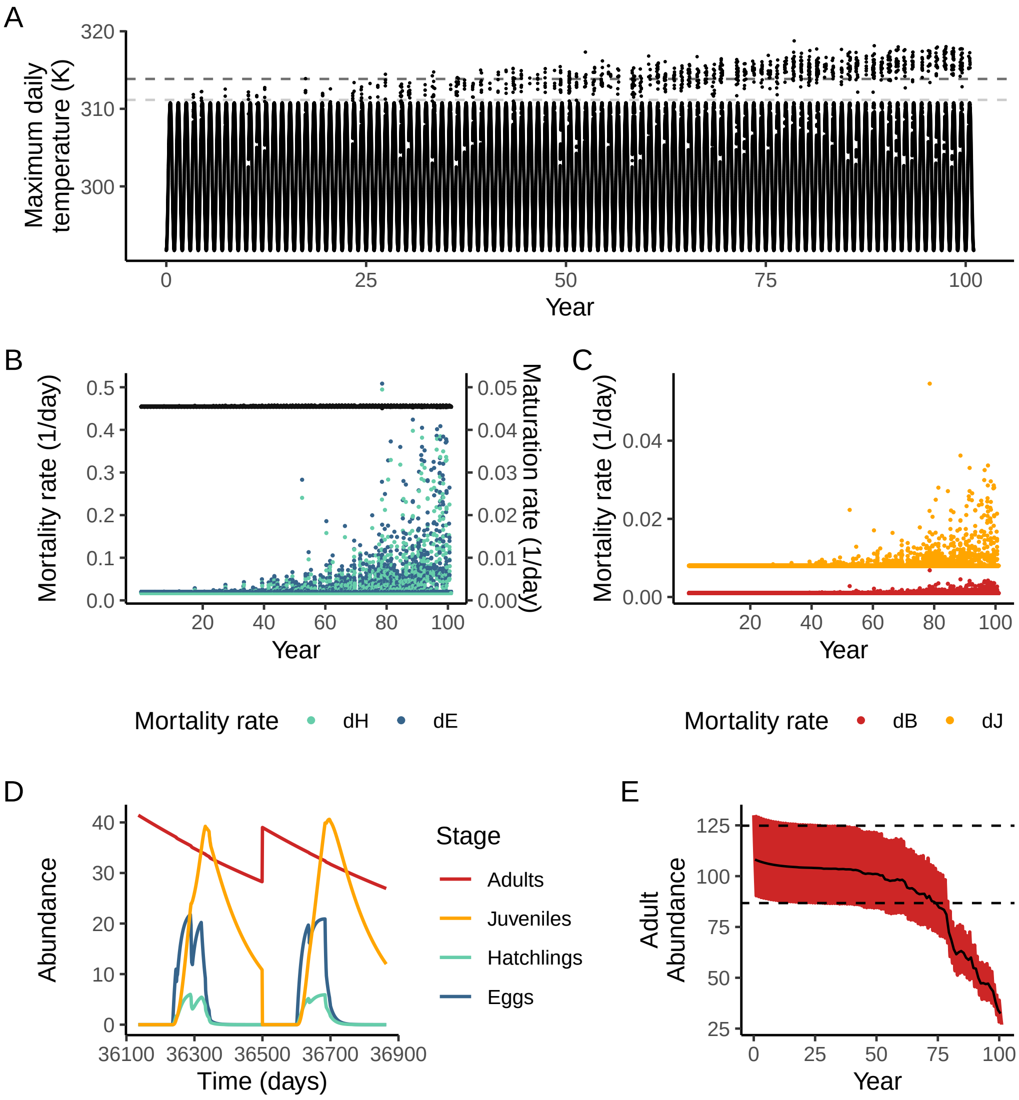

Figure 1.6: Population dynamics under a regime of stochastic hot extremes that become increasingly hotter over 100 years. **A** depicts the thermal regime, in which hot extremes exceed the temperature where adult incubation (light gray dashed line) and adult mortality rate (dark gray dashed line) are affected. The hot extremes impact the vital rates for both the ectothermic stages (**B**; egg maturation rate depicted with black points) and the endothermic stages (**C**). These impacts result in changes in abundance, visualized for the last two years of the simulation (**D**) as well as over all 100 years of the simulation (**E**; dashed lines depict maximum and minimum adult abundance under no hot extremes).

1.5 Discussion

An extensive body of research has documented avian population responses to warming and used these observed trends to develop population-specific models for projecting dynamics under climate warming (Fink *et al.* 2020; Hostetler *et al.* 2015; Nater *et al.* 2023; Rushing *et al.* 2016; Wilson, LaDeau, *et al.* 2011) . Despite these advances, our ability to generate predictions for the vast majority of bird species – for which detailed population dynamics information is scarce – remains limited (Conde *et al.* 2019; Lees *et al.* 2020; Proença *et al.* 2017). A promising approach for overcoming this limitation is to integrate climate effects on bird vital rates using a mechanistic understanding of bird physiology, and incorporate these effects across life stages in a dynamical, full-annual-cycle population model (Jenouvrier 2013; McKechnie, Hockey, *et al.* 2012; Urban *et al.* 2016; Urban 2019). Here, we draw on decades of work on ectotherm thermal ecology (reviewed in Angilletta 2009) and avian physiology (reviewed in McKechnie 2022) to develop such a framework. Our model generates stable dynamics under typical seasonal variation in temperature without warming, capturing the seasonality characteristic of most bird population dynamics. Our framework also reveals the undeniable role of temperature variation on arid-zone bird population dynamics: hot temperatures reached through dangerous levels of warming or through stochastic hot extremes can cause large declines in bird populations via direct effects on vital rates.

1.5.1 Impacts of warming on arid-zone passerines

Parameterized to represent desert-dwelling passerine birds, our model yields starkly different outcomes for population persistence depending on the magnitude of warming. We found that a 1.5-degree deterministic increase in mean temperature over 100 years – a degree of warming that corresponds to the best-case scenario of emissions reductions (IPCC 2021) – had nearly no effect on population dynamics (Figure 1.4). In contrast, a 5°C increase in mean temperatures over 100 years, corresponding to a high emissions scenario, caused complete extinction of the population. Adult birds are endotherms, and use behavior to buffer their ectothermic stages from temperature variation, so it is reasonable to expect that they can maintain performance across some amount of temperature variation. This finding suggests that even populations living fairly close to their thermal limits can withstand temperatures up to 1.5°C outside of their typical range of experienced temperatures without much cost to abundance, but that sufficiently high levels of warming can have devastating outcomes.

While the magnitude of warming plays an undeniable role in shaping bird population dynamics, our analyses also underscore the importance of accounting for the specific thermal patterns that give rise to warming. The same degree of increase in average annual temperature can come about from a variety of thermal regimes that vary considerably in how often and by how much they exceed critical thresholds for bird vital rates. For example, even when warming occurs as a steady, deterministic increase in average temperatures, the seasonal pattern of warming (e.g. a faster increase in winter minima or in summer maxima) dramatically alters outcomes for desert passerine populations. Across all magnitudes of warming, we repeatedly found that regimes where summer temperatures increased more quickly than winter temperatures led to larger declines in abundance, simply because increasing temperatures during the hottest time of the year exceeds threshold temperatures more quickly than in other regimes. In contrast, warmer winters regimes did not directly affect bird populations since the resulting temperatures were still well within the range of what birds tolerate.

Warming does not occur as a steady, deterministic trend, however. Nowhere is this more evident than in the numerous hot extreme periods felt across the globe (Habeeb *et al.* 2015; Luo *et al.* 2024; Rohini *et al.* 2016; Russo *et al.* 2014). Increases in the intensity, duration, and frequency of hot extremes can increase average temperatures, and comparing the impact of this form of warming to the deterministic trend analysis revealed a critical insight: while our ability to predict hot extremes is weak, their impact on desert passerine populations can be extremely strong. The same amount of warming over 100 years can be devastating to bird populations if that warming happens through stochastic hot extremes, yet unremarkable if temperatures generally follow a deterministic increase in mean annual temperatures. Furthermore, extreme temperatures can have large effects within as few as two decades – as we have already seen in several cases of mass mortality of desert birds due to hot extremes (McCowan & Griffith 2021; McKechnie, Rushworth, *et al.* 2021; Sharpe, Bayter, *et al.* 2021). Especially since hot extremes will not be evenly distributed around the world (Luo *et al.* 2024; Russo *et al.* 2014), accurately forecasting hot extreme periods in climate change scenarios remains a challenge, one that our work highlights as a top priority by revealing how not accounting for hot extremes could lead to considerable underestimation of climate change impacts on birds.

Several studies have used physiological mechanisms to assess warming consequences for arid-zone birds, specifically by estimating increases in lethal dehydration risk or cooling costs for adult birds during the summer (Albright, Mutiibwa, *et al.* 2017; Conradie *et al.* 2020; Ma *et al.* 2023; McKechnie & Wolf 2010; Riddell *et al.* 2019). In many cases, these studies have predicted severe repercussions of warming for desert birds, although the degree of predicted severity is geographically variable due to differences in regional climate projections (McCowan & Griffith 2021; McKechnie, Rushworth, *et al.* 2021; Sharpe, Bayter, *et al.* 2021). Our model expands on this work by introducing a modeling framework that is dynamic, year-round, and stage-structured, enabling us not only to account for temperature effects on other life stages and during other seasons, but also to quantify how warming impacts translate to changes in population abundance. The present parameterization of our model, which represents a general group of birds as opposed to a specific species, supports these previous studies' predictions about severe outcomes of warming for desert birds, and can be used to estimate the extent of population declines resulting from different temperature regimes. While our present study primarily used deterministic warming trends based on global averages, our model can also accommodate real temperature time series data, making it suitable to address regional differences in projected warming intensity around the world.

1.5.2 Beyond arid-zone passerines

Though we focused our analyses on desert-dwelling passerine birds, our framework provides a trait-based approach for making mechanistic predictions about warming impacts on a variety of avian systems, such that any of the underlying temperature response functions can be parameterized or adjusted for the biology of specific species of interest. Our general finding that the pattern of warming determines the net impact on population abundance is likely to hold true for other systems, both non-passerine and non-arid-zone, but we expect several specific results to differ.

Within arid-zone bird communities, the consequences of warming may vary in severity for some groups of species. For example, some non-passerine groups such as columbids and caprimulgids use different physiological mechanisms for thermoregulating, which in some cases confer higher thermotolerance (McKechnie, Whitfield, *et al.* 2016; O'Connor *et al.* 2017) that might result in less sensitivity to warming. On the other hand, some desert bird populations may inhabit places where temperatures routinely reach or exceed their mortality thresholds; for these populations, even 1.5°C of deterministic warming could be sufficient to impact vital rates and population abundance.

Outside of deserts, the ways the warming affects populations could differ. Parameterizing the model for non-desert species who do not live so close to their thermal limits is likely to show a limited effect of warming on bird populations, since the primary mechanism modeled is acute responses of vital rates to temperatures that exceed threshold values. Indeed, instead of triggering the acute high mortality observed in the arid-zone (McCowan & Griffith 2021; McKechnie, Rushworth, *et al.* 2021; Saunders *et al.* 2011; Sharpe, Bayter, *et al.* 2021) and predicted by our model, for example, warming could predominantly drive phenological shifts in migration and breeding (Romano *et al.* 2023). Such phenological shifts could expose breeding birds and early life stages to higher incidence of cold weather events (Regan & Sheldon 2023; Shipley *et al.* 2020)(Shipley or cause mismatches with resources or altered interactions with competitors and parasites (Ahola *et al.* 2007; Both, Bouwhuis, *et al.* 2006; Iler *et al.* 2021; McKinney *et al.* 2012; Saino *et al.* 2009). Furthermore, other climatic factors such as precipitation and drought can interact with temperature to determine outcomes on demographic rates (Albright, Pidgeon, *et al.* 2010; Bourne, Cunningham, *et al.* 2020b; Conrey *et al.* 2016; Gardner, Amano, *et al.* 2016; Garrett *et al.* 2022), and on their own can have significant impacts on bird populations (Anctil *et al.* 2014; Dossman *et al.* 2023; Smith *et al.* 2010; Studds & Marra 2007). Extending our framework to account for more diverse ways that temperature and other aspects of climate change affect bird populations (see Model Extensions) will be a challenging but important next step.

Expanding our framework within and beyond the arid-zone would benefit from additional empirical research into bird temperature responses. One reason for focusing our analyses on arid-zone birds was the availability of physiological and behavioral data on such species (e.g. Bourne, Ridley, McKechnie, *et al.* 2021; Bourne, Ridley, Spottiswoode, *et al.* 2021; McKechnie, Gerson, *et al.* 2021). Nevertheless, even for arid-zone birds, no single species has been sufficiently well described to provide precise values of each of the parameters in our mechanistic framework, highlighting an urgent need for further integration of theoretical and empirical approaches. In particular, much research has focused on temperature responses of adult and egg mortality (Conde *et al.* 2019; Jenouvrier 2013), with relatively less data available about how other life stages (e.g. hatchlings, juveniles) and processes (e.g. maturation, incubation, birth rate) are affected by temperature variation. One path towards a more comprehensive understanding of avian temperature responses is through coordinated global efforts, which could help establish research priorities and protocols that enable comparative and synthetic research (Urban *et al.* 2016; Urban 2019). Integrating such information with a mechanistic theoretical framework like the one we present here could help uncover geographic, phylogenetic, or functional patterns structuring physiological diversity and future temperature responses. For example, the heat tolerance limits and various other physiological properties of adult birds scale with body mass within phylogenetic groups (McKechnie, Gerson, *et al.* 2021), which points to the potential value of using our framework for generating comparative predictions of how climate sensitivity varies across species of different body size.

1.5.3 Model extensions

By integrating acute effects of climate warming on bird population dynamics, our model lays the groundwork for future theoretical development that captures more diverse temperature effects on birds. For example, even relatively low levels of warming that do not reach temperatures high enough to trigger acute mortality rate increases can still cause declines in body condition (Bourne, Ridley, Spottiswoode, *et al.* 2021; Bourne, Cunningham, *et al.* 2020a; Cunningham, Martin, *et al.* 2013; du Plessis *et al.* 2012), and therefore could generate carry-over effects across seasons (Norris 2005; Runge & Marra 2005) that impact survival and population abundance in the long term (Gardner, Amano, *et al.* 2016). Extending the framework to account for both acute and chronic responses to warming could entail defining discrete states within the avian life stages representing poor versus good body condition, which vary in temperature-dependent vital rate functions and have temperature-dependent transition probabilities between them. Using delay-differential equations to model delayed effects of exposure to high temperatures (such as egg incubation temperature affecting fledgling survival, observed in Berntsen & Bech (2016) and Nord & Nilsson (2016)) is another promising avenue.

Our model captures direct effects of warming on endothermic and ectothermic life stages of birds, but temperature variation can also indirectly affect bird population dynamics through changes to birds' resources (e.g. insect prey) and natural enemies (e.g. parasites and predators). For example, warming could increase insect abundance over short terms (Lehmann *et al.* 2020), thereby boosting survival and/or fecundity among insectivorous birds. Alternatively, higher temperatures could reduce insect abundance or shift insect phenology (Abarca & Spahn 2021; Harvey *et al.* 2023; Williams *et al.* 2015), causing mismatch between prey availability and nestling demand (Both, Van Turnhout, *et al.* 2009; Burgess *et al.* 2018; Vatka *et al.* 2011; Visser *et al.* 1998). Extending our modeling framework to explicitly incorporate trophic dynamics (e.g. Casas Goncalves & Amarasekare 2021) and phenological shifts would help capture this important dimension of avian responses to climate warming as well as the cascading responses across communities.

In nature, direct and indirect effects of temperature will interact with other abiotic factors to affect bird population dynamics. Habitat structure, topography, and other local factors mediate the operative temperatures that individual birds experience (Cunningham, Gardner, *et al.* 2021; Dzialowski 2005), and accounting for such variation can yield important insights into population- and species-level variation in how they respond to warming. Accurately predicting warming effects on population dynamics of birds outside of deserts, especially tropical zones, will require accounting for humidity, since high levels of humidity affect the physiology of thermoregulation (Gerson *et al.* 2019; van Dyk *et al.* 2019). Global climate change is also likely to entail shifts in precipitation regimes, including intensification of drought and rainfall across different regions (Douville *et al.* 2023). Such changes can have sizeable effects on bird populations (Anctil *et al.* 2014; Bourne, Cunningham, *et al.* 2020b; Canonne *et al.* 2023; Öberg *et al.* 2015), but require further theoretical and empirical research to mechanistically link variation in precipitation to bird vital rates (Boyle *et al.* 2020).

1.5.4 Conclusion

In summary, integrating the temperature responses of vital rates into a dynamic model that incorporates all avian life stages provides a powerful framework for projecting bird population dynamics under future climate warming. Our simulations reveal that stochastic hot extremes represent an immediate threat and that realistic levels of warming over the next century may cause severe declines in abundance. Our work represents a critical first step for developing a mechanistic understanding of the multifaceted impacts of climate warming on avian population dynamics.

Chapter 2

Integrating the effects of temperature-induced condition changes on bird population dynamics under climate warming

2.1 Abstract

Temperature variation can have acute effects on behavior, physiology, and vital rates that shape population trajectories under warming. The rising and extreme temperatures associated with warming can also cause changes to body condition that can persist beyond the exposure to such temperatures, but the relative importance of acute versus chronic responses to temperature in shaping population dynamics is unknown. Here we introduce a mechanistic framework that captures both the acute temperature responses of vital rates and the chronic temperature responses that manifest as costly poor condition. Using non-migratory arid-zone passerines as a case study, we investigate the relative importance of these temperature responses in shaping warming outcomes for bird populations. We find that, if recovery to good condition is sufficiently slow (e.g. > 10 days), temperature-induced chronic changes to condition can cause declines to population dynamics even for levels of warming that do not affect acute temperature responses of vital rates. Rapid recovery and low costs of being in poor condition, however, result in minimal impacts on abundance. At high magnitudes of warming, such as those expected under pessimistic emissions scenarios (e.g. 5°C of warming over 100 years), acute temperature responses have a primary role in shaping population outcomes, but chronic temperature responses of body condition can exacerbate declines. We also find that the seasonal patterns of warming could drive shifts in seasonal timing of poor condition. Finally, our framework underscores the importance of empirically evaluating the demographic consequences of temperature-induced condition declines for more robust predictions of bird population dynamics under global climate warming.

2.2 Introduction

Complex responses of bird behavior and physiology to temperature variation can impact the demographic responses that shape population dynamics, and become increasingly important to understand as climate warming shifts thermal regimes (IPCC 2021; Jenouvrier 2013; McLean, Lawson, *et al.* 2016; Pearce-Higgins *et al.* 2015). Temperature responses can be categorized as acute – i.e. directly responsive to the temperature only during exposure – or chronic, i.e. lasting beyond the period of exposure. For example, thermoregulatory costs have an acute response to temperature, in that they increase when birds experience unusually warm temperatures, but immediately reduce when temperatures become less extreme (McKechnie 2022; Riddell *et al.* 2019). On the other hand, extreme temperatures can cause lasting (chronic) changes to a bird's body condition, the effects of which persist even when temperatures are no longer extreme (Gardner, Amano, *et al.* 2016). While a robust body of research points to the importance of accounting for acute temperature responses when making predictions about population persistence under climate warming (Albright, Mutiibwa, *et al.* 2017; McKechnie & Wolf 2010, Chapter 1), the degree to which chronic changes to body condition caused by temperature extremes affect bird population dynamics remains unclear.

Evidence that even brief periods of exposure to elevated temperatures can have persistent effects on condition comes from studies of numerous species and across life stages (Belnap *et al.* 2019; Bourne, Ridley, Spottiswoode, *et al.* 2021; du Plessis *et al.* 2012; Gardner, Amano, *et al.* 2016; Nord & Giroud 2020; Sharpe, Cale, *et al.* 2019; Van Buskirk *et al.* 2010; van de Ven, McKechnie & Cunningham 2019; van de Ven, McKechnie, Er, *et al.* 2020). For example, adult male White-plumed Honeyeaters survived repeated exposure to >35°C, but were left with lower body mass than expected given their structural size (Gardner, Amano, *et al.* 2016). Exposure to periods of extreme cold weather can also induce increased thermoregulatory costs that result in reduced body condition (Williams *et al.* 2015), as has been shown to occur in Red-winged Fairy-wrens (Gardner *et al.* 2018). Temperature can also affect nestling body condition or body mass, both directly and through reductions in food provisioning by parents that occur during hot periods (Bourne, Ridley, Spottiswoode, *et al.* 2021; Cunningham, Martin, *et al.* 2013; van de Ven, McKechnie, Er, *et al.* 2020; Wiley & Ridley 2016).

For such temperature-induced changes in condition to affect bird population dynamics, variation in condition must translate into consequences for demographic processes such as survival, maturation, and birth. Although the long-term demographic effects of short-term exposure to warm temperatures affecting body condition are largely undescribed, a few illustrative examples point to the potential importance of integrating such effects into predictions of bird population dynamics under climate warming. Among adult male honeyeaters that experienced high temperatures, for example, poor body condition translated into lower survival across the subsequent year (Gardner, Amano, *et al.* 2016). Similarly, temperature-induced changes in nestling body mass have implications for future survival and reproductive success, since mass-at-fledging is a key predictor of juvenile survival (Martin *et al.* 2018; Mitchell *et al.* 2011; Monrós *et al.* 2002). Furthermore, non-optimal egg incubation temperatures can have lasting effects on body condition and survival, even extending into adulthood (Berntsen & Bech 2016; Hepp & Kennamer 2012; Nord & Nilsson 2016).

The timing and mechanistic basis of temperature-induced variation in condition are likely important determinants of the consequences for vital rates and population dynamics. For instance, birds in poor condition can have lower foraging efficiency (Geary *et al.* 2019) or be more susceptible to predation (Crino *et al.* 2017; Dierschke 2003), and thus experience higher mortality than birds in better condition. If extreme temperatures cause poor condition to occur during the breeding season, birds could have less energy to invest in reproduction, potentially leading to reduced birth rates that remain low even under normal temperatures (Martin 1987; Milenkaya *et al.* 2015; Ruffino *et al.* 2014). Reduced body condition during molting could impact quality of the newly molted feathers (Vágási *et al.* 2012), which could affect the bird's thermoregulatory abilities (Nilsson & Svensson 1996; Vágási *et al.* 2012), potentially making it less tolerant of extreme temperatures. The net effect of such changes will also depend on the duration over which poor body condition persists, which might range from a matter of days (e.g. if foraging under better thermal conditions for several days could enable a bird to regain its body mass and/or restore its energy reserves; Sharpe, Cale, *et al.* 2019; van de Ven, McKechnie & Cunningham 2019) to months or years (e.g. if poor feather quality causes low condition across seasons; Podlaszczuk *et al.* 2016)). In sum, temperature variation can affect body condition in various ways, and the ultimate impact on population dynamics could arise through numerous mechanisms and can have variable repercussions. Predicting how such effects translate into long-term consequences for bird population dynamics remains a key gap.

Here, we address this gap by expanding the mechanistic framework we developed in Chapter 1, which captures acute temperature effects on avian population dynamics, to include temperature effects on body condition and the resulting consequences for vital rates. We model discrete body condition states, with temperature-dependent transition rates into and out of condition states. We use our framework to investigate the relative importance of chronic effects of warming on body condition for population dynamics, focusing on arid-zone passerine birds as a case study. Specifically, we consider the impact of variable costs of being in poor vs. good body condition, the extent to which birds can recover good condition under favorable temperatures, and the impact of different seasonal patterns of climate warming on population dynamics.

2.3 Methods

2.3.1 Defining condition

Condition in birds is widely studied, but in the literature can refer to different traits, physiological processes, and repercussions. Broadly, condition refers to a state that affects some aspect of performance, and can be framed conceptually or operationally (Brown 1996). Operational considerations of condition often refer to body condition or energy reserves, estimated through measurement of fat reserves or body mass (Labocha & Hayes 2012), but can also refer to states such as degree of feather wear (Merilä & Hemborg 2000) or differences at the cellular level in oxidative stress (Berntsen & Bech 2021; Costantini 2008; Emami *et al.* 2021; von Schantz *et al.* 1999). Condition can be strongly affected by various factors such as precipitation and habitat quality (Brown & Sherry 2006; Marra, Studds, *et al.* 2015; Norris & Marra 2007; Smith *et al.* 2010), but here we focus on the aspects of body condition that respond to variation in temperature (e.g. Gardner, Amano, *et al.* 2016; Sharpe, Cale, *et al.* 2019). In principle, condition can vary along a continuous axis, but given limited information regarding how vital rates scale with condition, we discretize condition into “good” or “poor” condition states that differ in the parameterization of certain vital rates. Depending on the particular underlying mechanism that characterizes poor condition, the poor condition states could exhibit a higher mortality rate for a given temperature, increased sensitivity to high temperatures, and/or a lower per capita birth rate, for example. The general form of our model can accommodate numerous definitions of condition, with that caution that care should be taken to parameterize and interpret the model with a consistent definition of condition for a given investigation. In our analyses, we operationalize condition as representing high or low energy reserves, and we use empirical information about body condition and body mass to parameterize our model (see Model Analysis).

2.3.2 Model overview

We introduce a stage-structured model of avian population dynamics that incorporates effects of temperature on bird vital rates as well as condition. We extend the mathematical framework from Chapter 1 to include good and poor condition states for each life stage, with temperature-dependent transition rates between condition states (Figure 2.1). The general model allows birds in any life stage to transition from good condition to poor condition depending on temperature, and poor condition juveniles and adults to recover and return to good condition.

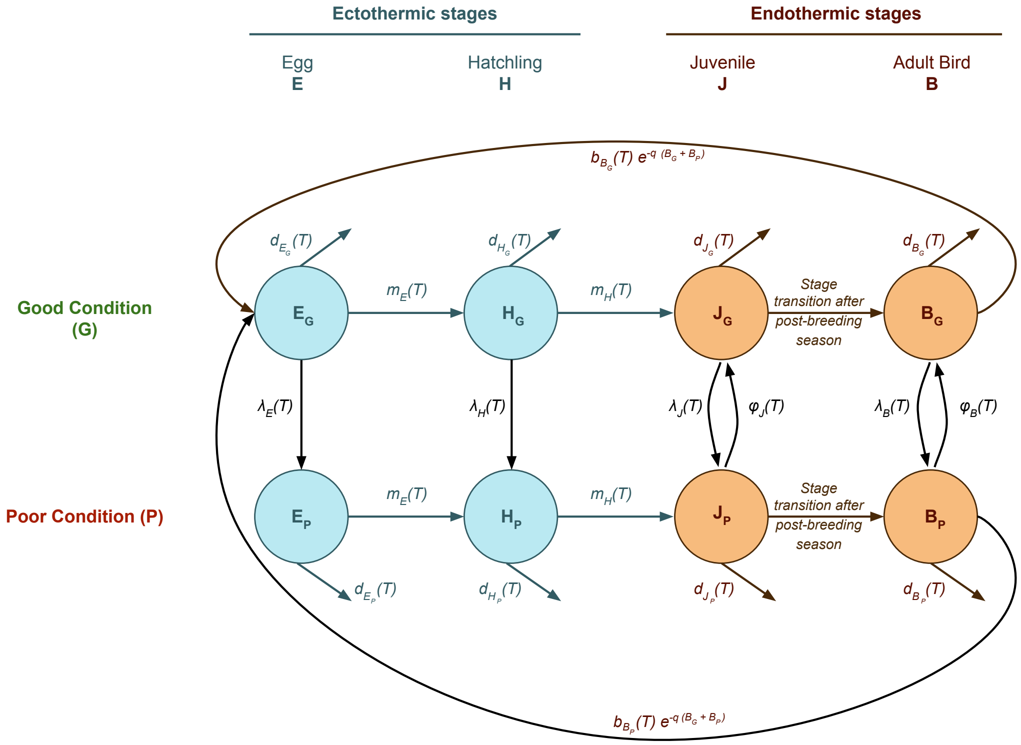

Figure 2.1: General stage- and condition-structured model of avian population dynamics with temperature-dependent vital rates. The model is the same as Chapter 1, with the following addition: each life stage is split into good and poor condition states. Good condition individuals transition to poor condition at temperature-dependent transition probability $\lambda_X(T)$ $(X = E, H, J, B)$, and poor condition juveniles and adults can transition back to good condition at temperature-dependent transition probability $\psi_Y(T)$ $(Y = J, B)$. The temperature-dependent mortality and birth rates for a given life stage depend on condition state.

The dynamics are given by:

Pre-breeding season $(0 \leq t \leq t_{pre})$

$$\begin{aligned}
\frac{dB_{G_{pre}}}{dt} &= -d_{B_G}(T)B_{G_{pre}} - \lambda_B(T)B_{G_{pre}} + \psi_B(T)B_{P_{pre}} \\
\frac{dB_{P_{pre}}}{dt} &= -d_{B_P}(T)B_{P_{pre}} + \lambda_B(T)B_{G_{pre}} - \psi_B(T)B_{P_{pre}}
\end{aligned}$$

initial conditions:

$$B_{G_{pre}}(0,0) = B_0 \text{ for } y = 0$$

$$B_{P_{pre}}(0,0) = 0 \text{ for } y = 0$$

$$B_{K_{pre}}(0,y) = B_{K_{post}}(365, y-1) \text{ for } y > 0 \text{ and } K = G, P$$

Breeding season $(t_{pre} + 1 \leq t \leq t_{br})$

$$\begin{aligned}
\frac{dE_{G_{br}}}{dt} &= (b_{B_G}(T)B_{G_{br}} + b_{B_P}(T)B_{P_{br}})e^{-q(B_{G_{br}}+B_{P_{br}})} - m_E(T)E_{G_{br}} - d_{E_G}(T)E_{G_{br}} - \lambda_E(T)E_{G_{br}} \\
\frac{dH_{G_{br}}}{dt} &= m_E(T)E_{G_{br}} - m_H(T)H_{G_{br}} - d_{H_G}(T)H_{G_{br}} - \lambda_H(T)H_{G_{br}} \\
\frac{dJ_{G_{br}}}{dt} &= m_H(T)H_{G_{br}} - d_{J_G}(T)J_{G_{br}} - \lambda_J(T)J_{G_{br}} + \psi_J(T)J_{P_{br}} \\
\frac{dB_{G_{br}}}{dt} &= -d_{B_G}(T)B_{G_{br}} - \lambda_B(T)B_{G_{br}} + \psi_B(T)B_{P_{br}}
\end{aligned}$$

$$\begin{aligned}
\frac{dE_{P_{br}}}{dt} &= \lambda_E(T)E_{G_{br}} - m_E(T)E_{P_{br}} - d_{E_P}(T)E_{P_{br}} \\
\frac{dH_{P_{br}}}{dt} &= \lambda_H(T)H_{G_{br}} + m_E(T)E_{P_{br}} - m_H(T)H_{P_{br}} - d_{H_P}(T)H_{P_{br}} \\
\frac{dJ_{P_{br}}}{dt} &= \lambda_J(T)J_{G_{br}} + m_H(T)H_{P_{br}} - d_{J_P}(T)J_{P_{br}} - \psi_J(T)J_{P_{br}} \\
\frac{dB_{P_{br}}}{dt} &= \lambda_B(T)B_{G_{br}} - d_{B_P}(T)B_{P_{br}} - \psi_B(T)B_{P_{br}}
\end{aligned}$$

initial conditions:

$$X_{K_{br}}(t_{pre}+1,y) = 0 \text{ for } X_K = E_K, H_K, N_K, J_K \text{ and } K = G, P$$

$$B_{K_{br}}(t_{pre}+1,y) = B_{K_{pre}}(t_{pre}+1,y)) \text{ for } K = G, P$$

Post-breeding season ($t_{br}+1 \leq t \leq 364$)

$$\begin{aligned}
\frac{dE_{G_{post}}}{dt} &= -m_E(T)E_{G_{post}} - d_{E_G}(T)E_{G_{post}} - \lambda_E(T)E_{G_{post}} \\
\frac{dH_{G_{post}}}{dt} &= m_E(T)E_{G_{post}} - m_H(T)H_{G_{post}} - d_{H_G}(T)H_{G_{post}} - \lambda_H(T)H_{G_{post}} \\
\frac{dJ_{G_{post}}}{dt} &= m_H(T)H_{G_{post}} - d_{J_G}(T)J_{G_{post}} - \lambda_J(T)J_{G_{post}} + \psi_J(T)J_{P_{post}} \\
\frac{dB_{G_{post}}}{dt} &= -d_{B_G}(T)B_{G_{post}} - \lambda_B(T)B_{G_{post}} + \psi_B(T)B_{P_{post}}
\end{aligned}$$

$$\begin{aligned}
\frac{dE_{P_{post}}}{dt} &= \lambda_E(T)E_{G_{post}} - m_E(T)E_{P_{post}} - d_{E_P}(T)E_{P_{post}} \\
\frac{dH_{P_{post}}}{dt} &= \lambda_H(T)H_{G_{post}} + m_E(T)E_{P_{post}} - m_H(T)H_{P_{post}} - d_{H_P}(T)H_{P_{post}} \\
\frac{dJ_{P_{post}}}{dt} &= \lambda_J(T)J_{G_{post}} + m_H(T)H_{P_{post}} - d_{J_P}(T)J_{P_{post}} - \psi_J(T)J_{P_{post}} \\
\frac{dB_{P_{post}}}{dt} &= \lambda_B(T)B_{G_{post}} - d_{B_P}(T)B_{P_{post}} - \psi_B(T)B_{P_{post}}
\end{aligned}$$

initial conditions:

$$X_{K_{post}}(t_{br}+1,y) = X_{K_{br}}(t_{br}+1,y) \text{ for } X = E, H, J, B \text{ and } K = G, P \tag{2.1}$$

where the state variables, E, H, J, and B represent, respectively, the abundances of eggs, hatchlings, juveniles, and adults, and the subscripts G and P indicate good or poor condition states. The parameter q depicts the intraspecific competition coefficient, the index y the year of the simulation, and t_{pre} and t_{br} the last days of the pre-breeding and breeding seasons, respectively. The functions $b_K(T)$ $(K = G, P)$, $m_X(T)$ $(X = E, H)$, and $d_{Z_K}(T)$ $(Z = E, H, J, A$ and $K = G, P)$ depict, respectively, the temperature responses of per capita birth, maturation, and mortality rates, and the functions $\lambda_X(T)$ $(X = E, H, J, B)$ and $\psi_Y(T)$ $(Y = J, B)$ depict for a given life stage the transition rates between, respectively, good to poor condition states and poor to good condition states. Note that the birth and mortality rates depend on condition state $(G,\ P)$.

2.3.3 Temperature-dependent transition rates between condition states

We derive functional forms for the rates of transition between condition states by assuming that birds can retain good body condition under most typical temperatures, but that condition deteriorates during extreme temperatures and can only be recovered when experiencing an ideal range of temperatures. While the functional shape of the temperature response of such transition rates has not be described in the literature, several studies have documented threshold maximum daily temperatures above or below which adult birds lose body mass or experience reductions in body condition over the course of 24 hours (Bourne, Ridley, McKechnie, *et al.* 2021; du Plessis *et al.* 2012; Gardner, Amano, *et al.* 2016; Gardner, Rowley, *et al.* 2018; Sharpe, Cale, *et al.* 2019; van de Ven, McKechnie & Cunningham 2019; van de Ven, McKechnie, Er, *et al.* 2020). We therefore use modified generalized normal functions to describe the temperature response of both the rate of transition from good to poor condition ($\lambda_X(T)$, $X = E, H, J, B$) and the rate of transition from poor to good condition ($\psi_Y(T)$, $Y = J, B$). The temperature responses functions of the condition transition rates are given by:

$$\begin{aligned}
\lambda_X(T) &= -\lambda_{X_{max}} e^{-\left(\frac{|T-T_\mu|}{\beta_\lambda}\right)^{\alpha_\lambda}} + \lambda_{X_{max}} \\
\psi_Y(T) &= \psi_{Y_{max}} e^{-\left(\frac{|T-T_\mu|}{\beta_\psi}\right)^{\alpha_\psi}}
\end{aligned} \tag{2.2}$$

where $\lambda_X(T)$ of stage $X = E, H, J, B$ is the transition rate from good to poor condition state; $\psi_Y(T)$ for stage $Y = J, B$ is the transition rate from poor to good condition state. $\lambda_{X_{max}}$ and $\psi_{Y_{max}}$ represent, respectively, the maximum values of $\lambda_X(T)$ and $\psi_Y(T)$; both functions are centered around temperature T_μ; β_Z ($Z = \lambda, \psi$) represents, respectively, the variation in $\lambda_X(T)$ and $\psi_Y(T)$ around T_μ; and α_Z ($Z = \lambda, \psi$) describes the kurtosis of the functions. We assume that $\psi(T)$ has a narrower breadth than $\lambda_X(T)$ (i.e., $\beta_\psi < \beta_\lambda$), since birds cannot recover to good condition at a temperature where they are also losing good body condition.

2.3.4 Model analysis

Parameterization

We focus our analysis on non-migratory arid-zone passerine birds as a case study. Such species live close to their thermoregulatory limits, and have been observed to suffer reductions in body condition as a result of high temperature exposure (Bourne, Ridley, Spottiswoode, *et al.* 2021; Gardner, Amano, *et al.* 2016; Sharpe, Cale, *et al.* 2019; Wiley & Ridley 2016). Having investigated the acute responses of vital rates to warming scenarios in Chapter 1, we use this same system to now evaluate the role of chronic responses to warming for population dynamics. We therefore parameterize all vital rate (birth, maturation, mortality) temperature response functions using the same parameterization from Chapter 1.

As a first step toward using our framework to investigate the impacts of temperature-induced changes in condition on population dynamics, we focus on the condition state of the adult life stage. We allow only adults to change from good to poor or from poor to good condition by setting $\lambda_X(T) = 0$ for $X = E, H, J$, and $\psi_J(T) = 0$. We use reported temperature thresholds (Supplemental Table S1) to parameterize the $\lambda_B(T)$ and $\psi_B(T)$ functions (Figure 2.2).

Thermal regimes

We investigate the model under no-warming and warming scenarios. For the no-warming scenario, we follow the framework from Chapter 1, which implements a deterministic thermal regime with both seasonal and diurnal variation in temperature. For warming scenarios, we use deterministic warming scenarios from Chapter 1, which enables us to investigate both changes in the magnitude of warming over 100 years (1.5-, 3-, or 5-degree increase in mean annual temperatures over 100 years) and in the variance in temperature over 100 years ("warmer winters" where the minimum annual temperature increases faster than the maximum, "warmer summers" where the maximum annual temperature increases faster than

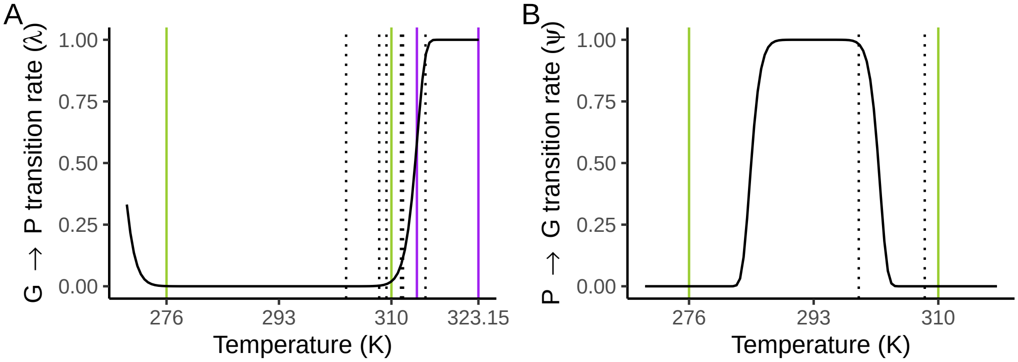

Figure 2.2: Temperature-dependent transition rate functions. **A** depicts the $\lambda_B(T)$, the rate of transition from good to poor condition for adults; **B** depicts the $\psi_B(T)$, the rate of transition from poor to good condition for adults. Vertical green lines depict the annual minimum and maximum temperatures under typical seasonal variation in temperature. In **A**, purple vertical lines indicate the endothermic upper mortality inflection point (T = 313.85 K) and the endothermic total mortality point (T = 323.15 K). Dashed vertical lines are maximum daily temperatures reported in the literature as thresholds above which adult birds experience a loss in body mass or body condition (Supplemental Table B.1). In **B**, dashed vertical lines are maximum daily temperatures reported in the literature as temperatures below which birds have a net daily increase in body mass (Supplemental Table B.1).

the minimum, and "baseline warming" where temperatures increase at the same rate).

As in Chapter 1, we focus on non-migratory arid-zone passerine birds, and thus define the deterministic no-warming and warming equations with parameters based on data from the Sonoran Desert.

Temperature response of adult condition

To investigate the relative importance of temperature-induced changes in adult condition state on population abundance, we explore two features that characterize the poor condition state: first, the extent to which good condition can be recovered, and second, the consequences of being in poor condition.

We begin by comparing the effect of three baseline warming scenarios with varying magnitude of warming (1.5-, 3-, or 5-degree increase in mean annual temperatures over 100 years) on population dynamics, for populations with and without the ability to recover good condition. For these, we define the cost of being in poor condition as having a 20% higher mortality rate (i.e., the poor condition adult mortality rate ($d_{B_P}(T)$) has the same shape as the good condition adult mortality rate ($d_{B_G}(T)$), and therefore the same temperature thresholds, but is shifted 20% higher).

Next, we assess the importance of the type and magnitude of the cost of being in poor condition. Specifically, we explore variation in the mortality rate shift as well as variation in the birth rate relative to good condition adults, while also exploring variation in $\psi_B(T)$ to compare differences in good condition recovery rate. For this analysis, we focus on 1.5° of baseline warming.

Finally, we investigate whether the seasonality of temperature-induced poor condition affects warming outcomes for populations. We use an alternate parameterization of $\lambda_B(T)$ which allows for good-to-poor condition state transitions due to cold temperatures ($< 5^\circ$C, Gardner, Rowley, *et al.* (2018)) experienced in winter under typical seasonal variation (no warming), as well as due to hot temperatures experienced under warming. We compare the effect on population abundance of different patterns of deterministic warming (warmer winters, warmer summers, and baseline warming).

All analyses were performed in R version 4.3.2 (R Core Team 2022).

2.4 Results

With our parameterization based on arid-zone passerine birds, transitions to poor condition can occur even for levels of warming that are not hot enough to generate acute effects on vital rates (i.e. baseline warming with a 1.5-degree increase in mean annual temperature over 100 years, which never exceeds mortality inflection points; Figure 2.3). These transitions from good to poor condition occur during a short window of peak summer temperatures. When birds in poor condition can recover rapidly into good condition, the peak of poor condition adults is small and lasts only a short period of time (Figure 3B). When birds cannot recover from poor to good condition, the population of poor condition birds grows as temperatures rise and is present in the population year-round (Figure 2.3C).

The effect on abundance of these good-to-poor condition transitions depends on whether adults can recover (Figure 2.4). Allowing poor condition birds to recover rapidly has a relatively small effect on abundance, though this effect increases with magnitude of warming. In contrast, if poor condition is permanent, populations can decline substantially. For example, 1.5 degrees of warming in a population of birds that cannot recover from poor condition is more detrimental than 3 degrees of warming when we do not account for temperature effects on condition.

We examined recovery rate and the cost of being in poor condition more closely under 1.5 degrees of warming. We found that fast rates of recovery (e.g. $<$ 10 days needed under favorable temperatures) considerably reduce the effect of condition on population abundance

(Figure 2.5). If recovery takes longer than 10 days under favorable temperatures, reductions in population abundance can be moderate to substantial, depending on the severity of the cost of being in poor condition. This trend holds true regardless of whether being in poor condition imposes a cost to adult birds' baseline mortality rates (Figure 2.5A), or to their birth rates (Figure 2.5B).

Bird populations in which transitions to poor condition can happen at typical cold temperatures experience good-to-poor condition state transitions in the winter, but recover as temperatures become seasonally warmer under typical seasonal variation (Figure 2.6A). Climate warming that arises primarily through increased winter temperatures eliminates these winter peaks (Figure 2.6B). If the same extent of average climate warming occurs due to increases in year-round temperatures (i.e. baseline warming), the winter season peaks of poor condition are reduced or eliminated, but new poor condition peaks arise during the summers (Figure 2.6C). The magnitude of these summer peaks is even higher under a warming regime that primarily increases summer temperatures; moreover, the nature of warming in this scenario means that the winter peaks also persist, albeit reduced in abundance (Figure 2.6D).

These changes in the timing and magnitude of poor condition peaks can have variable effects on the overall population sizes (Figure 2.7). Even under relatively high amounts of overall warming, if this warming arises due to warmer winters, there is a minor benefit to populations sizes. For other patterns of warming, warming is initially beneficial, but then the increasingly large summer peaks, combined with warming impacts on vital rates, outweigh any possible benefits (especially for 3 and 5C of warming).

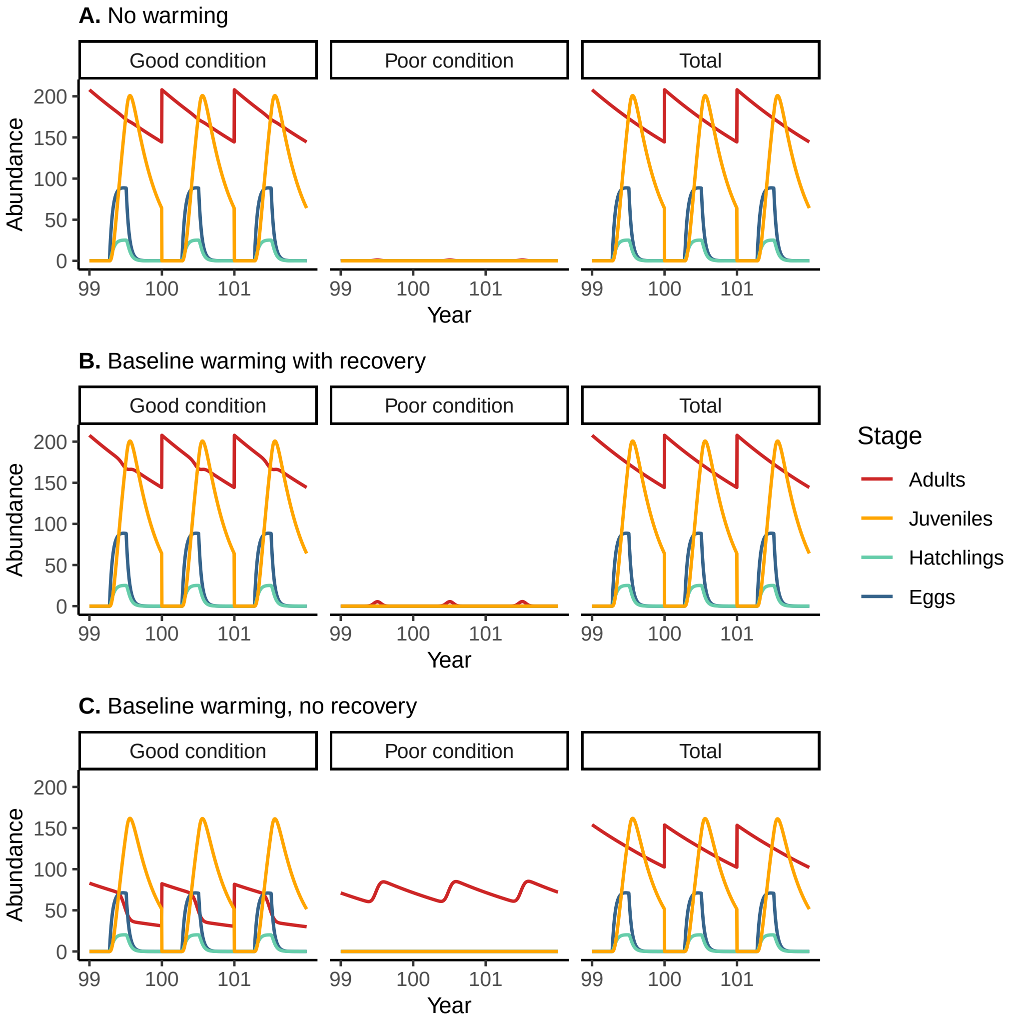

Figure 2.3: Abundance time series for the last two years of the simulation, under (A) no warming, (B) baseline warming (1.5 degrees over 100 years) with adults able to recover rapidly from poor to good condition (1 day recovery in optimal temperature), or (C) baseline warming (1.5 degrees over 100 years) with adults unable to recover to good condition. The cost of adult poor condition is a 20% higher mortality rate than the mortality rate for good condition adults. The abundances of good condition birds (first column) summed with abundance of poor condition birds (second column) give the total abundance (third column).

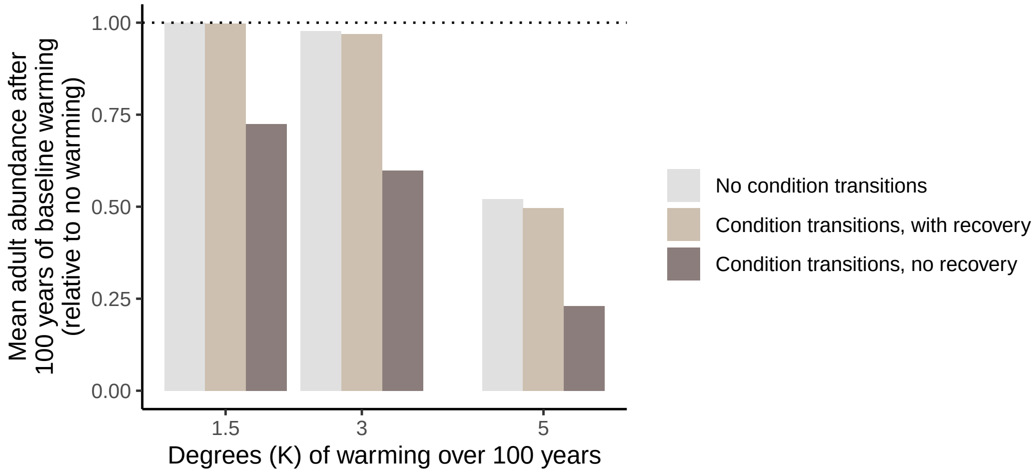

Figure 2.4: Mean adult abundance under different magnitudes of baseline warming (1.5, 3, or 5 degrees over 100 years) depends on whether we account for temperature effects on condition and whether poor condition is permanent. Simulations that do not include temperature-dependent condition are in gray; simulations that account for condition but permit rapid recovery (1 day recovery in optimal temperature) are in light brown; simulations that account for condition but do not allow any recovery are in dark brown.

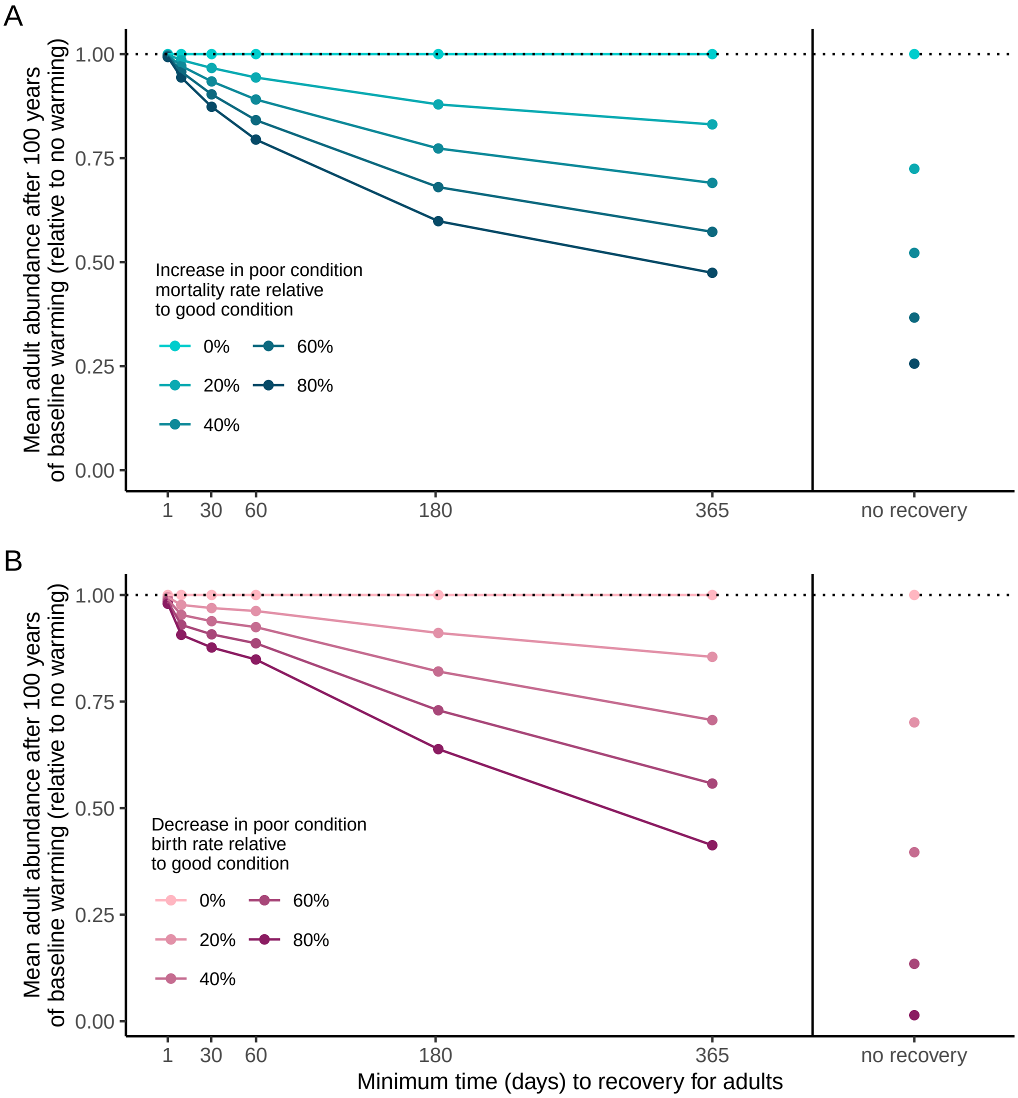

Figure 2.5: Mean adult abundance under baseline warming (1.5 degrees over 100 years) depends on the rate of recovery from poor to good condition and the cost of being in poor condition. whether cost is defined as (**A**) higher mortality rate or (**B**) lower birth rate for poor condition adults. The dotted horizontal line represents the abundance under no warming, with no transitions to poor condition. The x-axis is calculated as 1/the maximum rate of recovery to good condition, and can be interpreted as the recovery time needed in optimal temperature for recovery.

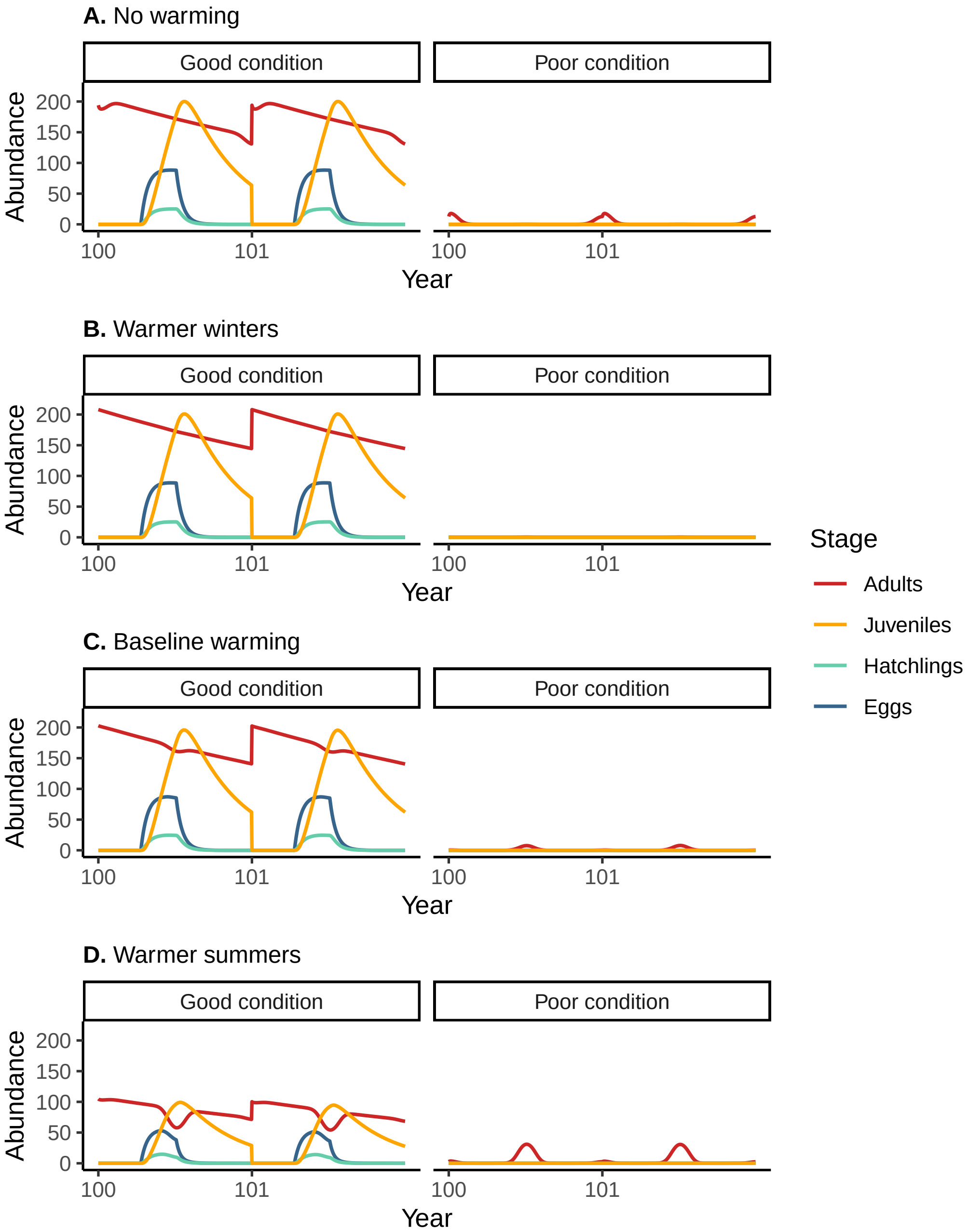

Figure 2.6: Timing of poor condition peaks varies with temperature regime, for a population that is sensitive to typical winter temperatures and can recover rapidly (1 day recovery in optimal temperature) to good condition. Panels depict abundance time series for the last two years of simulations under no warming (A) vs three warming scenarios with a 3-degree increase in average annual temperatures over 100 years: warmer winters (B), baseline warming (C), and warmer summers (D). The cost of adult poor condition is a 20% higher mortality rate than the mortality rate for good condition adults. Total abundance is not depicted here since the total depends on the effects of both direct temperature effects on vital rates and temperature-induced poor condition.

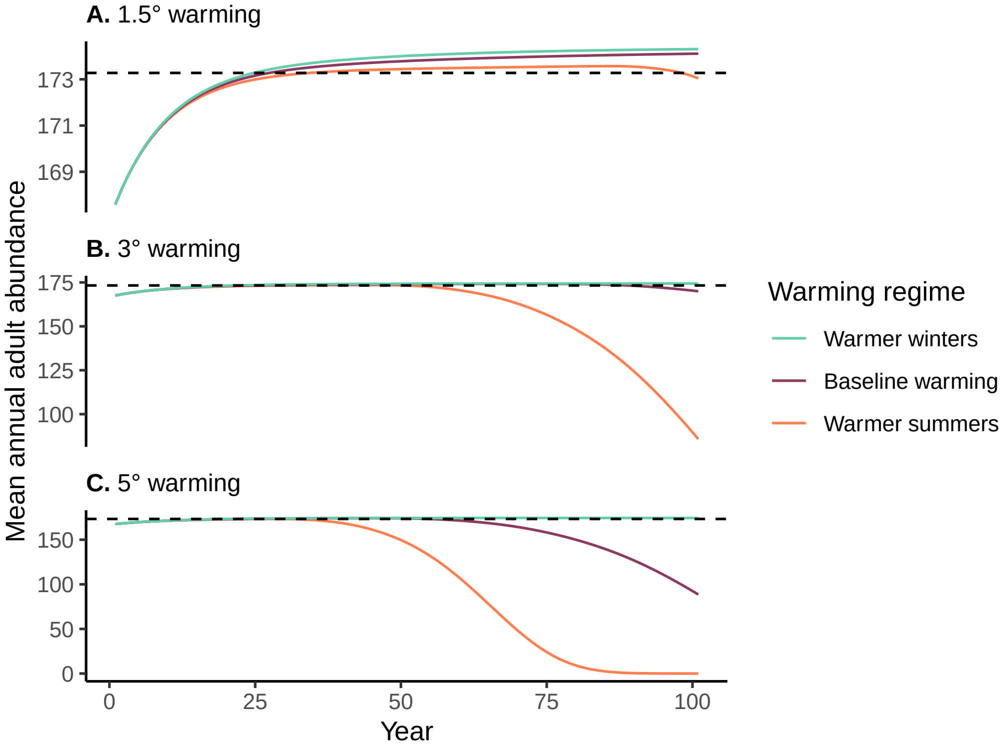

Figure 2.7: Mean annual abundance timeseries for a population with condition sensitive to typical winter temperatures and rapid recovery (1 day recovery in optimal temperature) to good condition, depicting simulations under three magnitudes of warming (A: 1.5 degrees; B: 3 degrees; C: 5 degrees) with different patterns of warming (turquoise: warmer winters; purple: baseline warming; orange: warmer summers). Dashed horizontal line represents mean annual abundance in year 100 for a simulation with no warming.

2.5 Discussion

We developed a novel theoretical framework to evaluate the effects of temperature-driven variation in condition on bird species' long-term population dynamics under climate warming, and analyzed the model using parameter values informed by the physiology of non-migratory arid-zone passerine birds. Our results indicate that under certain scenarios, warming-induced persistent changes to adult condition can result in reductions in abundance beyond what would be expected if birds experienced only acute (i.e. immediate) effects of warming on vital rates. We also find that different patterns of warming (e.g. warming that occurs due to higher temperatures throughout the year, vs. warming driven by an increase in summer temperatures alone) have different implications for how changes in condition affect long-term dynamics.

Our analysis yields two key findings regarding the role of temperature-induced condition changes on arid-zone passerine population dynamics. First, we find that the degree to which temperature-mediated changes to adult condition scale up to affect population dynamics depends on the cost associated with being in poor vs. good condition, and on the extent to which birds in poor condition can recover good condition under favorable temperatures (Figure 2.5). Specifically, when birds can rapidly recover into good condition, the impact of temperature-induced condition deterioration on abundance is low, even if costs of being in poor condition are high. In contrast, when the recovery rate from poor to good condition is sufficiently low, these chronic effects of temperature on condition can substantially reduce population abundance, even under low levels of warming that otherwise do not affect bird vital rates (1.5°C of baseline warming over 100 years; Figure 2.4). Thus, if adult poor condition is long-lasting or even irreversible, not accounting for chronic temperature responses of condition risks substantially underestimating the consequences of warming on arid-zone passerine populations, regardless of the predicted magnitude of future climate warming.

Whether or not such long-lasting condition changes arise due to warming temperatures, however, is likely to depend on the specific aspect of condition that is affected by temperature. For example, chronic responses of adult condition are often measured in terms of changes to body mass or fat reserves, which are likely recoverable on a short timescale, such as a matter of days (e.g. Sharpe, Cale, *et al.* 2019). On the other end of the spectrum, irreversible temperature-induced poor condition is easier to envision for early life stages, where temperature stress during early development can cause life-long changes to condition, such as degree of oxidative stress or differences in mass and morphology (Belnap *et al.* 2019; Berntsen & Bech 2021; Nord & Nilsson 2016). Even so, the rate of recovery to good condition for adults can be low if it results in cascading effects of poor condition (e.g., juvenile feather quality impacts the timing of energy-intensive molting, thus reducing energy reserves in a future season; Podlaszczuk *et al.* 2016). Lower recovery rates could also arise if we accounted for severity of poor condition (e.g., body mass is continually lost every day of exposure to elevated temperatures (du Plessis *et al.* 2012; van de Ven, McKechnie & Cunningham 2019), so the length of exposure should affect the total body mass lost, which must be recovered to return to good condition). Furthermore, as temperature rise and the intensity, frequency, and duration of extreme temperatures increase (IPCC 2021), the probability of being in poor condition while also experiencing elevated temperatures that do not allow for recovery could make interactive effects of temperature and poor condition on vital rates more important than poor condition recovery rate, simply because the circumstances permitting recovery are rarer.

Our second key result addresses the consequences of climate warming for arid-zone passerines that are sensitive to cold temperatures. We find that such species may experience a transient benefit of climate warming if warming occurs primarily due to warmer winter temperatures (Figure 2.7). Even under such conditions, however, these benefits are minor given our model parameterization. If summer temperatures increase at the same or faster rate as winter temperatures, any benefits of milder winters are likely to be overwhelmed by the negative effects of rising summer temperatures – especially under 3° or 5°C of warming over the next century. These results are consistent with recent work in Australia on changes in body condition and survival following different patterns of warming. In a study in western Australia, Red-winged Fairy-wrens experienced fewer cold extremes (< 5°C) and relatively mild summers, and showed a corresponding increase in body condition (Gardner, Rowley, *et al.* 2018), which is aligned with our finding that mitigating winter temperatures due to warming could improve body condition. In a study of banding data across semi-arid eastern Australia, improvements in survival during wintertime due to warming could not offset reductions in survival due to warmer summers (Gardner, Clayton, *et al.* 2022), as we predict for warming regimes that experience increases in both winter and summer temperatures.

Our analysis examining dynamics for cold-sensitive arid-zone passerines also highlights how differences in warming regimes could alter the timing of peak poor condition in a population. Under typical seasonal variation in temperature, adults transitioned to poor condition only during the winter (Figure 2.6A). Warming regimes that had significant increases in winter temperatures (i.e., warmer winters and baseline warming) could greatly reduce or even eliminate the number of adults transitioning to poor condition during the winter, but if summer temperatures also increased substantially (i.e., under baseline warming and warmer summers regimes) temperature-induced transitions to poor condition shifted to the summer (Figure 2.6B-D). Especially if temperature-induced poor condition is a transient state, the shift in timing of poor condition could have different impacts on population dynamics. Accounting for additional energy-demanding events that have specific seasonal timings across the annual cycle (e.g. molting and migration) could uncover additional impacts of poor condition on population dynamics. Additionally, given our previous finding that stochastic heat extremes can have outsized consequences for arid-zone passerine populations beyond those expected for an equivalent level of deterministic warming (see Chapter 1), evaluating the impacts of such stochastic extremes when temperature can also affect condition is a clear next step.

Of course, the relative importance of chronic responses of condition versus acute responses of vital rates on bird population dynamics could differ outside of the arid-zone. Birds that do not live as close to their thermal limits may not experience such strong acute vital rate responses to extreme temperatures, making the role of temperature-induced condition changes (which can arise even for temperatures that do not cause acute mortality) relatively more important. On the other hand, the relative importance of temperature for impacting condition could be lower than other factors such as habitat quality and/or precipitation (Brown & Sherry 2006; Marra, Studds, *et al.* 2015; Norris & Marra 2007; Smith *et al.* 2010). Indeed, drought has been shown to exacerbate temperature responses of condition (Bourne, Cunningham, *et al.* 2020b; Gardner, Amano, *et al.* 2016), although not in all cases (Van Buskirk *et al.* 2010). Furthermore, while we investigated cold sensitivity of body condition, we did not examine the potential role of chronic responses to stochastic extreme cold temperatures on population dynamics. Though the frequency of extreme cold events are generally declining due to climate change (Ummenhofer & Meehl 2017), in some areas of the world, phenological shifts in breeding timing could make exposure of early life stages (eggs, hatchling, nestlings) to extreme cold temperatures more common (Regan & Sheldon 2023; Shipley *et al.* 2020). Addressing the impact of such stochastic extremes is an important next step.

Our model lays the groundwork for future theoretical work aimed at evaluating the complex pathways through which climate warming can affect bird population dynamics. While the most general form of our modeling framework allows for temperature to affect condition at all life stages, our analyses focus only on the population dynamics consequences of temperature-induced changes to adult condition. Evaluating how variation in temperature-induced condition transitions of egg, hatchling, and nestling stages affect population dynamics is a key next step. This extension should account for potential direct effects of temperature on early-life stages as well as the indirect effects of temperature that can arise because of variation in adult provisioning of food to hatchlings and nestlings under warmer temperatures (Bourne, Ridley, Spottiswoode, *et al.* 2021; Cunningham, Kruger, *et al.* 2013; Wiley & Ridley 2016). Finally, a promising area for future development of this framework is to explicitly incorporate information about how bird vital rates scale with body mass, which is often measured in the field as an empirical proxy for body condition. Such a model would be ideally suited for comparative analyses of how acute and chronic temperature responses and their impact on population dynamics may vary across species.

Our model analysis builds on parameter values derived from a vast body of empirical research on temperature-dependent physiology of arid-zone passerine birds (Supplemental Table B.1, see also Chapter 1), but our work nevertheless underscores the importance of addressing key gaps in our empirical understanding of bird condition. Specifically, while numerous studies have documented changes in body condition due to exposure to extreme temperatures (e.g. Bourne, Ridley, Spottiswoode, *et al.* 2021; du Plessis *et al.* 2012; Gardner, Amano, *et al.* 2016; Sharpe, Cale, *et al.* 2019; van de Ven, McKechnie & Cunningham 2019; van de Ven, McKechnie, Er, *et al.* 2020), there is little quantitative evidence regarding how temperature-induced condition affects key vital rates, and on the rate at which birds in poor condition can recover to a good condition (Milenkaya *et al.* 2015). The consequences of variation in condition on bird performance during migration and breeding are relatively well-studied (Cooper *et al.* 2015; Marra, Hobson, *et al.* 1998; Marra & Holberton 1998; Studds & Marra 2005, 2007; Tonra *et al.* 2011), and extending this body of work to quantifying temperature-dependence of these effects is an important avenue for future empirical research as temperatures rise around the globe.

In conclusion, we present an integrative theoretical framework for generating quantitative predictions regarding the role of temperature-induced changes in bird condition on long-term bird population dynamics. We show that the consequences of such effects for desert-dwelling birds vary with how severely poor condition affects the vital rates that underlie bird population dynamics, and on the rate at which poor condition birds can regain good condition. We also show that under high (but realistic) levels of climate warming, the primary detriment to arid-zone bird population dynamics will arise from the acute effects of temperature on bird vital rates rather than through changes to condition. Finally, our work highlights key gaps in our empirical understanding of how temperature affects bird condition, and in how condition in turn affects the vital rates that determine long-term demography.

Chapter 3

Behavioral mechanisms underlying trait-mediated survival in a coral reef fish

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M.C. developed the analytical approach, conducted the statistical analysis, and wrote the manuscript with T.R. and S.S. T.R. collected field data with K.S. All authors contributed to writing and revisions.

3.1 Abstract

Fast growth and large size generally increase survivorship in organisms with indeterminate growth. These traits frequently covary, but where they do not, trade-offs often exist in the behavioral choices of organisms. Juvenile bicolor damselfish Stegastes partitus that settle to coral reefs at larger sizes generally experience enhanced survivorship but have slower juvenile growth rates. We hypothesized that differences in behavior may mediate this trade-off, so to test whether trait-related behaviors or the traits themselves enhance early survival, we combined individual behavioral observations with otolith (ear stone)-based daily growth measurements for juvenile S. partitus in the Florida Keys. Foraging, sheltering, and chasing behaviors of 256 fish were measured during five different months (2008-2009) and patterns of differential survival were similar to those from a 6-year (2003-2008) recruitment time-series. We found a trade-off between sheltering and foraging that significantly explained patterns in size-at-settlement: damselfish that settled at larger sizes spent less time sheltered and more time feeding high in the water column. Juvenile growth rates were unrelated to any of the sheltering-foraging behaviors, but instead were inversely related to adult conspecific density. Damselfish that settled near higher densities of conspecifics were subjected to increased territorial chasing. Chasing intensity interacted with settlement size such that large juveniles who were chased more frequently exhibited slower growth rates, whereas smaller settlers did not experience this energetic cost. Thus, the dominant survival strategy of S. partitus is to settle at a large size and spend more time foraging high in the water column while dodging

conspecifics at an energetic cost to their growth rates. Size-at-settlement is determined during the larval period and after settlement, this trait is key to subsequent behaviors and the strength of trait-mediated survival. Understanding how somatic growth, body size, and survival are intertwined in early life is necessary to help explain population dynamics.

3.2 Introduction

Predation is one of the major selective forces shaping the form and behavior of animals (Endler 1991). This is particularly true of the minuscule early life stages of marine organisms, which frequently endure high mortality rates due to predation (Houde 2002; Sogard 1997). Individuals with morphologies or behaviors that facilitate avoidance of or escape from predators will have a greater probability of surviving to reproductive maturity and increasing their fitness.

The Growth-Mortality Hypothesis (Anderson 1988), or as it has been recently renamed, the Growth-Survival Paradigm (GSP; Robert *et al.* (2023)), provides a theoretical framework for evaluating which traits may be selectively removed from a population by predators. Focused on the youngest life stages when all animals are most vulnerable to predation, the paradigm posits that individuals that grow faster, attain larger sizes-at-age, or have reduced early life stage durations experience enhanced survival. Much evidence has accumulated that suggests this may indeed be the case for a diversity of taxa (Arendt 1997), including fishes (e.g., Marshall *et al.* (2003), Searcy & Sponaugle (2001), and Semlitsch *et al.* (1988)).

However, fast growth is also known to be associated with reduced fitness (Alonso-Alvarez *et al.* 2007; Arendt 2003; Gotthard 2000; Olsson & Shine 2002; Rankin & Sponaugle 2011) and several potential trade-offs with accelerated growth may explain why slower growth can be beneficial. For example, rapid growth may be attained at the expense of development, tissue maintenance, and repair, and for fish, swimming capabilities (Arendt 1997). Compromise of these functions could result in a reduced ability to escape predation.

Conflicting field and laboratory results for different fish species over the past four decades have created some debate about the generality of the GSP. A recent review reconsidered the empirical evidence for the GSP and proposed a new synthetic framework that encompasses a range of patterns of selective survival (Robert *et al.* 2023). While the GSP and this new framework include reference to behaviors underpinning trait-based predation, it is challenging to document behaviors that are linked directly to survival.

Behavior likely mediates the relationship between growth, size, and vulnerability to predation. For instance, increased foraging activity or selection of certain foraging habitats may result in accelerated growth, but also greater visibility to predators (Biro, Abrahams, *et al.* 2006; Biro & Stamps 2008; Stamps 2007). These trade-offs have been proposed as drivers of the evolution of submaximal growth rates in some taxa (Biro, Abrahams, *et al.* 2006; Stoks *et al.* 2005). Additionally, initial size may further interact with behavior to influence growth and survival. For example, smaller fish are more vulnerable to gape-limited predation and therefore may be more wary and shelter more often or for longer durations (Sogard 1997). However, smaller individuals also typically have lower fat reserves, higher weight-specific metabolic requirements, and larger drag coefficients, and therefore may need to spend more time foraging than larger individuals (Krause *et al.* 1998; Wooton 1994).

For a common Western Atlantic reef fish, the bicolor damselfish, *Stegastes partitus*, individuals that preferentially survived the first few weeks on the reef (i.e., post-settlement) were those that were larger at settlement but had slower juvenile growth rates during the first week of life on the reef (Rankin & Sponaugle 2011). A similar relationship between juvenile growth and survival was observed in older juveniles of this species in the Bahamas (Johnson & Hixon 2010) and field experiments demonstrated that increased intraspecific chases reduced juvenile growth rates (Johnson 2008). Slower juvenile growth is contrary to both the current paradigm (Anderson 1988) and to observations of survival in other western Atlantic reef fishes (e.g., Grorud-Colvert & Sponaugle (2011) and Searcy & Sponaugle (2001)). The objective of the present study was to identify the behavioral mechanisms underlying these relationships among settlement size, juvenile growth rate, and survivorship.

While we have previously documented selective survival of large *S. partitus* settlers who grew more slowly as juveniles (Rankin & Sponaugle 2011), as well as changes in the patterns of selective survival with water temperature and lunar phase (Rankin & Sponaugle 2011, 2014), we were only able to speculate on the underlying behavioral mechanisms. In the present study, to tease apart the role of the early life history traits and test the hypothesis that survival-related behaviors underlie these selective patterns, we observed early juvenile behaviors of multiple cohorts of naturally settled juvenile *S. partitus* and coupled these with otolith-derived measurements of size and growth from the same individuals. Although otolith microstructure analysis is a common tool used to elucidate patterns in growth and mortality during the early life stages of fishes (e.g., Sponaugle (2010)), it has rarely been used in conjunction with field observations to link behavior with growth (but see, for example, McCormick & Meekan (2010) and Meekan *et al.* (2010)). Otolith microstructure analysis enables the estimation of daily size and growth rate at any point in the life history of an individual and the comparison of such traits at common points in the life of individuals who vary in their behavioral traits and survivorship.

3.3 Methods

3.3.1 Study species and site

The bicolor damselfish *Stegastes partitus* maintains benthic territories on spur and groove reefs in the Caribbean and Western Atlantic (Emery 1973), including dead coral rubble piles at the reef base (Rankin & Sponaugle 2014). Adults and juveniles are diurnal planktivorous, consuming a range of planktonic cyanobacteria (*Trichodesmium* sp.) and other zooplankton along with limited amounts of benthic algae (Emery 1968; Goldstein *et al.* 2017). Territories are important for acquiring food, shelter, and eventually mates, and are defended against conspecifics and potential predators. Adults are benthic brooders, with males guarding the embryos for 4̃ d until hatching (Robertson *et al.* 1988). Larvae have a pelagic larval duration of 1̃ mo., after which they arrive to nearshore reefs in multi-day pulses generally during the dark half of the lunar cycle (D'Alessandro *et al.* 2007; Grorud-Colvert & Sponaugle 2009). Larvae settle to reef and rubble areas, metamorphosing into juveniles overnight, a transition that is recorded in their otoliths (Sponaugle & Cowen 1996). Daily deposition of material on otoliths provides a continuous chronological record of size and growth. *S. partitus* is an ideal model species for studying relationships among size, early juvenile growth, and behavior because they are abundant, easy to sample as benthic juveniles, and remain strongly site-attached following settlement. All observations and measurements for the present study were obtained from newly settled fish in the upper Florida Keys. The main predators of S. partitus juveniles are unknown, but barracuda (*Sphyraena barracuda*), bar jack (*Caranx ruber*), and cero (*Scomberomorus regalis*) have been observed preying on adults (Emery 1968). Gut contents indicate that *S. partitus* are also preyed upon by trumpetfish (*Aulostomus maculatus*), but not muraenids or other nocturnal fishes (Randall 1967). More recently, *S. partitus* juveniles and adults have been shown to be readily consumed by the invasive Indo-Pacific lionfish (Albins & Hixon 2008; Green *et al.* 2011; Palmer *et al.* 2016).

3.3.2 Behavioral observations

Behavioral observations of recently settled *S. partitus* were made in July, August, and September 2008 and in May and July 2009 on Sand Island Reef (25°01.09'N, 80°22.08W) and Snapper Ledge Reef (24°58.92'N, 80°25.30'W) at an average depth of 8 m (range 5-12 m). All fish (n = 256) were collected after observations using quinaldine and MS-222 and stored in 95% ethanol to enable the comparison of behavioral observations to otolith-derived traits. Observations were conducted each day between 1030 and 1430 h, the peak period of activity for newly settled *S. partitus* (Rankin and Sponaugle, unpublished pilot study), and consistent with general feeding patterns of the species (Myrberg 1972). Furthermore, as boldness and aggression have been shown to be influenced by small within-day changes in water temperature in another damselfish *Pomacentrus moluccensis* (Biro, Beckmann, *et al.* 2010), the restriction of the time of day that observations were conducted minimized daily temperature fluctuations.

For all observations, a pair of SCUBA divers would haphazardly locate settled juveniles, position themselves 3 m away, and allow 2 min for the subject(s) to acclimate to their presence, comparable to other in situ behavioral studies of juvenile coral reef fish (Nedelec *et al.* 2017; White & Warner 2007). The divers would then observe the subject for 5 min, and using a timer, stopwatch, and data sheet, record for each fish: (1) total time spent sheltered, (2) number of times shelter was sought, maximum distance travelled (3) horizontally and (4) vertically from primary shelter. Sheltering was defined as when the fish was under or within the crevices of coral or rubble, often hidden from view. Maximum distance traveled horizontally and vertically was noted during the observation period, then measured using a pair of weights and a tape measure afterward. Since the number of adults surviving can be used as a proxy of habitat quality and potential aggressive pressure, we also visually estimated (5) density of adult conspecifics within a 1.5-m radius (7 m^2 area) around each fish's primary shelter, which is greater than the average territory size of 1 m^2 (Emery 1973), but within the range of how far conspecifics will travel to each other (Knapp & Warner 1991). In addition to these metrics, in 2009 (May and July), divers recorded for each fish the (6) number of times an individual was chased by a conspecific (n=168), and (7) number of bites an individual took in the water column (n=46). Separately, and for a limited number of fish (n=15), divers measured (8) burst swim speed in response to a predator. For this measurement, a model of a predator was used to elicit an escape response, and this was videotaped with a stereo camera at a frame rate of 30 s^{-}1 to estimate escape swimming speeds. Digital images were processed with VideoMach (Gromada v. 5.5.3) and analyzed in Image Pro Plus (Media Cybernetics v. 4.5). All fish were collected following a single observation period and stored in 95% EtOH to preserve their otoliths for microstructure analysis.

3.3.3 Otolith processing

Standard procedures were used to digitally measure the standard length (SL) of each fish, dissect and clear (in immersion oil) their otoliths, and read, innumerate, and measure increments (at 400X) along the longest axis of the clearest lapillus (sensu Sponaugle & Pinkard (2004)). All readings were made using an oil immersion 40X lens attached to a Leica DMLB microscope equipped with a polarized filter between the first stage and light source. Otolith images were captured by a Dage MTI video camera and analyzed using Image Pro Plus (v4.5; Media Cybernetics). Each otolith was read (increments enumerated) once blind (i.e., without sample information available) and saved as a digital file. Readings were validated as per Searcy & Sponaugle (2001). Otolith microstructure analysis was used to determine juvenile age (number of concentric increments following the settlement mark), mean juvenile growth rates (average of post-settlement otolith increment widths, in µm/day), and size-at-settlement (otolith radius-at-settlement, in µm).

3.3.4 Data analyses

Comparison of traits with 6-year recruitment time-series

To set the context for the study, we first re-analyzed a six-year (2003-2008) time-series of *S. partitus* recruitment (Rankin & Sponaugle 2014). In that study, the otoliths of a representative sample of newly settled juveniles were analyzed to obtain individual age and daily growth rates. While these data were used to examine lunar cyclic patterns in larval and settlement traits (Rankin & Sponaugle 2014), the present analysis focused on how average early life history traits change over time among young juveniles via differential survival. Our goal for this comparison was to ensure the data used in the present study aligned with the larger patterns evident in the six-year dataset.

Rankin & Sponaugle (2014) separated juveniles into two age groups – young fish 1-10 d old post-settlement and older fish, or survivors, 11-29 d old post-settlement – and found significant differences between the age groups with respect to size-at-settlement and juvenile growth rate (measured over the first two days of juvenile life). We reproduced that finding to compare to the present dataset (2008-2009 data), which has fewer fish, especially in the older juvenile group since the focus of the collection was the youngest recruits. We separated the fish into similar aged groups and used Mann-Whitney U tests to compare age groups for each dataset. Because the number of fish in the older age group in the present study was low, we also re-analyzed the time-series using age as a continuous variable. To avoid data loss and maximize relevance of the present dataset, we chose to use the entirety of the juvenile growth record (minus the last incomplete increment from the day of collection). We note that the mean juvenile growth rate during the first 2 days and mean growth rate over the entire juvenile period were significantly correlated (Pearson correlation, $r = 0.87$, $n = 814$, $p<0.001$; Supplementary Figure C.1); thus hereafter we used mean juvenile growth rate over the entire juvenile period.

We next examined whether there were individual-level trade-offs between settlement size and juvenile growth rate in both datasets. Since young fish in our dataset represent an 'initial' population prior to post-settlement selective pressures, and older fish are those who have survived selective mortality, i.e., 'survivors,' we expected to see a relationship between settlement size and juvenile growth rate in older fish, and not necessarily in the younger fish. Thus, we included an interaction term between settlement size and juvenile age for predicting juvenile growth rate, using a linear mixed model with collection site as a random intercept.

Otolith derived early life history traits and temperature

Temperature has been shown to influence growth-related early life history traits in *S. partitus* (Rankin & Sponaugle 2011). Therefore, to control for the influence of temperature over the multiple months of observations, we controlled for the temperature that fish experienced during their juvenile period. Daily water temperature values were obtained from the NOAA Buoy MLRF1 and averaged for each fish across their actual days of life. We used average temperature experienced during the juvenile period to predict juvenile growth rate and used the residuals from this linear regression as a temperature-standardized measure of juvenile growth rate.

Behavioral observations and relationships to traits

To test for associations between the two main traits (settlement size and juvenile growth) and different behaviors, we planned to run a principal component analysis (PCA) on all of the observed behaviors. Unfortunately, bite count was measured for only a portion of the fish in 2009 (n=46), so using it in the PCA would have substantially reduced our sample size. Instead, we examined those 2009 fish for a relationship between the Number of bites and Maximum vertical distance in the water column. Indeed, the number of bites by a fish in the water column was significantly related to the maximum vertical distance a fish travelled in the water column; thus, we assume for our purposes that the inclusion of Maximum vertical distance is associated with foraging success (Supplementary Figure C.2, Table S1). We also did not include the number of times chased by conspecifics in the PCA, since being chased is a behavior not instigated by the individual itself, and may be a consequence of behaviors we included in the PCA. Horn's Parallel Analysis for component retention (Horn 1965) indicated that we should use three principal components in the analysis.

To examine the relationship between juvenile fish behavior and the two primary early life history traits (settlement size and juvenile growth rate), we constructed three different hypotheses in the form of directed acyclic graphs (DAGs) that explain how each trait of interest relates to survival (approximated by juvenile age). In the first hypothesis, settlement size affects survival directly (e.g., through gape-limited predation) and/or indirectly via behavior. Settlement size also affects juvenile growth rate directly and/or indirectly via behavior. Juvenile growth rate in turn affects survival. In the second, adult density affects juvenile growth and survival directly (e.g., through competition, or because higher density indicates better habitat quality) and/or indirectly via the number of times an individual is chased by conspecifics. This second hypothesis was developed from observations that adult density and increased intraspecific chasing reduce growth in experimental fish (Johnson 2008). We factored in size-at-settlement as relative size may interact with chasing behavior to affect juvenile growth. We also included the possibility that fish behaviors (e.g., sheltering) could affect how often a fish is chased. Finally, the third hypothesis describes an energetic trade-off between swimming behavior (speed; measured for a small subset of fish) and juvenile growth that could arise if fast-growing fish invest in size over other important developmental and morphological processes, resulting in fast growers who swim more slowly. Slower growers are potentially faster swimmers and thus better able to escape predation, and therefore experience higher survivorship.

To assess all direct and indirect relationships represented in the DAGs, we used confirmatory path analysis (Shipley 2009). We represented each path with a linear mixed (LMM) or Poisson-distributed generalized linear mixed model (GLMM; when the response variable was count data, such as Number of times chased), with the collection site as a random intercept. In several cases, we were unable to fit a model with random effects due to singularity issues; in that instance, we fit a simpler model without the random effect term. We then used psem from piecewiseSEM (Lefcheck 2015) to assess the structure of the DAG by quantifying path coefficients for all hypothesized relationships and testing the goodness of fit of the model. All data processing and statistical analyses were conducted in R version 4.2.1 (R Core Team 2022). We used functions from the lmerTest package (Kuznetsova *et al.* 2017) for linear mixed models and the glmmTMB package (Brooks *et al.* 2017) for GLMMs.

3.4 Results

3.4.1 Comparison of traits with 6-year recruitment time-series

Comparison of the present dataset with a longer 6-yr recruitment time series yielded very similar patterns (Figure 3.1). Older juveniles, who had survived longer, had settled larger (Figure 3.1A,B), and grew more slowly during their first two days on the reef (i.e., post-settlement; Figure 3.1C,D). The shorter and longer datasets had the same significant pattern of directional selection in early juvenile growth (Mann-Whitney U: p = <0.001-0.01), and the same trend in settlement size. Likely due to low sample sizes in the present study (i.e., fewer older individuals), the pattern of larger settlers selectively surviving was not significant (Mann-Whitney U: p = 0.13). Using age as a continuous variable in generalized additive models to increase the power of the trait analysis provided a clearer view of the age-related changes in traits (settlement size in the 6-yr dataset and juvenile growth in both datasets: p $\leq$0.001-<0.01; Supplementary Figure C.3), though the trend of larger settlement size among older survivors in the present smaller dataset remained non-significant (p = 0.27).

In both datasets, there was a significant interaction between settlement size and juvenile age for predicting juvenile growth: settlement size and juvenile growth became increasingly negatively associated with age (i.e., survival) (current dataset: conditional $R^2 = 0.17$, $p_{\text{interaction}} = 0.015$; 6-yr dataset: conditional $R^2 = 0.40$, $p_{\text{interaction}} = 0.011$; Figure 3.2; Supplementary Tables C.2-C.3).

3.4.2 Behavioral observations and relationships to traits

The first axis (PC1) from the PCA of measured behaviors on the full dataset (n = 256) explained 41.9% of the variance and separated fish based on their sheltering versus foraging and other swimming behavior (Figure 3.3). Positive loading on PC1 represented fish that spent more time sheltering and did not travel long distances. PC2 and PC3 explained less

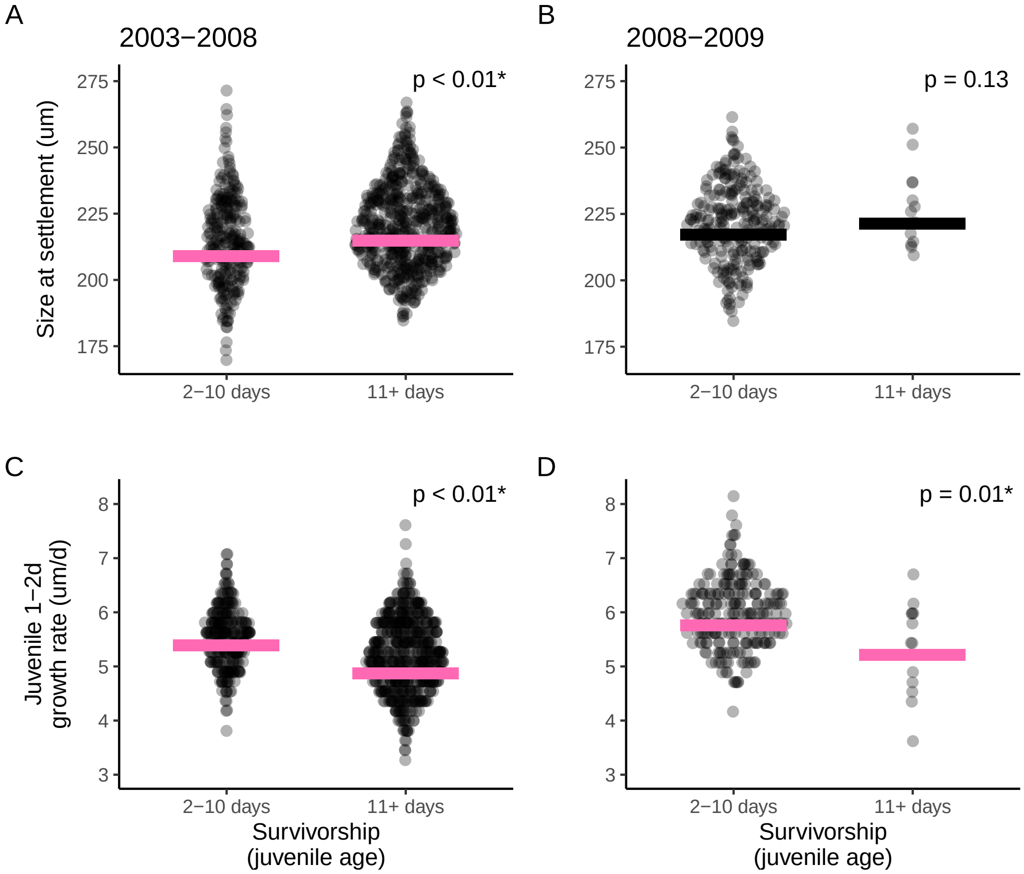

Figure 3.1: Comparison of early life traits between young and older juveniles for *S. partitus* data in the (**A, C**) 6-year (2003–2008) recruitment time series from Rankin and Sponaugle (24), and in the (**B, D**) present study (2008–2009). Fish age groups were defined similarly in each data set (young fish = 2–10 days old post-settlement; older fish = 11–29 days post-settlement). Settlement size (**A, B**) was derived from the position of the settlement mark on otoliths of individual fish; juvenile growth (**C, D**) was similarly computed by averaging daily otolith increment widths for the first 2 days of life on the reef. Pink lines indicate significantly different medians; black lines are non-significant but included to facilitate visualization. *indicates significance ($P < 0.05$).

variance (21.8% and 20.7%, respectively) and captured not how long fish sheltered, but *how* they sheltered (Supplementary Figure C.4). In both of these PCs, mean shelter time and the number of times sheltering loaded in opposite directions. Mean shelter time increases when a fish is sheltering fewer times, but for a long time period, as opposed to many short sheltering

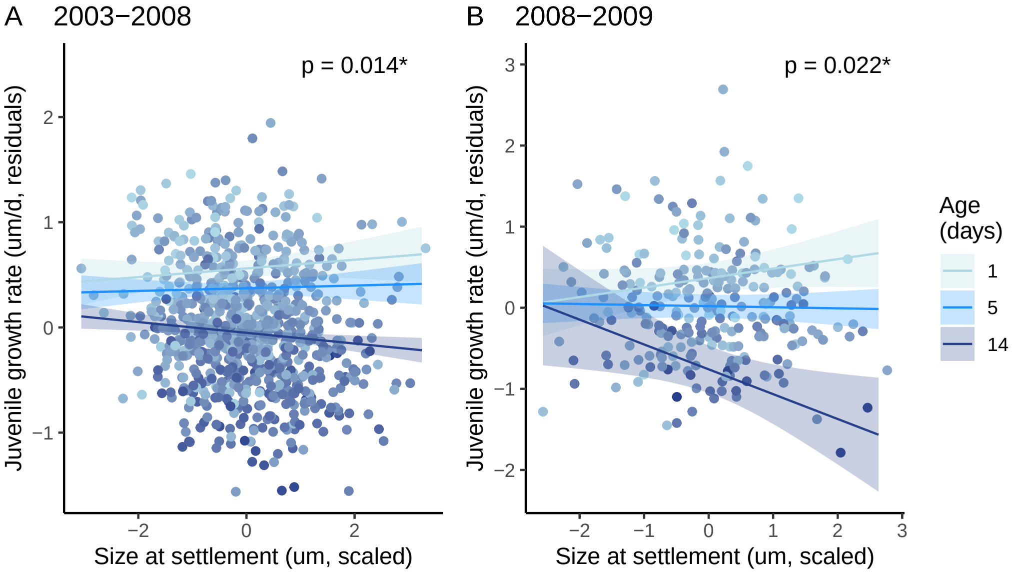

Figure 3.2: Mean juvenile growth rate as a function of settlement size for juvenile *Stegastes partitus* sampled as part of the **(A)** 6-year (2003–2008, n = 818) time series and in the **(B)** present dataset (2008–2009, n = 256). Data points are traits from individuals color-coded by juvenile age. Lines depict the significant interaction between settlement size and age (A: Linear mixed model; B: Linear model; Supplementary Tables C.2-C.4), with selected ages spanning the range of ages in the present dataset. *indicates significance ($P < 0.05$).

periods. Thus this trade-off can be interpreted as having long, infrequent bouts of sheltering versus short, frequent bouts of sheltering. PC2 can thus be interpreted as separating fish that travel far and shelter fewer times (but for longer), versus fish that do not travel far and shelter for short, frequent periods. PC3 separates fish that travel far horizontally and return frequently to shelter for short periods from those that do not travel far and remain sheltered for long periods (Supplementary Figure C.4).

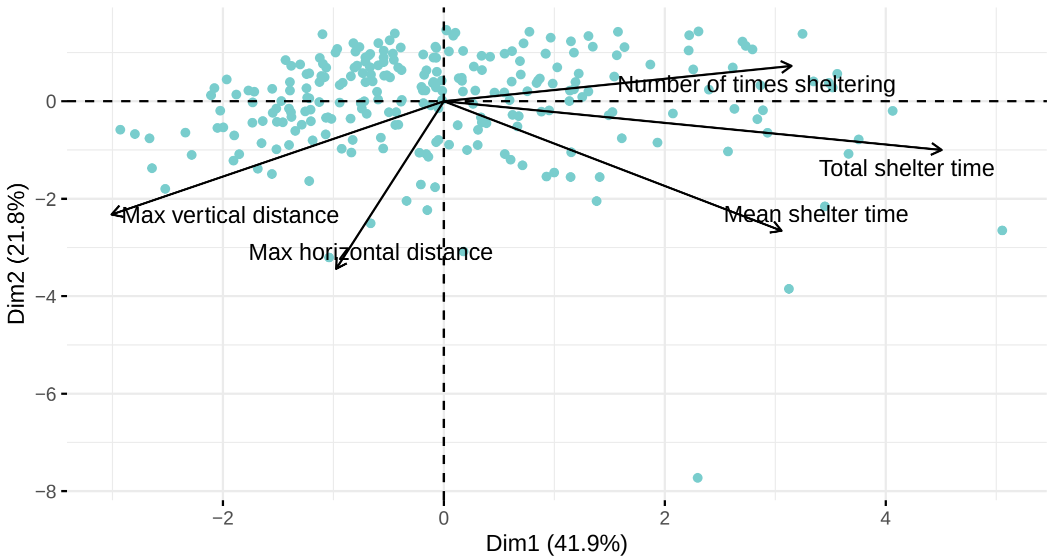

Figure 3.3: Primary dimensions (PC2 vs. PC1) in principal component analysis (PCA) of behaviors observed over 5 min for newly settled *Stegastes partitus* juveniles (n = 256). Observations were made over 5 different months in the Florida Keys. Behaviors are mean and total time spent sheltered, number of times shelter was sought (number of times sheltering), and maximum distance traveled horizontally (max horizontal distance) and vertically (max vertical distance) from the primary shelter.

Settlement size

PC1, the measure of time spent sheltered vs time spent foraging, was negatively related to size-at- settlement (LM: p = 0.008; Figure 3.4 A-B, Table S4), with larger fish spending less time hiding and more time traveling both horizontally and vertically in the water column. Settlement size did not predict PC2, but did predict PC3 (LM: p = 0.59 and LMM: p = 0.04, respectively; Figure 3.4A,C-D; Table S4). Interestingly, both PC1 and PC3 were significantly associated with survival (increasing juvenile age), and settlement size did not predict survival when controlling for these behavioral axes (Figure 3.4E; Table S4). In other words, the associations between PC1 and survival and between PC3 and survival are not simply spurious correlations that arise because they are each associated with settlement size. Instead, size-at-settlement is related to survival through size-related behaviors (Figure 3.4A). In an analysis with a smaller dataset (n = 168), relationships between behaviors and survival were harder to distinguish (due to reduced power), and the relationship between PC3 and survival was not significant (Figure 3.5E). However, there was a positive relationship between PC2 (distance traveled and frequency of sheltering) and survival.

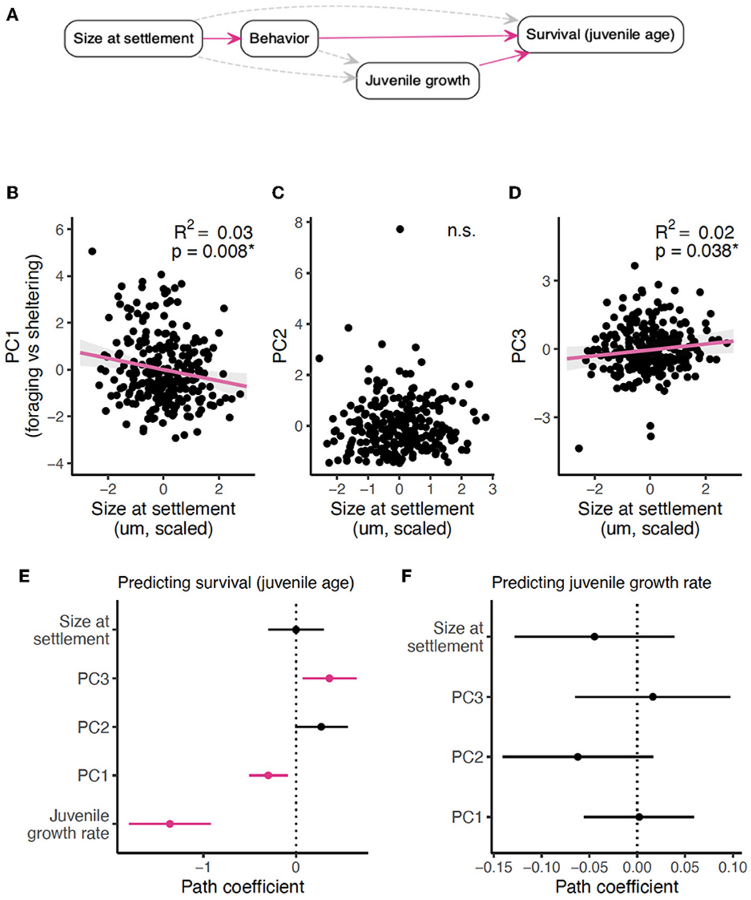

Figure 3.4: Confirmatory path analysis of *Stegastes partitus* settlement size, juvenile growth, and survival (n = 256). **(A)** Directed acyclic graph (DAG) outlining alternative hypotheses of how settlement size relates to survival (approximated by juvenile age) and juvenile growth rate: settlement size affects survival and juvenile growth rate directly and/or indirectly via behaviors. Solid pink arrows indicate significant relationships; gray dashed arrows indicate the relationships we investigated and found them to be non-significant. **(B–D)** Relationship between principal components and settlement size from a linear model **(B)** or from linear mixed models **(C, D)**. Marginal R^2-values are included to describe the variance captured by the main effects and interaction terms of each model. **(E)** Path coefficients from the component model of survivorship (juvenile age) of *S. partitus* as a function of settlement size, juvenile growth rate, and all PCs. **(F)** Path coefficients from component model of juvenile growth rate as a function of settlement size and all PCs. (E, F) Pink indicates significant relationships at a p-value of <0.05; black indicates non-significance ($p > 0.05$). For standardized path coefficients, see Supplementary Table C.4 For R^2-values of all component models, see Supplementary Table C.5 . For PCA biplots showing how the measured behaviors load on each axis, see Figure 3.3 and Supplementary Figure C.4 . indicates significance ($P < 0.05$). n.s. indicates non-significant.

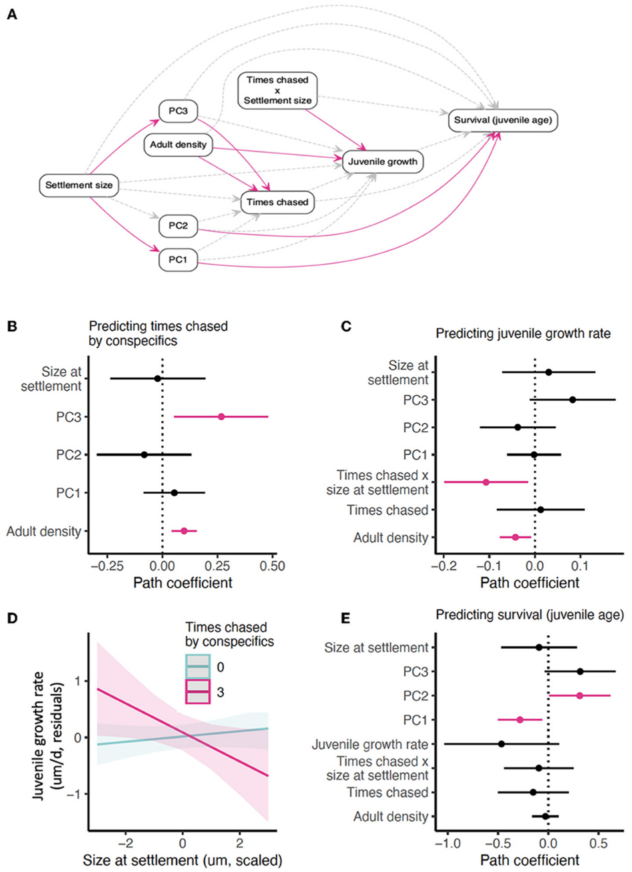

Figure 3.5: Confirmatory path analysis of *Stegastes partitus* adult density (habitat quality; aggressive pressure), chasing behaviors, and relationship to juvenile growth rate (n = 168). **(A)** Directed acyclic graph (DAG) outlining alternative hypotheses of how adult S. partitus density relates to juvenile growth rate and survival. Adult density could affect juvenile growth rate by impacting the frequency of conspecific chasing, or through another mechanism. Adult density may also directly impact survival, such as if the presence of adults indicates higher quality habitat, or indirectly through increased chasing. The effect of chasing on both growth and survival could depend on settlement size. Furthermore, foraging and sheltering behaviors could predict how frequently fish are chased by conspecifics. **(B)** Path coefficients from component model of adult density, settlement size, and behavioral axes on the number of times an individual was chased. **(C)** Path coefficients from the component model of adult density, behavioral axes, number of times chased, and the interaction of chased times and settlement size on juvenile growth rate. **(D)** Visualization of the interaction between the number of times chased and settlement size for predicting juvenile growth rate; 0 or 3 times chased were selected for simplicity of visualization. **(E)** Path coefficients from the component model of the same variables on survivorship (juvenile age). In the DAG, the solid pink line is a significant relationship; the gray dashed line indicates the lack of a significant relationship. (B, C, E) Pink color indicates a significant relationship from linear mixed models at $p < 0.05$; black color indicates non-significance ($p > 0.05$). For standardized path coefficients, see Supplementary Table C.6. For R^2-values of all component models, see Supplementary Table C.7. For PCA biplots showing how the measured behaviors load on each axis, see Figure 3.3 and Supplementary Figure C.4.

Juvenile growth

Although settlement size-related behaviors influenced juvenile *S. partitus* survival, surprisingly, the same behaviors captured by the PCA dimensions did not predict variation in juvenile growth rate (Figure 3.4F; Table S4). In fact, settlement size neither directly nor indirectly (via the behaviors in the PCA) predicted juvenile growth rate (Figure 3.4A,E-F; Table S4). Instead, when we considered fish for which we had data on chasing behavior (n = 168), settlement size affected juvenile growth rate through an interaction with how often fish were chased by conspecifics (Figure 3.5A,C-D; Table S6). Juvenile growth was unrelated to settlement size where no chases were observed, but when fish were chased multiple times during the 5-min observation period, juvenile growth became a negative function of settlement size—larger fish at settlement experienced slower juvenile growth, the dominant emergent relationship of surviving *S. partitus* (Figure 3.2). We also found that PC3, which captured far horizontal travel with frequent, short bouts of sheltering, predicted the number of times fish were chased by conspecifics.

As shown previously for this species (Johnson 2008), adult density was negatively associated with juvenile growth (Figure 3.5C; Table S6). Adult density was also directly related to the number of times an individual was chased (Figure 3.5B; Table S6). Despite these relationships, adult density and the interaction of chasing and settlement size did not predict survival (Figure 3.5E; Table S6). Furthermore, the significant relationship we found between juvenile growth and survival in the full dataset model (Figure 3.4A,E; Table S4) disappeared in this model (Figure 3.5A,E; Table S6). We note, however, that we had low power to detect relationships between measured variables and juvenile survival in this data subset, since this subset had fewer older fish than the full dataset (only 3 fish were 11+ days old and 9 fish 9+ days old, compared to 11 and 23 fish respectively in the full dataset).

Unfortunately, swim speed was only measured in 15 fish and since they were the same age when collected, we could not assess how swim speed related to survival. The inverse correlation between swim speed and juvenile growth was not significant, though we note that we had low power for this analysis (Supplementary Figure C.5B).

3.5 Discussion

For larval fishes to successfully recruit to adult populations, individuals need to survive the highly dangerous period of early life. Predators are known to target prey with particular traits (e.g., small sizes and slow growth; Anderson (1988)). Thus, settlers with particular traits may be more or less successful at navigating the hazardous first few weeks of life on the reef, potentially influencing the overall strength of recruitment to the population. The Growth-Survival Paradigm (GSP; Robert *et al.* (2023)) describes how we might expect the characteristics (or traits) of young fish to change over time due to predation pressure, but it is typically challenging to identify the mechanisms underlying observed shifts in traits. By combining otolith microstructure analysis and direct observations of behavior in individual fish, we have been able to pinpoint early life processes that create variation in the characteristics of survivors.

3.5.1 Consistency of behavioral dataset with a 6-yr recruitment time-series

Previous work with our focal species, the bicolor damselfish, *Stegastes partitus*, demonstrated that juveniles who settled at larger sizes and had slower juvenile growth experienced higher survival during the first few weeks of life on the reef (Johnson 2008; Johnson & Hixon 2010; Rankin & Sponaugle 2011, 2014). While differential survival of fish with large settlement sizes is consistent with the GSP, the success of slow growers is not. To identify the behaviors underlying this trait selection, we measured behaviors for 256 fishes and combined them with otolith-derived early life history traits. This dataset exhibited the same patterns in trait distributions over time as a 6-year monthly time series of recruitment in the Florida Keys (Rankin & Sponaugle 2014), justifying the use of this smaller dataset in examining behavior in the context of growth-related traits.

3.5.2 Relationship between settlement size and juvenile growth

For data from both the present study and the larger 6-year recruitment time-series, comparison of mean juvenile growth as a function of size-at-settlement revealed clear patterns associated with juvenile age. The relationship between the two traits changed from no relationship among the youngest juveniles to a significant inverse relationship among the oldest juveniles. Thus, this relationship is not inherent to the species or individual but instead emerges as a result of selective survival. While there was variation among individuals with regard to both variables, surviving older juveniles on average were those who settled at larger sizes and then had slower early juvenile growth. Although this relationship was not examined explicitly in previous studies, the inverse relationship among the traits of survivors is consistent with previous studies (Johnson 2008; Johnson & Hixon 2010; Rankin & Sponaugle 2011, 2014).

Size-at-settlement of *S. partitus* is determined during the larval period by larval growth rates and the number of days larvae spend growing at this rate in the plankton (i.e., pelagic larval duration, PLD; (Rankin & Sponaugle 2011, 2014)). Faster-growing damselfish larvae spend less time in the plankton (shorter PLD) and vice versa, with both traits "carrying over" to affect size-at-settlement. Regardless of seasonal fluctuations in water temperature or cyclic lunar phases, the size of settling S. partitus larvae sets the stage for juvenile survival (Rankin & Sponaugle 2011, 2014). Similar carry-over phenomena is common in other coral reef fishes with complex life histories (e.g., Dingeldein & White (2016) and Shima & Swearer (2010)).

3.5.3 Behaviors underlying selective changes in early life history traits

A PCA of the dataset in the present study (n=256) enabled us to collapse multiple observed behaviors into a single behavioral variable. PC1 captured the variance associated with the relative time fish spent sheltering vs the maximum distances fish swam in vertical and horizontal dimensions. Maximum vertical distance was also positively associated with the number of bites in the water column, thus serving as an indication of foraging success. Fundamentally, PC1 reflected the trade-off between foraging (planktivory) and sheltering. When fish are sheltered under a coral or other reef rubble, they are unable to feed on their preferred diet in the water column (Emery 1968, 1973).

We found a significant relationship between settlement size and the sheltering-foraging axis of behavior (PC1). Bicolor damselfish settling at larger sizes had lower PC1 scores, indicating reduced sheltering behavior and increased foraging high in the water column. Further, PC1 changed with juvenile age: survivors (old fish) had significantly lower PC1 scores, suggesting progressive removal of fish with high PC1 scores. Settlement size alone (i.e., controlling for PCs) did not predict survival. Together these results point to the behaviors that underlie observed patterns of selective mortality. Larger settlers need not shelter as much as smaller settlers and are able to forage higher in the water column, obtaining more zooplankton prey. Previous experiences being equal, larger individuals should be less vulnerable to gape-limited predation (Anderson 1988; Miller *et al.* 1988; Sogard 1997) and should therefore have the benefit of sustaining greater activity. This has been shown in Great Barrier Reef pomacentrid *Pomacentrus aboinensis*, where larger juveniles exhibited greater rates of foraging activity and aggression, but also experienced higher survivorship (Meekan *et al.* 2010). Larger lemon damselfish, *Pomacentrus moluccensis*, in Indonesia also sheltered less frequently (Gauff *et al.* 2018). Theoretical (Arendt 1997; Stamps 2007) and empirical evidence (Damsgard & Dill 1998; Hurst *et al.* 2005) suggests that smaller settlers should spend more time foraging and less time sheltered to accelerate their growth and "catch up" to their larger conspecifics, even though this should increase their exposure to visual predators. Instead, and consistent with other damselfishes, we observed the contrary: juvenile *S. partitus* that were smaller at settlement spent more time sheltered and travelled less far from those shelters.

Greater activity of larger settlers suggests that they are 'bolder', a trait that has been associated with higher survival in some species (Fuiman *et al.* 2010; Godin & Davis 1995; McCormick, Fakan, *et al.* 2018; Réale & Festa-Bianchet 2003). For instance, Fuiman *et al.* (2010) found that juveniles of another pomacentrid, *Pomacentrus wardi*, with reduced escape swimming speeds and lower boldness were more susceptible to predation. They suggested that boldness is a form of vigilance that reduces the risk of a predator attack, therefore increasing overall survival. Similarly, a lab experiment with guppies (*Poecilia reticulata*) found that bolder individuals tended to inspect predators, which resulted in fewer attacks (Godin & Davis 1995). McCormick, Fakan, *et al.* (2018) found that selection on the white-tailed damselfish *Pomacentrus chrysurus* was related to a suite of behavioral traits associated with boldness. Whether boldness is a trait that reduces vulnerability to predation, or simply covaries with other traits that increase survivorship is unknown.

3.5.4 Influence of adult conspecific density on juvenile growth

If larger settlers forage more than smaller settlers, why is higher survival associated with slower early juvenile growth? Johnson (2008) found that *S. partitus* grew more slowly in areas of high adult density. We examined this in our full dataset and found the same relationship: juvenile growth decreased significantly with increasing adult density. But surprisingly, juvenile growth was unrelated to any sheltering or foraging behaviors. Larval settlement into an area of the reef with high adult densities implies that the habitat is favorable (can successfully support higher numbers of conspecifics). While this area may be favorable for some reason (higher food supply, fewer predators, higher vigilance possible, etc.), settling in proximity to adult conspecifics also brings with it an increasing likelihood of being chased by conspecifics. Johnson (2008) found that more intraspecific chasing was associated with reduced juvenile growth for *S. partitus* in the Bahamas. Being chased requires evasion and burst swimming by the chased, and typically smaller fish, followed by quick sheltering. Such escape behavior disrupts an individual's foraging and requires energy expenditure. Agonistic behavior, such as chasing, can be physiologically costly (Briffa & Sneddon 2007) due to build-up of lactic acid, production and release of stress hormones (Briffa & Sneddon 2007; Wilson, Gatten, *et al.* 1990), injury (McDougall & Kramer 2007), and energy expenditure

(Neat *et al.* 1998). Repeated chasing would likely cause reduced growth in the fish being chased.

In our dataset that included chasing measurements, the number of times an individual was chased increased significantly with adult density, but this variable alone did not directly reduce juvenile growth. Instead, the number of times chased interacted with size-at-settlement to predict juvenile growth rate. Individuals who were not chased did not experience a tradeoff between size and juvenile growth. Among fish who were chased, larger fish had slower juvenile growth rates, and smaller fish had faster growth rates. This result for large fish is not surprising, as evading frequent chasers would require energy expenditure. More surprising is that small settlers who were chased frequently did not experience reduced juvenile growth rates. For those fish, it is possible that chases were of shorter intensity/duration, reducing the energetic cost of this evasive behavior, or evasive movement of smaller fishes simply does not cost as much energetically, such that these smaller fish are able to maintain relatively high juvenile growth rates.

We also found fish that were chased more were those who traveled farther horizontally, sheltering frequently but for brief periods of time. This behavior, captured by PC3, is associated with larger settlers, suggesting that larger fish venture farther into neighboring territories, which then results in chases. That adult density and the number of times an individual was chased interacting with settlement size significantly predicted juvenile growth points to the possibility of both behavioral and energetic mechanisms underlying the preferential survival of slow-growing juveniles. However, these variables did not predict survivorship, likely due to the low number of older fish in this data subset. Thus, we cannot distinguish whether these relationships are byproducts of size-dependent behaviors or drivers of survivorship in themselves.

3.5.5 Predator evasion, condition, and juvenile growth

Another non-mutually exclusive process that may play a role in the phenomenon of reduced juvenile growth of survivors is predator evasion via escape swimming. Fast swimmers could experience higher survivorship, yet pay a price in lower juvenile growth rates due to energetic costs of swimming performance. We could not measure in situ burst swim speeds following a simulated predator attack for many S. partitus juveniles and thus could not formally test this hypothesis; our data for 15 new settlers show a negative but non-significant correlation between burst swim speed and juvenile growth rate. While we did not have the power to evaluate this hypothesis, trade-offs between growth and swimming performance have been observed in other teleosts (Billerbeck *et al.* 2001; Kolok & Oris 1995; Sogard & Olla 2002) and amphibians (Arendt 2003).

Additional trade-offs can exist between condition (i.e., lipid reserves) and accelerated growth (Johansen *et al.* 2001; Sogard & Spencer 2004). For instance, (Johnson 2008) observed that high-condition *S. partitus* juveniles grew more slowly than low-condition juveniles and attributed this reduction in growth to more agonistic interactions among high-condition individuals. We did not measure condition in our study, but condition often covaries with size (Henderson *et al.* 1988; Schultz & Conover 1997; Thompson *et al.* 1991) and we observed that larger settlers were more active, grew more slowly as juveniles, and had higher survival (Rankin & Sponaugle 2011).

3.5.6 Conclusions

Size-at-settlement is a key trait influencing the survival of young *S. partitus* settlers. We found that preferential survival of large settlers is not merely a function of gape-limited predation but rather occurs via specific fish behaviors. Large settlers forage higher up in the water column, which could provide access to larger quantities of planktonic food and enhance survival. However, spending more time unsheltered likely engages more conspecific chasers. We found that being chased by conspecifics results in slower juvenile growth rates for large settlers than for small settlers, suggesting differences in the energetic costs of territorial behavior. Furthermore, the degree to which this extra energy expenditure is required depends on the reef 'neighborhood' fish settle into. Favorable habitats that support high adult densities could require additional energy expenditure on the part of juveniles, as resident adults chase the new arrivals.

Thus, the size at which settlers arrive to and enter the juvenile habitat plays a critical role in determining subsequent behaviors and trait-mediated survival. Because territorial defense and maintenance are necessary for fitness and conspecific agonistic behavior is a dominant part of damselfish life history, this phenomenon is likely to apply to other damselfish species in numerous locations. Understanding the role of agonistic behaviors in survival is important as changing habitat (territory size; Silveira *et al.* (2020)), depth (Goldstein *et al.* 2016), and environmental conditions (Silva-Pinto *et al.* 2020), including levels of predation pressure (Ferrari *et al.* 2019), can affect the frequency or intensity of damselfish agonistic behaviors. Such an understanding of how food availability, somatic growth, survival, and behavior are intertwined in early life is necessary to help explain population dynamics of small territorial fishes such as the bicolor damselfish.

3.6 Data availability statement

The datasets presented in this study can be found in NSF's BCO-DMO online repository: `https://www.bco-dmo.org/project/521586`

3.7 Ethics statement

Fish were collected under permits 07SR-524 and 07SR-1032A from the Florida Fish and Wildlife Conservation Commission and permits 2007-030 and 2007-018-A1 from the Florida Keys National Marine Sanctuary. All collections and fish handling procedures were approved under the University of Miami Animal Care and Use Permit 07-068. Conflict of Interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix A

Supplement for Chapter 1

A.1 Appendix S1

Table A.1: Empirical support for parameter choices used in Chapter 1. This table includes all parameters for each temperature-dependent vital rate function (equations found in Table 1), with possible proxies or measurements from the literature listed next to each. Example ranges of parameter values for each proxy are provided based on a thorough but non-comprehensive literature search, specifying values for arid-zone passerines separately from other birds (which could include non-arid-zone passerines as well as non-passerines from various habitats). N/A indicates that our literature search did not yield values for a given proxy. Finally, the proxy or measurement used for model simulations in the main text is described, and the value used in main-text simulations is listed. For parameters with units of temperature, we list values in Celcius in the table, but use Kelvin in our models. *See following page for table.*

Endothermic life stage or ectothermic life stage	Vital rate	Parameter	Name of parameter/description	Possible proxies or measurements for the parameter	Example ranges of values calculated for arid-zone passerines	Example ranges of values reported for other species	Which we use in this paper	Value used in simulations (we report Celcius here but use Kelvin in our models)
Endothermic	**Adult mortality**	T_Ll_dB	Lower mortality inflection point	T_lc (lower critical threshold of thermoneutrality, aka lower inflection point for resting metabolic rate)	27.1 C ± 4.9 (20.5–32.7; 6 lark species) (Kemp and McKechnie 2019, Williams 1999, Tieleman et al 2002)	Tropical non-arid zone passerines: 21-31 C (11 species; Monge et al 2022); Mediterranean passerines: 18.7 C ± 2.1 (16.4–22.6; 8 species; Gonzalez-Medina et al 2023)	This parameter does not affect our analyses since we focused on hot extremes; given the difficulty of determining mortality due only to cold and not also to starvation, we arbitrarily picked a temperature where mortality was observed in waxbills	2C
				Temperature where daily net body mass change is negative	<26C (Sharpe et al 2019)	N/A		
				Temperature where mortality rate increases (by measuring across multiple temperatures)	From a range of temperatures, mortality only observed in Black-throated Waxbills for 1.8 - 9C (semi-arid in parts of its range; Lasiewski et al 1964)	N/A		
		T_Ul_dB	Upper mortality inflection point	When Ta > normorthermic Tb	40.7C ± 0.6 (39.6–42.2; 30 species) (McKechnie et al 2021)	Narrow range, but variable depending on phylogenetic group (Prizinger et al 1991, McKechnie and Wolf 2019, McKechnie et al 2021)	When Ta > normorthermic Tb	40.7 C
				T_uc (upper critical threshold of thermoneutrality, aka upper inflection point for resting metabolic rate)	37.9C ± 3.2 (30.6–44.9; 30 species) (McKechnie et al 2021)	Tropical non-arid zone passerines: 30-40 C (11 species; Monge et al 2022); Mediterranean passerines: 32.8 C ± 1.4 (30–35; 8 species; Gonzalez-Medina et al 2023); some non-passerines do not have a T_uc (McKechnie et al 2021)		
				T_ec (inflection point of EWL)	39.3C ± 2.4 (33.3–45.6; 28 species) (McKechnie et al 2021)	Mediterranean passerines: 33.1 C ± 1.6 (29.4–34.4; 8 species; Gonzalez-Medina et al 2023)		
				Temperature when panting begins	40.2C ± 1.5 (35.9–42.3; 20 species) (McKechnie et al 2021)	Not all groups of birds pant; temperature of panting onset available for arid-zone non-passerines (McKechnie et al 2021)		
				Temperature where daily net body mass change is negative	35.5 - 42C (Sharpe et al 2019; du Plessis et al 2012; van de Ven et al 2019)	N/A		
		d_T_R_dB	dB within inflection points	1/average lifespan in days (doesn't account for temperature)	2 - 15+ years	Various depending on phylogeny; passerine max longevity on average 10 years (Wasser and Sherman 2010)	(1 - % survival)/365 (doesn't account for temperature)	0.001
				(1 - % annual survival)/365 (doesn't account for temperature)	0.0014 for verdins (Austin 1977)	0.0002 - 0.002, with variation by latitude (Ricklefs 1973; Ricklefs et al 2011; Martin et al 2015; Beauchamp 2023)		
				(1 - % annual survival)/365 in a lab setting controlling for temperature	N/A (unlikely to be feasible)	N/A (unlikely to be feasible)		
		T_LT_dB	Lower total mortality point	Cold temperature where mass mortality is observed (use a lower temperature to represent total mortality)	N/A	-16C in several shorebird species (Schwemmer et al 2014); Eastern Bluebirds and other species died in February 2021 across the US Midwest and South from -22C - 10C (Rolland et al 2023); numerous species affected by cold and weather reviewed in Newton 2007, including mass mortality of hundreds of warblers from a sudden drop in temperature to 1C (Deane 1914)	This parameter does not affect our analyses since we focused on hot extremes; we arbitrarily selected a temperature based on the cold temperature where mass mortality is observed and minimum tolerable temperature	-25C (thus aL_dB = 0.26)
				Instead use rate of increase in mortality rate (by measuring mortality rate across several temperatures)	N/A (unlikely to be feasible)	N/A (unlikely to be feasible)		
				Minimum tolerable operative temperature (calculated from summit metabolism, conductance, and minimum body temperature e.g. Londoño et al 2017)	N/A	For several Peruvian birds, minimum tolerable temperature was calculated to be -47C to -37C at night and -20C to -13C during the day depending on altitude (-37C and -13 for low-altitude; Londoño et al 2017)		
		T_UT_dB	Upper total mortality point	T_HTL (lab measure which is a proxy for lethal hyperthermia)	49.8 ± 2.0 (46–54; 30 species) (McKechnie et al 2021)	Arid-zone non-passerine HTLs in McKechnie et al 2021	HTL (lab measure which is a proxy for lethal hyperthermia)	50 C (thus aH_dB = 0.74)
				Hot temperature where mass mortality is observed (use a higher temperature to represent total mortality)	Mass mortality from single day heat event ranging from 43C to 49C (Finlayson 1932; Saunders 2011; McKechnie et al 2021); 4 adult Jacky winters died when daily max reached 49C (semi-arid; Sharpe et al 2021)	Mass mortality from single day hot extreme (44C) of penguins (Holt and Boersma 2022)		

			Lethal dehydration (would need to develop function relating %body mass lost due to EWL to a mortality rate or probability of mortality)	Calculated as cumulative measure over a range of diurnal temperatures; can't specify a single max temperature	N/A		
Juvenile mortality	T_LI_dJ	Lower mortality inflection point	T_lc (lower critical threshold of thermoneutrality, aka lower inflection point for resting metabolic rate)	N/A	T_lc calculated in Gonzalez-Medina et al 2023 are based on both adult and juvenile birds, but separate values aren't given by adult/juv	Use value from adults	6C
			Temperature where daily net body mass change is negative	N/A	N/A		
	T_UI_dJ	Upper mortality inflection point	When Ta > normorthermic Tb	N/A	N/A	Use value from adults	40.7 C
			T_uc (upper critical threshold of thermoneutrality, aka upper inflection point for resting metabolic rate)	N/A	T_uc calculated in Gonzalez-Medina et al 2023 are based on both adult and juvenile birds, but separate values aren't given by adult/juv		
			T_ec (inflection point of EWL)	N/A	T_ec calculated in Gonzalez-Medina et al 2023 are based on both adult and juvenile birds, but separate values aren't given by adult/juv		
			Temperature when panting begins	N/A	N/A		
	d_T_R_dJ	dJ within inflection points	(1 - % survival)/duration of juvenile stage (doesn't account for temperature)	Around 0.0081-0.0087 for verdins (Austin 1977)	Annual survival for fledglings starting late summer is generally 25-50% of adult survival, but highly variable (Ricklefs 1973; Beauchamp 2023; Cox et al 2014)	(1 - % survival)/duration of juvenile stage (doesn't account for temperature)	0.008
			(1 - % survival)/duration of juvenile stage, in a lab setting controlling for temperature	N/A (unlikely to be feasible)	N/A (unlikely to be feasible)		
	T_LT_dJ	Lower total mortality point	Cold temperature where mass mortality is observed (use a lower temperature to represent total mortality)	N/A	N/A	Use same rate of increase as that calculated for adults	aL_dJ = 0.26
			Instead use rate of increase in mortality rate (by measuring mortality rate across several temperatures)	N/A (unlikely to be feasible)	N/A (unlikely to be feasible)		
	T_UT_dJ	Upper total mortality point	T_HTL (lab measure which is a proxy for lethal hyperthermia)	N/A	N/A	Use same rate of increase as that calculated for upper mortality increase based on T_UT_dB (aka for adults)	aL_dJ = 0.74
			Hot temperature where mass mortality is observed (use a higher temperature to represent total mortality)	N/A	N/A		
			Lethal dehydration	N/A	N/A		
Birth rate	bB	Per capita birth rate	# eggs laid per adult per season/duration of breeding season	Verdins have 3-6 eggs; Canyon wrens have 4-6 eggs; Black-throated sparrows have 2-5 eggs; passerines with open cup nests in desert scrub have 3-4 eggs per clutch (Ricklefs 1980); species with other kinds of nests have more eggs (Jetz et al 2008)	Passerines with open cup nests in other habitats have 2-6.5 eggs per clutch (Ricklefs 1980); birds with closed nests tend to have larger clutches than open nests, and clutch size varies by how seasonal the habitat is and migratory behavior (Jetz et al 2008)	There is support for the birth rate varying with temperature (Schou et al 2021; Hurley et al 2018) or breeding halting due to extreme temperatures (Sharpe et al 2021), but for simplicity we use a constant value. We assume 2 clutches per breeding season	4 eggs x 2 clutches / 2 adults = 4 per breeding season
Temperature experienced due to incubation	I_L	Lower incubation threshold	Temperature where average adult nest attendance time reduces	N/A	N/A	This parameter does not affect our analyses since we focused on hot extremes; we arbitrarily selected 2.5C (a value just above the temperature below which adult mortality increases)	2.5C
			Temperature where adults experience costs due to nest attendance	N/A	N/A		
			Temperature where average temperature experienced by eggs decreases (incubation becomes less efficient)	N/A	Around 25C or lower for king rails (Clauser and McRae 2017); numerous species incubate in freezing temperatures but data on effectiveness of incubation at these temperatures is lacking; Canada Jays kept eggs about 10-15C higher than ambient temperature in ambient temperatures of -5 to -15C, tracking the ambient temperatures (Burant et al 2024)		
	I_H	Upper incubation threshold	Temperature where average adult nest attendance time reduces	Attendance reduces around 36C to about 20% reduction at 40C in Bourne et al 2021; all eggs abandoned >40C (Sharpe et al 2019) or >46C (Sharpe et al 2021)	N/A	Temperature where average adult nest attendance time reduces	38C
			Temperature where adults experience costs due to nest attendance	36.1C in Bourne et al 2021	N/A		

				Temperature where average temperature experienced by eggs increases (incubation becomes less efficient)	N/A	N/A		
		T_inc	Temperature experienced within incubation thresholds	Average temperature experienced during range of temperatures within incubation thresholds (field measurement)	see T_R_mE	see T_R_mE	see T_R_mE	37C
				Optimal temperature for egg maturation	see T_R_mE	see T_R_mE		
Ectothermic	**Egg maturation**	T_R_mE	Reference temperature where no enzyme inactivation due to temperature occurs	Any temperature for which maturation is measured within a normal range of temperatures	36.2 - 38.4C for zebra finches in Wada et al 2015	Around 35C in Clauser and McRae 2017; in general, eggs assumed to experience 30-40C regularly, and often colder than this (Huggins 1941; Webb 1987)	Temperature with best outcomes for zebra finches in Wada et al 2015	37C
				Optimal temperature for egg maturation	Mean incubation temperatures proposed as optimal temperatures: 37 and 38.6C for zebra finches (Wada et al 2015; Zann and Rossetto 1991)	Assumed to be between 36-40C for many species (Lundy 1969; Webb 1987; Conway and Martin 2000; DuRant et al 2013)		
		T_L_mE	Low temperature threshold	Low temperature where maturation halts	N/A	Assumed to be around 26C for many species, primarily based on work done in chickens (Lundy 1969; Conway and Martin 2000; DuRant et al 2013; but see Webb 1987)	Low temperature where maturation is assumed to halt	26C
		T_H_mE	High temperature threshold	High temperature where maturation halts (typically estimated for ectothermic species by fitting function to data)	N/A	Not reported; often assumed to correspond to when mortality at high temperatures happens, e.g. 40.5C (Conway and Martin 2000)	High temperature where maturation is assumed to halt	40.5C
		m_T_R_mE	Maturation rate at reference temperature	1/duration of egg stage (doesn't account for temperature)	Variable by species	Variable by species, e.g. Skutch 1945 and Martin et al 2007	1/duration of egg stage at the reference temperature	1/14 days
				1/duration of egg stage at the reference temperature	Incubation period lasts 12.8-14.9 days for zebra finches depending on incubation temperature (Wada et al 2015)	Incubation period lasts 16-19.7 days for Japanese quail (precocial species) depending on incubation temperature (Nord and Nilsson 2021)		
		A_mE	Determines shape of mE(T) around reference temperature	Fit from data on egg maturation at various temperatures	N/A	Maturation is faster at higher-than-optimal temperatures and slower at lower-than-optimal temperatures (Hepp et al 2015)	Selected so that maturation increases after optimal temperature (to capture how eggs hatch faster at higher-than-optimal temperatures)	7000
		A_L_mE	Determines shape of mE(T) around low temperature threshold	Fit from data on egg maturation at various temperatures	N/A	N/A	Selected so that maturation halts below low temperature threshold	-80000
		A_H_mE	Determines shape of mE(T) around high temperature threshold	Fit from data on egg maturation at various temperatures	N/A	N/A	Selected so that maturation halts above high temperature threshold	16000
	Egg mortality	T_Ll_dE	Lower mortality inflection point	Some number of degrees below optimum incubation temperature (arbitrary)	See egg maturation for optimal temperature	See egg maturation for optimal temperature	This parameter does not affect our analyses since we focused on hot extremes; we inferred that the inflection point where mortality changes (by measuring mortality rate across several temperatures) should be lower than 34C, so arbitrarily picked 32C	32C
				Inflection point where mortality changes (by measuring mortality rate across several temperatures)	35.9C impacted zebra finch long term survival, but not hatching rate (Bernsten and Bech 2016)	Wood duck eggs incubated at 34C had lower hatching rates than 36C (Hepp et al 2006)		
		T_Ul_dE	Upper mortality inflection point	Some number of degrees above optimum incubation temperature (arbitrary)	See egg maturation for optimal temperature	See egg maturation for optimal temperature	Inflection point where mortality changes (by measuring mortality rate across several temperatures)	38C
				Inflection point where mortality changes (by measuring mortality rate across several temperatures)	In the Jacky winter, hatching success declined > 35 °C (semi-arid; Sharpe et al 2021); in zebra finches, 38.4C reduced hatching rate relative to 37.4C, aka 1C above presumed optimum (Wada et al 2015); egg survival for Southern pied babblers less likely >35.4C (Bourne et al 2020)	N/A		
		d_T_R_dE	dE within inflection points	(1 - % survival)/duration of egg stage (doesn't account for temperature)	0.017 for verdins (Austin 1977)	0.005 to 0.08 in Ricklefs 1969a, 1969b, with higher values in humid tropics and values 0.01-0.03 in arid tropics	(1 - % survival)/duration of egg stage (doesn't account for temperature)	0.02
				(1 - % survival)/duration of egg stage, in a lab setting controlling for temperature	N/A	N/A		

		T_LT_dE	Lower total mortality point	Cold temperature where mass mortality is observed (use a lower temperature to represent total mortality)	N/A	N/A	Assume that freezing temperatures will result in complete mortality	0C (thus aL = 0.12)
				Rate of increase in mortality rate (by measuring mortality rate across several temperatures)	N/A	Webb 1987 shows reduced survivorship around 10C for limited exposures (Figure 4), and that eggs can experience very low temperatures for short durations and still survive		
		T_UT_dE	Upper total mortality point	Hot temperature where mass mortality is observed (use a higher temperature to represent total mortality)	In Jacky winter, all eggs died at >42.5 °C (semi-arid; Sharpe et al 2021); zebra finch eggs are very heat tolerant and withstood 51C (Griffith et al 2016)	Assumed to be 40.5C for most species (DuRant et al 2013); above 43.5C, king rail clutches had a very low chance of hatching (Clauser and McRae 2017); variable, 40-45C in Webb 1987	Hot temperature where mass mortality is observed	42.5C (thus aH = 0.87)
				Rate of increase in mortality rate (by measuring mortality rate across several temperatures)	N/A	Could potentially be calculated in Webb 1987 Figure 4, but not for individual species		
	Hatchling mortality	T_LI_dH	Lower mortality inflection point	Some number of degrees below optimum incubation temperature (arbitrary)	N/A	N/A	Use value from eggs	32C
				Inflection point where mortality changes (by measuring mortality rate across several temperatures)	N/A	N/A		
		T_UI_dH	Upper mortality inflection point	Some number of degrees above optimum incubation temperature (arbitrary)	N/A	N/A	Use value from eggs, since many of these estimates are based on nestlings defined as both ectothermic and endothermic stage of nestling development, and cannot easily separate direct and indirect effects of temperature	38C
				Inflection point where mortality changes (by measuring mortality rate across several temperatures)	Probability of nestling survival starts to decrease above 33.1C in Southern pied babblers (Bourne et al 2020); probability of fledging reaches <50% above 35.1C in hornbills (van de Ven et al 2020), but is at least partly due to food provisioning (indirect effects of temperature)	Nestling mortality rates increase around 35-38C in lesser kestrel, with probability of mortality reaching >50% at 40-44C (Catry et al 2015; Corregidor-Castro et al 2023); nestlings of rollers (non-passerines) can withstand 50C (Catry et al 2015); note that these estimates are based on nestlings defined as both ectothermic and endothermic stage of nestling development		
		d_T_R_dH	dN within inflection points	(1 - % survival)/duration of hatchling stage (doesn't account for temperature)	0.011 for nestling verdins (Austin 1977), though this includes both ectothermic and endothermic stage of nestling development	0.003 to 0.07 for nestlings in Ricklefs 1969a, 1969; note that these estimates are based on nestlings defined as both ectothermic and endothermic stage of nestling development	(1 - % survival)/duration of nestling stage (doesn't account for temperature)	0.017
				(1 - % survival)/duration of hatchling stage, in a lab setting controlling for temperature	N/A	N/A		
		T_LT_dH	Lower total mortality point	Cold temperature where mass mortality is observed (use a lower temperature to represent total mortality)	N/A	N/A	Use value from eggs	aL_dH = 0.12
				Rate of increase in mortality rate (by measuring mortality rate across several temperatures)	N/A	N/A		
		T_UT_dH	Upper total mortality point	Hot temperature where mass mortality is observed (use a higher temperature to represent total mortality)	No nestlings have survived >38C in Southern Pied Babblers (Bourne et al 2020)	86% cormorant chicks dead from multiple day heat wave (temperatures around 35-38C, Quintana et al 2022); mass mortality of penguin chicks (temperatures at least 44C, Holt and Boersma 2022); mortality in gull chicks after 1 day heat wave (Salzman 1982)	Use value from eggs, since many of these estimates are based on nestlings defined as both ectothermic and endothermic stage of nestling development	aH_dH = 0.87
				Rate of increase in mortality rate (by measuring mortality rate across several temperatures)	N/A	N/A		
	Hatchling maturation	mH	Hatchling maturation rate	1/length of average duration of hatchling stage (doesn't account for temperature)	Superb fairy-wrens develop endothermy in 7 days (Diehl et al 2023); canyon wren develops endothermy in 9-12 days (Ricklefs and Hainsworth 1968)	Development of endothermy after hatching occurs on day 4.5-12 for many passerines (Dunn 1975; Clark and Balda 1981; Clark 1982; Olson 1992)	1/length of average duration of nestling stage (doesn't account for temperature)	1/7 days

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A.2 Appendix S2

Here we show the effect of varying various parameters on adult abundance. In general, these analyses reveal that the results we present in the main text are robust to parameter choice. In some cases, changing parameters has very little effect on year 100 adult abundance. In others, the qualitative result (e.g. very low abundance at 5C of warming, high abundance at 1.5C warming, and some mid-level abundance at 3C of warming) is robust, while the exact abundance depends on parameter choice. In these cases, the analyses we present in this supplement demonstrate the potential for species with different life history traits to be differentially impacted by warming, and lay the groundwork for further exploration in this area.

A.2.1 Sensitivity analysis 1: egg maturation parameters

We begin by considering parameters that dictate the shape of the egg maturation temperature response function at normal-to-high temperatures. We focus on THmE, the upper maturation threshold, and two parameters that determine the shape of the temperature response function at normal-to-high temperatures, AmE and AHmE. Since the shape of this function can only be evaluated in warming scenarios, we ran the sensitivity analyses in three warming scenarios (warmer summers with 1.5, 3, and 5 degrees of warming).

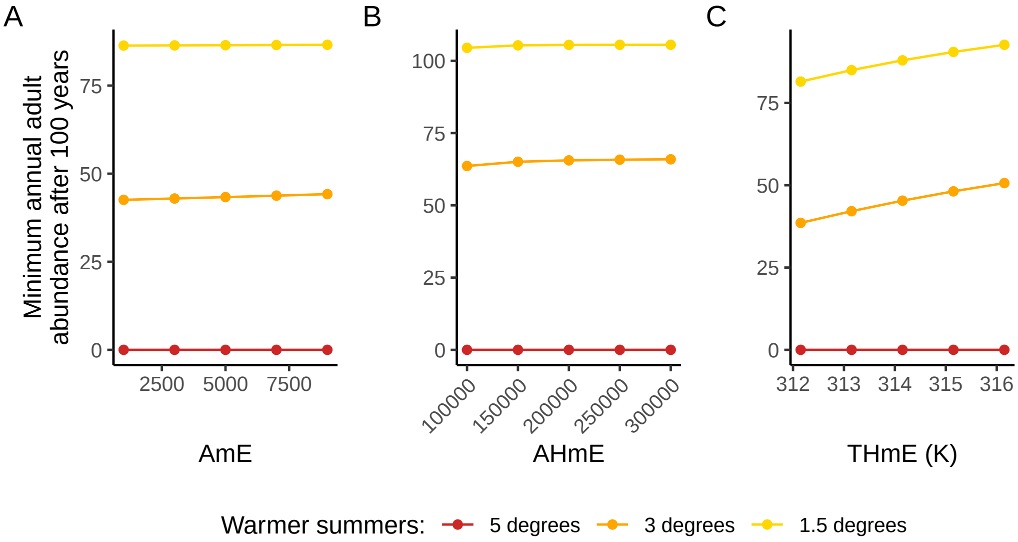

Figure A.1: Adult abundance does not respond strongly to three parameters that dictate the shape of the egg maturation function. Colors represent warming regimes (1.5, 3, or 5 degrees of warmer summers).

A.2.2 Sensitivity analysis 2: "base" parameters

Next, we show the effect of varying base mortality rates (i.e., mortality rates within lower and upper inflection points) and maturation rates (mH, the temperature-independent hatchling mortality rate, and mETR, the egg maturation rate at the reference temperature). Since these parameters affect dynamics regardless of warming, we explore their effect on adult abundance under typical seasonal variation. To compare the effects of the parameters to each other, we use a range of percentages of each parameter, but also present individual plots to show dynamics with reasonable ranges of values for each vital rate (Table S1).

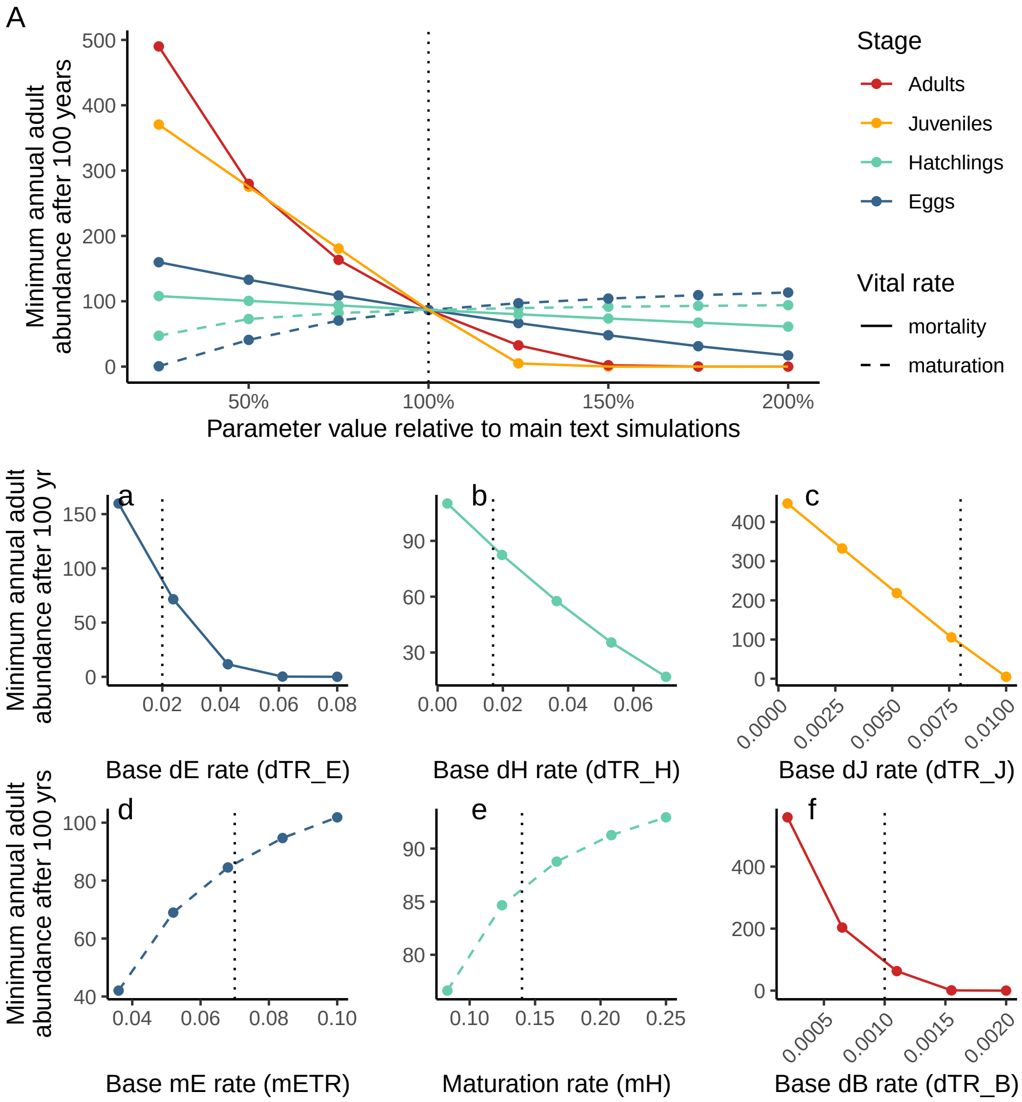

Figure A.2: Species that vary in life history traits (i.e. average lifespan, average incubation duration, and expected mortality rates of life stages) will vary in abundance, making these interesting axes in which to explore warming effects in future studies. Colors represent life stages (red = adults, yellow = juveniles, turquoise = hatchlings, and blue = nestlings), and line type represents the vital rate (solid line = mortality rate, dashed line = maturation rate of ectothermic stages). In **A**, all traits are overlaid so as to compare how percent changes in each parameter affect adult abundance relative to the values used in the simulation (dotted vertical line). In **a-f**, traits are represented individually using reasonable values for each parameter (with value used in the simulation marked with a dotted vertical line).

A.2.3 Sensitivity analysis 3: parameters whose units are temperature

The final set of parameters we explore are those related to upper inflection points (for mortality rate and incubation functions) and rates of increase above those upper inflection points. Since these are temperature thresholds that are only crossed in warming scenarios, we ran the sensitivity analyses with three warming scenarios (warmer summers with 1.5, 3, and 5 degrees of warming).

When varying upper inflection points, we kept the rates of increase (and all other parameters) the same as the values used in main text simulations. When varying rates of increase, we kept the upper inflection points the same as main text simulations and calculated new rates of increase by considering a range of total mortality points. For each parameter, we ran the simulation with 10 alternative temperatures, considering 5 degrees on either side of the parameter. There were exceptions for two stages: the upper inflection point and total mortality points for the egg and hatchling stages were about 4.5 degrees apart, so we did not consider total mortality points 5 degrees lower than the value used in main text simulations, since that would make the total mortality point a lower temperature than the upper inflection point.

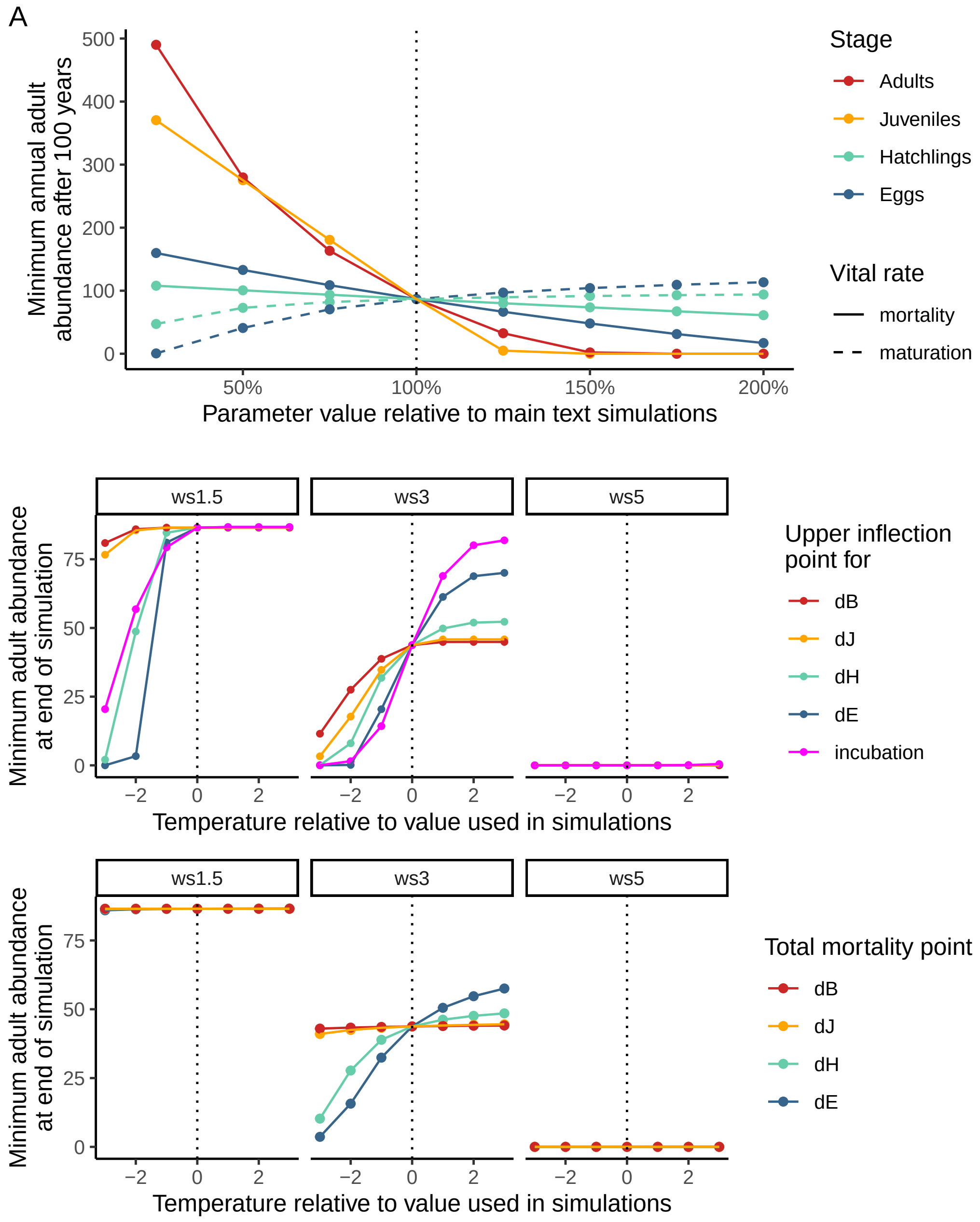

Figure A.3: Species differing in sensitivity of the mortality rate to temperature did not vary in outcome at 5 degrees of warming, but lowering the upper mortality inflection point (aka reducing thermotolerance). Colors represent life stages (red = adults, yellow = juveniles, turquoise = hatchlings, and blue = nestlings) or incubation rate (pink).Vertical panels represent warming regimes (1.5, 3, or 5 degrees of warmer summers). Dotted vertical lines represent values used in simulation. **A** depicts variation in the upper inflection point of the mortality rate for different life stages, or the upper threshold for the incubation rate. **B** depicts variation in the total mortality point, which dictates the rate of increase above the upper mortality inflection point.

A.3 Additional Supplemental Figures

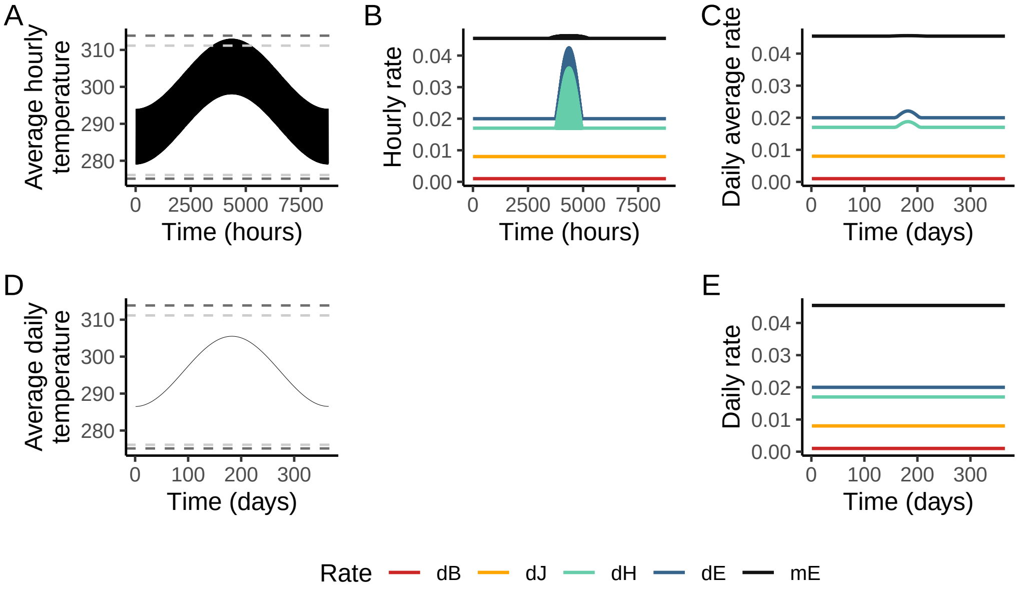

Figure A.4: Averaging hourly vital rates is important for capturing how temperature impacts bird populations. Temperatures and bird vital rates are displayed for the last year of a warming simulation where average annual temperature increases by 3°C over 100 years, with annual variation in temperature increasing because of increasingly warmer summers. (A) Hourly temperatures during the summer exceed the temperature at which bird vital rates are no longer constant. The model calculates vital rates for each hour (B), and averages them to get daily average rates to use in the simulation (C). Using average daily temperatures (D) instead of hourly temperatures to calculate daily average rates (E) results in constant vital rates across the year, since the average daily temperatures do not exceed the temperature at which bird vital rates are no longer constant.

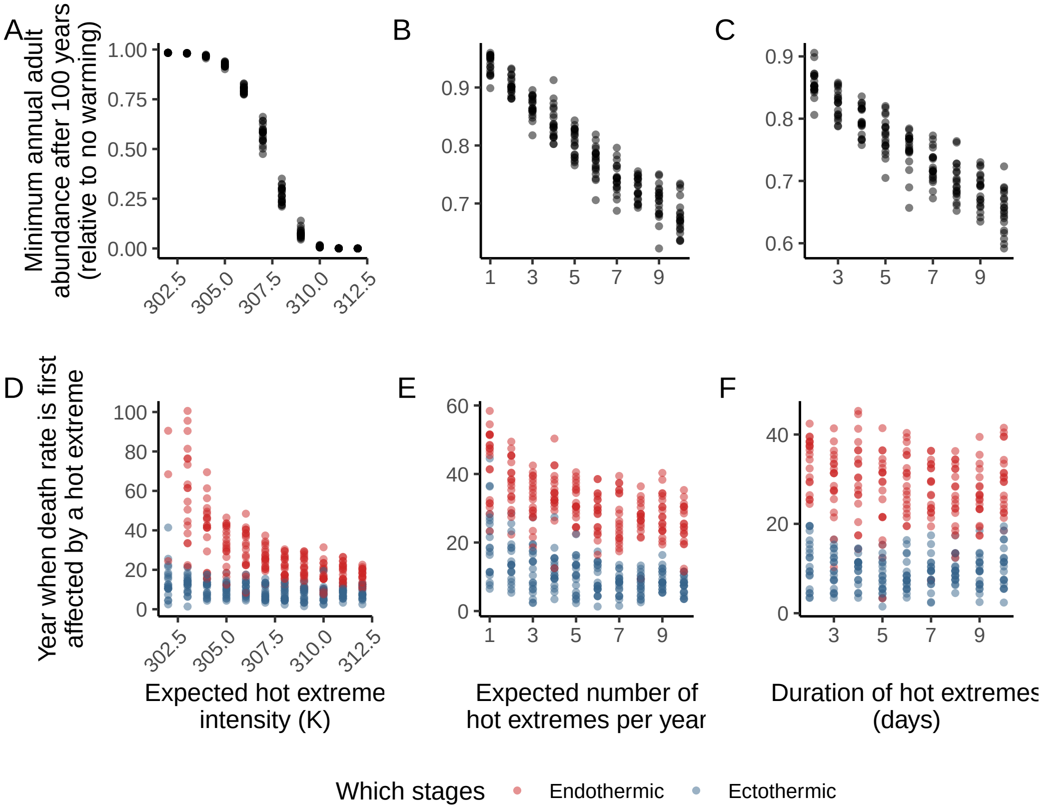

Figure A.5: Averaging hourly vital rates is important for capturing how temperature impacts bird populations. Temperatures and bird vital rates are displayed for the last year of a warming simulation where average annual temperature increases by 1.5°C over 100 years, with annual variation in temperature increasing because of increasingly warmer summers. (A) Hourly temperatures during the summer exceed the temperature at which bird vital rates are no longer constant. The model calculates vital rates for each hour (B), and averages them to get daily average rates to use in the simulation. Using average daily temperatures instead of hourly temperatures (D) to calculate daily average rates (E) results in constant vital rates across the year, since the average daily temperatures do not exceed the temperature at which bird vital rates are no longer constant.

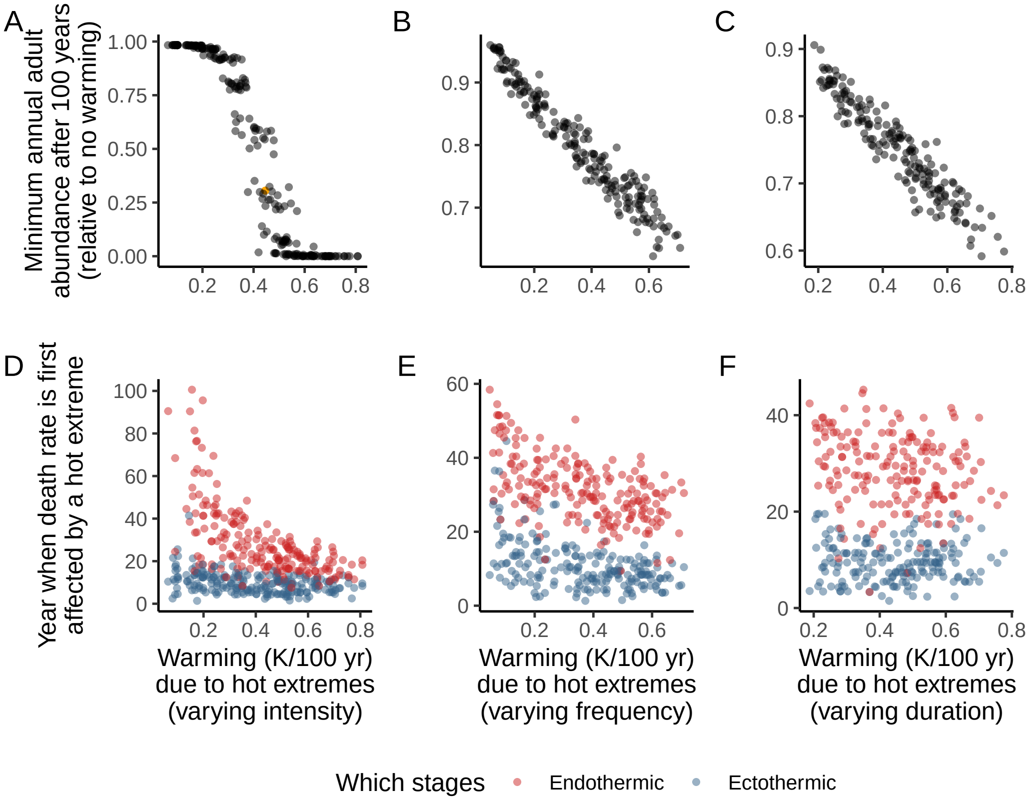

Figure A.6: Averaging hourly vital rates is important for capturing how temperature impacts bird populations. Temperatures and bird vital rates are displayed for the last year of a warming simulation where average annual temperature increases by 1.5°C over 100 years, with annual variation in temperature increasing because of increasingly warmer summers. (A) Hourly temperatures during the summer exceed the temperature at which bird vital rates are no longer constant. The model calculates vital rates for each hour (B), and averages them to get daily average rates to use in the simulation. Using average daily temperatures instead of hourly temperatures (D) to calculate daily average rates (E) results in constant vital rates across the year, since the average daily temperatures do not exceed the temperature at which bird vital rates are no longer constant.

Appendix B

Supplement for Chapter 2

B.1 Appendix S1

Table B.1: Information on temperature-induced condition changes (causes, consequences/costs, and recovery).Orange cells contain threshold temperatures displayed in Figure 2A; blue cells contain threshold temperatures displayed in Figure 2B. *See following page for table.*

		Adults										Hatchling/nestling/fledgling					Egg	
		Possible mechanisms for T -> change in condition			Thresholds/patterns for T -> change in condition			Condition recovery rate	Costs of poor condition			Thresholds/patterns for T -> change in condition	Costs of poor condition				Long term costs of egg incubation temperature	
Paper	Species	Onset of heat-dissipating behaviors (HDBs)	Reduction in foraging effort or efficiency	Reduction in offspring provisioning	Adult net 0 24hr mass (diurnal mass gain = noctural mass loss)	Adult 0 diurnal mass gain (net negative daily loss corresponding to nocturnal mass loss)	Other measure of adult mass or body condition loss	Adults able to recover body condition?	Adult body condition affects adult survival	Adult condition affects egg or nest success	Nests abandoned/breeding not attempted	Hatchling/nestling mass loss or relatively smaller	Delay or advance in fledging (nestling maturation)	Hatchling/nestling temps affect fledgling mass	Hatchling/nestling temps affect later success	Fledging temperatures affect success	Egg incubation temperature affects nestling size	Egg incubation temperature affects long term survival
du Plessis et al 2012	Southern Pied Babbler (Turdoides bicolor)	Tmax ~ 34C (McKechnie et al 2021 reports 38.2C in lab)	reduced efficiency not effort with higher Tmax and when doing HDBs	n/a	Tmax 35.5C for nonbreeding adults	Tmax 38.5C for nonbreeding adults	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Wiley and Ridley 2016	Southern Pied Babbler (Turdoides bicolor)	n/a	n/a	decrease in provisioning with increased Tmax	n/a	n/a	n/a	n/a	n/a	n/a	n/a	11 day old nestling mass decreases with number of days Tmax > 35.5C	n/a	n/a	n/a	n/a	n/a	n/a
Bourne et al 2021 Behavioral Ecology	Southern Pied Babbler (Turdoides bicolor)	n/a	total biomass caught increased with Tmax until ~32.3C, above which is declined with Tmax	provisioning effort negatively associated with temperature	n/a	n/a	n/a	n/a	n/a	n/a	n/a	high temps associated with smaller hatchling/nestling body mass. SEM shows that temp affects day 5 mass directly, and temp plus provisioning affects day 11 mass	n/a	n/a	day 5 and day 11 mass each predict probability of fledging from nest	n/a	n/a	n/a
Bourne et al 2021 Conservation Physiology	Southern Pied Babbler (Turdoides bicolor)	n/a	n/a	n/a	n/a	daily mass loss increases with increasing Tmax above 36.1C (breeding/incubating adults)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Bourne et al 2022 Ibis	Southern Pied Babbler (Turdoides bicolor)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	high temps during nestling stage associated with smaller body mass	n/a	n/a	n/a	temperatures after fledging negatively associated with survival to day 90 (nutritional independence) (acute response to temp, not effect of mass necessarily)	n/a	n/a
Bourne et al 2020 Proc B	Southern Pied Babbler (Turdoides bicolor)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	high temps during nestling stage associated with smaller body mass	decline in age at fledging between mean Tmax = 37.3-38C (above 38C all young die) (acute response to temp, not effect of mass necessarily)	n/a	day 11 mass predicts probability of survival to day 90	n/a	n/a	n/a
Cunningham et al 2013 PLoS ONE	Common Fiscal (Lanius collaris)	n/a (McKechnie et al 2021 reports 40C in lab)	n/a	reduction in provisioning at high Tmax for large broods	n/a	n/a	n/a	n/a	n/a	n/a	n/a	6 day old hatchlings mass neg. affected by Tmax (maybe harder to detect for nestlings)	n.s. but positive increase in time to fledging with mean Tmax of nesting period >35C (acute response to temp, not effect of mass necessarily)	n.s. but negative effect; temps on days 8 and 10 matter most for fledgling mass. Tmax > 33C	n/a	n/a	n/a	n/a
Catry et al 2015	Lesser Kestrel and Common Roller	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	lower mass with higher Tmax for both species (for roller, depends on nest type)	n/a	lower mass from heat event affects fledging mass for kestrels, not rollers	n/a	n/a	n/a	n/a
van de Ven et al 2019	Southern Yellow-billed Hornbill	n/a	reduced efficiency not effort with higher Tmax, and reduced efficiency depending on microhabitat	n/a	maybe ~26C for breeding males	Tmax > 38.4C for breeding males	n/a	yes	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
van de Ven et al 2020	Southern Yellow-billed Hornbill	n/a	n/a	decrease in provisioning with increased Tmax	breeding females lose body mass regardless of temperature	Tmax > 31.4C for breeding females	n/a	n/a	n/a	yes, larger females had higher success (could last in nest longer probably)	references cannibalism/nest abandonment; see vdV thesis	nestling net 24 hr mass loss Tmax > 40.6C; mass reduced with higher Tmax and with lower provisioning	delay of 2.6 days for every 1C increase in Tmax (acute response to temp, not effect of mass necessarily)	Tmax during nestling period reduced nestling mass right before fledging	n/a	n/a	n/a	n/a
Pattison et al 2022	Southern Yellow-billed Hornbill	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	fewer nesting attempts when hotter	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Sharpe et al 2019	Jacky Winter	~30-35C	n/a	n/a	n/a	n/a	net mass loss when Tmax >= 42C or < 26C	yes, over several days without hot extremes	not short-term survival, mortality seemed due to acute T not cumulative mass loss; didn't investigate long-term survival	n/a	abandoned eggs >40C	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Gardner et al 2016	White-plumed Honeyeater	n/a	n/a	n/a	n/a	n/a	body condition (based on body mass) lower if Tmax > 35C for several days during low rain years	n/a	males had lower chance of survival to next year if condition was low. Female survival low, could be because they are smaller	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Gardner et al 2018	Red-winged Fairy Wren (Malurus elegans) and White-browed Scrubwren (Sericornis frontalis)	n/a	n/a	n/a	n/a	n/a	body condition improved with fewer cold minima for both species and declined with Tmax > 30C for fairy wrens, no change for scrubwrens	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Pattison and Smit 2017	Rufous-eared Warbler (Malcorus pectoralis)	~25-30C	reduced foraging effort and success (along with other behaviors reduced) while panting increased	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Salaberria et al 2013	Spotless Starlings (Sturnus unicolor)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	high temps during nestling stage associated with smaller body mass for second broods, which experience hotter conditions than first broods	n/a	n/a	n/a	n/a	n/a	n/a
Nord and Nilsson 2016	Blue Tit (Cyanistes caeruleus)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	not reported	incubation temp interacted with body mass to predict nestling survival to winter and to next breeding season. Cold and high incubation temps had lower adult body masses compared to mid incubation temp
Hepp and Kennamer 2012	Wood Duck (Aix sponsa)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	incubation at cold temp led to smaller nestling body mass	ducks incubated at colder temps were less likely to fledge & to be recaptured as adults, and had lower reproductive success (albeit small sample size)
Berntsen and Bech 2016	Zebra finch (Taeniopygia guttata)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	not reported	cooler incubation temp didn't affect egg or nestling survival, but DID reduce long term survival after fledging
Berntsen and Bech 2021	Zebra finch (Taeniopygia guttata)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	incubation temperature didn't affect nestling body mass or adult body mass	uncovered possible mechanism for reduction in long term survival observed in prev paper: eggs incubated at cooler temp have more oxidative stress, and it accumulates through time
Belnap et al 2019	Bobwhite quail	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	cooler-than-optimal incubation temperatures had smaller body size (hotter-than-optimal had smaller tarsi but body mass didn’t change)	didn't measure long term survival, but cooler- and hotter-than-optimal chicks had locomotory issues

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Appendix C

Supplement for Chapter 3

C.1 Supplemental figures

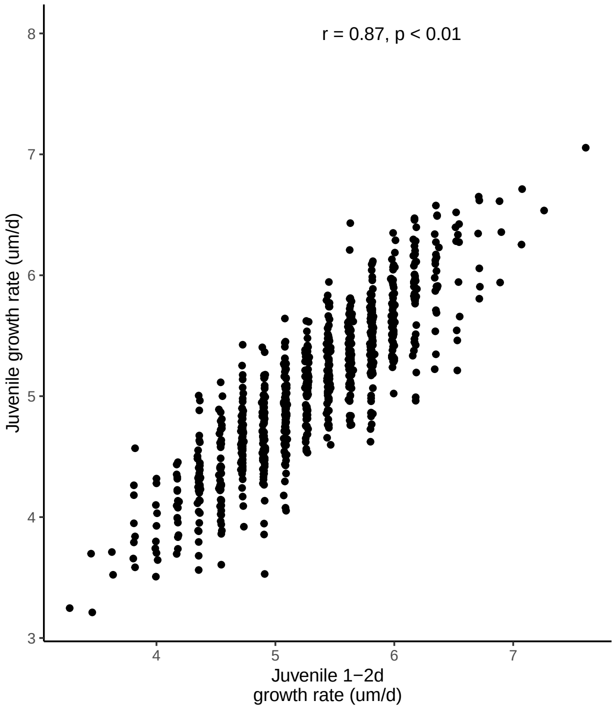

Figure C.1: Significant correlation between two different measures of *Stegastes partitus* juvenile growth rate data in the present study (n = 256): the mean daily growth rate across the first two days of the juvenile period as reported in Rankin and Sponaugle (2014) and the mean growth rate over the entire juvenile period (i.e. from settlement to collection).

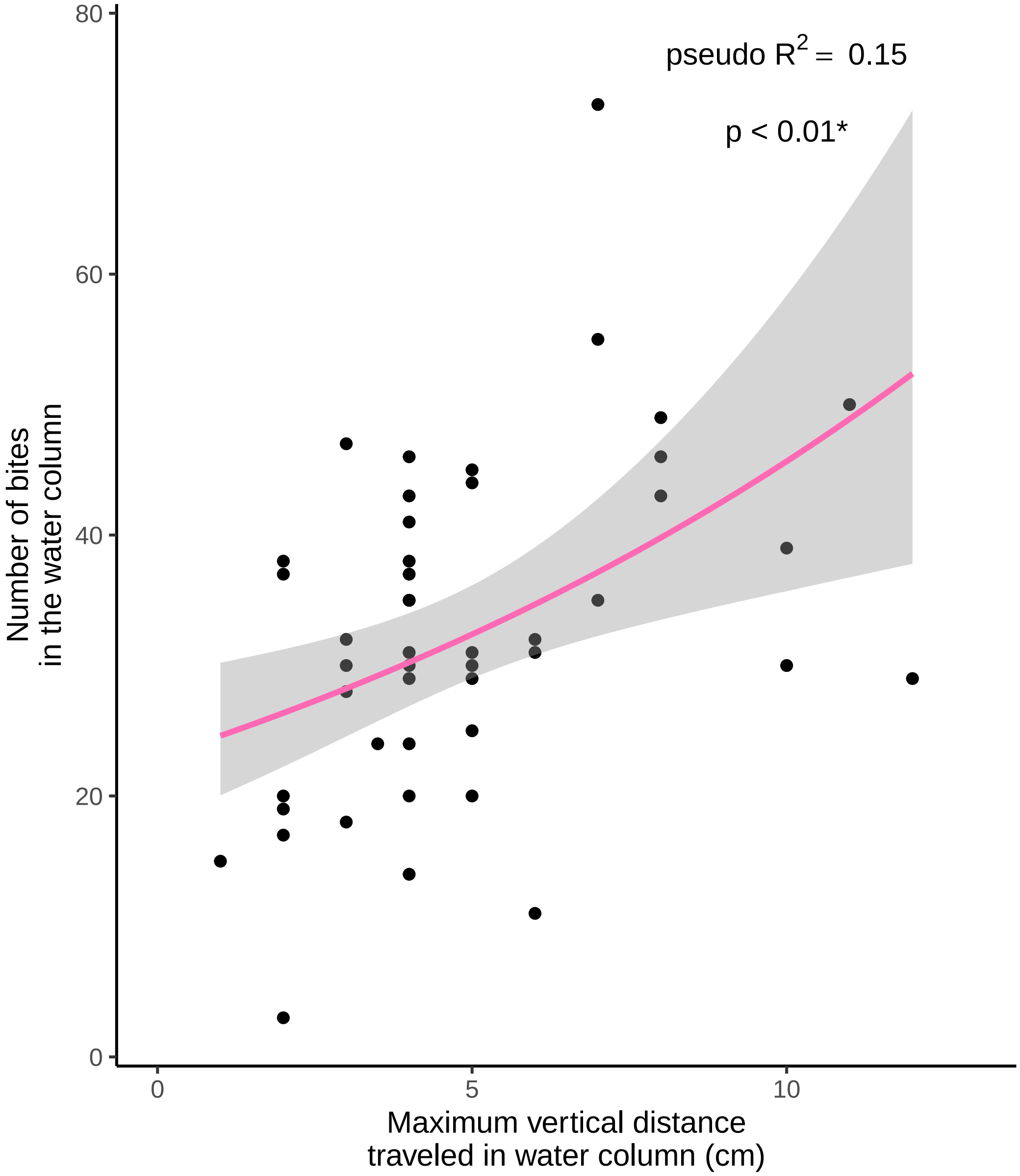

Figure C.2: Number of bites taken in the water column by newly settled juvenile *Stegastes partitus* over a 5-min observation period vs maximum vertical distance travelled by the same individual during that period. Pink line indicates a significant relationship (negative binomial-distributed generalized linear model: $p<0.001$). Number of bites taken in the water column was measured for a subset ($n = 46$) of fish from 2009.

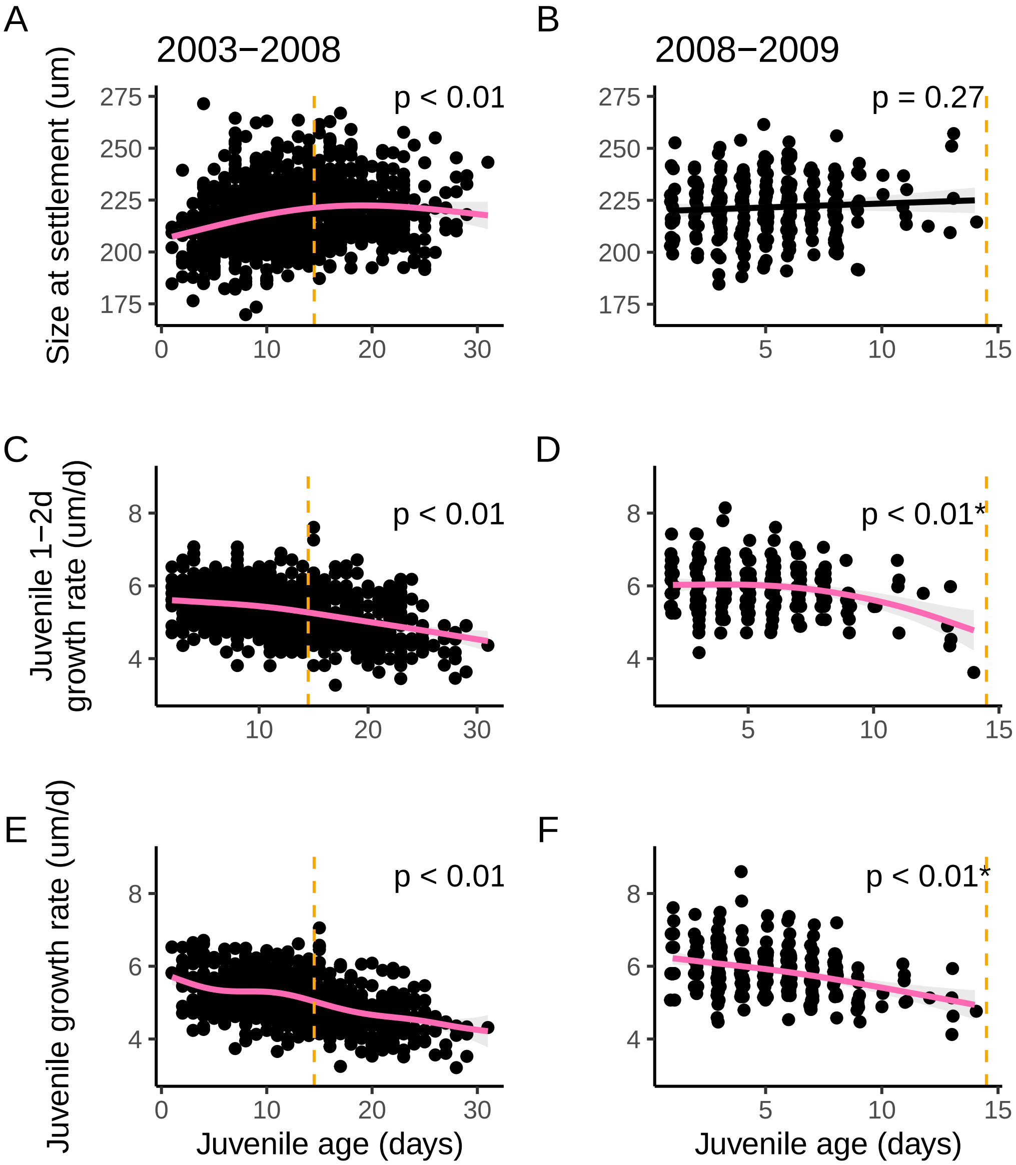

Figure C.3: Comparison of *Stegastes partitus* early life traits across juvenile age for data in the (A,C,E) 6-yrrecruitment time-series (n = 818) from Rankin and Sponaugle (2014) and in the (B,D,F) present study (n =256). Data plotted for continuous aged juveniles, with pink lines representing significant relationships and black lines non-significant relationships from generalized additive models (GAMs). Settlement size (A,B) was derived from the position of the settlement mark on otoliths of individual fish. Juvenile 1-2d growth rate (C,D) was computed from mean otolith increment widths for the first two days of life on the reef, while juvenile growth rate (E,F) was computed from mean otolith increment widths across the entire juvenile period (from settlement to collection). Vertical dashed orange line indicates scope of the present study(oldest fish = 14 days old).

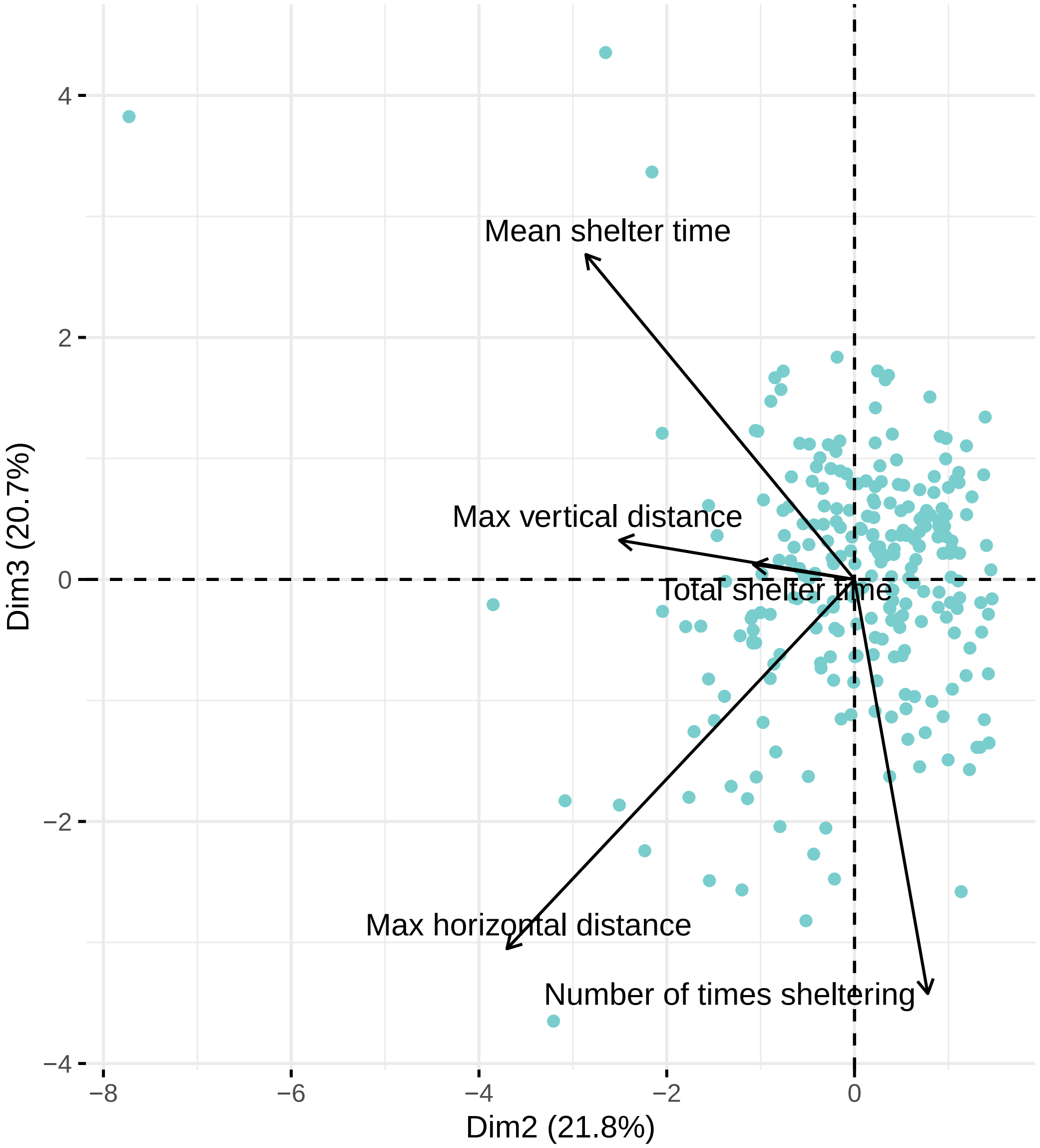

Figure C.4: PC3 vs PC2 in principal component analysis (PCA) of behaviors observed over 5 min for newly settled *Stegastes partitus* juveniles (n = 256), observed over 5 months in the Florida Keys. Behaviors are mean and total time spent sheltered, number of times shelter was sought (Number of times sheltering), maximum distance travelled horizontally (Max horizontal distance) and vertically (Max vertical distance) from the primary shelter

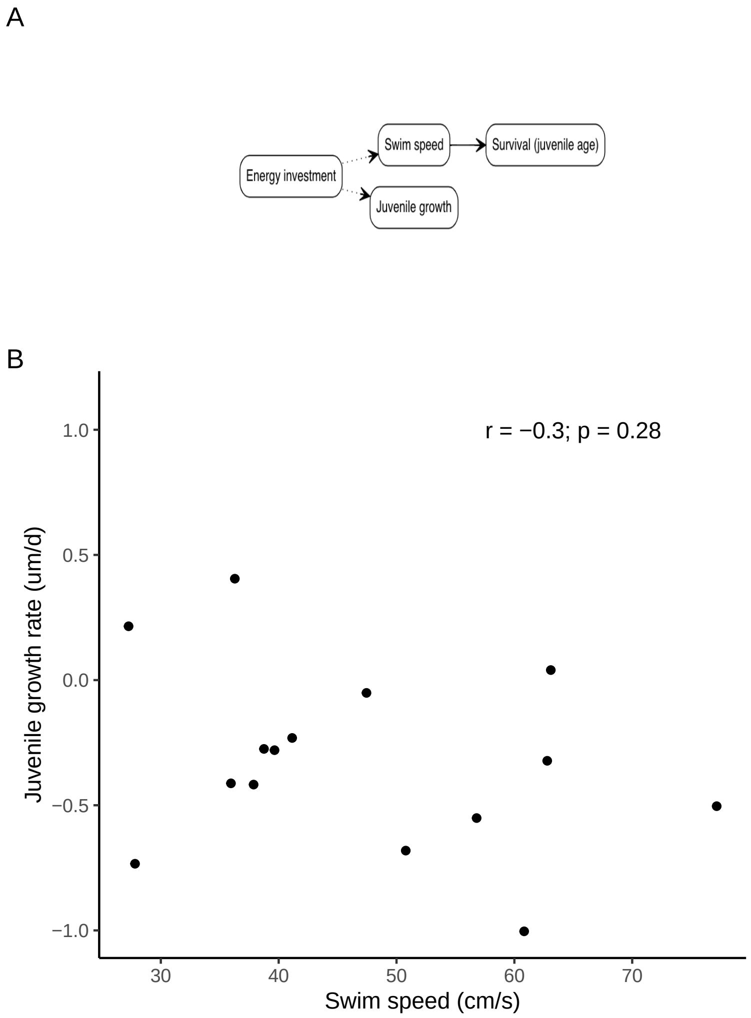

Figure C.5: *Stegastes partitus* energetic trade-offs in predator evasion. (A) Directed acyclic graph (DAG) outlining a hypothesis for how juvenile *S. partitus* slow juvenile growth rate could be related to increased survival. Energy allocation (unmeasured in our study) could lead to a trade-off between juvenile growth and swim speed, and faster swim speeds could increase chance of survival. A significant correlation between swim speed and juvenile growth rate would support this hypothesis. Black dotted lines indicate potential causal relationships between unmeasured and measured variables; black solid line indicates potential causal relationship between measured variables. Due to the small sample size, we did not perform a path analysis on this DAG and instead investigated (B) the correlation between juvenile growth rate and burst swim speed in response to a simulated predator attack. Swim speed measured in situ for n=15 new settlers using a stereo camera. We report the non-significant Pearson's correlation and p-value on the figure

C.2 Supplemental tables

Table C.1: Generalized linear model (GLM) with a negative binomial error structure predicting number of times fish take bites in the water column.

	Estimate	Std. Error	z value	p value
(Intercept)	3.13	0.12	25.28	<0.001
Max vertical distance	**0.07**	**0.02**	**3.08**	**0.002**

Table C.2: Linear mixed effects model (LMM) predicting juvenile growth rate (um/d, residuals) in the 2008-2009 dataset, with random intercepts for collection site.

	Estimate	Std. Error	df	t value	p value
(Intercept)	0.45	0.11	4.50	4.26	0.010
Settlement size	0.15	0.09	249.51	1.75	0.081
Juvenile age	**-0.09**	**0.01**	**251.60**	**-5.84**	**<0.001**
Settlement size x juvenile age	**-0.03**	**0.01**	**251.47**	**-2.30**	**0.022**

Table C.3: LMM predicting juvenile growth rate (um/d, residuals) in the 2003-2008 dataset, with random intercepts for collection site.

	Estimate	Std. Error	z value	p value
(Intercept)	0.61	0.04	14.67	<0.001
Settlement size	0.05	0.04	1.22	0.223
Juvenile age	**-0.05**	**0.00**	**-16.05**	**<0.001**
Settlement size x juvenile age	**-0.01**	**0.00**	**-2.47**	**0.014**

Table C.4: Path coefficients for the DAG in Figure 3.4A. The model is well fit to the data (C-statistic = 1.33, df = 6, p-value = 0.97). A p-value < 0.05 would indicate that the hypothesized structure in the DAG is not supported by the data. Estimates correspond to partial regression coefficients and can be interpreted as the expected change in the response given a unit change in the predictor. Standardized estimates are calculated by scaling these estimates by the ratio of the standard deviation of the predictor over the standard deviation of the response.

Response	Predictor	Estimate	Std.Estimate	Std.Error	DF	Crit.Value	P.Value
PC1	**Settlement size**	**-0.24**	**-0.17**	**0.09**	**254**	**-2.69**	**0.008**
PC2	Settlement size	-0.04	-0.03	0.07	254	-0.54	0.591
PC3	**Settlement size**	**-0.13**	**-0.13**	**0.06**	**256**	**-2.08**	**0.038**
Juvenile age	**Juv. growth rate**	**-1.36**	**-0.35**	**0.23**	**250**	**-6.03**	**<0.001**
Juvenile age	Settlement size	0.00	0.00	0.15	250	0.01	0.989
Juvenile age	**PC1**	**-0.30**	**-0.16**	**0.10**	**250**	**-2.84**	**0.005**
Juvenile age	PC2	-0.28	-0.11	0.14	250	-1.91	0.057
Juvenile age	**PC3**	**-0.36**	**-0.14**	**0.15**	**250**	**-2.46**	**0.015**
Juv. growth rate	PC1	0.00	0.00	0.03	251	0.08	0.939
Juv. growth rate	PC2	0.06	0.10	0.04	251	1.55	0.123
Juv. growth rate	PC3	-0.02	-0.03	0.04	251	-0.40	0.691
Juv. growth rate	Settlement size	-0.04	-0.07	0.04	251	-1.05	0.297

Table C.5: R-squared values for component models for the DAG in Figure 3.4A.

Response	Family	Link	Mixed model	Marginal R2	Conditional R2
PC1	Gaussian	identity	No	0.03	NA
PC2	Gaussian	identity	No	0.00	NA
PC3	Gaussian	identity	Yes	0.02	0.08
Juvenile age	Gaussian	identity	No	0.19	NA
Juvenile growth rate	Gaussian	identity	No	0.01	NA

Table C.6: Path coefficients for the DAG in Figure 3.5A. The model is well fit to the data (C-statistic = 13.55, df = 12, p-value = 0.33). A p-value < 0.05 would indicate that the hypothesized structure in the DAG is not supported by the data. Estimates correspond to partial regression coefficients and can be interpreted as the expected change in the response given a unit change in the predictor. Standardized estimates are calculated by scaling these estimates by the ratio of the standard deviation of the predictor over the standard deviation of the response.

Response	Predictor	Estimate	Std.Estimate	Std.Error	DF	Crit.Value	P.Value
Times chased	**Adult density**	**0.10**	**0.13**	**0.03**	**162**	**3.44**	**0.001**
Times chased	Settlement size	-0.02	-0.01	0.11	162	-0.19	0.848
Times chased	PC1	0.05	0.04	0.07	162	0.78	0.435
Times chased	PC2	0.08	0.04	0.11	162	0.75	0.454
Times chased	**PC3**	**-0.27**	**-0.14**	**0.11**	**162**	**-2.47**	**0.014**
Juv. growth rate	**Adult density**	**-0.04**	**-0.19**	**0.02**	**159**	**-2.43**	**0.016**
Juv. growth rate	Times chased	0.01	0.02	0.05	159	0.26	0.792
Juv. growth rate	Settlement size	0.03	0.05	0.05	160	0.58	0.560
Juv. growth rate	PC3	-0.08	-0.14	0.05	145	-1.74	0.084
Juv. growth rate	PC1	0.00	0.00	0.03	160	-0.05	0.959
Juv. growth rate	PC2	0.04	0.07	0.04	159	0.89	0.375
Juv. growth rate	**Chased:Settlmt size**	**-0.11**	**-0.19**	**0.05**	**159**	**-2.29**	**0.024**
Juvenile age	Juv. growth rate	-0.47	-0.13	0.29	159	-1.60	0.111
Juvenile age	Times chased	-0.15	-0.06	0.18	158	-0.84	0.404
Juvenile age	Settlement size	-0.09	-0.04	0.19	159	-0.48	0.634
Juvenile age	PC3	-0.32	-0.14	0.18	157	-1.78	0.076
Juvenile age	**PC2**	**-0.31**	**-0.15**	**0.16**	**158**	**-2.01**	**0.046**
Juvenile age	**PC1**	**-0.28**	**-0.20**	**0.11**	**159**	**-2.54**	**0.012**
Juvenile age	Adult density	-0.03	-0.03	0.07	158	-0.43	0.665
Juvenile age	Chased:Settlmt size	-0.09	-0.04	0.17	158	-0.54	0.593
PC1	**Settlement size**	**-0.26**	**-0.16**	**0.12**	**166**	**-2.11**	**0.036**
PC2	Settlement size	0.01	0.01	0.09	166	0.08	0.936
PC3	**Settlement size**	**-0.21**	**-0.20**	**0.08**	**168**	**-2.68**	**0.007**

Table C.7: R-squared values for component models for the DAG in Figure 3.5A

Response	Family	Link	Mixed model	Marginal R2	Conditional R2
Times chased	Poisson	log	No	0.13	NA
Juvenile growth rate	Gaussian	identity	Yes	0.08	0.10
Juvenile age	Gaussian	identity	Yes	0.09	0.13
PC1	Gaussian	identity	No	0.03	NA
PC2	Gaussian	identity	No	0.00	NA
PC3	Gaussian	identity	Yes	0.04	0.10

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