Individual Behavioral Variation in a Highly-Mobile Marine Predator: Plasticity, Experience, and Fitness Outcomes

Erik W. Johansson

A dissertation
submitted in partial fulfillment of the
requirements for the degree of:

Doctor of Philosophy

University of Washington

2026

Reading Committee:
Briana Abrahms, Chair
P. D. Boersma
Berry Brosi

Program Authorized to Offer Degree:
Biology

University of Washington

Abstract

Individual Behavioral Variation in a Highly-Mobile Marine Predator: Plasticity, Experience, and Fitness Outcomes

Erik W. Johansson

Chair of the Supervisory Committee:
Briana Abrahms
Department of Biology

In this dissertation, I examine variation in the foraging and breeding behavior of a marine predator. I describe patterns underlying this variation, measure fitness consequences of alternative behavioral strategies, and highlight the role of previous experience as a driver of behavioral decisions. First, I conduct the first test of correlated behavioral plasticities in a wild population and show that expressions of plasticity are coupled; not only does behavioral plasticity vary across a population, but the level of behavioral plasticity expressed by an individual is correlated across distinct behaviors. Second, I find that the fitness consequences of coordinated reproductive plasticity are mediated by environmental conditions. While plasticity improves reproductive success in the context of highly productive ocean conditions, it does not buffer against the negative reproductive impacts of highly unproductive conditions. Third, I use metrics of foraging success derived from high-resolution biologging data to reveal that previous success impacts broad-scale movement decisions and fine-scale foraging activity allocation. I highlight this state-behavior feedback as a mechanism that can produce and maintain interindividual behavioral variation. Together, this dissertation advances our understanding of behavioral variation by drawing connections across movement, foraging, and cognitive ecology.

Contents

Acknowledgements **4**
Introduction **5**
Chapter 1: Patterns of Individual Variation in Plasticity Across Multiple Behaviors in Wild Vertebrates **8**
1.1 Abstract 8
1.2 Introduction 9
1.3 Methods 12
1.4 Results 16
1.5 Discussion 18
1.6 Supplementary Material 22
Chapter 2: Consequences of Individual Variation in Plasticity in Wild Vertebrates **29**
2.1 Abstract 29
2.2 Introduction 30
2.3 Methods 32
2.4 Results 35
2.5 Discussion 38
2.6 Supplementary Material 42
Chapter 3: Previous Foraging Success Shapes Behavioral Decision-Making Across Scales **47**
3.1 Abstract 47
3.2 Introduction 48
3.3 Methods 52
3.4 Results 57
3.5 Discussion 61
3.6 Supplementary Material 65
Conclusion **71**
Bibliography **75**

Acknowledgements

This work would not have been possible without the support, guidance, and kindness of so many others. First and foremost, thank you to my advisor Briana Abrahms, for her unwavering encouragement and direction throughout the years of this work. I am also deeply grateful to my Committee members, Dee Boersma, Berry Brosi, and Andrew Berdahl, for their invaluable feedback and support.

Thank you to the members of the Abrahms Lab who have provided support and community over the years: Leigh West, Kasim Rafiq, Anna Nisi, TJ Clark-Wolf, Meredith Honig, Marie-Pier Poulin, Katherine Stewart and Kyra McClelland; as well as the many members of the Center for Ecosystem Sentinels, in particular: Eric Wagner, Ginger Rebstock, Katie Holt, Pearl Wellington, and Kalyna Durbak. For Chapters 1 and 2, I am thankful to the members of the Prugh lab for their helpful feedback, and am especially grateful for statistical guidance from Tim Jones. For Chapter 3, I owe thanks to the Berdahl and Sridhar labs for their valuable input.

The data used for all three chapters were collected at Punta Tombo, Argentina, made possible by permits and logistical support from the Province of Chubut Government Offices of Flora and Fauna and of Tourism, many long-lasting relationships between the Center for Ecosystem Sentinels and Argentine collaborators, as well as countless volunteers over the past four decades. I'd like to thank in particular those who I spent time with at Punta Tombo and whose work most directly contributed to the datasets used in the research presented here: Katie Holt, Dee Boersma, Kevin Robinson, Chloe Rabinowitz, Kalyna Durbak, Meredith Honig, Bryn Carter, and Sofia Denkovski.

Introduction

The diversity and flexibility of animal behavioral expressions has drawn scientific interest for centuries, and carries consequences for individual fitness, population resilience, and ecological processes (Dall et al., 2012; Gross et al., 2010; Réale et al., 2010). While traditional approaches in behavioral ecology averaged behavior across individuals and contexts, interest in the variation around these averages has grown over the past two decades (Wolf and Weissing, 2012), enabled by advances in data collection technology, computing power, and ecological theory (Hertel et al., 2020; Nathan et al., 2008; Sih et al., 2004b). Empirical work documenting patterns in this behavioral variation has been conducted across taxa and behaviors, with examples in mammals, fish, birds, reptiles, amphibians, and invertebrates (Bolnick et al., 2003), spanning behaviors involved in movement, foraging, and reproduction. This work has revealed that the variation around average behavioral expression is more than noise. The expression of a behavior can vary consistently across individuals (inter-individual behavioral variation; Stamps, 2016), or within an individual across time or contexts (intra-individual behavioral variation; Beever et al., 2017), and expression can be correlated across behaviors (Sih et al., 2004a). Despite a growing interest in animal behavioral variation, gaps remain in our understanding of the patterns underlying behavioral variation, the ecological and evolutionary consequences of behavioral variation, and the mechanisms that produce and sustain behavioral variation.

Attempts to describe patterns in animal behavioral variation has led to a framework that partitions the variation into behavioral type (mean expression), behavioral plasticity (change in expression across a gradient), and behavioral predictability (residual variation in expression) (Dingemanse et al., 2010; Hertel et al., 2020). There can be consistent inter-individual differences across any of these partitions – individuals can vary in their average behavior (Bell, 2004), their levels of behavioral plasticity (Stamps and Biro, 2016), and their levels of behavioral predictability (Hertel et al., 2021) – and a key development in animal behavior was the realization that these differences can be correlated across behaviors (Sih et al., 2004b). Early work on these behavioral correlations focused on correlated average behaviors, such as average individual aggressiveness towards conspecifics and average individual boldness in response to predators (Bell, 2004). Higher resolution data on behavioral expression and environmental context, alongside a growing statistical toolkit aimed at describing these behavioral correlations,

has opened the door to exploring correlations in behavioral plasticity and predictability as well (O'Dea et al., 2022). Correlated behavioral plasticities are of particular interest because of the crucial role of plasticity in responding to rapid environmental change (Beever et al., 2017). Correlated behavioral plasticities in wild populations remain untested, despite a growing recognition of their importance (Sheehy and Laskowski, 2023).

The drivers and consequences of animal behavioral variation are another frontier of behavioral ecology (Dingemanse and Wolf, 2013). Empirical work has documented individual fitness consequences of interindividual variation in behavioral type (Dingemanse et al., 2004; Smith and Blumstein, 2008) as well as interindividual variation in behavioral plasticity (Nussey et al., 2007). Beyond individual consequences, behavioral variation also plays an important role in population persistence; variation within a population provides a portfolio effect, in which some individuals persist in environmental contexts that are catastrophic for other individuals, enabling population persistence across a range of conditions (Schindler et al., 2010). Given the important consequences of behavioral variation, there is growing interest in the mechanisms that produce and sustain the patterns of variation that we observe in wild populations (Dingemanse et al., 2010; Sih et al., 2015). One of these mechanisms that remains underexplored is the feedback between behavioral decisions and the outcomes of those decisions; this coupling can lead to divergence in interindividual behavioral expression (Sih et al., 2015). This feedback also hints at a broader challenge to describing the drivers and consequences of behavioral variation: a comprehensive approach requires high-resolution, longitudinal data on animal behavior, the contexts in which the behavior is expressed, and the outcomes of behavioral choices. Reflecting a universal challenge in ecological research (Levin, 1992), both the contextual drivers of behavior and the consequences of behavior can operate across multiple scales. This makes research on drivers and consequences of behavioral variation especially challenging for long-lived, highly mobile vertebrate species that are among the taxa most threatened by global change (Runge et al., 2014).

With this dissertation, I address three topics at the frontier of behavioral ecology using a dataset on the movement, foraging, and reproductive behavior of Magellanic penguins (*Spheniscus magellanicus*) from the Punto Tombo colony in Chubut, Argentina. In Chapter 1, I conduct the first test of correlated behavioral plasticities in a wild population across four behaviors. Specifically, I test whether individuals that display high plasticity in one behavior are

more likely to also display high plasticity in other behaviors, suggesting a generalized plasticity, or whether those individuals are more likely to display low plasticity in other behaviors, suggesting an allocation of plasticity. In Chapter 2, I use the dataset of individual behavioral plasticity estimates from Chapter 1 to examine the reproductive consequences of generalized behavioral plasticity across environmental contexts. By comparing the reproductive success of individuals that display varying plasticity across a range of environmental conditions, I test whether plasticity confers a reproductive advantage by buffering disadvantageous environments. In Chapter 3, I turn to drivers of behavioral variation by exploring the role of previous decision outcomes on subsequent decision-making. Using high-resolution biologging data collected over the previous two breeding seasons, I test the effect of foraging success on broad-scale movement decisions and fine-scale activity allocation, and discuss the implications of my findings on the maintenance of interindividual behavioral variation.

Chapter 1: Patterns of Individual Variation in Plasticity Across Multiple Behaviors in Wild Vertebrates

Authors: Erik Johansson, P. Dee Boersma, Timothy Jones, Briana Abrahms

***Note**: This chapter was published jointly with Chapter 2:*

Johansson, E., Boersma, P. D., Jones, T., Abrahms, B. 2024. Plasticity syndromes in wild vertebrates: Patterns and consequences of individual variation in plasticity across multiple behaviours. *Ecol. Lett.* 27, e14473. https://doi.org/10.1111/ele.14473

1.1 Abstract

Behavioral plasticity is an important mechanism allowing animals to cope with changing environments. Theory has hypothesized the existence of 'plasticity syndromes' – positive correlations in plasticity across multiple behaviors within an individual – affording a generalized ability to respond to environmental change. However, the occurrence of correlated plasticities in natural populations remains untested. Using a 40-year dataset on free-ranging Magellanic penguins, we find evidence of both positively and negatively correlated behavioral plasticities. Plasticity was positively correlated between two foraging behaviors and between two reproductive behaviors, but negatively correlated across foraging and reproductive behaviors; these findings suggest shared mechanisms underlying plasticity in certain behaviors. Such results highlight the complex patterns of plasticity across behaviors, individuals, and environments.

1.2 Introduction

As animals confront increasingly variable environments, understanding the ecological processes that promote their resilience is critical. One important mechanism for species responding to environmental change is the capacity to vary behavioral expression across contexts, i.e., 'behavioral plasticity' (Pigliucci et al., 2006). Behavioral plasticity occurs in diverse taxa, and across functional behavioral categories (e.g., reproduction, foraging, dispersal; Beever et al., 2017). Because many behaviors are highly sensitive to the environment (Snell-Rood, 2013) and can be expressed quickly, they can serve as a fast-acting coping mechanism for individuals experiencing anomalous environmental conditions.

Behavioral plasticity is expected to confer fitness benefits in rapidly changing environments (Beever et al., 2017). However, behavioral plasticity might also exact costs under non-anomalous, or average, conditions (Piper, 2011; West-Eberhard, 2003); highly plastic individuals may be less able to take advantage of predictable resources due to a lack of familiarity (Switzer, 1993; Wolf et al., 2009), and may experience costs in the form of time and energy dedicated to maintaining cognitive and sensory apparatuses and sampling for environmental cues (Dingemanse and Wolf, 2013). Assessing the performance trade-offs of behavioral plasticity in wild populations under variable environmental conditions remains challenging because it requires repeatedly sampling individual behavior over a range of environments. Moreover, the population consequences of plasticity can be particularly difficult to determine because behavioral plasticity can vary substantially across individuals within a population.

Consistent variation in behavior among individuals within a population is increasingly recognized in animal ecology (Dall et al., 2012; Réale et al., 2010; Wolf and Weissing, 2012), and can drive variation in survival, reproduction, and dispersal (Cote et al., 2010; Dingemanse and Réale, 2005; Schuett et al., 2011). While previous research has highlighted variation in average behavioral expression across individuals, such as individual variation in aggression or exploratory behavior (Bell et al., 2009), there is growing interest in patterns and consequences of interindividual variation in behavioral plasticity (Stamps, 2016). However, studies of interindividual behavioral variation are complicated by the range of behaviors animals express. Quantifying behavioral syndromes – i.e., suites of behaviors with correlated expression (Sih et al., 2004b) – allows us to consider the drivers and consequences of multiple behaviors

simultaneously. For example, evidence of a positive correlation between aggression and exploration in the great tit (*Parus major*) enabled researchers to identify fluctuating selection pressures on avian behavioral strategies more holistically (Dingemanse et al., 2004). Such syndromes have been identified in many taxa (Sih et al., 2004a), and both theoretical and empirical work have shown behavioral syndromes can be important predictors for observed ecological patterns (Sih et al., 2012).

While both behavioral plasticity and behavioral syndromes can shape ecological and evolutionary patterns, little attention has been paid to the integration of these phenomena. Recent theory has hypothesized the existence of 'plasticity syndromes' – positive correlations of plasticity across multiple behaviors within an individual (Fig. 1.1a-c) – which may afford a generalized ability to respond plastically to environmental change (Hertel et al., 2020; Sheehy and Laskowski, 2023; Westneat et al., 2019). Alternatively, populations could exhibit 'plasticity allocation' – negative correlations of plasticity across behaviors (Fig. 1.1d-f) – indicating a tradeoff in plasticity expression among behaviors. As plasticity is generally described as the slope of a behavioral response across an environmental gradient, these hypotheses concern correlations in the magnitude, i.e. the absolute slope, of behavioral plasticities. Determining whether and how the absolute magnitude of plasticity is correlated across multiple behaviors is critical to understanding a population's adaptive capacity to environmental change and the selective pressures on the evolution of behavioral plasticity (Dingemanse and Wolf, 2013; Sheehy and Laskowski, 2023).

These hypotheses remain largely untested in natural systems due to a lack of sufficient repeated measurements of multiple behaviors across individuals and environmental contexts. Despite recent efforts to investigate plasticity syndromes in natural animal populations (Hertel et al., 2021; Laforge et al., 2023), the only existing evidence of correlations in plasticity across behaviors comes from a laboratory population of zebrafish (O'Dea et al., 2022). In addition, understanding the fitness consequences of behavioral plasticity in long-lived species, and how such consequences may vary across environmental contexts, requires very long-term data to track both environmentally- and behaviorally-driven variation in fitness outcomes. This is especially challenging to observe for long-lived, highly mobile vertebrate species that are among the taxa most threatened by global change (Runge et al., 2014).

Here, we employ a 40-year dataset, including repeated behavioral observations on more than 1800 Magellanic penguins (*Spheniscus magellanicus*) from a colony experiencing environmentally-driven population decline, to examine the patterns and consequences of correlations in plasticity across multiple behaviors. We considered three alternative hypotheses: 1) a 'plasticity syndrome hypothesis', in which a positive correlation in plasticity across behaviors would indicate a shared driver or mechanism of plasticity (O'Dea et al., 2022; Sheehy and Laskowski, 2023); 2) a 'plasticity allocation hypothesis', in which a negative correlation would reflect a trade-off such that plasticity in one behavior constrains the plasticity of another behavior (Sheehy and Laskowski, 2023); and 3) a null hypothesis in which the absence of a correlation across behaviors would indicate that the plasticity of those behaviors are not coupled and instead respond independently.

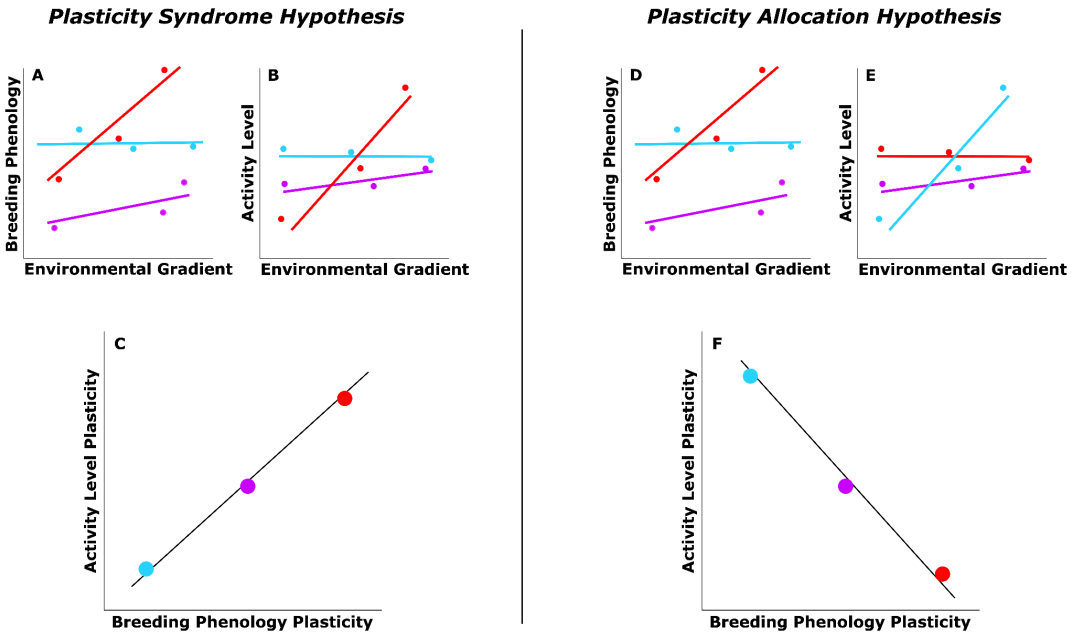


Figure 1.1 Conceptual figure demonstrating individual behavioral plasticity trends (A, B, D, E), estimated from repeated measures of individual behavior (here, breeding phenology and activity level as hypothetical examples) across environmental gradients (e.g., temperature, rainfall). Behavioral plasticity is variation in behavior across contexts, and its magnitude can be quantified as the slope of the lines shown in (A, B, D, E). Slope values are plotted against each other in the bottom graphs (C, F), which show the relationships between individual plasticity across two behaviors. Slope values are positively correlated in the plasticity syndrome hypothesis (A-C) and negatively correlated in the plasticity allocation hypothesis (D-F).

1.3 Methods

1.3.1 Study System

This study was carried out at the Punta Tombo Magellanic penguin colony in Chubut, Argentina (44°03′ S, 65°13′ W; Fig. 1.2a-b), where we have been following marked individuals since 1982 (Boersma et al., 1990) and satellite-tracking foraging adults since 1996 (Rebstock et al., 2022). Due to environmental change and human impacts, this colony has declined from ~400,000 breeding pairs in the 1980s to less than 200,000 breeding pairs in 2023 (García-Borboroglu et al., 2006; Holt and Boersma, 2022; Rebstock et al., 2016).

Males arrive at the colony following their migration season in mid-September. Breeding adults frequently mate with the same partner for multiple years (Wagner et al., 2022). Females arrive shortly after males; eggs are typically laid in early October, but laying date is variable and has become later over time (Cappello and Boersma, 2021). During the nestling period in November-February, both parents provision chicks with food collected on multi-day foraging trips (lasting 2.9 ± 1.8 days). During these trips, penguins swim dozens of kilometers to at-sea foraging grounds and exhibit high inter-individual variation in their fidelity to previous foraging sites (Boersma and Rebstock, 2009; Wilson et al., 2005). Starvation is the primary cause of chick mortality (Boersma and Rebstock, 2014), making efficient foraging vital to reproductive success (Boersma and Rebstock, 2009; Boersma et al., 2015; Rebstock et al., 2022).

1.3.2 Behavioral Data

We identified four behaviors known to be important for individual fitness: egg laying date (Cappello and Boersma, 2021), mate switching (Wagner et al., 2022), foraging trip distance (Boersma and Rebstock, 2009), and foraging site fidelity (Rebstock et al., 2022). To ensure sufficient sample sizes for estimating individual plasticity, we constrained our datasets on all behaviors to individuals for whom we had at least four observations of the given behavior.

We determined egg laying date – the Julian day the first egg of a clutch was laid – by regularly checking nests of marked individuals (Cappello and Boersma, 2021). Records were restricted to those known within two days of confidence, resulting in 6102 records on 810 individuals (Table S1.2). We recorded mate switching as a binary behavior, dependent on whether the individual mated with the same breeding partner as the previous year or switched to

a new partner. We only considered cases where both mates from the previous year were seen, resulting in 9657 records on 1330 individuals (Table S1.2).

Foraging trip data were collected using Argos satellite and Global Positioning System (GPS) tags deployed on breeding adults during chick rearing (Table S1.1; see Rebstock et al., 2022 for tagging procedures). All trip data were regularized to a 30-minute fix interval using the state-space model Crawl (Johnson et al., 2008), and only multi-day trips were included, as the biological drivers are expected to differ for shorter excursions (Rebstock et al., 2022). This resulted in 1414 trip distance records on 163 individuals and 875 site fidelity records on 106 individuals (Table S1.2). We defined foraging trip distance as the maximum distance from the colony reached during a trip, and foraging site fidelity as the distance between the endpoints of consecutive foraging trips (Rebstock et al., 2022).

1.3.3 Environmental Data

We extracted environmental data known to influence each of the four behaviors. We matched egg laying dates with measurements of the Southern Annular Mode (SAM) (Fig. 1.2c), as laying date is significantly influenced by ocean conditions(Rebstock and Boersma, 2018). SAM describes the strength of the westerly winds surrounding Antarctica, which determine the latitude of currents carrying cold and nutrient-rich water to the Patagonian Shelf Marine Ecosystem. Negative SAM values are associated with high oceanic productivity in this region (Lovenduski and Gruber, 2005), and have a positive effect on adult survival of other seabirds; the inverse is true during positive SAM phases (Ventura et al., 2021). SAM is also correlated with penguin reproductive phenology in other regions (Hindell et al., 2012).

We matched mate switching data with rainfall measurements, as penguins are more likely to switch mates following early reproductive failure (Wagner et al., 2022), which is most frequently caused by high rainfall events (Boersma and Rebstock, 2014). We recorded precipitation (+/- 0.1mm) daily at the study site using a rain gauge (Boersma and Rebstock, 2014), and calculated an annual metric of rainfall as the log-transformed average amount of rain per day during the egg-laying and early nestling period, from October-December (Fig. 1.2d).

As foraging trips occurred on a daily, rather than annual scale, we matched trip metrics (distance and site fidelity) with daily oceanographic measurements. We extracted daily, 4 km resolution sea surface temperature values from the ‘nceiPH53sstd1day’ dataset using the

'rerddapXtracto' package in R (Mendelssohn, 2023). These values were averaged over the foraging area, defined as the 99% minimum convex polygon of trip endpoints, to obtain a single value representing daily oceanographic conditions (Fig. 1.2e). Although the relationship between sea surface temperature and prey availability is complex and variable (Silva et al., 2016), previous research has found that Magellanic penguin chicks grow larger under low sea surface temperature conditions (Barrionuevo et al., 2018).

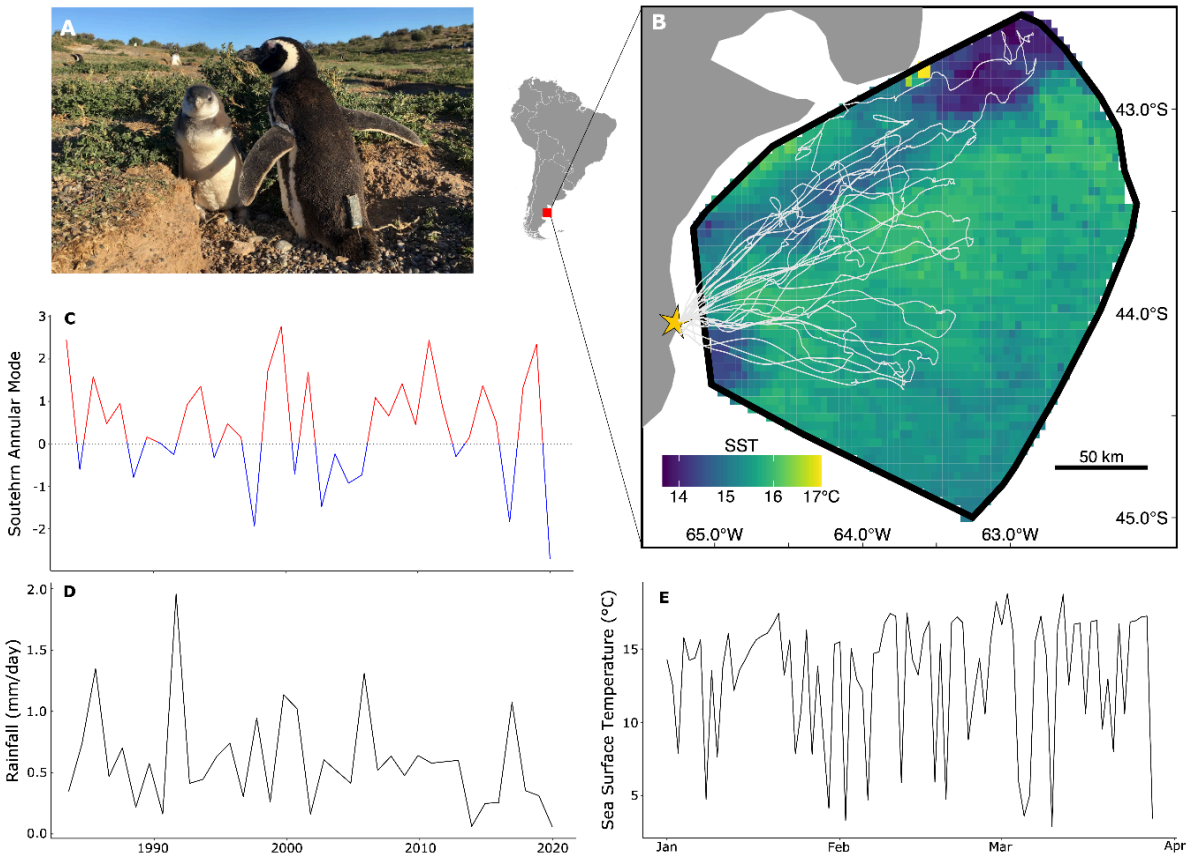


Figure 1.2 (A) Breeding adults have been satellite tracked since 1996 to quantify foraging trip metrics during chick rearing. (B) The location of the Punta Tombo Magellanic penguin colony (gold star). Foraging area in January-February – defined by the 99% minimum convex polygon of foraging trip endpoints – is outlined in black. Select foraging tracks are shown in gray, as well as sea surface temperature values from January 4, 2020. (C) Southern Annular Mode (SAM) indices from 1983-2020, with positive phases in red and negative phases in blue. The SAM index is used as a broad-scale proxy of ocean productivity in this region. (D) Rainfall measurements during the early stages of chick rearing from 1983-2020. (E) Average Sea Surface Temperature (SST) measurements in the foraging area through the fledging season of 2020.

1.3.4 Single-Behavior Models

To identify important factors driving each behavior, we ran model selection on four sets of generalized linear mixed effects models (GLMMs). Each model had the same basic structure, with behavior as the response, an environmental variable as a fixed effect, a random intercept for each individual, and a random slope for individual variation in the effect of the environmental variable. We considered additional fixed and random effects, including year, sex, previous mate, and previous fledging success, to control for potential sources of variation. All model fitting was performed using the 'lme4' package (Bates et al., 2015) in R version 4.3.1 (R Core Team, 2023); see Appendix S1.1 for details on model selection procedure. To investigate correlations across behaviors, the selected single-behavior model structures were incorporated into double-behavior models.

1.3.5 Double Hierarchical Generalized Linear Models

Individual behavioral plasticity can be estimated from mixed-effects models using best linear unbiased predictor estimates (Betini and Norris, 2012; Carter et al., 2012), but using these estimates in further analyses ignores their uncertainty (Houslay and Wilson, 2017). Double hierarchical generalized linear models (DHGLMs) are able to include the estimation of individual plasticity in multiple behaviors, as well as their correlation, in a single model (Hertel et al., 2020). As a result, despite requiring very large amounts of data, DHGLMs are considered the best tool available for identifying plasticity correlations given their ability to fully propagate uncertainty from the base data into estimates of behavioral correlation (Hertel et al., 2021; O'Dea et al., 2022; Sheehy and Laskowski, 2023). We fit three bivariate DHGLMs to estimate correlations in plasticity (Appendix S1.2): one model compared two breeding behaviors (egg laying date and mate choice); one model compared two foraging behaviors (foraging distance and foraging site fidelity); and one model compared a breeding behavior with a foraging behavior (egg laying date and foraging distance).

Each DHGLM was fitted as a Bayesian model using the statistical software Stan connected to R via the RStan interface (Carpenter et al., 2017; Stan Development Team, 2023). By using a Bayesian framework, we were able to include all individuals with data for a given behavior in the parameter estimations specific to that behavior, while estimating correlations across two behaviors using only individuals with data on both behaviors. To allow the data to

dominate parameter estimation, all parameters were defined via vague prior distributions (Lambert et al., 2005; see Table S1.12). Models were estimated using Markov chain Monte Carlo via 4 chains, with a minimum warm-up period of 2000 iterations, or until convergence (based on trace plots of among chain mixing and convergence criteria (R-hat $\leq$ 1.05); (Vehtari et al., 2021)). Following convergence a minimum of 2000 iterations were performed to estimate posterior distributions of model parameters (Vehtari et al., 2021). Because we were interested in the absolute magnitude of plasticity (Sheehy and Laskowski, 2023), we transformed individual plasticity estimates post-hoc by multiplying all plasticity estimates of individuals with negative mean plasticity values by -1. This enables a direct comparison of the magnitude of plasticity across individuals and behaviors, while preserving the posterior distribution shape and the uncertainty of the plasticity estimate.

To interpret the strength of plasticity correlations, we used the metrics of probability of direction (*pd*) and highest density interval (HDI) to characterize the certainty in the posterior distributions of our Bayesian models. *pd* ranges from 0.5-1.0 and measures the probability with which an effect has a particular sign (Makowski et al., 2019). *pd* values should be interpreted as the existence, rather than the significance, of an effect (Makowski et al., 2019), with higher values indicative of greater certainty of a relationship in either a positive or negative direction. Following Weller et al. (2022) and Murphy et al. (2023), we considered *pd* values >0.75 as evidence that a correlation likely exists. The HDI is the range of values where the probability of a parameter lying between those points equals a set amount, but placed so that all points within this interval have a higher probability density than points outside this interval (Makowski et al., 2019). We report the 89% HDI here, as recommended for Bayesian analyses (Kruschke, 2014; McElreath, 2016).

1.4 Results

1.4.1 Single-Behavior Models

For mate switching, with the response as probability of staying with the same mate, model selection supported rainfall (estimate: -0.17; 95% CI: [-0.28, -0.06]), previous fledging success (estimate: 1.32; 95% CI: [1.16, 1.48]), and previous mate (estimate: 0.98; 95% CI: [0.82, 1.14]) as fixed effects. Individuals were more likely to switch mates following years of high rainfall, as nest failure was higher in these years (Wagner et al., 2022). For lay date, model

selection supported the inclusion of SAM (estimate: 1.15; 95% CI: [0.32, 1.98]) and year (estimate: 0.29; 95% CI: [0.20, 1.36]) as fixed effects; egg laying is later following years with lower productivity as measured by SAM values.

For foraging behaviors, model selection supported the inclusion of sea surface temperature (distance: estimate: 3.18; 95% CI: [1.07, 5.32]; site fidelity: estimate: 1.64; 95% CI: [-0.25, 3.49]), and sex (distance: estimate: -5.36; 95% CI: [-16.32, 5.93]; site fidelity: estimate: -1.52; 95% CI: [-12.85, 9.69]) as fixed effects for both models, with females as the reference group. Under higher sea surface temperature conditions, foraging trip distance increased and foraging site fidelity decreased.

For all behavioral categories, model selection supported random individual slopes with respect to the environmental predictor, indicating interindividual variation in behavioral plasticity. Inclusion of a random intercept for year was also supported in all models, indicating substantial inter-annual variability in behavior beyond any trend captured by the fixed effect year terms.

1.4.2 DHGLMs

Parameter estimates from the DHGLMs broadly agreed with the estimates from the single-behavior models (Tables S11-12); mate switching increased with higher rainfall (Fig. 1.3a) and egg laying was delayed following higher SAM conditions (Fig. 1.3b), while trip distance increased and site fidelity decreased with higher sea surface temperature conditions (Fig. 1.3c-d). Interindividual variation in plasticity was found for each behavior (Appendix S1.4).

Plasticity in lay date and plasticity in mate switching were positively correlated (DHGLM posterior distribution median = 0.24; *pd* = 0.84; HDI = [-.14, 0.60]; Fig. 1.3e). Plasticity estimates were also positively correlated between foraging trip distance and foraging site fidelity behaviors (median = 0.28; *pd* = 0.84; HDI = [-0.12, 0.68]; Fig. 1.3g). Plasticity in lay date and foraging trip distance behaviors were negatively correlated (median = -0.28; *pd* = 0.77; HDI = [-0.75, 0.26]; Fig. 1.3f). Metrics for all model parameters are reported in Table S1.12.

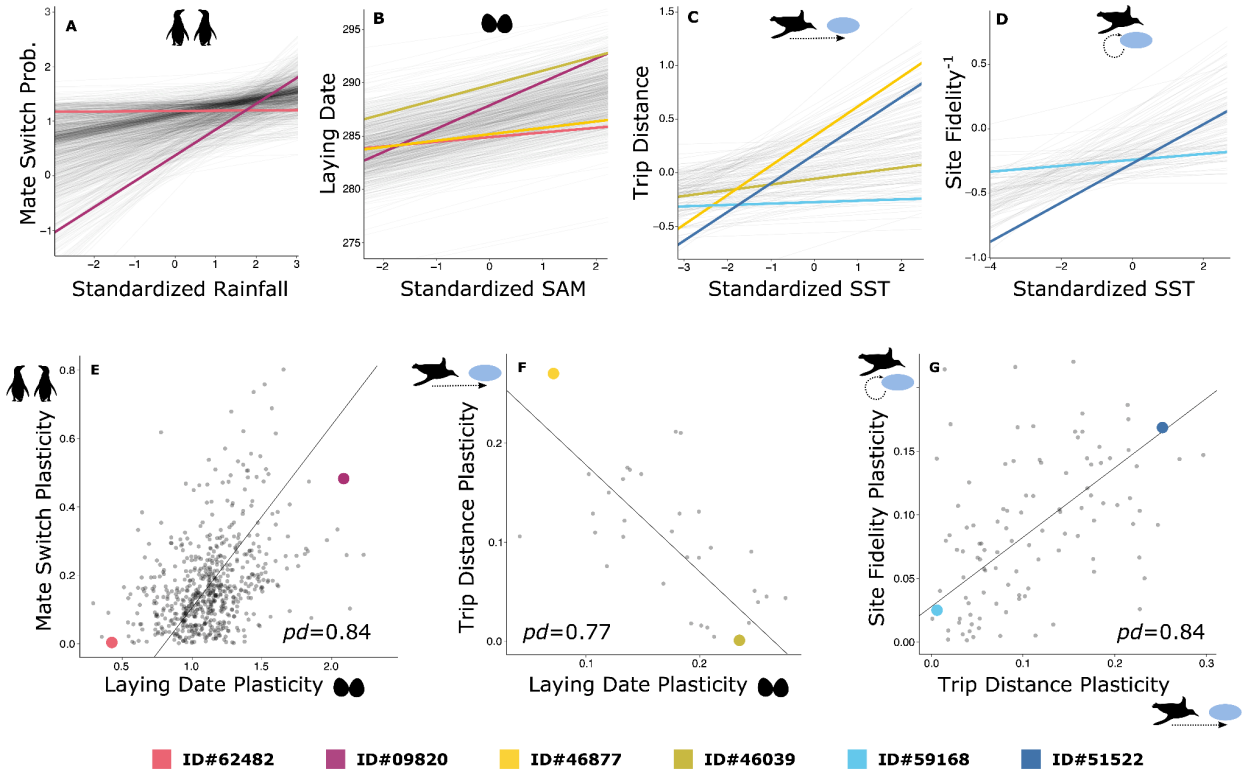


Figure 1.3 (A-D) Individual behavioral plasticity magnitude estimates from double-hierarchical generalized linear models (DHGLMs) for four behaviors (A-mate switching, B-egg laying date, C-foraging distance, and D-foraging site fidelity). Each line represents a single individual, with the slope of that line representing the magnitude of individual plasticity. Six individuals are highlighted in color for demonstration. Correlations of plasticity estimates across behaviors for each DHGLM are shown in (E-G), with each individual represented as a point and lines representing the line of best fit drawn from a Deming regression (Appendix S1.3). The probability of direction (*pd*) metric ranges from 0.5 to 1; here we consider $pd > 0.75$ as support of a correlation.

1.5 Discussion

By leveraging long-term data, our results provide empirical support for correlated plasticities in a free-ranging animal population for the first time. We paired 40 years of field data on reproductive and foraging behaviors with environmental data to reveal patterns of individual plasticity across behaviors in a long-lived vertebrate species, and found that individual plasticity was positively correlated across certain key behaviors and negatively correlated across others. These findings provide empirical support for both the plasticity syndrome and plasticity allocation hypotheses (Dingemanse and Wolf, 2013; Sheehy and Laskowski, 2023), highlighting

the complexity of coupled plasticity patterns. Our study underscores the importance of very long-term data for revealing the diversity of plasticity across behaviors, individuals, and environments, which is critical for predicting how populations will respond to ongoing environmental change.

Individuals in this population differed in both their average behavior and their plasticity across four behaviors, which adds to a growing literature documenting interindividual variation in behavioral plasticity in wild populations (Araya-Ajoy and Dingemanse, 2017; Brommer et al., 2008; Nakayama et al., 2016). The ecological importance and adaptive role of interindividual behavioral variation in variable environments is well documented (Bolnick et al., 2011). Variation within a population provides a portfolio effect, in which some individuals persist in environmental contexts that are catastrophic for other individuals, enabling population persistence across a range of conditions (Schindler et al., 2010). The maintenance of this interindividual behavioral variation is therefore an important biological process to examine as the environment continues to change (Dingemanse and Wolf, 2013).

Our study did not directly test for the proximate mechanisms maintaining individual variation in behavioral plasticity in this population, but existing theory provides potential explanations. Individual variation in demographic or internal states could facilitate this diversity; we tested for these effects where our data allowed, but there could be unaccounted-for variations that make it more or less beneficial for individuals to be plastic (e.g. disease, hunger state). Additionally, this variation could be maintained through a combination of spatiotemporal resource heterogeneity and intraspecific competition, where the benefits of individual plasticity depend on the plasticity of other individuals (Dall et al., 2004; Wolf, 2009; Wolf et al., 2011). Lastly, correlated behavioral plasticities may impose constraints on behavior that contribute to interindividual variation (Sheehy and Laskowski, 2023). Specifically, if the plasticity of two behaviors is tightly coupled, the observation of interindividual variation in one behavior may be driven by a plastic response in a coupled behavior. It is therefore crucial to consider individual plasticity across multiple behaviors at once.

The direction and strength of evidence for correlated plasticities varied among pairs of behaviors, indicating that plasticity correlations are behavior-specific. In addition, although the posterior distributions and *pd* metrics for all models lent evidence of plasticity correlations, high levels of uncertainty are evident in the model results. We found support for a plasticity syndrome

between two breeding behaviors (mate switching and egg laying date; Fig. 3e), which indicates that when environmental conditions change, plastic individuals respond in a coordinated way by adjusting multiple features of their breeding behavior. We also found support for a plasticity syndrome between two foraging behaviors (foraging distance and site fidelity; Fig. 3g). Similarly, this suggests that when oceanographic conditions change in the foraging area, plastic individuals tend to adjust multiple features of their foraging.

Positive correlations in plasticity across multiple behaviors may reflect common behavioral or physiological mechanisms underlying distinct expressions of plasticity (Sheehy and Laskowski, 2023). These correlations may be maintained by positive feedbacks: behaving plastically in one context may lessen the cost of behaving plastically in another context, either through the development of a shared physiological pathway or simply through gaining experience with responding plastically (Wolf et al., 2008). For example, the coordinated plasticities across foraging behaviors described here are in response to a single environmental variable and could therefore share sensory pathways. It is also plausible that responding plastically in one behavior necessitates more flexibility in another behavior if the two behaviors are tightly linked ecologically, for example as in territoriality and singing to attract mates (Sheehy and Laskowski, 2023). In Magellanic penguins, coordinated breeding routines are essential to successfully raising chicks; switching mates could necessitate flexibility in those routines as the new pair learn to coordinate the timing of their breeding behaviors. There could also be adaptive pressure for correlated behavioral plasticities, driven by the benefit of responding to multi-faceted environmental change with a suite of behavioral responses (Hossie et al., 2017).

In contrast, we found support of a plasticity allocation between a breeding behavior and a foraging behavior (egg laying date and trip distance; Fig 3f), suggesting that behaving plastically in one functional behavioral category may actually constrain the ability of an individual to behave plastically in another behavioral category. Negatively correlated plasticities indicate a tradeoff between expressing plasticity among behaviors. Some costs (e.g., developing and maintaining physiological pathways, exploring new environments) may have to be paid, at least in part, for each expression of plasticity (O'Dea et al., 2022; Snell-Rood, 2013). These costs may well overlap for some pairs of plasticity expressions more than for others. For example, developing responsiveness to sea temperature may aid in multiple expressions of plasticity in

foraging behavior. This could explain why we find plasticity syndromes among some behaviors and plasticity allocation among other behaviors in this system; the mechanisms underlying these expressions of plasticity could be shared among some behaviors and not shared among others.

The occurrence of correlated plasticities has far-reaching consequences for ecology and evolution (O'Dea et al., 2022; Sheehy and Laskowski, 2023), but our understanding of these consequences has been limited by a lack of empirical work (Dingemanse and Wolf, 2013). Our study provides a first look at correlated plasticities and their fitness consequences in a wild population. Future work should explore the context-dependency of correlated plasticities: whether correlated behavioral plasticity patterns are more common in certain populations, under certain external circumstances, or in individuals of a specific demographic class is crucial to understanding the implications of these correlations. Correlated individual plasticities have the potential to either facilitate or constrain adaptive change in populations, depending on whether selection favors plasticity in both behaviors or selects for plasticity in one behavior and against plasticity in another behavior (Bell and Sih, 2007; Dingemanse and Dochtermann, 2013). Similar empirical work in other natural systems will allow us to determine how widespread correlated plasticities syndromes are, in what circumstances they are most likely to occur, and their impact on individual fitness, population resilience, and ecological patterns.

1.6 Supplementary Material

Table S1.1 Models of satellite tags used for tracking Magellanic penguin foraging trips.

Model	Years	Manufacturer
Argos PTTs		
ST10	1996-2004, 2008	Telonics+
ST20	2003-2010, 2012-2015	Telonics+
SPOT-275C	2017-2019	Wildlife Computers
GPS tags		
F2G 134A	2012-2018	PathTrack
F5G 334A/434A	2017-2019	SirTrack
nanoFix-GEO	2019, 2021-2022	PathTrack

Table S1.2 Sample size and error distributions for four behaviors used in modeling.

Behavior	Observations	Individuals	Error Distribution
Egg laying date	6102	810	Normal
Mate switching	9657	1330	Bernoulli
Foraging trip distance	1414	163	Normal
Foraging site fidelity	875	106	Normal

Appendix S1.1 Single-behavior model selection procedure.

For each behavior, we first constructed models that contained all potential fixed effects for that behavior, but varied in the specification of random effects. We selected the random effects structure by fitting all permutations of random effects and choosing the model with the lowest small sample size-corrected Akaike's Information Criterion (AICc; Zuur et al., 2009). We then selected among all permutations of fixed effects based on AICc, holding the random effects structure constant (Zuur et al., 2009). Full model selection results are reported in Tables S1.3-1.10, and parameter estimates for the selected models are reported in Table S1.11.

Table S1.3 Model selection: random effects for lay day model

Formula	delta AICc
SAM + year + (1|year) + (SAM|id)	0.00
SAM + year + (SAM|id)	1747.18
SAM + year	2502.81

Table S1.4 Model selection: fixed effects for lay day model

Formula	delta AICc
SAM + year + (1|year) + (SAM|id)	0.00
year + (1|year) + (SAM|id)	4.68
SAM + (1|year) + (SAM|id)	23.79
1 + (1|year) + (SAM|id)	27.93

Table S1.5 Model selection: random effects for mate switch model

Formula	delta AICc
rain + year + prev_mate + prev_fledge + (1|year) + (rain|id)	0.00
rain + year + prev_mate + prev_fledge + (rain|id)	20.83
rain + year + prev_mate + prev_fledge	102.37

Table S1.6 Model selection: fixed effects for mate switch model

Formula	delta AICc
rain + prev_mate + prev_fledge + (1|year) + (rain|id)	0.00
rain + year + prev_mate + prev_fledge + (1|year) + (rain|id)	1.12
year + prev_mate + prev_fledge + (1|year) + (rain|id)	5.33
prev_mate + prev_fledge + (1|year) + (rain|id)	7.27
rain + year + prev_fledge + (1|year) + (rain|id)	139.02
rain + prev_fledge + (1|year) + (rain|id)	139.26
year + prev_fledge + (1|year) + (rain|id)	139.26
prev_fledge + (1|year) + (rain|id)	152.04
rain + prev_mate + (1|year) + (rain|id)	288.45
rain + year + prev_mate + (1|year) + (rain|id)	289.16
year + prev_mate + (1|year) + (rain|id)	294.55
prev_mate + (1|year) + (rain|id)	297.72
rain + year + (1|year) + (rain|id)	425.59
rain + (1|year) + (rain|id)	426.04
year + (1|year) + (rain|id)	434.21
1 + (1|year) + (rain|id)	440.53

Table S1.7 Model selection: random effects for trip distance model

Formula	delta AICc
SST + year + sex + (1|year) + (SST|id)	0.00
SST + year + sex + (SST|id)	49.45
SST + year + sex	238.29

Table S1.8 Model selection: fixed effects for trip distance model

Formula	delta AICc
SST + sex + (1|year) + (SST|id)	0.00
SST + year + sex + (1|year) + (SST|id)	1.72
sex + (1|year) + (SST|id)	5.07
SST + (1|year) + (SST|id)	5.25
year + sex + (1|year) + (SST|id)	6.82
SST + year + (1|year) + (SST|id)	7.00
1 + (1|year) + (SST|id)	10.49
year + (1|year) + (SST|id)	12.27

Table S1.9 Model selection: random effects for site fidelity model

Formula	delta AICc
SST + year + sex + (1|year) + (SST|id)	0.00
SST + year + sex + (SST|id)	22.81
SST + year + sex	46.31

Table S1.10 Model selection: fixed effects for site fidelity model

Formula	delta AICc
SST + sex + (1|year) + (SST|id)	0.00
SST + year + sex + (1|year) + (SST|id)	0.45
sex + (1|year) + (SST|id)	2.58
year + sex + (1|year) + (SST|id)	3.10
SST + year + (1|year) + (SST|id)	3.83
1 + (1|year) + (SST|id)	5.87
year + (1|year) + (SST|id)	6.43
SST + (1|year) + (SST|id)	9.96

Table S1.11 Parameter estimates from single-behavior models

Model	Parameter	Parameter Estimate	95% CI
Lay date	SAM	1.151	[0.317, 1.982]
	Year	0.285	[0.205, 0.364]
Mate switch	Rain	-0.169	[-0.275, -0.006]
	Previous mate	0.978	[0.818, 1.140]
	Previous fledge	1.321	[1.163, 1.484]
Trip distance	SST	3.180	[1.070, 5.320]
	Sex	-5.355	[-16.324, 5.933]
Site fidelity	SST	1.640	[-0.250, 3.486]
	Sex	-1.524	[-12.845, 9.669]

Mate switch = probability of mating with same individual as previous breeding season
Previous mate = whether the previous-season's mate was the same individual as two seasons ago

Previous fledge = whether individual successfully fledged any chick in the prior breeding season
Site fidelity = distance between endpoints of sequential foraging trips

Appendix S1.2 Specification of double-hierarchical generalized linear models (DHGLMs).

The general structure of each DHGLM had the following core components. Each behavioral response variable, $y^1$and y^2, and associated environmental correlates, x^1 and x^2 (note that superscripts denote behavior, not powers) were related to each other according to

$$g\left(\mu_{i,j}^1\right) = (\beta_0^1 + \alpha_i^1) + (\beta_1^1 + \delta_i^1)x_{i,j}^1$$

$$g\left(\mu_{i,j}^2\right) = (\beta_0^2 + \alpha_i^2) + (\beta_1^2 + \delta_i^2)x_{i,j}^2$$

$$y_{i,j}^1 \sim D(\mu_{i,j}^1, \theta^1)$$

$$y_{i,j}^2 \sim D(\mu_{i,j}^2, \theta^2)$$

where i denotes individual, j denotes observation within individual, $\mu_{i,j}$ is the expected value for individual i at observation j, $g()$ is the GLMM link function (identity for foraging trip distance, site fidelity, and egg laying date responses, logit for mate switching), β_0 and β_1 are the population-level intercept and slopes, α_i and δ_i are the individual (random) level differences in intercept and slope, respectively, and D is the assumed observation level distribution (normal for foraging trip distance, site fidelity, and egg laying date responses, bernoulli for mate fidelity), with additional parameter Θ controlling variation in response (normal: σ^2, Bernoulli is not needed). Additional parameters identified as important predictors for each behavior from the single-behavior models were included as predictors of that behavior in the DHGLMs.

We define a model for the individual random effects (slope and intercept) such that they are not-independent, but rather co-vary according to a multivariate normal distribution centered on zero:

$$\begin{matrix}\alpha_i^1 \\ \alpha_i^2 \\ \delta_i^1 \\ \delta_i^2\end{matrix} \sim MVN\left(\boldsymbol{\mu} = \begin{matrix}0 \\ 0 \\ 0 \\ 0\end{matrix}, \Sigma = \begin{matrix}(\sigma_{\alpha^1})^2 & & & \\ \rho_{\alpha^1,\alpha^2}\sigma_{\alpha^1}\sigma_{\alpha^2} & (\sigma_{\alpha^2})^2 & & \\ \rho_{\alpha^1,\delta^1}\sigma_{\alpha^1}\sigma_{\delta^1} & \rho_{\alpha^2,\delta^1}\sigma_{\alpha^2}\sigma_{\delta^1} & (\sigma_{\delta^1})^2 & \\ \rho_{\alpha^1,\delta^2}\sigma_{\alpha^1}\sigma_{\delta^2} & \rho_{\alpha^2,\delta^2}\sigma_{\alpha^2}\sigma_{\delta^2} & \rho_{\delta^1,\delta^2}\sigma_{\delta^1}\sigma_{\delta^2} & (\sigma_{\delta^2})^2\end{matrix}\right)$$

The variance-covariance matrix of this distribution consists of diagonal elements that control the variation among individual level responses within each behavior, and off-diagonal

elements that control the degree of covariation between individual level factors via the inclusion of correlation parameters, ρ. The correlation parameters affect the degree to which intercepts and slopes are correlated within behavioral responses (i.e., ρ_{α^1,δ^1} represents the correlation between intercepts and slopes of behavior 1) but also between behaviors (i.e., ρ_{δ^1,δ^2} represents the correlation between slopes of behavior 1 and slopes of behavior 2). If correlated plasticities existed between two behavioral responses, we would expect a non-zero correlation between the slopes of behavior 1 and 2 (i.e., $\rho_{\delta^1,\delta^2} \neq 0$).

Models were estimated using Markov chain Monte Carlo via 4 chains, with a minimum warm-up period of 2000 iterations, or until convergence (based on trace plots of among chain mixing and convergence criteria (R-hat ≤ 1.05); (Vehtari et al., 2021)). Following convergence, a minimum of 2000 iterations were performed to estimate posterior distributions of model parameters (Vehtari et al., 2021).

Appendix S1.3 Deming regression of plasticity correlation estimates.

Deming regression was used to draw best-fit lines for Figures 3e-g, which allowed us to take into account uncertainty in both the predictor and the response for these models. Models were weighted by $\sqrt{sd_x^2 + sd_y^2}$, where sd_x is the standard deviation of the plasticity estimate along the *x* axis and is the standard deviation of the plasticity estimate along the *y* axis.

Appendix S1.4 Magnitude of variation in individual plasticity.

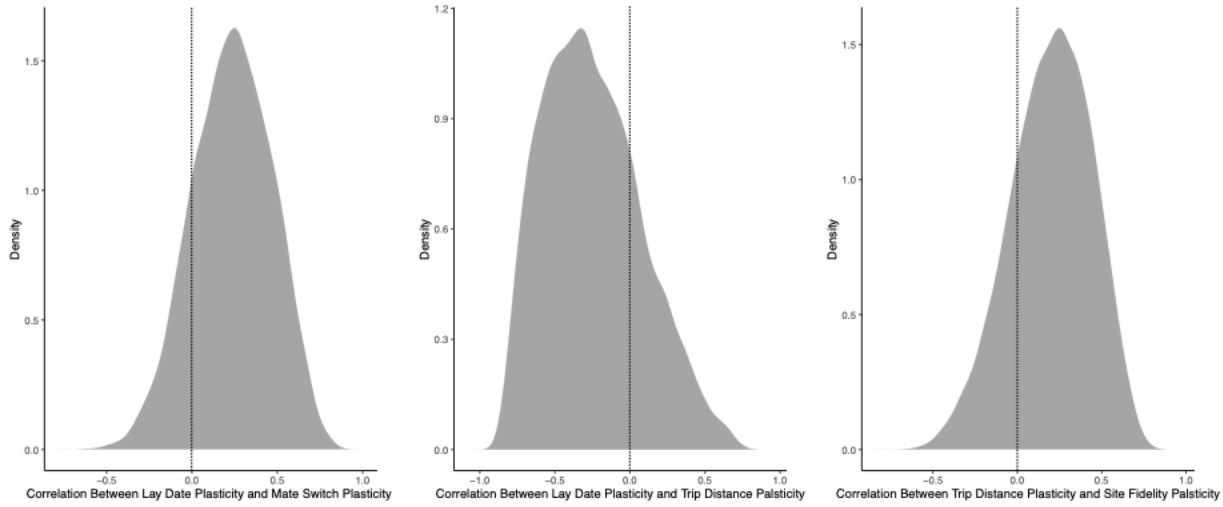
For each DHGLM, we defined the magnitude of variation in individual plasticity for each behavior as the coefficient of variation in the slope estimates of that behavior, defined as:
CV = σ/μ, where σ is the vector of MCMC standard deviation values from the model and μ is the vector of MCMC slope estimates from the model. Here, we report the median and 89% highest density interval for each coefficient of variation in plasticity from each model. For the lay date and mate switch model, CV_{lay_date} = 0.57 [0.26, 1.13] and CV_{mate_switch} = 2.31 [0.97, 4.54]. For the lay date and trip distance model, CV_{lay_date} = 0.61 [0.27, 1.17] and $CV_{trip\_distance}$ = 2.24 [0.51, 5.65]. For the trip distance and site fidelity model, $CV_{trip\_distance}$ = 1.67 [0.60, 3.13] and $CV_{site\_fidelity}$ = 1.47 [0.00, 3.84].

Table S1.12 Parameter estimates from DHGLMs

Model	Parameter	Prior Distribution	Median Estimate	*pd*	89% HDI
Lay date (LD) - Mate switch (MS)	LD Intercept	Normal (mean=0, sd=100)	286.36	1.00	[285.56, 287.13]
	SAM (LD predictor)	Normal (0, 100)	1.185	1.00	[0.48, 1.89]
	MS Intercept	Normal (0, 100)	1.031	1.00	[0.89, 1.19]
	Rainfall (MS predictor)	Normal (0, 100)	-0.161	1.00	[-0.25, -0.07]
	Year (LD predictor)	Normal (0, 100)	0.287	1.00	[0.22, 0.35]
	Prev_Fledge (MS predictor)	Normal (0, 100)	1.323	1.00	[1.19, 1.46]
	Prev_Mate (MS predictor)	Normal (0, 100)	0.991	1.00	[087, 1.13]
	cor(LD int, LD slope)	LKJ(eta=1)	0.074	0.79	[-0.07, 0.23]
	cor(LD int, MS int)	LKJ(1)	-0.201	0.98	[-0.36, -0.05]
	cor(LD int, MS slope)	LKJ(1)	-0.106	0.75	[-0.37, 0.16]
	cor(LD slope, MS int)	LKJ(1)	0.069	0.64	[-0.23, 0.36]
	cor(LD slope, MS slope)	LKJ(1)	0.241	0.84	[-0.14, 0.60]
	cor(MS int, MS slope)	LKJ(1)	0.484	1.00	[0.22, 0.78]
Trip distance (TD) - Site fidelity (SF)	TD Intercept	Normal (0, 100)	0.079	0.79	[-0.09, 0.24]
	SST (TD predictor)	Normal (0, 100)	0.092	1.00	[0.04, 0.14]
	SF Intercept	Normal (0, 100)	-0.170	0.76	[-0.56, 0.20]
	SST (SF predictor)	Normal (0, 100)	0.083	0.99	[0.02, 0.14]
	Sex (TD predictor)	Normal (0, 100)	-0.119	0.77	[-0.38, 0.15]
	Sex (SF predictor)	Normal (0, 100)	-0.196	0.82	[-0.53, 0.15]
	cor(TD int, TD slope)	LKJ(1)	0.587	0.99	[0.27, 0.91]
	cor(TD int, SF int)	LKJ(1)	0.212	0.84	[-0.13, 0.54]
	cor(TD int, SF slope)	LKJ(1)	0.165	0.69	[-0.36, 0.69]
	cor(TD slope, SF int)	LKJ(1)	0.081	0.59	[-0.46, 0.59]
	cor(TD slope, SF slope)	LKJ(1)	0.279	0.84	[-0.12, 0.68]
	cor(SF int, SF slope)	LKJ(1)	0.403	0.85	[-0.11, 0.91]
Lay date (LD) -Trip distance (TD)	LD Intercept	Normal (0, 100)	-0.015	0.57	[-0.15, 0.12]
	SAM (LD predictor)	Normal (0, 100)	0.198	0.99	[0.08, 0.31]
	TD Intercept	Normal (0, 100)	0.279	0.94	[-0.01, 0.58]
	SST (TD predictor)	Normal (0, 100)	0.070	0.98	[0.02, 0.12]
	Year (LD predictor)	Normal (0, 100)	0.048	1.00	[0.04, 0.06]
	Sex (TD predictor)	Normal (0, 100)	-0.249	0.93	[-0.51, 0.02]
	cor(LD int, LD slope)	LKJ(1)	0.071	0.77	[-0.08, 0.22]
	cor(LD int, TD int)	LKJ(1)	-0.053	0.60	[-0.38, 0.28]
	cor(LD int, TD slope)	LKJ(1)	-0.245	0.73	[-0.80, 0.31]
	cor(LD slope, TD int)	LKJ(1)	-0.497	0.89	[-0.96, 0.03]
	cor(LD slope, TD slope)	LKJ(1)	-0.281	0.77	[-0.75, 0.26]
	cor(TD int, TD slope)	LKJ(1)	0.492	0.97	[0.14, 0.84]

LKJ = Lewandowski-Kurowicka-Joe; distribution used for positive definite symmetric matrices with unit diagonals (uniform: eta = 1; small correlations favored: eta > 1; large correlations favored: eta < 1).

Figure S1.1 Correlated Plasticity HDIs



Posterior distributions of correlations among behavioral plasticities from each DHGLM model.

Chapter 2: Consequences of Individual Variation in Plasticity in Wild Vertebrates

Authors: Erik Johansson, P. Dee Boersma, Timothy Jones, Briana Abrahms

***Note**: This chapter was published jointly with Chapter 1:*

Johansson, E., Boersma, P. D., Jones, T., Abrahms, B. 2024. Plasticity syndromes in wild vertebrates: Patterns and consequences of individual variation in plasticity across multiple behaviours. *Ecol. Lett.* 27, e14473. https://doi.org/10.1111/ele.14473

2.1 Abstract

Behavioral plasticity is an important mechanism allowing animals to cope with changing environments. The precise fitness consequences of this strategy under various environmental regimes varies. Plasticity is thought to buffer individuals from the negative effects of anomalously poor environments, but support for this hypothesis in wild populations is mixed. Using a 40-year dataset on free-ranging Magellanic penguins, we find that coordinated plasticity across reproductive behaviors did not strongly affect lifetime reproductive success, but its effect on interannual performance varied significantly by environmental context: plasticity reduced success in average oceanic conditions, increased success in anomalously productive conditions and, contrary to expectation, did not buffer against anomalously unproductive conditions. Such results highlight the interactive consequences of plasticity across behaviors, individuals, and environments, and the context-dependent role that correlated plasticities play in the adaptive capacity of populations to environmental change.

2.2 Introduction

As animals confront increasingly variable environments, understanding the ecological processes that promote their resilience is critical. One important mechanism for species responding to environmental change is the capacity to vary behavioral expression across contexts, i.e., 'behavioral plasticity' (Pigliucci et al., 2006). Behavioral plasticity occurs in diverse taxa, and across functional behavioral categories (e.g., reproduction, foraging, dispersal; Beever et al., 2017). Because many behaviors are highly sensitive to the environment (Snell-Rood, 2013) and can be expressed quickly, they can serve as a fast-acting response mechanism for individuals experiencing anomalous environmental conditions.

Behavioral plasticity is expected to confer fitness benefits in rapidly changing environments (Beever et al., 2017). However, behavioral plasticity might also exact costs under non-anomalous, or average, conditions (Piper, 2011; West-Eberhard, 2003); highly plastic individuals may be less able to take advantage of predictable resources due to a lack of familiarity (Switzer, 1993; Wolf et al., 2009), and may experience costs in the form of time and energy dedicated to maintaining cognitive and sensory apparatuses and sampling for environmental cues (Dingemanse and Wolf 2013). Assessing the performance trade-offs of behavioral plasticity in wild populations under variable environmental conditions remains challenging because it requires repeatedly sampling individual behavior over a range of environments. Moreover, the population-level consequences of plasticity can be particularly difficult to determine because behavioral plasticity can vary substantially across individuals within a population.

Consistent variation in behavior among individuals within a population is increasingly recognized in animal ecology (Dall et al., 2012; Réale et al., 2010; Wolf and Weissing, 2012), and can drive variation in survival, reproduction, and dispersal (Cote et al., 2010; Dingemanse and Réale, 2005; Schuett et al., 2011). While previous research has highlighted variation in average behavioral expression across individuals, such as individual variation in aggression or exploratory behavior (Bell et al., 2009), there is growing interest in patterns and consequences of interindividual variation in behavioral plasticity (Stamps, 2016). However, studies of interindividual behavioral variation are complicated by the range of behaviors animals express. Quantifying behavioral syndromes – i.e., suites of behaviors with correlated expression (Sih et al., 2004a) – allows us to consider the drivers and consequences of multiple behaviors

simultaneously. For example, evidence of a positive correlation between aggression and exploration in the great tit (*Parus major*) enabled researchers to identify fluctuating selection pressures on avian behavioral strategies more holistically (Dingemanse et al., 2004). Such syndromes have been identified in many taxa (Sih et al., 2004b), and both theoretical and empirical work have shown behavioral syndromes can be important predictors for observed ecological patterns (Sih et al., 2012).

While both behavioral plasticity and behavioral syndromes can shape ecological and evolutionary patterns, little attention has been paid to the integration of these phenomena. Recent theory has hypothesized the existence of 'plasticity syndromes' – positive correlations of plasticity across multiple behaviors within an individual – which may afford a generalized ability to respond plastically to environmental change (Hertel et al., 2020; Sheehy and Laskowski, 2023; Westneat et al., 2019). Alternatively, populations could exhibit 'plasticity allocation' – negative correlations of plasticity across behaviors – indicating a tradeoff in plasticity expression among behaviors. As plasticity is generally described as the slope of a behavioral response across an environmental gradient, these hypotheses concern correlations in the magnitude, i.e. the absolute slope, of behavioral plasticities. Determining whether and how the absolute magnitude of plasticity is correlated across multiple behaviors is critical to understanding a population's adaptive capacity to environmental change and the selective pressures on the evolution of behavioral plasticity (Dingemanse and Wolf, 2013; Sheehy and Laskowski, 2023).

These hypotheses remain largely untested in natural systems due to a lack of sufficient repeated measurements of multiple behaviors across individuals and environmental contexts. In addition, understanding the fitness consequences of behavioral plasticity in long-lived species, and how such consequences may vary across environmental contexts, requires very long-term data to track both environmentally- and behaviorally-driven variation in fitness outcomes. This is especially challenging to observe for long-lived, highly mobile vertebrate species that are among the taxa most threatened by global change (Runge et al., 2014).

Here, we employ a 40-year dataset, including repeated behavioral observations on more than 1800 Magellanic penguins (*Spheniscus magellanicus*) from a colony experiencing environmentally-driven population decline, to examine the consequences of plasticity across multiple behaviors. Specifically, we examined the relationship between behavioral plasticity and reproductive performance across varied environmental conditions to test the hypothesis that

behavioral plasticity and environment have an interactive effect on fitness. We predicted that behavioral plasticity would be positively correlated with reproductive success under anomalous environmental conditions and negatively correlated with reproductive success under average environmental conditions.

2.3 Methods

2.3.1 Study System

This study was carried out at the Punta Tombo Magellanic penguin colony in Chubut, Argentina (44°03′ S, 65°13′ W), where we have been following marked individuals since 1982 (Boersma et al., 1990). Due to environmental change and human impacts, this colony has declined from ~400,000 breeding pairs in the 1980s to less than 200,000 breeding pairs in 2023 (García-Borboroglu et al., 2006; Holt and Boersma, 2022; Rebstock et al., 2016).

Males arrive at the colony following their migration season in mid-September. Breeding adults frequently mate with the same partner for multiple years (Wagner et al., 2022). Females arrive shortly after males; eggs are typically laid in early October, but laying date is variable and has become later over time (Cappello and Boersma, 2021).

2.3.2 Behavioral and Reproductive Success Data

We identified two reproductive behaviors known to impact penguin fitness: egg laying date (Cappello and Boersma, 2021) and mate switching (Wagner et al., 2022). To ensure sufficient sample sizes for estimating individual plasticity, we constrained our datasets on all behaviors to individuals for whom we had at least four observations of the given behavior.

We determined egg laying date – the Julian day the first egg of a clutch was laid – by regularly checking nests of marked individuals (Cappello and Boersma, 2021). Records were restricted to those known within two days of confidence, resulting in 6102 records on 810 individuals (Table S1). We recorded mate switching as a binary behavior, dependent on whether the individual mated with the same breeding partner as the previous year or switched to a new partner. We only considered cases where both mates from the previous year were seen, resulting in 9657 records on 1330 individuals (Table S1).

Our metric of reproductive success was fledging success (Boersma and Rebstock, 2009; Wagner et al., 2022), defined annually for each individual as whether they had any chicks that

fledged that year (Rebstock et al., 2022), which we determined by regularly checking the nests of marked individuals throughout the breeding season. Chicks start to fledge in January (Cappello and Boersma, 2021); any chick weighing at least 1800g after January 10 and not found dead was considered fledged (Boersma and Rebstock, 2014; Rebstock et al., 2022).

2.3.3 Environmental Data

We extracted environmental data known to influence each of the behaviors. We matched egg laying dates with measurements of the Southern Annular Mode (SAM), as laying date is significantly influenced by ocean conditions (Rebstock and Boersma, 2018). SAM describes the strength of the westerly winds surrounding Antarctica, which determine the latitude of currents carrying cold and nutrient-rich water to the Patagonian Shelf Marine Ecosystem. Negative SAM values are associated with high oceanic productivity in this region (Lovenduski and Gruber, 2005), and have a positive effect on adult survival of other seabirds; the inverse is true during positive SAM phases (Ventura et al., 2021). SAM is also correlated with penguin reproductive phenology in other regions (Hindell et al., 2012).

We matched mate switching data with rainfall measurements, as penguins are more likely to switch mates following early reproductive failure (Wagner et al., 2022), which is most frequently caused by high rainfall events (Boersma and Rebstock, 2014). We recorded precipitation (+/- 0.1mm) daily at the study site using a rain gauge (Boersma and Rebstock, 2014), and calculated an annual metric of rainfall as the log-transformed average amount of rain per day during the egg-laying and early nestling period, from October-December.

2.3.4 Behavioral Plasticity Modeling

Individual behavioral plasticity can be estimated from mixed-effects models using best linear unbiased predictor estimates (Betini and Norris, 2012; Carter et al., 2012), but using these estimates in further analyses ignores their uncertainty (Houslay and Wilson, 2017). Double hierarchical generalized linear models (DHGLMs) are able to include the estimation of individual plasticity in multiple behaviors, as well as their correlation, in a single model (Hertel et al., 2020). As a result, despite requiring very large amounts of data, DHGLMs are considered the best tool available for identifying plasticity correlations given their ability to fully propagate uncertainty from the base data into estimates of behavioral correlation (Hertel et al., 2021; O'Dea

et al., 2022; Sheehy and Laskowski, 2023). We fit a bivariate DHGLM to estimate correlations in plasticity (Appendix S1.2) between two breeding behaviors (egg laying date and mate choice).

The DHGLM was fitted as a Bayesian model using the statistical software Stan connected to R via the RStan interface (Carpenter et al., 2017; Stan Development Team, 2023). By using a Bayesian framework, we were able to include all individuals with data for a given behavior in the parameter estimations specific to that behavior, while estimating correlations across two behaviors using only individuals with data on both behaviors. To allow the data to dominate parameter estimation, all parameters were defined via vague prior distributions (Lambert et al., 2005; see Supplementary Material). Models were estimated using Markov chain Monte Carlo via 4 chains, with a minimum warm-up period of 2000 iterations, or until convergence (based on trace plots of among chain mixing and convergence criteria (R-hat $\leq$ 1.05); (Vehtari et al., 2021)). Following convergence a minimum of 2000 iterations were performed to estimate posterior distributions of model parameters (Vehtari et al., 2021). Because we were interested in the absolute magnitude of plasticity (Sheehy and Laskowski, 2023), we transformed individual plasticity estimates post-hoc by multiplying all plasticity estimates of individuals with negative mean plasticity values by -1. This enables a direct comparison of the magnitude of plasticity across individuals and behaviors, while preserving the posterior distribution shape and the uncertainty of the plasticity estimate.

To interpret the strength of plasticity correlations, we used the metrics of probability of direction (*pd*) and highest density interval (HDI) to characterize the certainty in the posterior distributions of our Bayesian models. *pd* ranges from 0.5-1.0 and measures the probability with which an effect has a particular sign (Makowski et al., 2019). *pd* values should be interpreted as the existence, rather than the significance, of an effect (Makowski et al., 2019), with higher values indicative of greater certainty of a relationship in either a positive or negative direction. Following Weller et al. (2022) and Murphy et al. (2023), we considered *pd* values >0.75 as evidence that a correlation likely exists. The HDI is the range of values where the probability of a parameter lying between those points equals a set amount, but placed so that all points within this interval have a higher probability density than points outside this interval (Makowski et al., 2019). We report the 89% HDI here, as recommended for Bayesian analyses (Kruschke, 2014; McElreath, 2016).

2.3.5 Reproductive Success Modeling

To first establish whether broad-scale environmental conditions influence population-level reproductive success, we fit a logistic generalized linear mixed-effect model with SAM as a continuous predictor and fledging success as a binary response, including random intercepts for individual and year. Next, to examine the potential fitness consequences of behavioral plasticity, we paired individual behavioral plasticity estimates extracted from the DHGLM with annual individual reproductive success measurements. To consider the effects of divergent environmental conditions on the relationship between plasticity and reproductive success, we considered an interaction between plasticity and discrete environmental phases based on SAM indices. Specifically, we compared performance under 'average' conditions versus extremely anomalous conditions, defined as being above or below the 95th or 5th percentiles of SAM values, respectively (Clark-Wolf et al., 2023; Pardo et al., 2017). We accordingly separated records from years when SAM was above the 95th percentile (≥2.44), below the 5th percentile (≤ -1.96), and between the 45th-55th percentiles, (i.e., average conditions, ≥0.32, ≤0.57). Using these groupings, we fit a logistic mixed-effect generalized linear model with fledging success as a binary response, an interaction between SAM as a categorical predictor and plasticity as a continuous predictor, and random intercepts for individual and year.

To describe the consequences of plasticity in more than one behavior, rather than in a single behavior, we used a joint metric for the continuous predictor of plasticity (see Supplementary Material). Specifically, we used a joint metric for laying date plasticity and mate switching plasticity,. Finally, to identify any effect of plasticity on long-term (rather than interannual) reproductive success, we ran a weighted least squares regression using the 'stats' package in R (R Core Team, 2023), with joint plasticity as the sole predictor, total fledglings per years-monitored as the response, and weighted by years-monitored (min=7, max=32, mean=13.7).

2.4 Results

2.4.1 Behavioral Plasticity

Parameter estimates from the DHGLMs (Tables S11-12) reveal that mate switching increased with higher rainfall (Fig. 2.1a) and egg laying was delayed following higher SAM conditions (Fig. 2.1b). Interindividual variation in plasticity was found for each behavior

(Appendix S1.4). Plasticity in lay date and plasticity in mate switching were positively correlated (DHGLM posterior distribution median = 0.24; *pd* = 0.84; HDI = [-.14, 0.60]; Fig. 2.1c). Metrics for all model parameters are reported in Table S1.12.

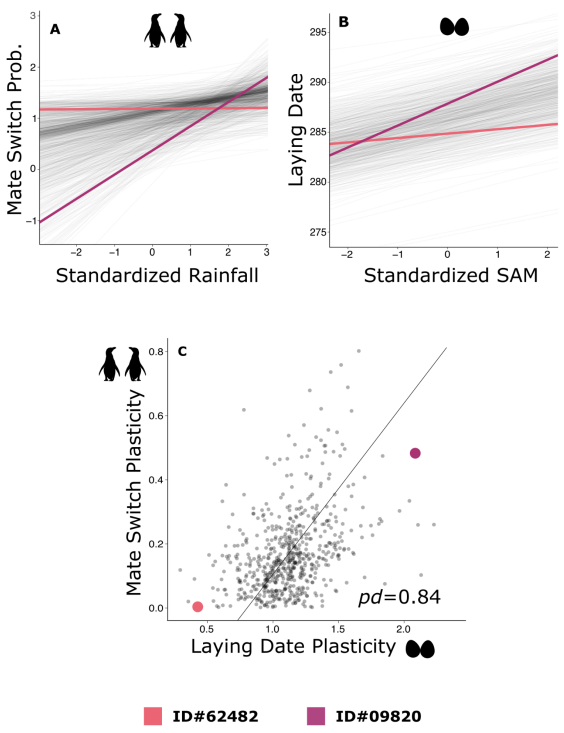


Figure 2.1 (A-B) Individual behavioral plasticity magnitude estimates from double-hierarchical generalized linear models (DHGLMs) for mate switching and egg laying date. Each line represents a single individual, with the slope of that line representing the magnitude of individual plasticity. Two individuals are highlighted in color for demonstration. Correlations of plasticity estimates across behaviors are shown in (C), with each individual represented as a point and lines representing the line of best fit drawn from a Deming regression (See Supplementary Material). The probability of direction (*pd*) metric ranges from 0.5 to 1; here we consider *pd* > 0.75 as support of a correlation.

2.4.2 Reproductive Success

At a population level, annual reproductive success was negatively correlated with SAM; fledging success was lower following less productive phases of SAM (estimate: -0.34; 95% CI: [-0.39, -0.30]; conditional R^2: 0.31; Fig. 2.2). Plasticity weakly affected long-term reproductive success, with a very small effect size (estimate: -0.04; 95% CI: [-0.09, 0.00]; R^2: 0.01; Fig. 2.2). However, there was a significant interaction between plasticity in reproductive behaviors and SAM on annual reproductive success (conditional R^2: 0.32). Following phases of anomalously high oceanic productivity, plasticity was positively correlated with fledging success (estimate: 1.46; 95% CI: [0.12, 2.89]; Fig. 2.2). Under average conditions, plasticity was negatively correlated with fledging success (estimate: -0.96; 95% CI: [-1.59, -0.33]; Fig. 2.2). In contrast, under anomalously low oceanic productivity, this relationship was not significant (estimate:

-0.11; 95% CI: [-1.74, 1.44]) and fledging success was very low across the population (Fig. 2.2). Full parameter estimates are reported in Supplementary Material.

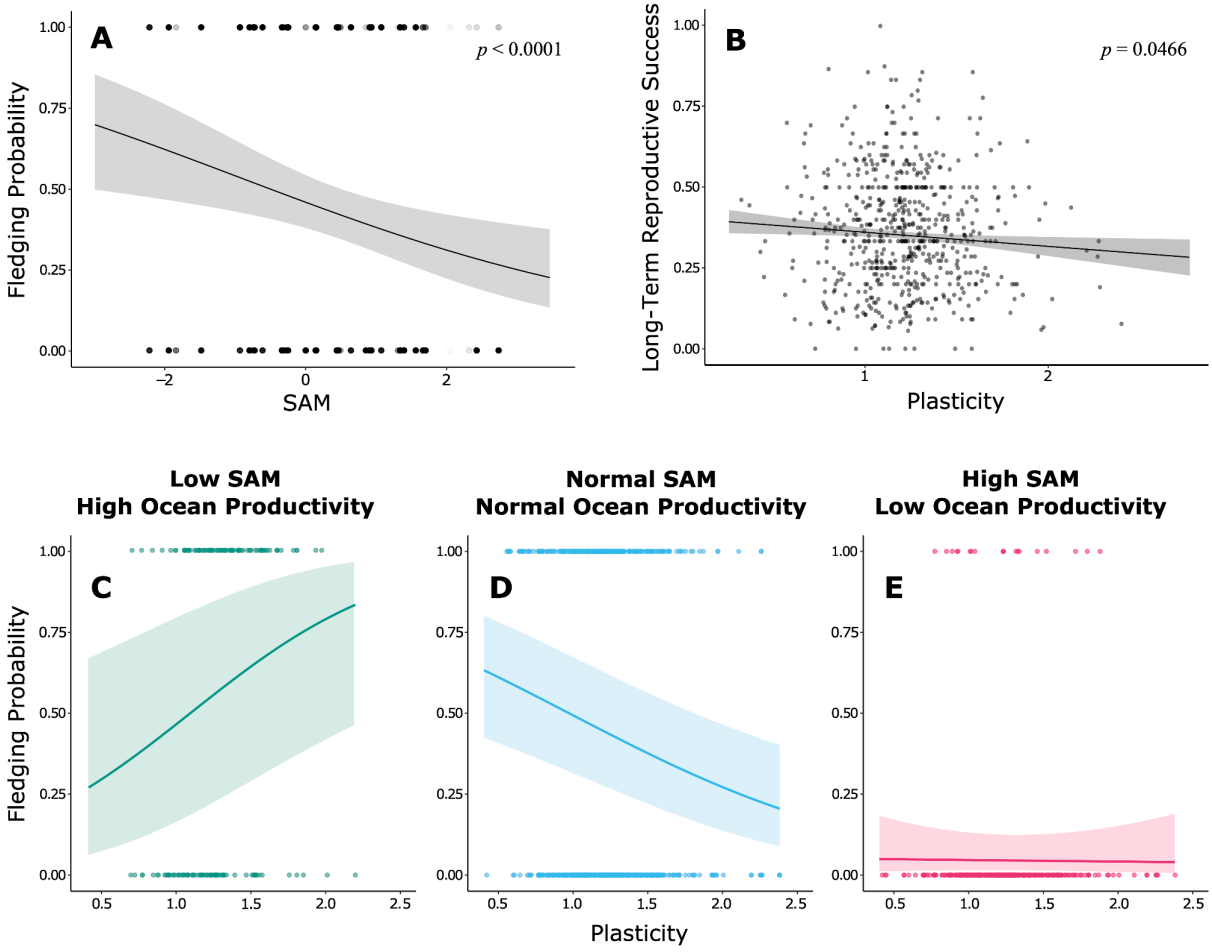


Figure 2.2 (A) Reproductive success is negatively correlated with the Southern Annular Mode (SAM), indicating that high phases of SAM result in bad reproductive conditions and low phases of SAM provide good reproductive conditions. (B) Plasticity has a weakly negative effect on long-term reproductive success. (C-E) The effect of plasticity on annual reproductive success is mediated by environmental context. Under extremely low phases of SAM (C), more plastic individuals perform better than less plastic individuals. Under normal SAM conditions (D), more plastic individuals perform worse than less plastic individuals. Under extremely high phases of SAM (E), no individuals perform well regardless of plasticity.

2.5 Discussion

By leveraging long-term behavioral data, our results indicate that the fitness-related benefits of behavioral plasticity are mediated by environmental context. We paired 40 years of field data on reproductive and foraging behaviors with environmental data to reveal that individual plasticity was positively correlated across distinct reproductive behaviors. We also found that environmental conditions mediated the relationship between individual plasticity and reproductive success. Plasticity was positively correlated with reproductive success in years with anomalously productive ocean conditions, but during years of normal ocean productivity this trend was reversed, indicating that plasticity may allow individuals to take advantage of good conditions rather than buffer against bad ones. Our study underscores the importance of very long-term data for revealing the consequences of plasticity across behaviors, individuals, and environments, which is critical for predicting how populations will respond to ongoing environmental change.

Individuals in this population varied in both their average behavior and their plasticity across behaviors, which adds to a growing literature documenting interindividual variation in behavioral plasticity in wild populations (Araya-Ajoy and Dingemanse, 2017; Brommer et al., 2008; Nakayama et al., 2016). The ecological importance and adaptive role of interindividual behavioral variation in variable environments is well documented (Bolnick et al., 2011). Variation within a population provides a portfolio effect, in which some individuals persist in environmental contexts that are catastrophic for other individuals, enabling population persistence across a range of conditions (Schindler et al., 2010). The maintenance of this interindividual behavioral variation is therefore an important biological process to examine as the environment continues to change (Dingemanse and Wolf, 2013).

Our study did not directly test for the proximate mechanisms maintaining individual variation in behavioral plasticity in this population, but existing theory provides potential explanations. Individual variation in demographic or internal states could facilitate this diversity; we tested for these effects where our data allowed, but there could be unaccounted-for variations that make it more or less beneficial for individuals to be plastic (e.g. disease, hunger state). Additionally, this variation could be maintained through a combination of spatiotemporal resource heterogeneity and intraspecific competition, where the benefits of individual plasticity

depend on the plasticity of other individuals (Dall et al., 2004; Wolf, 2009; Wolf et al., 2011). Lastly, correlated behavioral plasticities may impose constraints on behavior that contribute to interindividual variation (Sheehy and Laskowski, 2023). Specifically, if the plasticity of two behaviors is tightly coupled, the observation of interindividual variation in one behavior may be driven by a plastic response in a coupled behavior. It is therefore crucial to consider individual plasticity across multiple behaviors at once.

We found support for a plasticity syndrome between two breeding behaviors (mate switching and egg laying date), which indicates that when environmental conditions change, plastic individuals respond in a coordinated way by adjusting multiple features of their breeding behavior. Positive correlations in plasticity across multiple behaviors may reflect common behavioral or physiological mechanisms underlying distinct expressions of plasticity (Sheehy and Laskowski, 2023). These correlations may be maintained by positive feedbacks: behaving plastically in one context may lessen the cost of behaving plastically in another context, either through the development of a shared physiological pathway or simply through gaining experience with responding plastically (Wolf et al., 2008). In Magellanic penguins, coordinated breeding routines are essential to successfully raising chicks; switching mates could necessitate flexibility in those routines as the new pair learn to coordinate the timing of their breeding behaviors. There could also be adaptive pressure for correlated behavioral plasticities, driven by the benefit of responding to multi-faceted environmental change with a suite of behavioral responses (Hossie et al., 2017).

We found that the reproductive consequences of behavioral plasticity were mediated by environmental conditions. As predicted, individuals that were more plastic performed better under anomalously productive ocean conditions, successfully fledging chicks significantly more frequently than their less plastic counterparts (Fig. 4c). We found the opposite relationship under normal conditions, in which plasticity was negatively correlated with reproductive success (Fig. 4d). This supports our expectation that more plastic individuals should perform worse than less plastic individuals under normal environmental conditions because less plastic individuals have optimized their behavior to average conditions (Abrahms et al., 2018). Contrary to our predictions, however, reproductive success was uniformly low under poor oceanographic conditions, such that plasticity did not improve performance (Fig. 4e). We expected that individuals that are able to adjust their breeding behaviors to anomalous conditions – whether

good or bad – would gain a reproductive advantage over less responsive individuals. However, the nestling period – i.e., the time between chick hatching and fledging – is shortening in this population (Cappello and Boersma, 2021). Behavior can only be adjusted to a degree; delaying egg laying in years of low ocean productivity (Fig. 3b) may not be beneficial as it would reduce the nestling period even further.

These findings suggest that a diversity of individual plasticity levels could be sustained by heterogeneous environmental conditions across years. Indeed, we found only a very weak effect of individual plasticity on reproductive success across all years (Fig. 4b), indicating that there is minimal difference in the lifetime reproductive success of plastic and non-plastic individuals. These results align with recent work on northern elephant seals (*Mirounga angustirostris*), which found that plasticity and foraging success were positively correlated in good ocean conditions, negatively correlated in normal conditions, and not correlated in poor conditions (Abrahms et al., 2018). Such insights can help explain the long-term maintenance of behavioral diversity within these populations.

The occurrence of correlated plasticities has far-reaching consequences for ecology and evolution (O'Dea et al., 2022; Sheehy and Laskowski, 2023), but our understanding of these consequences has been limited by a lack of empirical work (Dingemanse and Wolf, 2013). Our study provides a first look at fitness consequences of correlated plasticities in a wild population. Correlated individual plasticities have the potential to either facilitate or constrain adaptive change in populations, depending on whether selection favors plasticity in both behaviors or selects for plasticity in one behavior and against plasticity in another behavior (Bell and Sih, 2007; Dingemanse and Dochtermann, 2013). Similar empirical work in other natural systems will allow us to determine how widespread correlated plasticities syndromes are, in what circumstances they are most likely to occur, and their impact on individual fitness, population resilience, and ecological patterns.

Finally, behavioral plasticity is often pointed to as a mechanism for coping with changing environmental conditions (Beever et al., 2017). Our findings provide nuance to this expectation, indicating that behavioral plasticity may allow individuals to take advantage of unusually good environmental conditions, but that its universal benefit under poor conditions should not be assumed. This has important implications for the long-term persistence of the Punta Tombo penguin colony, which was once the largest Magellanic penguin population but is experiencing

rapid population decline (Boersma and Rebstock, 2014; Clark-Wolf et al., 2023). The long-term trend of SAM is increasing (Lee et al., 2019), suggesting that foraging conditions will likely continue to degrade in this region. Based on our findings, behavioral plasticity is an inadequate mechanism for individuals in this population to cope with this change. More broadly, our study provides new insight into the occurrence of correlated behavior plasticity in the wild, and the context-dependent role that correlated plasticities may play in the adaptive capacity of populations to long-term environmental change.

2.6 Supplementary Material

Table S2.1 Sample size and error distributions for four behaviors used in modeling.

Behavior	Observations	Individuals	Error Distribution
Egg laying date	6102	810	Normal
Mate switching	9657	1330	Bernoulli

Appendix S2.1 Specification of double-hierarchical generalized linear model (DHGLMs).

The general structure of the DHGLM had the following core components. Each behavioral response variable, $y^1$and y^2, and associated environmental correlates, x^1 and x^2 (note that superscripts denote behavior, not powers) were related to each other according to

$$g\left(\mu_{i,j}^1\right) = (\beta_0^1 + \alpha_i^1) + (\beta_1^1 + \delta_i^1)x_{i,j}^1$$

$$g\left(\mu_{i,j}^2\right) = (\beta_0^2 + \alpha_i^2) + (\beta_1^2 + \delta_i^2)x_{i,j}^2$$

$$y_{i,j}^1 \sim D(\mu_{i,j}^1, \theta^1)$$

$$y_{i,j}^2 \sim D(\mu_{i,j}^2, \theta^2)$$

where i denotes individual, j denotes observation within individual, $\mu_{i,j}$ is the expected value for individual i at observation j, $g()$ is the GLMM link function (identity for foraging trip distance, site fidelity, and egg laying date responses, logit for mate switching), β_0 and β_1 are the population-level intercept and slopes, α_i and δ_i are the individual (random) level differences in intercept and slope, respectively, and D is the assumed observation level distribution (normal for foraging trip distance, site fidelity, and egg laying date responses, bernoulli for mate fidelity), with additional parameter Θ controlling variation in response (normal: σ^2, Bernoulli is not needed). Additional parameters identified as important predictors for each behavior from the single-behavior models were included as predictors of that behavior in the DHGLMs.

We define a model for the individual random effects (slope and intercept) such that they are not-independent, but rather co-vary according to a multivariate normal distribution centered on zero:

$$\begin{matrix}\alpha_i^1 \\ \alpha_i^2 \\ \delta_i^1 \\ \delta_i^2\end{matrix} \sim MVN\left(\boldsymbol{\mu} = \begin{matrix}0 \\ 0 \\ 0 \\ 0\end{matrix}', \Sigma = \begin{matrix}(\sigma_{\alpha^1})^2 & & & \\ \rho_{\alpha^1,\alpha^2}\sigma_{\alpha^1}\sigma_{\alpha^2} & (\sigma_{\alpha^2})^2 & & \\ \rho_{\alpha^1,\delta^1}\sigma_{\alpha^1}\sigma_{\delta^1} & \rho_{\alpha^2,\delta^1}\sigma_{\alpha^2}\sigma_{\delta^1} & (\sigma_{\delta^1})^2 & \\ \rho_{\alpha^1,\delta^2}\sigma_{\alpha^1}\sigma_{\delta^2} & \rho_{\alpha^2,\delta^2}\sigma_{\alpha^2}\sigma_{\delta^2} & \rho_{\delta^1,\delta^2}\sigma_{\delta^1}\sigma_{\delta^2} & (\sigma_{\delta^2})^2\end{matrix}\right)$$

The variance-covariance matrix of this distribution consists of diagonal elements that control the variation among individual level responses within each behavior, and off-diagonal elements that control the degree of covariation between individual level factors via the inclusion of correlation parameters, ρ. The correlation parameters affect the degree to which intercepts and slopes are correlated within behavioral responses (i.e., ρ_{α^1,δ^1} represents the correlation between intercepts and slopes of behavior 1) but also between behaviors (i.e., ρ_{δ^1,δ^2} represents the correlation between slopes of behavior 1 and slopes of behavior 2). If correlated plasticities existed between two behavioral responses, we would expect a non-zero correlation between the slopes of behavior 1 and 2 (i.e., $\rho_{\delta^1,\delta^2} \neq 0$).

The model was estimated using Markov chain Monte Carlo via 4 chains, with a minimum warm-up period of 2000 iterations, or until convergence (based on trace plots of among chain mixing and convergence criteria (R-hat ≤ 1.05); (Vehtari et al., 2021)). Following convergence, a minimum of 2000 iterations were performed to estimate posterior distributions of model parameters (Vehtari et al., 2021).

Table S2.2 Parameter estimates from reproductive success models

Response	Parameter	Parameter Estimate	95% CI
Annual reproductive success	SAM	-0.389	[-0.664, -0.111]
Long-term reproductive success	Plasticity	-0.044	[-0.087, -0.001]
Annual reproductive success	Intercept	0.936	[0.252, 2.138]
(Joint plasticity)	Plasticity	-0.956	[-1.594, -0.335]
	High SAM	-3.828	[-6.398, -1.298]
	Low SAM	-2.538	[-4.238, 0.129]
	Plasticity*High SAM	0.845	[-0.782, 2.395]
	Plasticity*Low SAM	2.417	[1.072, 3.843]
Annual reproductive success	Intercept	0.931	[-0.260, 2.135]
(Lay date plasticity)	Plasticity	-0.966	[-1.616, -0.332]
	High SAM	-3.869	[-6.446, -1.335]
	Low SAM	-2.690	[-5.432, 0.008]
	Plasticity*High SAM	0.891	[-0.762, 2.471]
	Plasticity*Low SAM	2.588	[1.172, 4.093]
Annual reproductive success	Intercept	0.057	[-0.909, 1.026]
(Mate switch plasticity)	Plasticity	-1.593	[-3.128, -0.106]
	High SAM	-2.945	[-4.729, -1.197]
	Low SAM	0.120	[-1.998, 2.235]
	Plasticity*High SAM	0.778	[-3.375, 4.363]
	Plasticity*Low SAM	1.925	[-0.363, 4.250]

Table S1.12 Parameter estimates from DHGLMs

Model	Parameter	Prior Distribution	Median Estimate	*pd*	89% HDI
Lay date (LD) - Mate switch (MS)	LD Intercept	Normal (mean=0, sd=100)	286.36	1.00	[285.56, 287.13]
	SAM (LD predictor)	Normal (0, 100)	1.185	1.00	[0.48, 1.89]
	MS Intercept	Normal (0, 100)	1.031	1.00	[0.89, 1.19]
	Rainfall (MS predictor)	Normal (0, 100)	-0.161	1.00	[-0.25, -0.07]
	Year (LD predictor)	Normal (0, 100)	0.287	1.00	[0.22, 0.35]
	Prev_Fledge (MS predictor)	Normal (0, 100)	1.323	1.00	[1.19, 1.46]
	Prev_Mate (MS predictor)	Normal (0, 100)	0.991	1.00	[087, 1.13]
	cor(LD int, LD slope)	LKJ(eta=1)	0.074	0.79	[-0.07, 0.23]
	cor(LD int, MS int)	LKJ(1)	-0.201	0.98	[-0.36, -0.05]
	cor(LD int, MS slope)	LKJ(1)	-0.106	0.75	[-0.37, 0.16]
	cor(LD slope, MS int)	LKJ(1)	0.069	0.64	[-0.23, 0.36]
	cor(LD slope, MS slope)	LKJ(1)	0.241	0.84	[-0.14, 0.60]
	cor(MS int, MS slope)	LKJ(1)	0.484	1.00	[0.22, 0.78]

LKJ = Lewandowski-Kurowicka-Joe; distribution used for positive definite symmetric matrices with unit diagonals (uniform: eta = 1; small correlations favored: eta > 1; large correlations favored: eta < 1).

Appendix S2.2 Definition of joint plasticity metric.

We applied a polar transformation to lay date plasticity estimates and mate switch plasticity estimates to capture an overall measure of plasticity across the two behaviors. Joint plasticity was defined as $\sqrt{\beta_1^1 + \beta_1^2}$, where β_1^1 = lay date plasticity and β_1^2 = mate switch plasticity. This transformation was done on the mean of the posterior distribution of individual plasticity estimates.

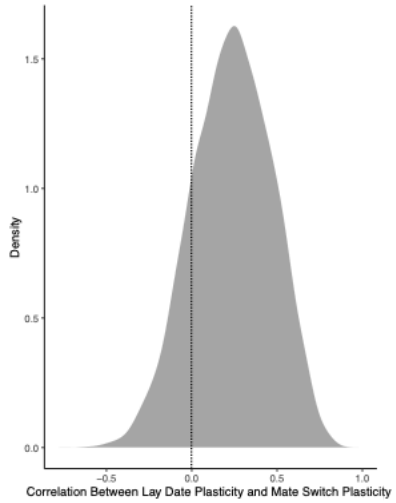
Appendix S2.3 Deming regression of plasticity correlation estimates.

Deming regression was used to draw best-fit lines for Figures 3e-g, which allowed us to take into account uncertainty in both the predictor and the response for these models. Models were weighted by $\sqrt{sd_x^2 + sd_y^2}$, where sd_x is the standard deviation of the plasticity estimate along the *x* axis and is the standard deviation of the plasticity estimate along the *y* axis.

Appendix S2.4 Magnitude of variation in individual plasticity.

For the DHGLM, we defined the magnitude of variation in individual plasticity for each behavior as the coefficient of variation in the slope estimates of that behavior, defined as:
CV = σ/μ, where σ is the vector of MCMC standard deviation values from the model and μ is the vector of MCMC slope estimates from the model. Here, we report the median and 89% highest density interval for each coefficient of variation in plasticity. For the lay date and mate switch model, CV_{lay_date} = 0.57 [0.26, 1.13] and CV_{mate_switch} = 2.31 [0.97, 4.54].

Figure S2.1 Correlated Plasticity HDI



Posterior distributions of correlations among behavioral plasticities from DHGLM model.

Chapter 3: Previous Foraging Success Shapes Behavioral Decision-Making Across Scales

Authors: Erik Johansson, P. Dee Boersma, Briana Abrahms

3.1 Abstract

Animal behavior arises from a decision-making architecture that incorporates the accumulated outcomes of previous behaviors. Cognitive ecology provides a theoretical framework for describing the effect of previous behavior outcomes on decision-making, and examples in wild populations appear in movement and foraging ecology, in the form of memory-based movement models and state-dependent foraging models, respectively. However, existing empirical work remains poorly integrated; research typically addresses a single mechanism operating at a single scale. Here, we reveal how marine predators (*Spheniscus magellanicus*) use the outcomes of their previous behavior – foraging success – to shape both broad-scale movement decisions and fine-scale decisions of foraging effort allocation. Our results highlight a general phenomenon of personal histories playing an important role in decision-making across scales. This dynamic coupling of behavioral decisions and the outcomes of those decisions is a cornerstone of adaptive, goal-directed behavior and can drive the emergence of intraindividual behavioral variation.

3.2 Introduction

Decision-making is fundamental to animal behavior, and the outcomes of these decisions determine individual fitness and shape ecological processes (Budaev et al., 2019). Efforts to describe and predict animal behavior have revealed that optimal decisions reflect both the current needs of the individual and the environmental information available to it. However, what an individual currently needs and what it knows about its environment depends, in part, on the outcomes of its previous behavioral decisions. For example, escaping a predator can incur costs and alter the energetic state of an individual as well as its knowledge of the risk landscape. This demonstrates a common feedback underlying animal behavior: current needs and environmental information impact behavioral decision-making, and the outcomes of these decisions can subsequently impact the needs and environmental information of the individual at future time steps (Sih et al., 2015). This feedback reveals a general mechanism through which previous experiences improve the ability of individuals to respond dynamically to changes in their internal state and their understanding of the world, and can also drive the diversity of behavior we observe within and across individuals.

Research on the feedback between previous experience and behavioral decisions appears across the ecological disciplines of cognitive, foraging, and movement ecology. Previous work in cognitive ecology has formalized this feedback and used it to explain a range of behaviors including foraging boldness (Rands et al., 2003), aggressive interactions (Chase et al., 1994), and threat avoidance. Conceptual models describe a decision-making architecture in which behavioral choices are made by integrating current stimuli and internal states to weigh conflicting needs of the individual (Budaev et al., 2019). These internal states encode representations of both physiological conditions, such as energy reserves, and environmental context, such as predation threat, and can persist at a range of scales. Thus, models from cognitive ecology often implicitly incorporate previous experiences via their integration of an animal's internal state. This state-behavior feedback has been used to describe inter-individual variation in behavior (Sih et al., 2015). For example, individuals with high energy reserves are more bold well foraging than individuals with low energy reserves, allowing them to forage more efficiently, resulting in persistent behavioral differences among individuals (Luttbeg and Sih, 2010). Outcomes of previous decisions determine the goals and information that guide

subsequent behavioral decisions, and are therefore essential to the aim of describing and predicting animal behavior.

Alongside the work in cognitive ecology to describe the feedback pathway connecting behavioral decisions to previous decision outcomes, empirical work in other ecological disciplines has examined this pathway in wild populations. In foraging ecology, this feedback has been explored through the use of Bayesian foraging models – which predict foraging decisions based on prior expectations and current rates of prey encounter – and dynamic state variable models – where accumulated energetic states moderate how animals respond to current conditions (McNamara and Houston, 1986; Valone, 2024). These efforts highlight fine-scale adjustments to foraging activity based on the accumulated energetic state of the individual, the current prey availability it experiences, and its prediction of broader prey availability (Watanabe et al., 2014). While the exact role of these factors in determining foraging decisions can be described under highly-controlled experimental conditions (Webb et al., 2024), they remain difficult to resolve in wild populations under natural conditions, where fine-scale behavioral data are more difficult to collect and confounding factors are more difficult to control (Houston et al., 2025).

Meanwhile, empirical work in movement ecology has revealed spatial memory as a mechanism linking previous experience to decisions of when and where to move (Merkle et al., 2019; Nathan et al., 2008). A primary challenge of decision-making is managing uncertainty resulting from incomplete information about the environment (Dall et al., 2005); animals that use spatial memory to update their beliefs about the environment can improve their movement decision-making in heterogeneous environments (Fagan et al., 2013). Similar to environmental information gained through current sensory input, memory can drive selection for or against available locations (Gurarie et al., 2022; Van Moorter et al., 2009). The direction and strength of this selection, however, will depend on what the individual previously experienced at that location – escaping a predator will elicit a different selection than consuming a resource. This nuance has remained underexplored in movement ecology, mainly due to the challenge of pairing spatial data with information on individual experiences of decision outcomes.

Movement ecology and foraging ecology both address the feedback between previous experience and behavioral decision-making described in cognitive ecology, but they often address distinct mechanisms and studies often operate from the viewpoint of a single scale.

Increasingly rich datasets on the context and outcomes of behavioral decisions in wild populations presents the opportunity to link these perspectives and begin addressing the generalized feedback mechanism between experience and decision-making empirically and holistically. An integrated approach to the study of previous experience and decision-making is necessary to reveal interactions that may occur across expressions of this pathway. The fields of cognitive, foraging, and movement ecology are also strengthened by each other; an interdisciplinary approach provides an opportunity to reveal underappreciated drivers of animal movement and interindividual behavioral variation. Studies that examine the role of previous experience on decision making across scales and mechanisms – including updates to current needs and environmental knowledge – from within the same system represent a clear next step.

Here, we examine how the outcomes of previous experiences shape animal decision-making at fine and broad scales by leveraging a dataset that pairs high-resolution data on foraging behaviors and outcomes with movement data on a marine top predator, *Spheniscus magellanicus* (Magellanic penguin). This species forages on patchy, ephemeral prey during underwater dives, and acts as a central place foraging during the breeding season. The natural history of breeding seabirds provides two distinct biologically-meaningful scales of behavior at which to explore decision-making – the dive-scale and the trip-scale. Previous work in these and other seabird systems have found evidence of spatial memory (Rebstock et al., 2022), and in rare cases memory of foraging success (Carroll et al., 2018), impacting trip-level movement decisions. Other work in similar systems has used dive-level foraging decisions to test predictions from optimal foraging theory (Watanabe et al., 2014). This system is therefore well suited to explore the effect of previous experience on decision-making across scales.

We simultaneously collected GPS location data spanning multiple foraging trips and high-resolution acceleration data that reveals dive-level prey pursuit behavior from breeding adult penguins. Linking theory from movement, foraging, and cognitive ecology, we test the hypothesis that the outcome of previous experiences – previous foraging success – should influence foraging decisions at both broad and fine scales. Specifically, we test the following predictions:

P1 (Broad-scale): Individuals will prefer trips that revisit the foraging area used on the previous trip, and this preference will be stronger following more successful foraging trips.

P2 (Fine-scale): Foraging effort will increase with current foraging success, but this effect will be moderated by previous foraging success, such that: (2a) the effect of current success on effort will be weaker (2a) – or alternatively, stronger (2b) – following high previous success than it will be following low previous success.

Support for P1 would reveal that broad-scale movement decisions are impacted by previous foraging success at the scale of days, while support for P2 would reveal that fine-scale effort allocation decisions are impacted by foraging success at the scale of minutes to hours. Support for P2a would suggest that individuals are more responsive following low previous success, increasing their effort under good current conditions to make up for an energetic deficit. Whereas support for P2b would suggest that individuals are more responsive following high previous success, decreasing their effort under poor current conditions and relying on their energetic reserves. Together, these analyses provide an integrated look at how the outcomes of previous experience drives animal decision-making across scales.

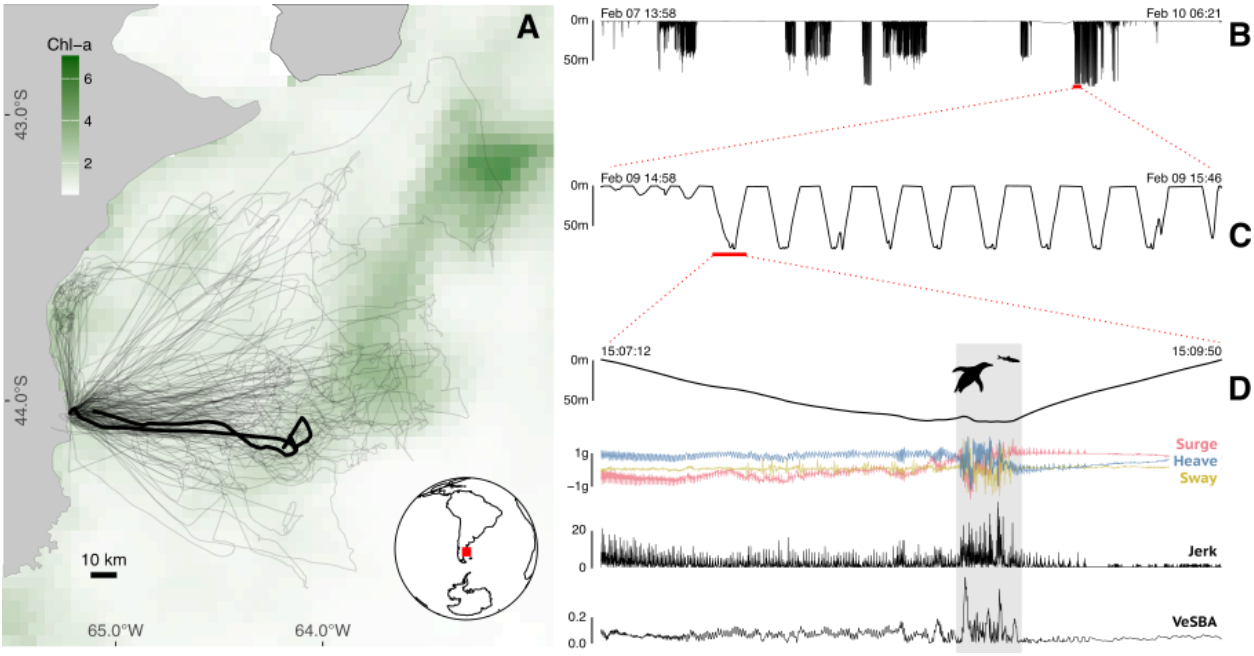


Figure 3.1 Movement and behavioral data collection. A. Foraging trips of breeding adult Magellanic penguins from Punta Tombo during the 2024 and 2025 post-guard seasons, with chlorophyll-a concentration from the week of February 7, 2024. B. Diving profile of highlighted foraging trip. C. Diving profile of hour-long foraging bout D. Profile and accelerometry-derived metrics from single dive, highlighting signature of prey pursuit.

3.3 Methods

3.3.1 Study System

This study was carried out at the Punta Tombo Magellanic penguin colony in Chubut, Argentina (44°03′ S, 65°13′ W), which is the breeding grounds for >100,000 breeding pairs. Females lay eggs in October, and both parents care for the eggs and chicks until fledging. During the January–February nestling period, parents provision chicks with food collected on multi-day foraging trips (Figure 3.1A). During these trips, penguins travel to at-sea foraging grounds, often returning to the same areas repeatedly. Efficient foraging during these trips is vital to reproductive success (Boersma and Rebstock, 2009; Rebstock et al., 2022), as starvation is the primary cause of chick mortality at this time of year (Boersma and Rebstock, 2014).

Magellanic penguins are diving predators, foraging primarily on Argentine anchovy (*Engraulis anchoita*) and occasionally on other forage fish, shrimp, and squid (Scolaro et al., 1999; Yorio et al., 2017). Based on prey capture data from intra-mandibular angle sensors, single dives may include capture of up to 13 prey items (Wilson, 2003). Prey capture events are characterized by rapid changes in instantaneous power (Wilson et al., 2010) resulting from rapid movement as the penguin lunges at prey, often approaching it from below (Simeone and Wilson, 2003). Magellanic penguins have an extremely high capture rate, catching prey that they snap at >99% of the time (Wilson et al., 2010).

3.3.2 Data collection and processing

Over two January-February nestling periods (2024, 2025), we deployed AxyTrek loggers (Technosmart, Italy, 69g) – equipped with tri-axial accelerometers (25Hz), GPS sensors (5-min daytime, 10-min nighttime fix rate), and time-pressure sensors (1Hz) – on 68 breeding males and females (see Rebstock et al., 2022 for tagging procedures). After filtering to exclude records with low satellite signal strength, location data from each deployment were used to fit a continuous-time correlated random walk state space model (Crawl; Johnson et al., 2008). Only data from multi-day foraging trips were retained, as the behavioral drivers are expected to differ for shorter excursions (Rebstock et al., 2022). Pressure data were adjusted for sensor drift using a zero offset correction function and used to assign diving periods and depth using the DiveMove package (Luque, 2007; Figure 3.1B-C). To isolate foraging dives and improve prey-pursuit detection, only dives ≥5m deep were retained (Kokubun et al., 2015; Takahashi et al., 2003). As

each dive was not individually geospatially referenced, dive locations had to be matched with GPS data and the uncertainty in dive locations varied with the interval between surrounding GPS fixes. To propagate this uncertainty in subsequent analyses, we drew 20 samples from the posterior distribution of the state vectors at the time of each dive using the fitted state space models, yielding a set of 20 equally plausible locations for each dive.

For both broad-scale and fine-scale analyses, we included sex and number of chicks being fed, determined through regular nest observations, as these are known drivers of variation in movement and foraging behavior. We also included at-sea chlorophyll-a concentration in both analyses to account for current environmental cues. Chlorophyll is a known indicator of ocean primary productivity, and is correlated with successful foraging in this population (Rebstock et al., 2022). We used the dataset collected by the Ocean Colour Climate Change Initiative, which we extracted from the NOAA ERDDAP data server using the 'rerddapXtracto' package (Mendelssohn, 2023). We used the recommended bias correction procedure (Sathyendranath et al., 2024) and log-transformed raw values before including them in our analyses. All data processing and model fitting was conducted in R version 4.3.1 (R Core Team, 2023).

3.3.3 Broad-Scale Analysis

To test the hypothesis that previous foraging success should influence foraging decisions at a broad-scale, we fit a conditional logistic regression model using trip-level utilization distributions of dive locations. For each actual ('used') foraging trip – defined by the set of dive locations during that trip – 20 plausible ('available') trips were simulated by randomly selecting a used trip and rotating it at random around the colony location, ensuring that all dive locations remained at-sea. The number of available trips was chosen based on sensitivity testing (see Supplementary Material). This approach provided a representative sample of the available foraging area using movement-constrained availability sampling (Avgar et al., 2016; Thurfjell et al., 2014). We then used the set of points defining each used and available trip to generate 95% kernel density estimated utilization distributions with a bandwidth of 4km and grid resolution of 2km to match the spatial resolution of environmental variables (Wakefield et al., 2015). Trip foraging success was defined as the inverse of energetic expenditure, as data from weighbridges at the colony revealed that penguins gain similar amounts of weight on all foraging trips during this breeding period, regardless of trip duration and energetic cost (Figure 3.2). This is likely

because breeding individuals will remain at-sea until they have accessed sufficient prey to feed their chicks. Energetic expenditure is thus a straightforward metric of trip-level foraging success; shorter, less energetically costly trips result in more overall and more frequent chick provisioning. Energetic expenditure was calculated for each trip from raw acceleration records using the approach described in Wilson et al. 2010. In brief, we converted acceleration to metabolic power using a species-specific equation (see Supplementary Materials). Trip-level chlorophyll conditions were calculated by averaging chlorophyll values across the utilization distribution and the timespan of the trip.

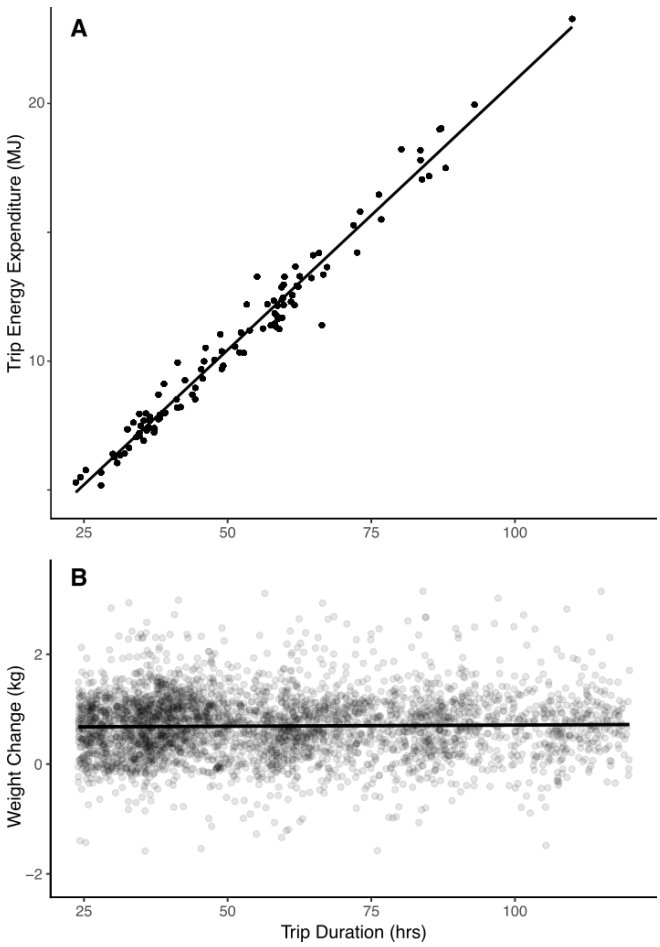


Figure 3.2 Foraging trips that last longer result in greater energetic expenditure (A), but do not result in higher weight gain (B). In our analysis, trip-level foraging success was defined as the inverse of trip-level energetic expenditure; trips that used less energy were more successful.

For each pair of consecutive trips by the same individual, spatial overlap was calculated between the first and second used trips – as well as the first used trip and all available second trips – using Bhattacharyya's affinity metric (Abrahms et al., 2018; Arthur et al., 2015; Figure 3.3A). Overlap was used as a metric of whether, and to what extent, individuals revisited previously-used foraging areas. With each

stratum defined by matched sets of used and available trips, we fit the conditional logistic regression model using the clogit function in the 'survival' package (Therneau, 2026), with chlorophyll concentration, previous trip overlap, and interactions between overlap and sex, overlap and number of chicks, and overlap and previous trip success as predictors, with a binary used (1) or available (0) variable as the response. We ran 20 imputations of the model to carry forward the uncertainty in dive locations and pooled the coefficient estimates and standard errors (Rubin, 1987; Schafer, 1999). We also ran a null model for comparison (see Supplementary Material).

3.3.4 Fine-Scale Analysis

To test the hypothesis that previous foraging success should influence foraging decisions at a fine-scale, we fit a mixed-effects generalized linear model to predict dive-level foraging effort in response to current and previous foraging success. Dive-scale foraging success was assigned based on the presence or absence of prey pursuit events. To identify prey pursuit events, we used acceleration data from diving periods to calculate normalized metrics of VeSBA (sum of static body acceleration; Ainley and Wilson, 2023) and jerk (differential of acceleration; tagtools package, DeRuiter et al., 2025) at 25Hz. VeSBA measures turn speed while jerk measures changes in acceleration (Figure 3.1D); both have been shown to be indicators of the rapid movements associated with prey capture in marine predators (Ainley and Wilson, 2023; Ydesen et al., 2014). We used these metrics to assign behavioral states to diving periods using unsupervised Gaussian mixture models, with solutions found using the expectation maximization algorithm (mclust package; Chimienti et al., 2016; Scrucca et al., 2016). We selected a model structure with five latent behavioral classes based on LIC (integrated complete-data likelihood; Biernacki et al., 2000) and the biological interpretability of the resulting classes, each of which corresponded to a distinct behavior (prey pursuit, ascent, descent, high-activity swimming, and low-activity swimming; see Supplemental Material) (Chimienti et al., 2016; Scrucca et al., 2016). Based on these assignments, each dive was classified as a 'prey pursuit dive' or 'non-prey pursuit dive' according to whether the dive included consecutive assignments to the prey pursuit cluster. These dive-level classifications were compared with expert assignments to estimate model sensitivity and specificity, and the stability of the choice of consecutive assignments and

assignment probability thresholds was tested with a sensitivity analysis (see Supplementary Materials).

For each dive, we then defined subsequent foraging effort as the time spent diving over the four minutes following the end of the dive. We defined current foraging success as the number of prey-pursuit dives over the four dives immediately preceding the focal dive, and previous foraging success as the number of same-day prey pursuit dives preceding the focal dive divided by elapsed time (Figure 3.4A). The thresholds defining current success and subsequent effort were chosen to isolate fine-scale foraging behavior adjustments in response to current conditions. A sensitivity analysis was run over current success and foraging effort thresholds to test the robustness of the results, and the full dataset of dives was subsampled to every five dives to reduce residual autocorrelation (see Supplementary Materials). Local environmental conditions for each dive were calculated as the mean chlorophyll concentration within a 3×3 grid-cell neighborhood (approximately 10 × 10 km) centered on the dive location on the same calendar date. Mixed effect linear models were fit using the glmmTMB package (Brooks et al., 2017) with effort as the response and chlorophyll, sex, number of chicks, and an interaction between current and previous foraging success as fixed effects, along with a random effect for trip. We again ran 20 imputations of the model to carry forward the uncertainty in dive locations, and pooled the results (Rubin, 1987; Schafer, 1999).

3.4 Results

A total of 171 multi-day foraging trips were recorded from the 68 tagged individuals, with an average of 2.7 trips and a range of 1-7 trips per individual. Trips lasted an average of 53.7 ± 17.1 hours and ended an average of 81.6 ± 25.1 km from the colony. Average trip energetic expenditure was 10.9 ± 3.5 megajoules. 107 pairs of consecutive trips were identified across 52 individuals. Individuals averaged 186 ± 118 dives >5m per day and 508 ± 256 dives >5m per trip, with 28.7 ± 11.2% being classified as prey-pursuit dives. Average dive depth (males: 25.3 ± 23.5; females: 15.2 ± 12.3m) and duration (males: 70.0 ± 34.7s; females: 57.4 ± 25.3s) differed between males and females. Previous foraging success (3.5 ± 3.8 prey pursuit dives per hour), current foraging success (1.1 ± 1.3 prey pursuit dives), and foraging effort (63.8 ± 31.1s diving) were calculated for every dive in the dataset.

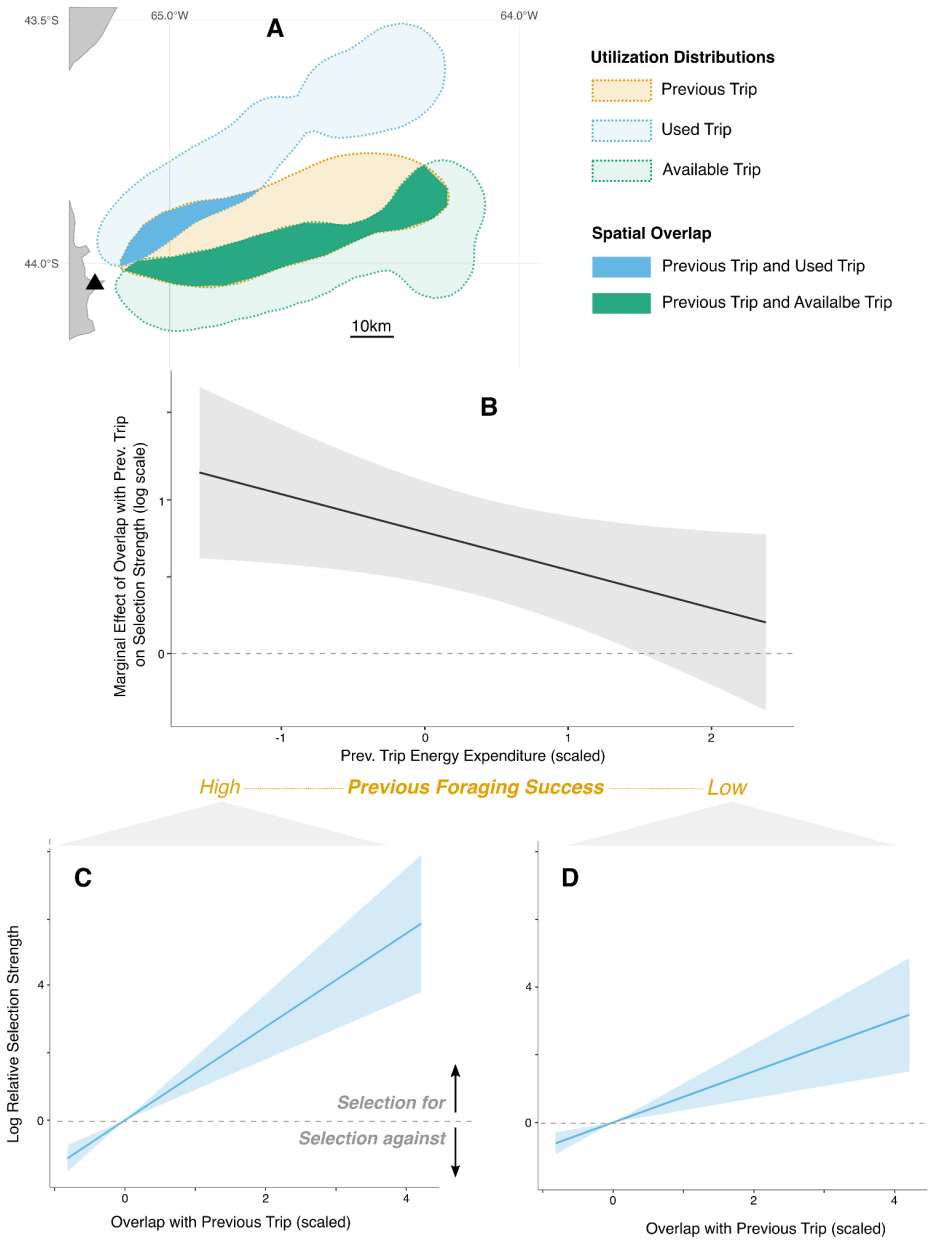


Figure 3.3 Broad-scale analysis approach and results. A. 95% utilization distributions estimated via kernel density estimation for an observed ('used') foraging trip, the previous observed trip taken by the same individual, and a generated 'available' foraging trip. Overlap between previous and used/available trips calculated using Bhattacharyya's affinity metric. B. The effect of spatial overlap with previous trip on selection strength was moderated by previous trip energy expenditure. C. Following more successful foraging trip (lower energy expenditure) individuals showed a stronger preference for returning to previously visited areas. D. Following less successful foraging trips, individuals showed a weaker - but still positive - preference for overlap with the previous trip.

3.4.1 Broad-Scale

We found strong evidence that foraging penguins selected trips that revisited foraging areas used on their previous trip (b = 0.750; SE = 0.373; $p < 0.044$) and weak evidence that they were selected trips that overlapped areas of high chlorophyll-a concentration (b = 0.300; SE = 0.168; $p < 0.074$). We found marginal support for the prediction (P1) that selection for revisiting foraging areas used on the previous trip was affected by the previous trip's success (b = -0.209; SE = 0.115; $p < 0.069$). The preference for revisiting previous foraging areas was high following previous trips that were highly successful; however, foragers showed only a slight preference for revisiting foraging areas following trips that were low-success (Figure 3.3B-D). There was no moderating effect of sex or number of chicks on the preference for revisiting foraging areas. These findings reveal that movement decisions in this system depend not only on current environmental conditions but also on personal histories – both where an individual has previously visited and what it previously experienced; individuals showed a stronger preference for returning to previously visited foraging areas when their previous foraging success in those areas was higher.

3.4.2 Fine-Scale

In support of P2, we found strong evidence that foraging effort was affected by current foraging success (b = 0.019; SE = 0.004; $p < 0.001$), previous foraging success (b = -0.051; SE = 0.006; $p < 0.001$), and their interaction (b = 0.016; SE = 0.004; $p < 0.001$), as well as by sex (b = 0.114; SE = 0.029; $p < 0.001$; ref. = Female). Effort was not affected by chlorophyll-a concentration or number of chicks. Current foraging success and foraging effort were positively correlated, but the strength of this effect depended on previous foraging success (Figure 3.4B-D). Specifically, in support of P2b, the positive effect of current success on foraging effort was strongest following periods of high previous success. At low levels of previous success effort was consistently high, whereas at high levels of previous success effort was responsive to current conditions, remaining high when conditions were good but declining in poorer conditions. This similarly reveals a foraging strategy that depends on personal histories; individuals only reduce their foraging effort when their previous success was high and their current success is low.

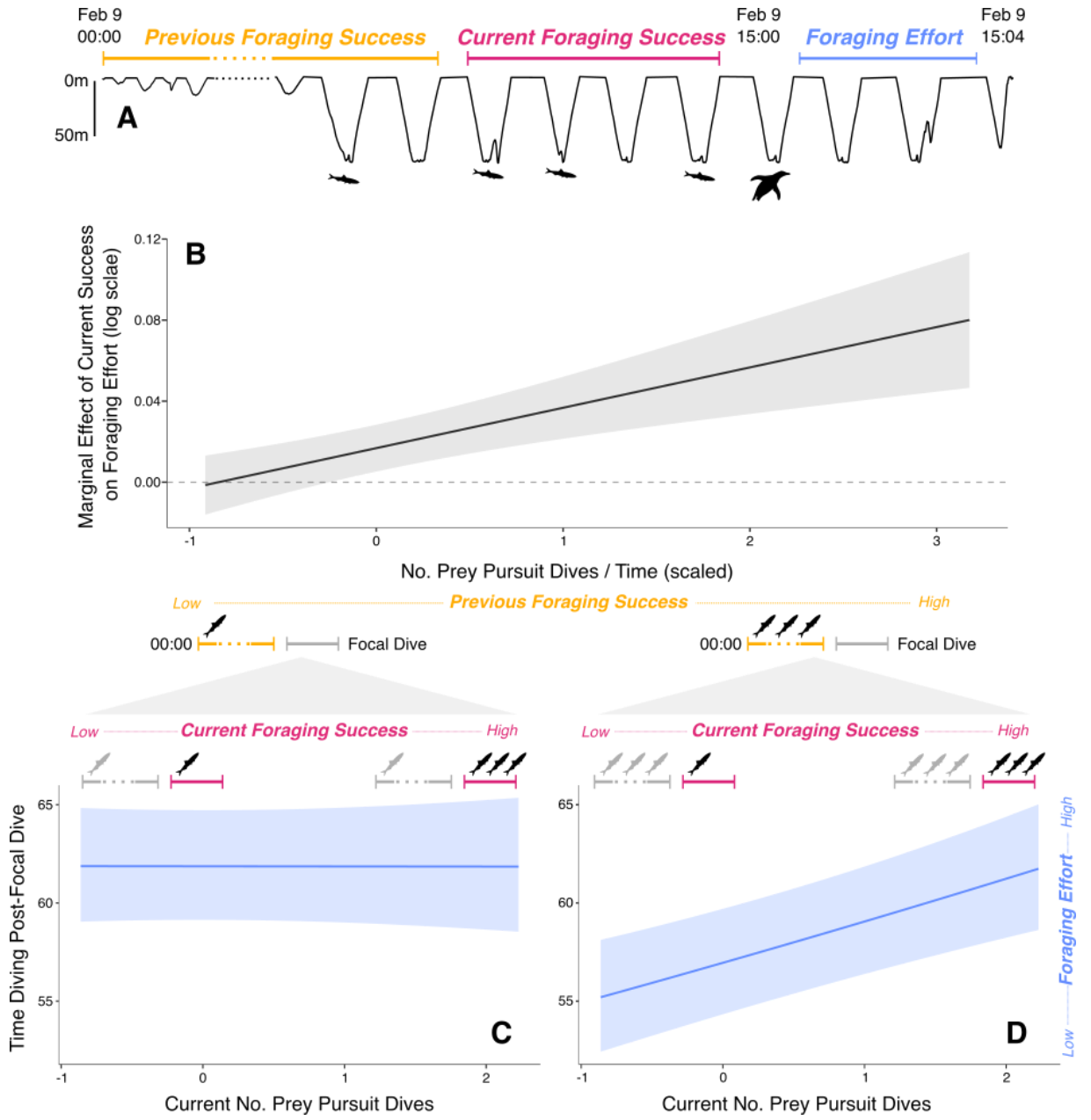


Figure 3.4 Fine-scale analysis approach and results. A. For each dive, current foraging success was defined as the number of prey pursuit dives over the past 4 dives; previous foraging success was defined as the number of prey pursuit dives since the start of that day, standardized by time since 00:00; subsequent foraging effort was defined as the time spent diving over the 4 minutes following the focal dive. B. The effect of current foraging success on subsequent foraging effort was moderated by previous foraging success. C. Following low previous success, effort was consistently high regardless of current success. D. Following high previous success, effort decreased as current foraging success decreased.

3.5 Discussion

By leveraging data on foraging predators that pairs movement patterns with high-resolution data on foraging decisions and outcomes, our results reveal the important effect of previous experiences on both broad- and fine-scale foraging decisions. We used tracking data across multiple consecutive foraging trips to show that central place foragers are more likely to return to foraging areas that they've previously visited, especially if their previous foraging experience was highly successful (P1), demonstrating the role of previous success in informing broad-scale movement decisions. We used concurrent accelerometry-derived indicators of foraging effort of the same individuals to show that, at a fine scale, these animals modulate their foraging effort based on both their current and previous foraging success (P2). Despite operating at different scales (between versus within foraging trips) and describing different behaviors (where to go versus how much energy to put into foraging), these results point to a general phenomenon of personal histories playing an important role in animal decision-making. Recognizing this as a generalized pathway that cuts across disciplinary boundaries improves our ability to predict behavioral decisions in novel contexts and reveals an important source of interindividual variation in behavior.

The results we present here, and the broader phenomenon they reflect of the outcomes of experiences impacting decisions across scales, supports theory in cognitive ecology positing a decision-making architecture that views animal behavior as goal-directed (Budaev et al., 2019). Animals track outcomes of previous decisions to update their internal representation of their own state and the world around them, and integrate these representations to identify goals and choose behaviors to meet those goals. This pathway is adaptive in cases where experience generates reliable information. At a broad scale, e.g., between foraging trips, previous foraging performance should be a reliable predictor of future prey availability when the prey landscape is spatially and temporally autocorrelated (Carroll et al., 2018; Ranc et al., 2021). Decisions of where and when to move can be reliably informed by experience at similar scales to the autocorrelation in the system. At a fine scale, e.g., within a foraging trip, recent foraging success should modify the internal state of the individual, tracking its energetic state relative to its needs and calibrating effort allocation (Watanabe et al., 2025). The weight of this information on decisions must be appropriately calibrated with other needs such as breeding or predation avoidance (Budaev et al., 2019). Our findings suggest distinct mechanisms of information use

operating at different scales, but reveal a general functional pathway of using previous experience to manage uncertainty and navigate competing priorities in decision-making.

Our finding that the decision of whether to visit a foraging area depends on whether the individual had previously visited that area supports existing empirical work in movement ecology (Fagan et al., 2013; Merkle et al., 2014). Site fidelity – which arises from a preference for visiting previously-visited locations – is widely documented in central place foragers, including in this system (Rebstock et al., 2022; Regan et al., 2024; Wakefield et al., 2015). Previous experience can modulate this preference; many animals only show site fidelity following good performance, using a win-stay lose-switch strategy (Carroll et al., 2018; Morrison et al., 2021; Switzer, 1993). While previous work on win-stay lose-switch strategies have largely focused on the effects of previous reproductive success outcomes in the context of selecting breeding sites (Byrne and Silla, 2023; Chalfoun and Martin, 2010), here we show that the effect of previous performance on probability of return similarly applies in the context of an animal's foraging behavior and success. In other systems, a preference for previously-visited locations can lead to the development of stable home ranges (Van Moorter et al., 2009); animals may also show an avoidance of recently visited locations, for example if depleted prey require time to replenish, or if territory markings take time to decay (Gurarie et al., 2022). Pairing location data with information on what the animal experienced at those locations is essential for understanding why documented movement patterns emerge. Our results indicate that individuals at this colony are foraging on prey patches that remain temporally persistent at broad spatial scales (1-10s km) over several days, and that individuals employ a win-stay lose-switch strategy to flexibly adjust their choice of foraging areas. These results add to a growing literature on previous experience modulating movement decisions, and highlight the importance of accounting for what animals have experienced, not just where they have been, in animal movement modeling.

At a fine-scale, we found that the decision of how much effort to put into foraging depends on an individual's current and previous foraging success within the same trip. Theoretical work in foraging ecology predicts this integration of current and previous success. For example, the marginal value theorem states that patch residency time should depend on both local and long-term patch quality (Charnov, 1976). More recent empirical tests of the marginal value theorem have emphasized that long-term patch quality is best defined by personal

experiences of the resource landscape rather than omniscient knowledge (Watanabe et al., 2014). Similarly, research on state-dependent foraging has emphasized that foraging decisions are made in the context of a string of decisions and their outcomes, not in isolation (Denryter et al., 2020). While memory generally provides information about external conditions, previous experience at this fine scale can drive decision-making through changes to the perceived physiological state (McNamara and Houston, 1986; Sih et al., 2015). Our finding that foraging animals adjust their response to current foraging success based on their previous foraging success is likely operating through this pathway; individuals with higher previous foraging success are more satiated and less likely to continue foraging when conditions are poor. That individuals with low previous foraging success continue high-effort foraging in poor conditions highlights the foraging pressure they experience while raising young. Meanwhile, individuals with high previous foraging success display the luxury of being selective in the timing of their foraging.

A key insight gained from focusing on the pathway of experience outcomes impacting decisions-making is that consistent differences in behavior among individuals can arise through differences in their personal histories. Interindividual behavioral variation has been a rapidly growing topic of interest in ecology (Dall et al., 2012; Réale et al., 2010; Wolf and Weissing, 2012). Recent work has documented this variation across behaviors, contexts, and taxa (Hertel et al., 2021; Johansson et al., 2024; Stamps, 2016) with demonstrated impacts on population persistence, for example through the portfolio effect (Schindler et al., 2010). However, the drivers of interindividual behavioral variation remain underexplored. While differences in genotypes, phenotypes, or parental effects account for some of this variation, differences in personal histories likely also drive behavioral variation among individuals, with diverging (or converging) effects due to positive (or negative) feedbacks between behavioral decisions and the needs and knowledge of the individual (Sih et al., 2015). Personal histories may also interact with other drivers of interindividual behavioral variation: for example, males in this system tend to forage at greater depths than females; this sex-specific driver of interindividual behavioral variation could result in different personal histories for males and females, as their foraging success will differ within the same prey landscape, leading to further diverging behavior as their foraging success determines subsequent movement. Complete accounts of behavioral variation across individuals must therefore consider the outcomes of the previous experiences of those individuals. While behavioral variation is present in our dataset, and we show that previous

experiences drive some of that variation, extending this to test whether the feedback between experience and behavior leads to stable, alternative behavioral types was beyond the scope of this study.

Our work reveals that previous foraging success is used to inform movement and foraging decisions across spatiotemporal scales in a wild animal population. We use these findings to highlight a general phenomenon of personal histories impacting animal decision-making that is traditionally studied at specific scales and within the frameworks of specific disciplines. As a result, we emphasize the importance of accounting for personal histories when describing and predicting behavioral decisions. This phenomenon also occurs at scales beyond what we explore here; for example, maternal effects could be considered an inter-generational impact of previous experience on subsequent decision-making (e.g., female bluebirds nesting in high-density breeding areas produce sons that are more likely to disperse; Duckworth and Badyaev, 2007). Although the precise mechanisms connecting experience to the behavioral decisions of when to forage, where to move, and whether to disperse may vary, treating the generalized pathway as a subject of focus will encourage cross-disciplinary insights, advance our understanding of adaptive decision-making and interindividual behavioral variation, and improve our ability to predict behavioral decisions in novel contexts.

3.6 Supplementary Material

Table S3.1 Prey pursuit validation of 300 dives across all deployments. Validation was done using expert assignments based on plots of depth and acceleration-derived metrics. Sensitivity indicates ability to detect prey pursuit dives correctly; specificity indicates ability to detect non-prey pursuit dives correctly; true skill statistic = sensitivity + specificity - 1, and

Assignment Certainty	**90%**				**95%**				**99%**			
Consecutive Points	**2**	**4**	**8**	**16**	**2**	**4**	**8**	**16**	**2**	**4**	**8**	**16**
True Positives	73	73	72	72	73	73	72	72	73	72	71	66
False Negatives	1	1	2	2	1	1	2	2	1	2	3	8
True Negatives	221	225	233	245	225	231	240	246	237	242	247	249
False Positives	35	31	23	11	31	25	16	10	19	14	9	7
Sensitivity	0.986	0.986	0.973	0.973	0.986	0.986	0.973	0.973	0.986	0.973	0.959	0.892
Specificity	0.863	0.879	0.910	0.957	0.879	0.902	0.938	0.961	0.926	0.945	0.965	0.973
True Skill Statistic	0.850	0.865	0.883	0.930	0.865	0.889	0.910	0.934	0.912	0.918	0.924	0.865

Figure S3.1 Representative example of unsupervised clustering model assignments for a single deployment, with metrics of a single prey-pursuit dive from the deployment.

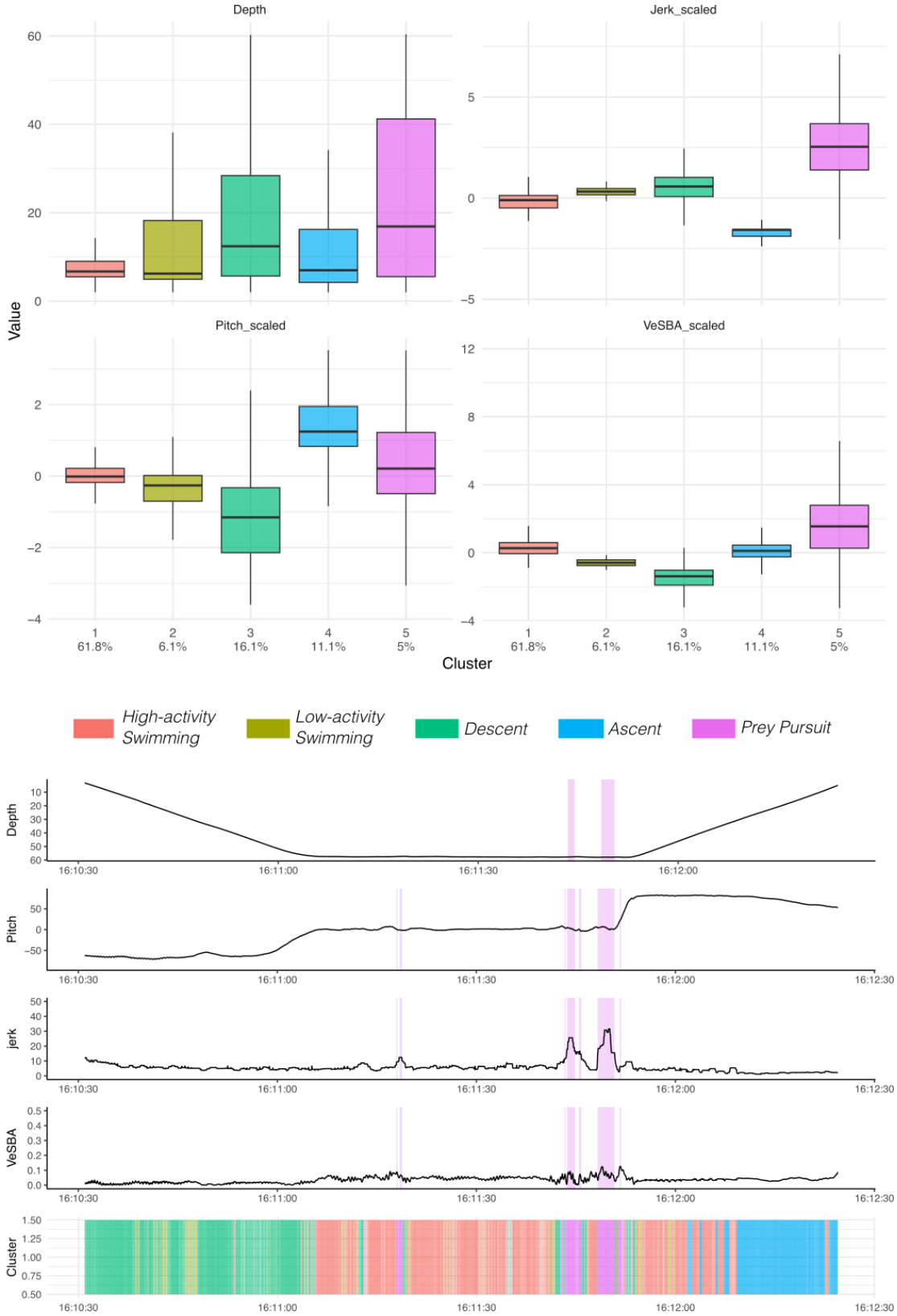


Figure S3.2 Parameter sensitivity for fine-scale analysis. Sensitivity to the number of dives used to define current foraging success (1, 2, 4, 8, 16), the number of minutes used to calculate subsequent foraging effort (1, 2, 4, 8, 16), and the threshold for assigning prey pursuit (8 consecutive cluster assignments over 99%, 16 consecutive over 95%, 16 consecutive over 95%) are shown for key coefficients. Estimates are highly consistent except at very low (<4) values of the current_success threshold.

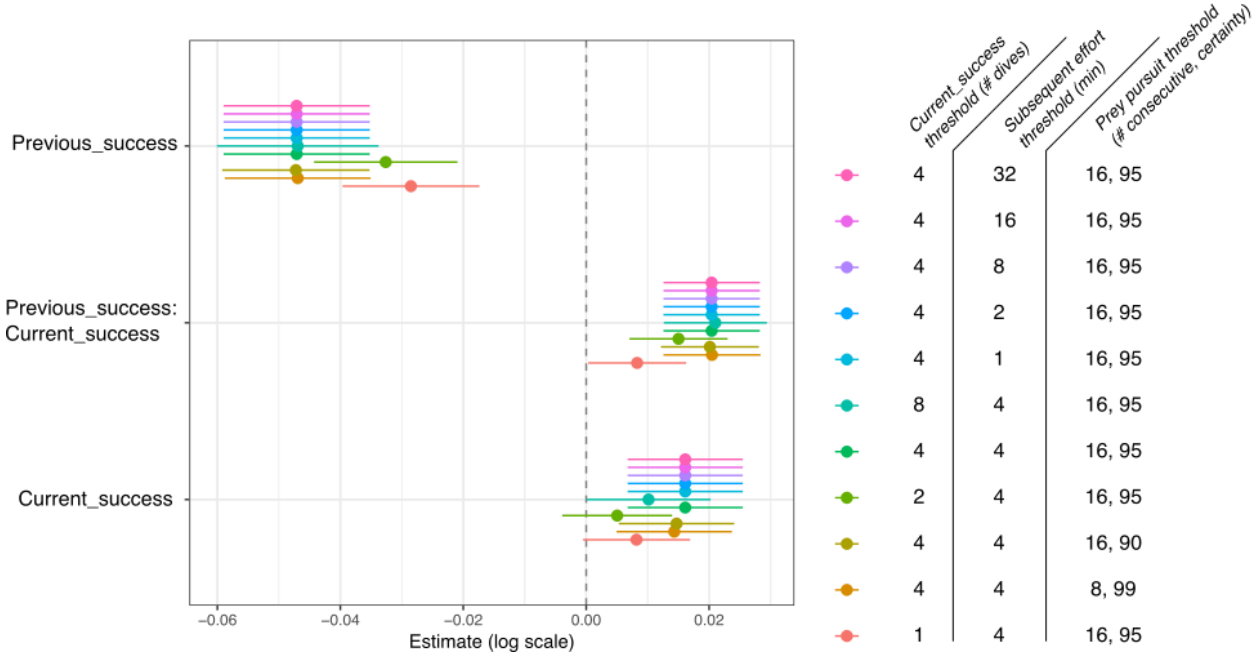


Figure S3.3 Residual autocorrelation for fine-scale analysis across a range of thinning parameters; 10 random trips shown. A thinning parameter of T4 includes every 4th dive in the analysis; main analysis uses a thinning parameter of T6 to minimize autocorrelation while preserving a usable sample size.

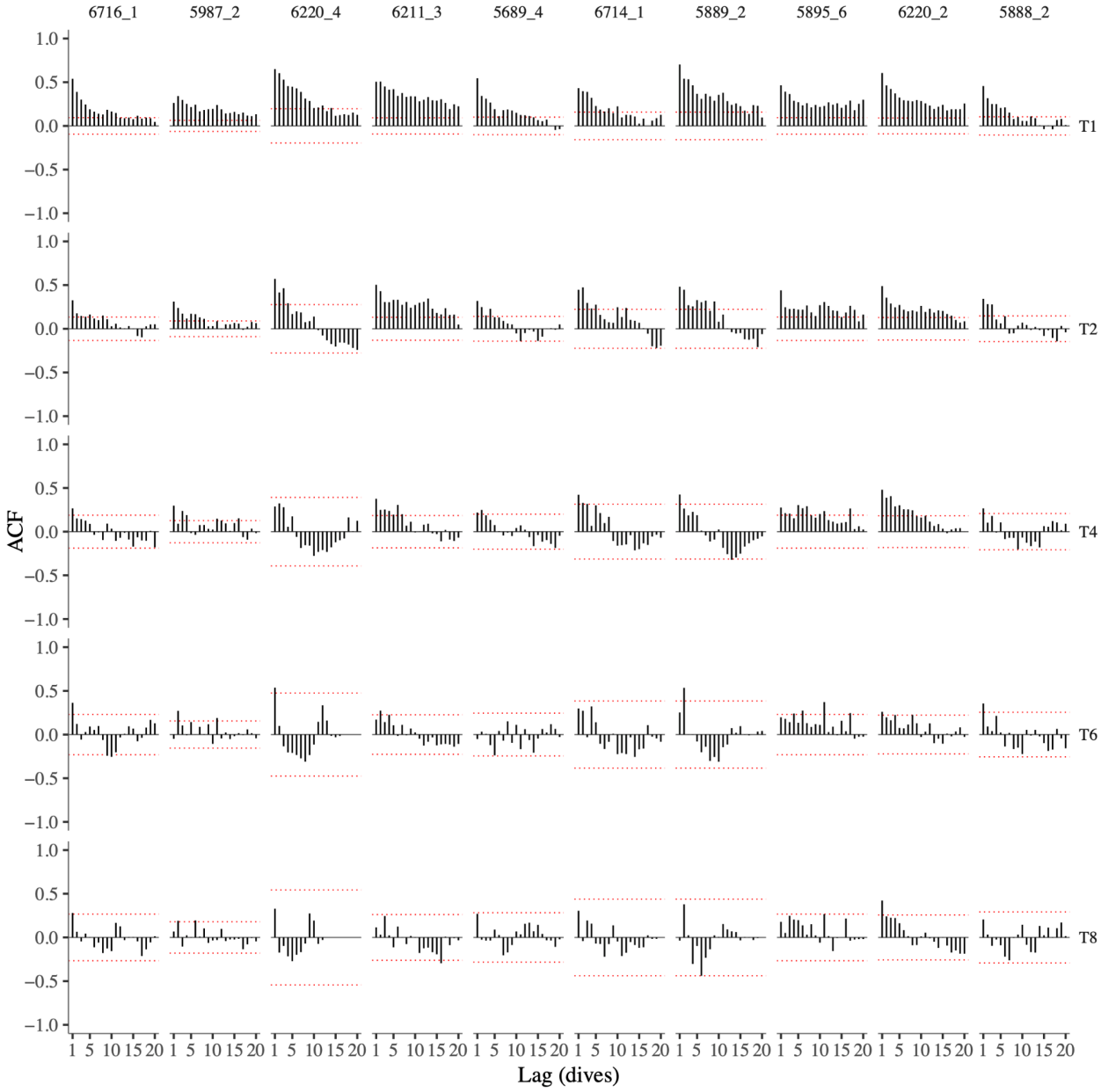


Figure S3.4 Simulated null model for broad-scale analysis. Each plot shows 999 simulated p-values of model coefficients after randomly re-assigning the 'used' trip within each stratum. Pink lines mark p=0.05, and labels indicate proportion of simulated p-values < 0.05. None of these proportions exceed 5%. This indicates that low p-values are not an artifact of model structure.

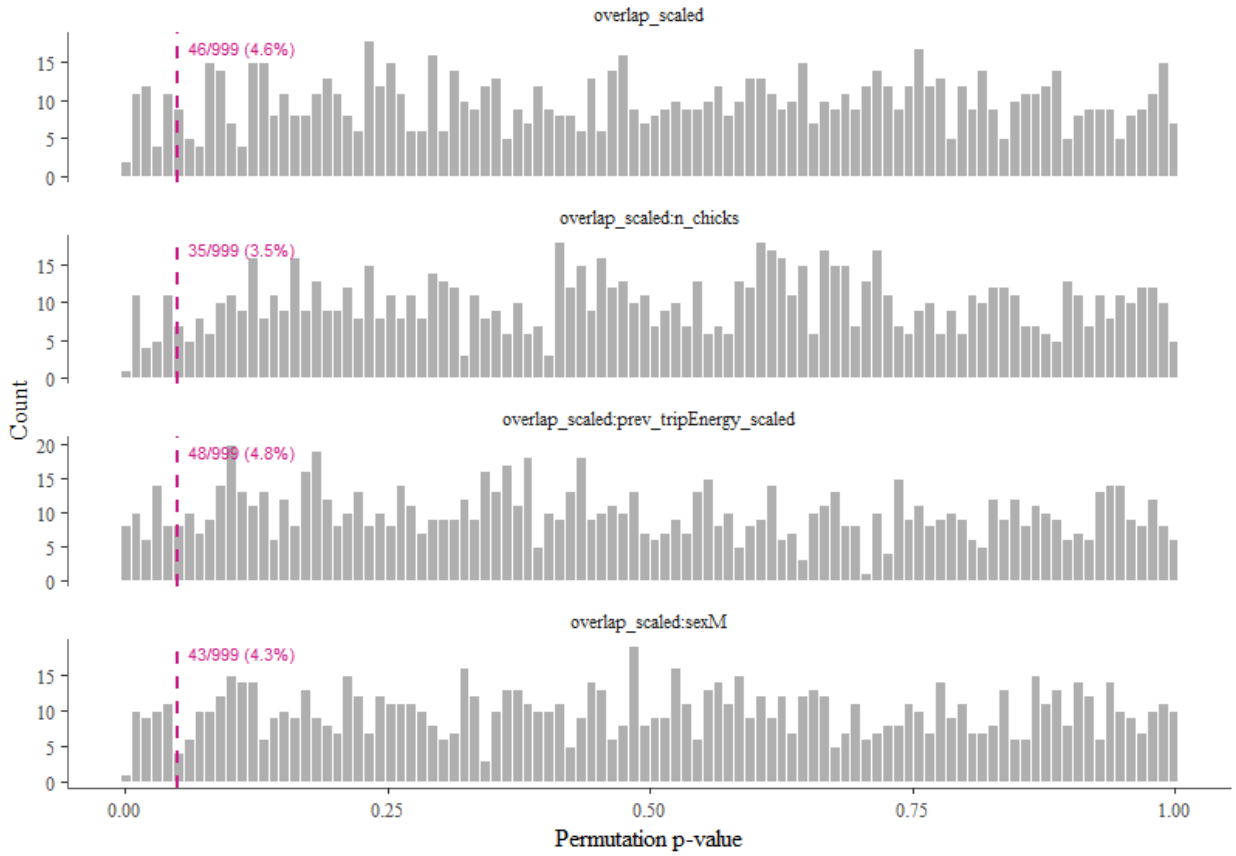
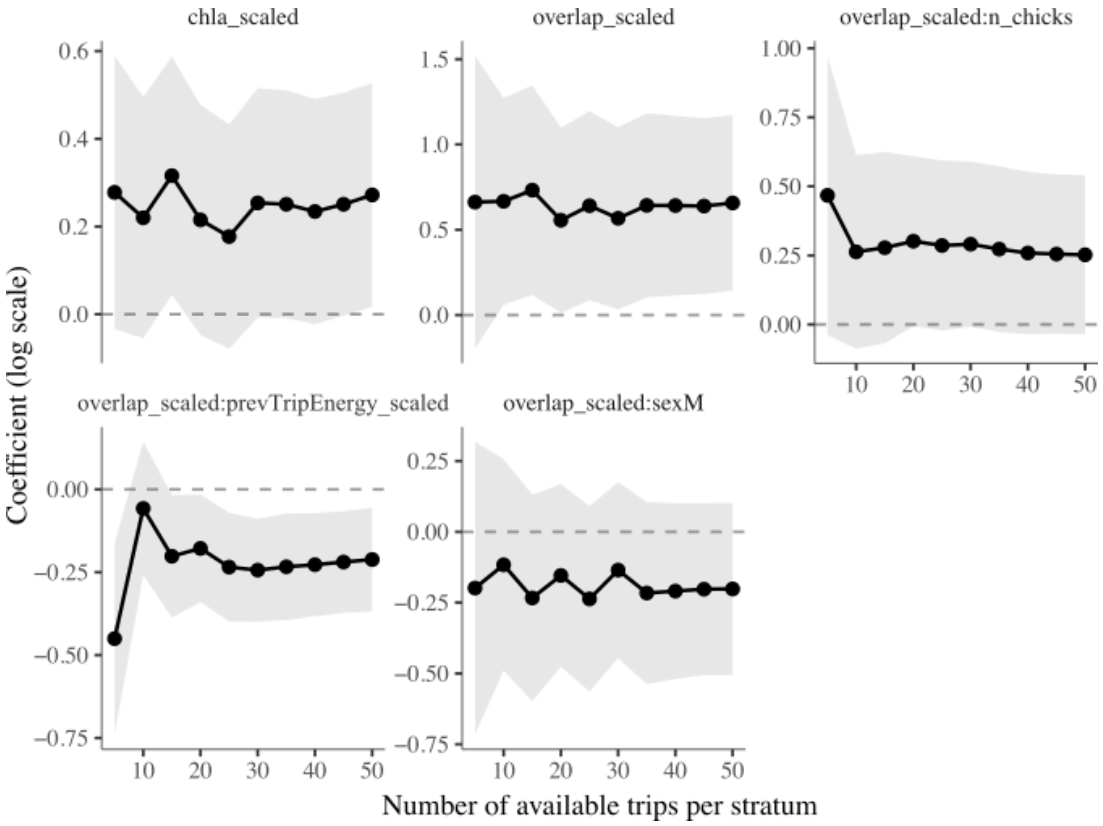


Figure S3.5 Sensitivity of model coefficients to number of non-used values per stratum (5-50) in broad-scale analysis. Non-used values per stratum correspond to the number of 'available trips' used for comparison to each 'used trip' in the conditional logistic regression model. Coefficient values stabilize by 20-25, and confidence intervals do not shrink dramatically with increasing strata size.



Conclusion

In Chapter 1, I described the first test of correlated plasticities in a wild population, revealing a positive correlation between plasticity in some behaviors and a negative correlation between plasticity in other behaviors. I then showed in Chapter 2 that the fitness consequences of coordinated expressions of plasticity depended on the environmental context: plasticity improved reproductive success in unusually productive environments, but did not buffer individuals against the negative consequences of unusually unproductive environments. Finally, in Chapter 3 I highlighted a common pathway through which previous experience drives animal decision-making, and therefore behavioral variation, across scales. Together, these chapters provide a holistic account of interindividual behavioral variation in a long-lived, highly mobile species – from the mechanisms that generate variation, to a description of novel patterns in this variation, to the reproductive consequences across environmental contexts. While there has been a surge of interest in behavioral variation (Beever et al., 2017; Dall et al., 2012; Stamps, 2016), most existing work still remains focused on documenting patterns of this variation, such as describing the range of behavioral expression across individuals (Bell et al., 2009) or correlations in behavioral expression within individuals (Hertel et al., 2020). As we continue to have access to higher-resolution and longer-term behavioral datasets, we are increasingly able to test hypotheses of what causes the patterns of behavioral variation we observe, and what the consequences of these patterns are for individuals, populations, and ecosystems. Doing so is essential for placing the study of behavioral variation in a broader ecological and evolutionary context. The consequences of a pattern in behavioral variation depends on its cause, making the joint study of cause and consequence more informative than either alone.

While this dissertation takes a holistic approach to the study of interindividual behavioral variation, it is still a fragmented account of behavioral variation in this population. Notably, I did not track a single behavioral pattern from its cause to its individual and ecological consequences, mainly due to data limitations. Magellanic penguins are annual breeders, so measuring the reproductive consequences of behavioral plasticity across environmental contexts required using long-term behavioral data. On the other hand, measuring the role of personal histories on fine-scale foraging behavior required high resolution biologging data that were only available over a span of two breeding seasons. My primary aim with each chapter was to test hypotheses at

the edge of current understanding, rather than prioritize integration across chapters. As revealed by my work on correlated plasticities (and extensive existing work on behavioral syndromes (Sih et al., 2004b)), even an approach focused on the causes and consequences of variation in a single behavior would remain incomplete because behaviors co-vary such that any single behavior is embedded in a broader suite of correlated traits. My analyses in all three chapters are also purely correlational. The results I present therefore describe plausible relationships, supported by data collected from free-living animals. I also used statistical approaches designed for analyzing observational data from wild populations (Hertel et al. 2020). However, these relationships remain untested experimentally; I did not manipulate the individuals or their environment to establish control groups. As with other ecological questions, progress on our understanding of behavioral variation will come from iteration between experiments, to establish causation, and observational studies such as those in this dissertation, to establish that laboratory or captive findings translate to ecologically meaningful contexts.

Understanding the causes and consequences of interindividual behavioral variation is particularly important for the long-lived, highly mobile species that are among the taxa most threatened by global change (Runge et al., 2014). The Punta Tombo Magellanic penguin colony is experiencing documented population decline, and faces risks from environmental change as well as more direct anthropogenic impacts (García-Borboroglu et al., 2006; Holt and Boersma, 2022; Rebstock et al., 2016). Behavioral plasticity is known to be a critical mechanism promoting resilience in the face of environmental change (Beever et al., 2017). Magellanic penguins are already displaying long-term adjustments to their phenology (Cappello and Boersma 2021) and foraging areas (Boersma et al. 2009) in response to changing conditions. In Chapter 1, I showed that these animals also adjust their mate choice, reproductive timing, and foraging in response to environmental change. However, just because individuals are adjusting their behavior does not mean they are successfully coping with changing conditions; these adjustments may come with accompanying costs, such as shortened breeding seasons or more energetically costly foraging patterns, or may simply be insufficient to overcome the challenges presented by new environments. In the case of mate choice and reproductive phenology in the penguins at Punta Tombo, I showed in Chapter 2 that, despite individuals varying in their level of plasticity, all individuals had low reproductive success in poor environmental conditions. Magellenic penguins can live over 30 years in the wild, and the study of how they respond to

changes must also account for personal histories. In Chapter 3, I showed that foraging penguins are more likely to return to areas they have foraged at previously if they previously experienced high foraging success in those areas. This is a beneficial strategy if the prey landscape is relatively stable between the initial visit and the subsequent visit to the area. But changing environments and anthropogenic factors may interrupt this synchrony. For example, bycatch is a risk for foraging penguins, and returning to stable prey patches could increase overlap with fishing vessels. Behavioral variation is hypothesized to improve population persistence, but exploring the precise mechanisms and consequences of this variation will remain important for describing and predicting the persistence of this population of Magellenic penguins and populations of other long-lived species.

The work I've presented here contributes to a growing literature documenting patterns, causes, and consequences of behavioral variation among and within individuals (Dingemanse et al., 2004; Hertel et al., 2021; Sih et al., 2012; Wolf and Weissing, 2012). My research addressed some known gaps in this literature (Johansson et al. 2024), and also highlighted important areas of future work. In Chapter 1, I presented the first test of correlated plasticities in a wild population, and showed that these correlations can be positive or negative. Much more work could be done to see how common these patterns are in other behaviors and systems. It would be particularly interesting to explore this at broader and finer scales of behavior. In Chapter 2, I showed that low- and high-plasticity individuals have similar long-term reproductive success, despite varying in their annual reproductive success under normal and high-quality environmental conditions. An extension of this work could examine whether the long-term reproductive success of these groups would remain balanced under projected long-term changes in environmental conditions, or at what point they would become unbalanced. In Chapter 3, I explored state-behavior feedbacks as a mechanism of behavioral variation. These feedbacks can generate divergent or convergent behavior over time, depending on whether the feedback is positive or negative (Sih et al. 2015). With a longer-term longitudinal study, one could ask whether the feedbacks I described here are positive or negative, and as such whether they drive behavioral divergence or convergence as a function of foraging history. Fine-scale adjustments in effort are likely to be convergent; less effort should result in lower foraging success, resulting in higher effort. On the other hand, broad-scale adjustments in selection of foraging area may be divergent; successful trips to particular areas of the foraging region cause individuals to return to

these areas, and their familiarity with local features could increase their foraging success, potentially leading to spatial segregation in foraging grounds. This dissertation addressed open questions in our understanding of interindividual behavioral variation, but our understanding of the patterns, causes and consequences of this variation remains far from complete. Further advancing this understanding requires integrating existing conceptual frameworks across disciplines and pairing collection of long-term behavioral data in wild populations with rigorous statistical approaches.

Bibliography

Abrahms, B., Hazen, E.L., Bograd, S.J., Brashares, J.S., Robinson, P.W., Scales, K.L., Crocker, D.E., Costa, D.P., 2018. Climate mediates the success of migration strategies in a marine predator. Ecol Lett 21, 63–71. https://doi.org/10.1111/ele.12871

Ainley, D.G., Wilson, R.P., 2023. The Aquatic World of Penguins: Biology of Fish-Birds, Fascinating Life Sciences. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-031-33990-5

Araya-Ajoy, Y.G., Dingemanse, N.J., 2017. Repeatability, heritability, and age-dependence of seasonal plasticity in aggressiveness in a wild passerine bird. J Anim Ecol 86, 227–238. https://doi.org/10.1111/1365-2656.12621

Arthur, B., Hindell, M., Bester, M., Trathan, P., Jonsen, I., Staniland, I., Oosthuizen, W.C., Wege, M., Lea, M.-A., 2015. Return Customers: Foraging Site Fidelity and the Effect of Environmental Variability in Wide-Ranging Antarctic Fur Seals. PLoS ONE 10, e0120888. https://doi.org/10.1371/journal.pone.0120888

Avgar, T., Potts, J.R., Lewis, M.A., Boyce, M.S., 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods Ecol Evol 7, 619–630. https://doi.org/10.1111/2041-210X.12528

Barrionuevo, M., Ciancio, J., Marchisio, N., Frere, E., 2018. Parental body condition and high energy value of fish determine nestling success in Magellanic penguin (Spheniscus magellanicus). Mar Biol 165, 105. https://doi.org/10.1007/s00227-018-3358-3

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Soft. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Dunham, J.B., Gahl, M.K., Smith, F.A., Lawler, J.J., 2017. Behavioral flexibility as a mechanism for coping with climate change. Front Ecol Environ 15, 299–308. https://doi.org/10.1002/fee.1502

Bell, A.M., 2004. Behavioural differences between individuals and two populations of stickleback (Gasterosteus aculeatus): Behavioural syndromes. Journal of Evolutionary Biology 18, 464–473. https://doi.org/10.1111/j.1420-9101.2004.00817.x

Bell, A.M., Hankison, S.J., Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis. Animal Behaviour 77, 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Bell, A.M., Sih, A., 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). Ecology Letters 10, 828–834. https://doi.org/10.1111/j.1461-0248.2007.01081.x

Betini, G.S., Norris, D.R., 2012. The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. Animal Behaviour 83, 137–143. https://doi.org/10.1016/j.anbehav.2011.10.018

Biernacki, C., Celeux, G., Govaert, G., 2000. Assessing a mixture model for clustering with the integrated completed likelihood. IEEE Trans. Pattern Anal. Machine Intell. 22, 719–725. https://doi.org/10.1109/34.865189

Boersma, P., Rebstock, G., 2009. Foraging distance affects reproductive success in Magellanic penguins. Mar. Ecol. Prog. Ser. 375, 263–275. https://doi.org/10.3354/meps07753

Boersma, P., Rebstock, G.A., García-Borboroglu, P., 2015. Marine protection is needed for Magellanic penguins in Argentina based on long-term data. Biological Conservation 182, 197–204. https://doi.org/10.1016/j.biocon.2014.12.005

Boersma, P., Stokes, D.L., Yorio, P.M., Davis, L., Darby, J., 1990. Reproductive variability and historical change of Magellanic Penguins (Spheniscus magellanicus) at Punta Tombo, Argentina. Penguin biology 7, 15–44.

Boersma, P.D., Rebstock, G.A., 2014. Climate Change Increases Reproductive Failure in Magellanic Penguins. PLoS ONE 9, e85602. https://doi.org/10.1371/journal.pone.0085602

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26, 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., Forister, M.L., 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist 161, 1–28. https://doi.org/10.1086/343878

Brommer, J.E., Rattiste, K., Wilson, A.J., 2008. Exploring plasticity in the wild: laying date–temperature reaction norms in the common gull *Larus canus*. Proc. R. Soc. B. 275, 687–693. https://doi.org/10.1098/rspb.2007.0951

Brooks, M., E., Kristensen, K., Benthem, K., J. ,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., Bolker, B., M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9, 378. https://doi.org/10.32614/RJ-2017-066

Budaev, S., Jørgensen, C., Mangel, M., Eliassen, S., Giske, J., 2019. Decision-Making From the Animal Perspective: Bridging Ecology and Subjective Cognition. Front. Ecol. Evol. 7, 164. https://doi.org/10.3389/fevo.2019.00164

Byrne, P.G., Silla, A.J., 2023. Lifetime breeding-site and nest-site fidelity in a declining terrestrial toadlet: evidence for a win-stay/lose-shift strategy. Front. Conserv. Sci. 4, 1226658. https://doi.org/10.3389/fcosc.2023.1226658

Cappello, C.D., Boersma, P.D., 2021. Consequences of phenological shifts and a compressed breeding period in Magellanic penguins. Ecology 102. https://doi.org/10.1002/ecy.3443

Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., Riddell, A., 2017. Stan: A Probabilistic Programming Language. J. Stat. Soft. 76, 1–32. https://doi.org/10.18637/jss.v076.i01

Carroll, G., Harcourt, R., Pitcher, B.J., Slip, D., Jonsen, I., 2018. Recent prey capture experience and dynamic habitat quality mediate short-term foraging site fidelity in a seabird. Proc. R. Soc. B. 285, 20180788. https://doi.org/10.1098/rspb.2018.0788

Carter, A., Goldizen, A., Heinsohn, R., 2012. Personality and plasticity: temporal behavioural reaction norms in a lizard, the Namibian rock agama. Animal Behaviour 7.

Chalfoun, A.D., Martin, T.E., 2010. Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a "win-stay, lose-switch" strategy? Oecologia 163, 885–892. https://doi.org/10.1007/s00442-010-1679-0

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Chase, I.D., Bartolomeo, C., Dugatkin, L.A., 1994. Aggressive interactions and inter-contest interval: how long do winners keep winning?. Animal Behaviour 48, 393–400. https://doi.org/10.1006/anbe.1994.1253

Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I.M., Travis, J.M.J., Scott, B.E., 2016. The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. Ecology and Evolution 6, 727–741. https://doi.org/10.1002/ece3.1914

Clark-Wolf, T.J., Dee Boersma, P., Rebstock, G.A., Abrahms, B., 2023. Climate presses and pulses mediate the decline of a migratory predator. Proc. Natl. Acad. Sci. U.S.A. 120, e2209821120. https://doi.org/10.1073/pnas.2209821120

Cote, J., Clobert, J., Brodin, T., Fogarty, S., Sih, A., 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Phil. Trans. R. Soc. B 365, 4065–4076. https://doi.org/10.1098/rstb.2010.0176

Dall, S., Giraldeau, L., Olsson, O., Mcnamara, J., Stephens, D., 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology & Evolution 20, 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Dall, S.R.X., Bell, A.M., Bolnick, D.I., Ratnieks, F.L.W., 2012. An evolutionary ecology of individual differences. Ecol Lett 15, 1189–1198. https://doi.org/10.1111/j.1461-0248.2012.01846.x

Dall, S.R.X., Houston, A.I., McNamara, J.M., 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters 7, 734–739. https://doi.org/10.1111/j.1461-0248.2004.00618.x

Denryter, K., Cook, R.C., Cook, J.G., Parker, K.L., Gillingham, M.P., 2020. State-dependent foraging by caribou with different nutritional requirements. Journal of Mammalogy 101, 544–557. https://doi.org/10.1093/jmammal/gyaa003

DeRuiter, S., Johnson, M., Sweeney, D., McNamara-Oh, Y.J., Fynewever, S., Tejevbo, R., Marques, T., Wang, Y., Ogedegbe, S., 2025. tagtools: Work with Data from High-Resolution Biologging Tags.

Dingemanse, N., Réale, D., 2005. Natural selection and animal personality. Behaviour 142. https://doi.org/10.1163/156853905774539445

Dingemanse, N.J., Both, C., Drent, P.J., Tinbergen, J.M., 2004. Fitness consequences of avian personalities in a fluctuating environment. Proc. R. Soc. Lond. B 271, 847–852. https://doi.org/10.1098/rspb.2004.2680

Dingemanse, N.J., Dochtermann, N.A., 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. J Anim Ecol 82, 39–54. https://doi.org/10.1111/1365-2656.12013

Dingemanse, N.J., Kazem, A.J.N., Réale, D., Wright, J., 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology & Evolution 25, 81–89. https://doi.org/10.1016/j.tree.2009.07.013

Dingemanse, N.J., Wolf, M., 2013. Between-individual differences in behavioural plasticity within populations: causes and consequences. Animal Behaviour 85, 1031–1039. https://doi.org/10.1016/j.anbehav.2012.12.032

Duckworth, R.A., Badyaev, A.V., 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proc. Natl. Acad. Sci. U.S.A. 104, 15017–15022. https://doi.org/10.1073/pnas.0706174104

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W., Papastamatiou, Y.P., Forester, J., Mueller, T., 2013. Spatial memory and animal movement. Ecol Lett 16, 1316–1329. https://doi.org/10.1111/ele.12165

García-Borboroglu, P., Boersma, P.D., Ruoppolo, V., Reyes, L., Rebstock, G.A., Griot, K., Heredia, S.R., Adornes, A.C., Da Silva, R.P., 2006. Chronic oil pollution harms Magellanic penguins in the Southwest Atlantic. Marine Pollution Bulletin 52, 193–198. https://doi.org/10.1016/j.marpolbul.2005.11.004

Gross, K., Pasinelli, G., Kunc, H.P., 2010. Behavioral Plasticity Allows Short‐Term Adjustment to a Novel Environment. The American Naturalist 176, 456–464. https://doi.org/10.1086/655428

Gurarie, E., Bracis, C., Brilliantova, A., Kojola, I., Suutarinen, J., Ovaskainen, O., Potluri, S., Fagan, W.F., 2022. Spatial Memory Drives Foraging Strategies of Wolves, but in Highly Individual Ways. Front. Ecol. Evol. 10, 768478. https://doi.org/10.3389/fevo.2022.768478

Hertel, A.G., Niemelä, P.T., Dingemanse, N.J., Mueller, T., 2020. A guide for studying among-individual behavioral variation from movement data in the wild. Mov Ecol 8, 30. https://doi.org/10.1186/s40462-020-00216-8

Hertel, A.G., Royauté, R., Zedrosser, A., Mueller, T., 2021. Biologging reveals individual variation in behavioural predictability in the wild. J Anim Ecol 90, 723–737. https://doi.org/10.1111/1365-2656.13406

Hindell, M.A., Bradshaw, C.J.A., Brook, B.W., Fordham, D.A., Kerry, K., Hull, C., McMahon, C.R., 2012. Long‐term breeding phenology shift in royal penguins. Ecology and Evolution 2, 1563–1571. https://doi.org/10.1002/ece3.281

Holt, K.A., Boersma, P.D., 2022. Unprecedented heat mortality of Magellanic Penguins. Ornithological Applications 124, duab052. https://doi.org/10.1093/ornithapp/duab052

Hossie, T., Landolt, K., Murray, D.L., 2017. Determinants and co‐expression of anti‐predator responses in amphibian tadpoles: a meta‐analysis. Oikos 126, oik.03305. https://doi.org/10.1111/oik.03305

Houslay, T.M., Wilson, A.J., 2017. Avoiding the misuse of BLUP in behavioural ecology. Behavioral Ecology 28, 948–952. https://doi.org/10.1093/beheco/arx023

Houston, A.I., Fayet, A., McNamara, J.M., 2025. Optimal diving: patch quality, depth, and marginal value. Behavioral Ecology 37, araf141. https://doi.org/10.1093/beheco/araf141

Johansson, E., Boersma, P.D., Jones, T., Abrahms, B., 2024. Plasticity syndromes in wild vertebrates: Patterns and consequences of individual variation in plasticity across multiple behaviours. Ecology Letters 27, e14473. https://doi.org/10.1111/ele.14473

Johnson, D.S., London, J.M., Lea, M.-A., Durban, J.W., 2008. CONTINUOUS-TIME CORRELATED RANDOM WALK MODEL FOR ANIMAL TELEMETRY DATA. Ecology 89, 1208–1215. https://doi.org/10.1890/07-1032.1

Kokubun, N., Lee, W.Y., Kim, J.-H., Takahashi, A., 2015. Chinstrap penguin foraging area associated with a seamount in Bransfield Strait, Antarctica. Polar Science 9, 393–400. https://doi.org/10.1016/j.polar.2015.10.001

Kruschke, J., 2014. Doing Bayesian Data Analysis: A Tutorial with R, JAGS, and Stan. Academic Press.

Laforge, M.P., Webber, Q.M.R., Vander Wal, E., 2023. Plasticity and repeatability in spring migration and parturition dates with implications for annual reproductive success. Journal of Animal Ecology 92, 1042–1054. https://doi.org/10.1111/1365-2656.13911

Lambert, P.C., Sutton, A.J., Burton, P.R., Abrams, K.R., Jones, D.R., 2005. How vague is vague? A simulation study of the impact of the use of vague prior distributions in MCMC using WinBUGS. Statist. Med. 24, 2401–2428. https://doi.org/10.1002/sim.2112

Lee, D.Y., Petersen, M.R., Lin, W., 2019. The Southern Annular Mode and Southern Ocean Surface Westerly Winds in E3SM. Earth and Space Science 6, 2624–2643. https://doi.org/10.1029/2019EA000663

Levin, S.A., 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology 73, 1943–1967. https://doi.org/10.2307/1941447

Lovenduski, N.S., Gruber, N., 2005. Impact of the Southern Annular Mode on Southern Ocean circulation and biology. Geophysical Research Letters 32, 2005GL022727. https://doi.org/10.1029/2005GL022727

Luttbeg, B., Sih, A., 2010. Risk, resources and state-dependent adaptive behavioural syndromes. Phil. Trans. R. Soc. B 365, 3977–3990. https://doi.org/10.1098/rstb.2010.0207

Makowski, D., Ben-Shachar, M.S., Lüdecke, D., 2019. bayestestR: Describing Effects and their Uncertainty, Existence and Significance within the Bayesian Framework. Journal of Open Source Software 4, 1541. https://doi.org/10.21105/joss.01541

McElreath, R., 2016. Statistical Rethinking: A Bayesian Course with Examples in R and Stan. CRC Press/Taylor & Francis Group.

McNamara, J.M., Houston, A.I., 1986. The Common Currency for Behavioral Decisions. The American Naturalist 127, 358–378. https://doi.org/10.1086/284489

Mendelssohn, R., 2023. rerddapXtracto: Extracts Environmental Data from “ERDDAP” Web Services.

Merkle, J.A., Fortin, D., Morales, J.M., 2014. A memory‐based foraging tactic reveals an adaptive mechanism for restricted space use. Ecology Letters 17, 924–931. https://doi.org/10.1111/ele.12294

Merkle, J.A., Sawyer, H., Monteith, K.L., Dwinnell, S.P.H., Fralick, G.L., Kauffman, M.J., 2019. Spatial memory shapes migration and its benefits: evidence from a large herbivore. Ecology Letters 22, 1797–1805. https://doi.org/10.1111/ele.13362

Morrison, T.A., Merkle, J.A., Hopcraft, J.G.C., Aikens, E.O., Beck, J.L., Boone, R.B., Courtemanch, A.B., Dwinnell, S.P., Fairbanks, W.S., Griffith, B., Middleton, A.D., Monteith, K.L., Oates, B., Riotte‐Lambert, L., Sawyer, H., Smith, K.T., Stabach, J.A.,

Taylor, K.L., Kauffman, M.J., 2021. Drivers of site fidelity in ungulates. Journal of Animal Ecology 90, 955–966. https://doi.org/10.1111/1365-2656.13425

Murphy, C.M., Weller, D.L., Ovissipour, R., Boyer, R., Strawn, L.K., 2023. Spatial Versus Nonspatial Variance in Fecal Indicator Bacteria Differs Within and Between Ponds. Journal of Food Protection 86, 100045. https://doi.org/10.1016/j.jfp.2023.100045

Nakayama, S., Laskowski, K.L., Klefoth, T., Arlinghaus, R., 2016. Between- and within-individual variation in activity increases with water temperature in wild perch. BEHECO arw090. https://doi.org/10.1093/beheco/arw090

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. U.S.A. 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Nussey, D.H., Wilson, A.J., Brommer, J.E., 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. J Evolution Biol 20, 831–844. https://doi.org/10.1111/j.1420-9101.2007.01300.x

O'Dea, R.E., Noble, D.W.A., Nakagawa, S., 2022. Unifying individual differences in personality, predictability and plasticity: A practical guide. Methods Ecol Evol 13, 278–293. https://doi.org/10.1111/2041-210X.13755

Pardo, D., Jenouvrier, S., Weimerskirch, H., Barbraud, C., 2017. Effect of extreme sea surface temperature events on the demography of an age-structured albatross population. Phil. Trans. R. Soc. B 372, 20160143. https://doi.org/10.1098/rstb.2016.0143

Pigliucci, M., Murren, C.J., Schlichting, C.D., 2006. Phenotypic plasticity and evolution by genetic assimilation. Journal of Experimental Biology 209, 2362–2367. https://doi.org/10.1242/jeb.02070

Piper, W.H., 2011. Making habitat selection more "familiar": a review. Behav Ecol Sociobiol 65, 1329–1351. https://doi.org/10.1007/s00265-011-1195-1

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ranc, N., Moorcroft, P.R., Ossi, F., Cagnacci, F., 2021. Experimental evidence of memory-based foraging decisions in a large wild mammal. Proc. Natl. Acad. Sci. U.S.A. 118, e2014856118. https://doi.org/10.1073/pnas.2014856118

Rands, S.A., Cowlishaw, G., Pettifor, R.A., Rowcliffe, J.M., Johnstone, R.A., 2003. Spontaneous emergence of leaders and followers in foraging pairs. Nature 423, 432–434. https://doi.org/10.1038/nature01630

Réale, D., Dingemanse, N.J., Kazem, A.J.N., Wright, J., 2010. Evolutionary and ecological approaches to the study of personality. Phil. Trans. R. Soc. B 365, 3937–3946. https://doi.org/10.1098/rstb.2010.0222

Rebstock, G., Boersma, P., 2018. Oceanographic conditions in wintering grounds affect arrival date and body condition in breeding female Magellanic penguins. Mar. Ecol. Prog. Ser. 601, 253–267. https://doi.org/10.3354/meps12668

Rebstock, G.A., Abrahms, B., Boersma, P.D., 2022. Site fidelity increases reproductive success by increasing foraging efficiency in a marine predator. Behavioral Ecology 33, 868–875. https://doi.org/10.1093/beheco/arac052

Rebstock, G.A., Boersma, P.D., García-Borboroglu, P., 2016. Changes in habitat use and nesting density in a declining seabird colony. Popul Ecol 58, 105–119. https://doi.org/10.1007/s10144-015-0523-0

Regan, C.E., Bogdanova, M.I., Newell, M., Gunn, C., Wanless, S., Harris, M.P., Lopez, S.L., Benninghaus, E., Bolton, M., Daunt, F., Searle, K.R., 2024. Seabirds show foraging site and route fidelity but demonstrate flexibility in response to local information. Mov Ecol 12, 46. https://doi.org/10.1186/s40462-024-00467-9

Rubin, D.B., 1987. Multiple Imputation for Nonresponse in Surveys, 1st ed, Wiley Series in Probability and Statistics. Wiley. https://doi.org/10.1002/9780470316696

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G., Fuller, R.A., 2014. Conserving mobile species. Frontiers in Ecol & Environ 12, 395–402. https://doi.org/10.1890/130237

Schafer, J.L., 1999. Multiple imputation: a primer. Stat Methods Med Res 8, 3–15. https://doi.org/10.1177/096228029900800102

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. Nature 465, 609–612. https://doi.org/10.1038/nature09060

Schuett, W., Dall, S.R.X., Baeumer, J., Kloesener, M.H., Nakagawa, S., Beinlich, F., Eggers, T., 2011. Personality variation in a clonal insect: The pea aphid, Acyrthosiphon pisum. Developmental Psychobiology 53, 631–640. https://doi.org/10.1002/dev.20538

Scolaro, J.A., Wilson, R.P., Laurenti, S., Kierspel, M., Gallelli, H., Upton, J.A., 1999. Feeding Preferences of the Magellanic Penguin over Its Breeding Range in Argentina. Waterbirds: The International Journal of Waterbird Biology 22, 104. https://doi.org/10.2307/1521999

Scrucca, L., Fop, M., Murphy, T., Brendan, Raftery, A., E., 2016. mclust 5: Clustering, Classification and Density Estimation Using Gaussian Finite Mixture Models. The R Journal 8, 289. https://doi.org/10.32614/RJ-2016-021

Sheehy, K.A., Laskowski, K.L., 2023. Correlated behavioural plasticities: insights from plasticity evolution, the integrated phenotype and behavioural syndromes. Animal Behaviour 200, 263–271. https://doi.org/10.1016/j.anbehav.2023.04.007

Sih, A., Bell, A., Johnson, J.C., 2004a. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution 19, 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., Bell, A.M., Johnson, J.C., Ziemba, R.E., 2004b. Behavioral Syndromes: An Integrative Overview. The Quarterly Review of Biology 79, 241–277. https://doi.org/10.1086/422893

Sih, A., Cote, J., Evans, M., Fogarty, S., Pruitt, J., 2012. Ecological implications of behavioural syndromes. Ecology Letters 15, 278–289. https://doi.org/10.1111/j.1461-0248.2011.01731.x

Sih, A., Mathot, K.J., Moirón, M., Montiglio, P.-O., Wolf, M., Dingemanse, N.J., 2015. Animal personality and state–behaviour feedbacks: a review and guide for empiricists. Trends in Ecology & Evolution 30, 50–60. https://doi.org/10.1016/j.tree.2014.11.004

Silva, C., Andrade, I., Yáñez, E., Hormazabal, S., Barbieri, M.Á., Aranis, A., Böhm, G., 2016. Predicting habitat suitability and geographic distribution of anchovy (Engraulis ringens) due to climate change in the coastal areas off Chile. Progress in Oceanography 146, 159–174. https://doi.org/10.1016/j.pocean.2016.06.006

Simeone, A., Wilson, R.P., 2003. In-depth studies of Magellanic penguin (Spheniscus magellanicus) foraging: can we estimate prey consumption by perturbations in the dive profile? Marine Biology 143, 825–831. https://doi.org/10.1007/s00227-003-1114-8

Smith, B.R., Blumstein, D.T., 2008. Fitness consequences of personality: a meta-analysis. Behavioral Ecology 19, 448–455. https://doi.org/10.1093/beheco/arm144

Snell-Rood, E.C., 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. Animal Behaviour 85, 1004–1011. https://doi.org/10.1016/j.anbehav.2012.12.031

Stamps, J.A., 2016. Individual differences in behavioural plasticities: Behavioural plasticities. Biol Rev 91, 534–567. https://doi.org/10.1111/brv.12186

Stamps, J.A., Biro, P.A., 2016. Personality and individual differences in plasticity. Current Opinion in Behavioral Sciences 12, 18–23. https://doi.org/10.1016/j.cobeha.2016.08.008

Stan Development Team, 2023. RStan: the R interface to Stan.

Switzer, P.V., 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7, 533–555. https://doi.org/10.1007/BF01237820

Takahashi, A., Dunn, M., Trathan, P., Sato, K., Naito, Y., Croxall, J., 2003. Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. Mar. Ecol. Prog. Ser. 250, 279–289. https://doi.org/10.3354/meps250279

Therneau, T., 2026. A Package for Survival Analysis in R.

Thurfjell, H., Ciuti, S., Boyce, M.S., 2014. Applications of step-selection functions in ecology and conservation. Mov Ecol 2, 4. https://doi.org/10.1186/2051-3933-2-4

Valone, T.J., 2024. Probabilistic inference and Bayesian‐like estimation in animals: Empirical evidence. Ecology and Evolution 14, e11495. https://doi.org/10.1002/ece3.11495

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S., Gaillard, J., 2009. Memory keeps you at home: a mechanistic model for home range emergence. Oikos 118, 641–652. https://doi.org/10.1111/j.1600-0706.2008.17003.x

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., Bürkner, P.-C., 2021. Rank-Normalization, Folding, and Localization: An Improved Rˆ for Assessing Convergence of MCMC (with Discussion). Bayesian Anal. 16. https://doi.org/10.1214/20-BA1221

Ventura, F., Lukacs, P., Granadeiro, J., Matano, R., Catry, P., 2021. Demographic responses to environmental change of the black-browed albatross, sentinel of the Patagonian Shelf Large Marine Ecosystem. Mar. Ecol. Prog. Ser. 668, 107–120. https://doi.org/10.3354/meps13743

Wagner, E.L., Cappello, C.D., Boersma, P.D., 2022. Should I stay or should I go: factors influencing mate retention and divorce in a colonial seabird. Animal Behaviour 192, 133–144. https://doi.org/10.1016/j.anbehav.2022.08.002

Wakefield, E.D., Cleasby, I.R., Bearhop, S., Bodey, T.W., Davies, R.D., Miller, P.I., Newton, J., Votier, S.C., Hamer, K.C., 2015. Long-term individual foraging site fidelity—why some gannets don't change their spots. Ecology 96, 3058–3074. https://doi.org/10.1890/14-1300.1

Watanabe, Y.Y., Ito, M., Takahashi, A., 2014. Testing optimal foraging theory in a penguin–krill system. Proc. R. Soc. B. 281, 20132376. https://doi.org/10.1098/rspb.2013.2376

Webb, J., Steffan, P., Hayden, B.Y., Lee, D., Kemere, C., McGinley, M., 2024. Foraging Under Uncertainty Follows the Marginal Value Theorem with Bayesian Updating of Environment Representations. https://doi.org/10.1101/2024.03.30.587253

Weller, D.L., Murphy, C.M., Johnson, S., Green, H., Michalenko, E.M., Love, T.M.T., Strawn, L.K., 2022. Land Use, Weather, and Water Quality Factors Associated With Fecal Contamination of Northeastern Streams That Span an Urban-Rural Gradient. Front. Water 3, 741676. https://doi.org/10.3389/frwa.2021.741676

West-Eberhard, M.J., 2003. Developmental Plasticity and Evolution. Oxford University Press. https://doi.org/10.1093/oso/9780195122343.001.0001

Westneat, David.F., Potts, L.J., Sasser, K.L., Shaffer, J.D., 2019. Causes and Consequences of Phenotypic Plasticity in Complex Environments. Trends in Ecology & Evolution 34, 555–568. https://doi.org/10.1016/j.tree.2019.02.010

Wilson, R., 2003. Penguins predict their performance. Mar. Ecol. Prog. Ser. 249, 305–310. https://doi.org/10.3354/meps249305

Wilson, R., Shepard, E., Gómez Laich, A., Frere, E., Quintana, F., 2010. Pedalling downhill and freewheeling up; a penguin perspective on foraging. Aquat. Biol. 8, 193–202. https://doi.org/10.3354/ab00230

Wilson, R.P., Scolaro, J.A., Grémillet, D., Kierspel, M.A.M., Laurenti, S., Upton, J., Gallelli, H., Quintana, F., Frere, E., Müller, G., Straten, M.T., Zimmer, I., 2005. How do Magellanic Penguins Cope with Variability in Their Access to Prey? Ecological Monographs 75, 379–401. https://doi.org/10.1890/04-1238

Wolf, M., 2009. Adaptive individual differences: The evolution of animal personalities. [s.n.], Groningen.

Wolf, M., Frair, J., Merrill, E., Turchin, P., 2009. The Attraction of the Known: The Importance of Spatial Familiarity in Habitat Selection in Wapiti Cervus elaphus. Ecography 32, 401–410.

Wolf, M., Van Doorn, G.S., Weissing, F.J., 2011. On the coevolution of social responsiveness and behavioural consistency. Proc. R. Soc. B. 278, 440–448. https://doi.org/10.1098/rspb.2010.1051

Wolf, M., Van Doorn, G.S., Weissing, F.J., 2008. Evolutionary emergence of responsive and unresponsive personalities. Proc. Natl. Acad. Sci. U.S.A. 105, 15825–15830. https://doi.org/10.1073/pnas.0805473105

Wolf, M., Weissing, F.J., 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology & Evolution 27, 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Ydesen, K.S., Wisniewska, D.M., Hansen, J.D., Beedholm, K., Johnson, M., Madsen, P.T., 2014. What a jerk: prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). Journal of Experimental Biology jeb.100016. https://doi.org/10.1242/jeb.100016

Yorio, P., González-Zevallos, D., Gatto, A., Biagioni, O., Castillo, J., 2017. Relevance of forage fish in the diet of Magellanic penguins breeding in northern Patagonia, Argentina. Marine Biology Research 13, 603–617. https://doi.org/10.1080/17451000.2016.1273529

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R, Statistics for Biology and Health. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387-87458-6