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Variabilité interindividuelle des réponses à l'environnement et conséquences sur la fitness individuelle chez le manchot pygmée.

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Wintz J, **Joly NB**, Jenouvrier S, Chiaradia A, Georges JY, Saraux C. Early growth trajectories affect fitness-related life history traits in little penguins (*in prep.*)

Lemonnier C, Bost CA, Bize P, **Joly NB**, Stier A, Robin JP, Handrich Y, Cillard A, Montblanc M, Viblanc VA. Short-term foraging plasticity of a deep diver, the king penguin (Aptenodytes patagonicus) in response to constraints at-sea: an experimental study. (*in prep.*)

Guillet L, Dupuis B, **Joly NB**, Chimienti M, Kato A, Ropert-Coudert Y, Hentati Sundberg J, Chiaradia A, Saraux C. (2023) Chasing the fish with little penguins: spatial and temporal variability in relation to environmental conditions. (*in prep.*)

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Joly NB, Chiaradia A, Georges JY, Saraux C (2022). The efficient breeder's guide to posterity: Main drivers of individual differences in fitness of little penguins. Poster presentation. *Ecology & Behavior Conference, Strasbourg, France*

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Other achievements:

Fieldwork

During 3 months in 2022, Participation to the data collection for the on-going long-term monitoring, including animal handling and weighing, microchipping and logger implantation/retrieval. This fieldwork was also the opportunity for me to closely collaborate with the research team in Australia.

Conference & seminar organization

Secretary of the organizing committee: Ecology & Behavior Conference, Strasbourg (2022): *Organization of an international conference dedicated to students with free accommodation, lunch and coffee break for 150 attendees during 3 days, participation in the scientific committee in charge of the abstract selection, conference program, welcoming of attendees and management of talk and poster sessions*.

DEPE Scientific Meetings (2021-2023): *Member of the organizing committee. Organization of a weekly lab seminar, including management of presentation program and invitation of external researchers.*

Teaching and supervising experience

Teaching at University of Strasbourg (2022): *64h of teaching to two different groups (~30 students each) of undergraduate students. Practical courses of animal phylogeny, evolution and diversity, including class preparation (visual support, biological samples, suitable resources) in interaction with other presenters as well as post-class feedback.*

Master 2 Student Supervision: Effect of early-growth conditions on adult vital rates (2023): *Co-supervision of a Master student, Justine Wintz, during 6 months including the creation of a master project, regular advancement meetings and supervision of conducted analysis and thesis redaction.*

Collaboration at Woods Hole Oceanographic Institution

Five-week trip in the WHOI laboratory (U.S.A) to exchange with Stéphanie Jenouvrier (Assistant Scientist with tenure at WHOI) in order to learn population matrix modelling and develop future projects.

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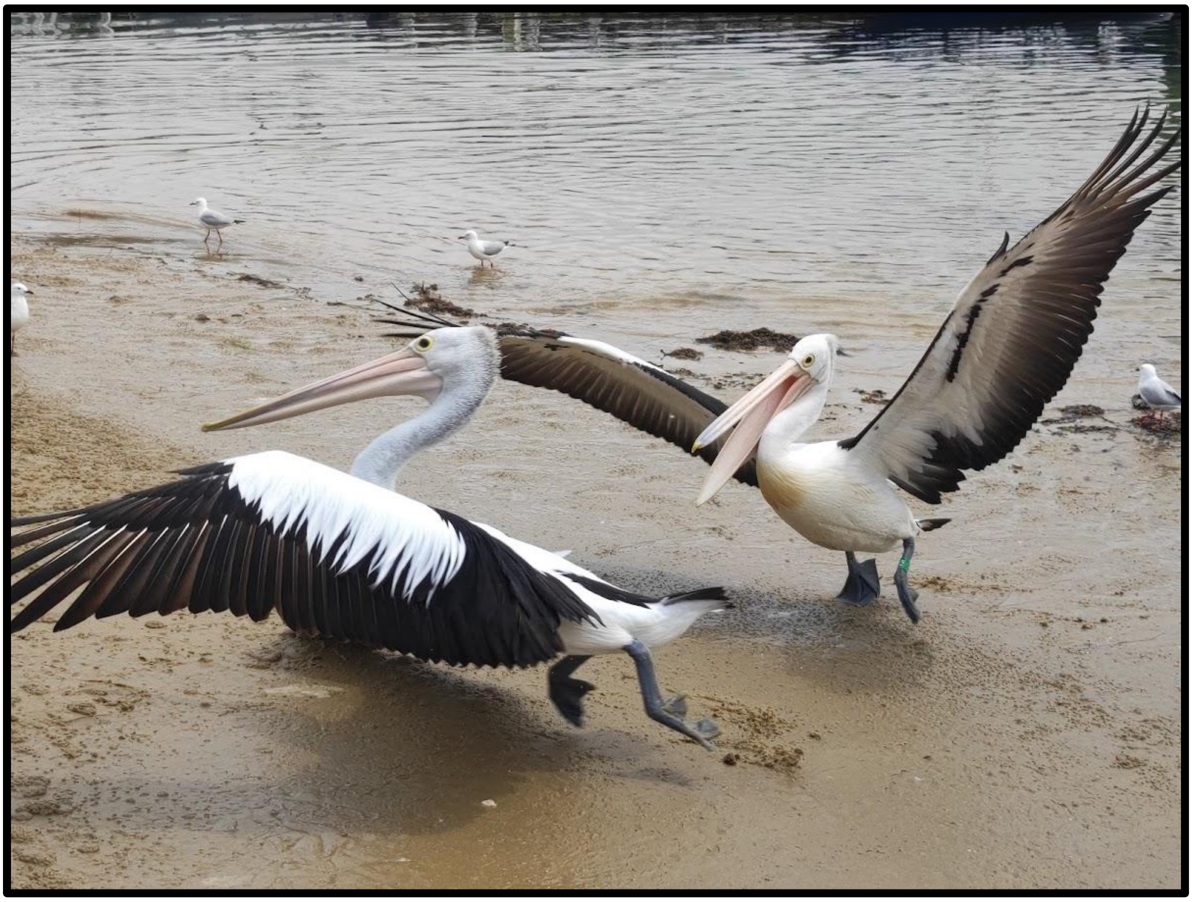
Chapter I: Introduction

On the importance of variability among individuals



1. A short history of evolutionary concepts

a) The widely debated definition of “species”

Living species evolve in interaction with other species (*i.e.* communities, McIntosh 1995) in given yet changing ecosystems (*i.e.* the physico-chemical and ecological conditions they live in, Tansley 1935). While the description of the interactions of a species with its environment can be summed-up by the last sentence, the philosophical definition of a species in itself is and has always been very complex (Hull 1965) and somewhat arbitrary (Mayr 1957). It is however referring to concrete evolutionary phenomenon, and biological species concept has been extensively defined by the work of people such as Ernst Mayr through the entire 20th century (1942, 1957, 1963, 1968, and 1996). Species can be defined as the main unit of evolution and summed up, in its largest although incomplete definition, as a group of organisms presenting geographic contiguity, morphological similarities and interbreeding capacities (Mayr 1996, Wheeler and Meier 2000, *Figure 1*).

While species concept is a very powerful tool to study evolutionary processes, it is largely insufficient to encompass the complexity of life and its evolution. Indeed, all so-called species present more or less patchy distribution with different levels of geographical insulation and individual flux across the patches (Dempster 2012). Thus, biological species concept has been largely criticized through time for being too restrictive and impractical, excluding speciation in non-breeding or morphologically similar organisms, but also defining speciation in organisms with recent or incomplete insulation (Sokal and Crovello 1970, Wiley 1978).

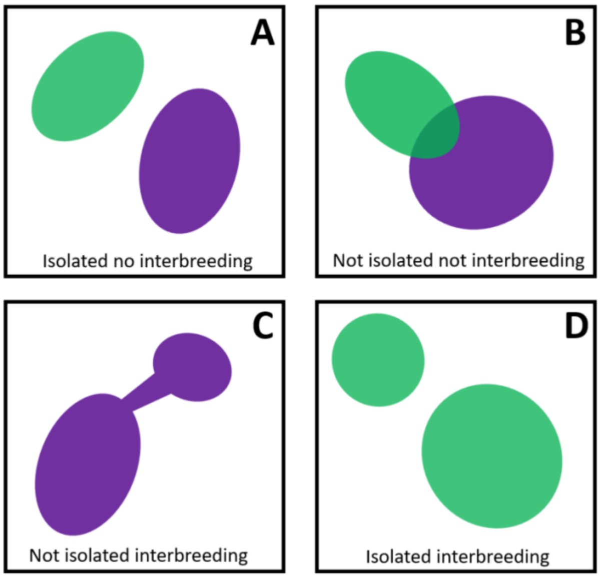


Figure 1: different cases of potential speciation

To deal with these inconsistencies, novel concepts of species have been described in the literature from the middle of the 20th century. For example, Simpson (1961) defined the evolutionary species as “a lineage (an ancestral-descendant sequence of population) evolving separately from others and with its own unitary evolutionary role and tendencies”. Rosen (1979) also proposed the phylogenetic species to be “a population or group of populations defined by one or more apomorphous (*i.e.* new character) features”. While these species concepts all possess some flaws and weaknesses that make them somewhat arbitrary and/or incomplete (thus unsatisfying, yet that will not be debated here; see Wheeler and Meier 2000), they have in common to rely on the population concept to try and define what a species is.

b) The population as the main unit to study the living

While the definition of a species is and has always been a debate in the biologist community, the definition of a population might prove as a useful tool to work on evolution concepts. Although it presents some subtleties (Clark et al. 1967), a population is most of the time defined as a group of organisms of the same species sharing a common space and temporality with the capacity to interact and breed with each other (Williams et al. 2002, Dempster 2012). While this definition itself relies on the species concept for convenience, it could easily be removed from the equation without lacking clarity, as the notion of inter-breeding itself is necessary to both the definition of a species and a population. Of course, this concept is also somewhat limited as populations are rarely isolated entities with equally patched interactions. Rather, fluxes of individuals exist among them, giving birth to concepts such as metapopulation (Hanski 1999). However, the

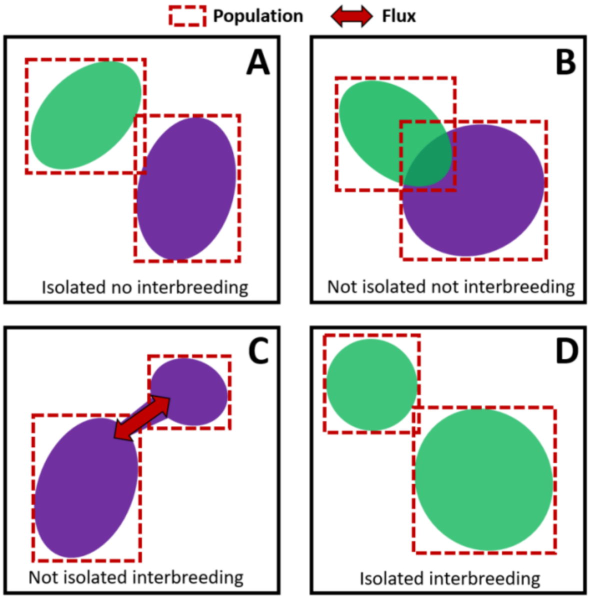


Figure 2: Defining populations in species

amount of variability among these patches is usually small and measurable, which makes it easy to treat as a unit sharing common eco-evolutionary characteristics (Dempster 2012, *Figure 2)*. As such, population rather than species is often used to study eco-evolutionary processes.

c) Assessing population changes through time

One of the main interests of population as a tool to study evolution, apart from its clear definition, is the ability to easily study its variation in time. Population dynamics in space and time is one of the oldest subject of biology, formally studied since the 17th century (see Egerton 1968). Studies of population were first developed for very practical reasons, such as monitoring of harmful (Juliano 2007) and hunted species (Caro 1999) or more recently management of endangered and invasive species (Thomson 2005). During the early 20th century, population changes through time, now called demography, started to be studied from an evolutionary perspective while people such as Fisher (1930) established links between population growth and natural selection. But the field of demography really took importance in the second half of the twentieth century after the popularization of the use of more complex mathematic models and especially matrices to assess the growth of populations in time (Hansen 1989), as theorized by Leslie in the 40s' (Leslie 1945, 1948). In such models, populations are described as structured (*e.g.* by age or body size) groups of individuals with different fertility and survival. Since then, the use of population dynamics (*i.e.* population changes in size through time) has become an increasingly important part of evolutionary theory (Charlesworth 1994).

While the population concept describes the space framework in which a group of individuals interacts, demography gives an insight of the temporal variations inside this framework (*Figure 3*). As such, population dynamics can be described as the manifestation at the population scale of the combined effect of environment and evolution processes on individuals. Thus, while population can be seen as a powerful tool to study the evolution of the living, individual is the key factor of its dynamics. Yet, traditional population modelling tends to consider a population as a whole, in which age is the only factor of variability in individual fertility and survival, in such a way that every individual of a population is considered as having the exact same vital rates as any other individual of its age class (Leslie 1945, 1948).

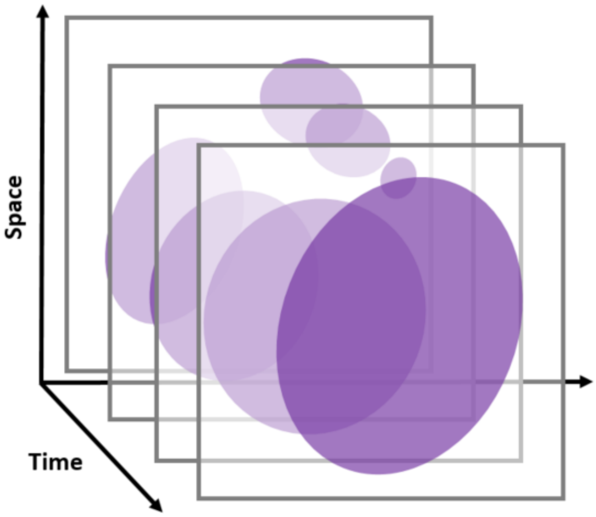


Figure 3: Concept of population dynamics

2. From population to individuals

a) More recent concept of population centered around individuals

All individuals are unique, whether it is in their morphology, physiology or behavior (*i.e.* phenotypes). As such, considering populations or species as an aggregate of individuals with their own specificities is not that much of a novelty in biology, as it is at the core of evolutionary theory since Darwin. In 1949, Mayr (*see citation below*) even conceptualized a single species world, described as a reproductive community of individuals, each being different and breeding with others depending on their similarities.

> *"It is quite possible to think of a world in which species do not exist but are replaced by a single reproductive community of individuals, each one different from every other one, and each one capable of reproducing with those other individuals that are most similar to it. Each individual would then be the center of a concentric series of circles of genetically more and more unlike individuals."* (Mayr 1949)

Yet, this concept of population being an aggregate of more or less similar individuals is hardly translated in the assessment of population dynamics and evolutionary processes and has been relatively neglected by ecologists for a long time (Wellington 1957). Even if these inter-individual differences are somewhat acknowledged in population modelling through the age-dependent population projection (*i.e.* individuals are different in fertility and survival probability depending on their age, Leslie 1945, 1948), it is largely insufficient to encompass the complexity of the differences that can exist among individuals of a same population.

More recently, ecologists started to focus more on the effects of inter-individual variability on population dynamics. In 1988 already, Lomnicki dedicated an entire book on the different ways population dynamics modelling could be affected by the individual differences that can exist within a population (Lomnicki 1988). A few years later, the first theoretical population dynamics models formally including differences among individuals were established, showing the substantial effect it could have on population growth and how system dependent it is (Bjørnstad and Hansen 1994, Doebeli and de Jong 1999). These studies mainly emphasized on the stabilizing effect of inter-individual differences on population in inherently unstable conditions. In practice, a few high quality individuals is potentially sufficient to limit population crashes in the case of unfavorable environmental conditions given that they can gather the limited amount of resources available (*see example B on Figure 4*). On the contrary, in a stable environment driven by short-term fluctuations (which is the most common cases a population may face), environment fluctuations should allow the coexistence of more diverse phenotypes across the population through processes such as cohort effect (Lindstrom and Kokko 2002), inducing more fluctuations in population demography (*see example A on Figure 4*).

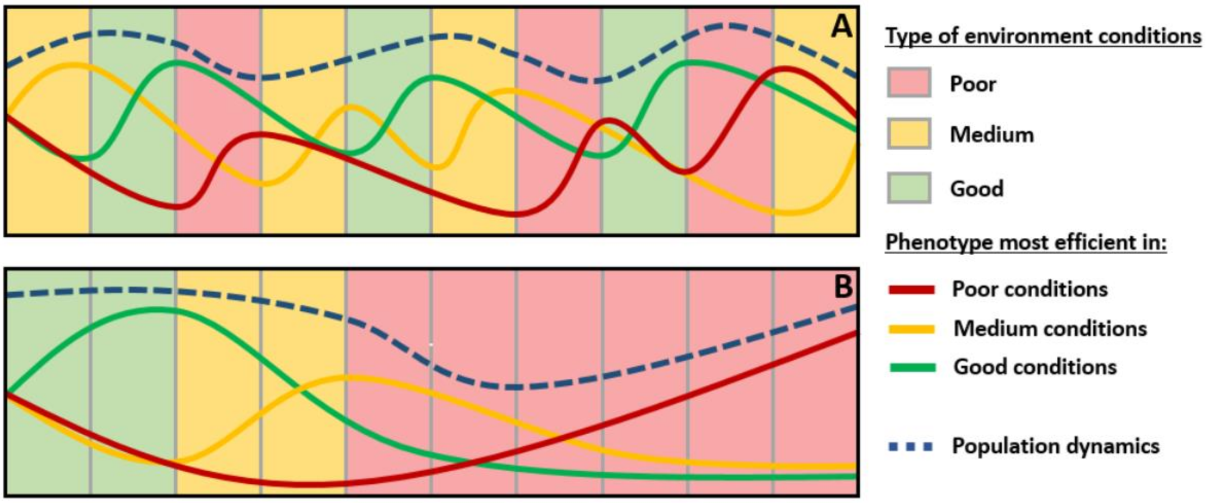


Figure 4: Individual variability and population dynamics in fluctuating (A) and more constant (B) environments

In any case, whether it is a factor of stabilization or destabilization of population dynamics, variability among individuals can have substantial effects on population growth and stability. Thus, inter-individual variability has to be taken into account, and even properly modelled, while making deterministic population projections and assessing evo-demographic questions. Easily written, but the task of modelling a population as an aggregate of unique individuals is properly gigantic and overwhelming, as the sources of variability are multiple, and each of them is at the base of many individual specificities.

b) Different individuals experience different lives

Assuming every individual is unique, one must acknowledge that every individual life is different. Life history is an old evolutionary concept (*See citation below*) that defines the way an individual produces offspring during its lifetime according to the environmental constraints it faces (Cole 1954, Williams 1966). In other words, life-history theory describes the way the limited energy available for an individual is allocated across its different life-history traits, that is to say any trait that is likely to somehow affect its contribution to the population (*i.e.* the amount of offspring it produces during its life).

> *"It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction." (Fisher 1930)*

The concept of life history is of great help in evolutionary and demographic contexts as the traits become the main unit of selection, and the individual reaction norm becomes the main tool of its measurement, including fixed characteristics but also plasticity. In other words, individual's current state is affected by its previous actions, and the current environmental conditions. Therefore, an optimal life history can be described as the optimal trajectory taken by an individual given the current conditions it faces (Brommer 2000). The power of the concept of life history resides in its capacity to encapsulate all the sources of variability that will drive an individual's performances across its life.

3. Sources of variability among individuals

a) Individual quality as a driver of inter-individual variability

When thinking about differences in individuals' lifetime performances, the first thing that comes in mind (especially when referring to evolutionary concepts) is inheritance. Indeed, evolution implies that individuals are all intrinsically different because the genes they were given by their parents as well as the way these genes combined are unique to every individual. This genetic inheritance becomes even more unique in the light of environment, under which genes will express differently, giving birth to as many unique phenotypes as there are of both genotypes and environmental conditions (Wright 1930, Fisher 1930). The number of combinations is therefore literally infinite, making each individual unique in its purest mathematical definition. Darwin himself noticed how inheritance combined with environmental conditions was at the core of variability in the living, especially at the individual level (*See citation below*).

> *"But at present, after drawing up a rough copy on this subject, my conclusion is that external conditions do extremely little, except in causing mere variability. This mere variability (causing the child not closely to resemble its parent) I look at as very different from the formation of a marked variety of new species." (Darwin 1856)*

Individual quality is not a recent concept as it has been used as an evolutionary concept since the beginning of inter-individual variability studies. In the '70s, several studies for example used the term of quality to respectively define offspring growth, individual secondary sexual characters and body mass (Hirshfield and Tinkle 1975, Zahavi 1975, Kenward 1978). However, this term was for a long time used without establishing a clear definition of quality, resulting in multiple and sometimes conflicting uses of the terminology. More recent studies have focused on the definition of individual "quality" and its implication in an eco-evolutionary context (Gaillard et al. 2003, Wilson and Nussey 2010, Bergeron et al. 2011). According to these studies, individual quality refers to a variable component of a phenotype in a population that can be used to rank individuals along a continuum of combinations of particular quantitative traits and assesses how individuals with different quality scores contribute to the evolutionary trajectory of a population. In other words, quality is a continuous metric of fixed inter-individual differences in phenotype along a gradient from the "best" to the "worst" contributor to the population. From the trait perspective, this unequal contribution is the resultant of the positive covariation between several traits with high

Figure 5: Individual quality gradient

demand in energy, thus performing in different aspects of life history all together (*e.g.* breeding success and longevity, *Figure 5*).

Capacity to perform ultimately relies on the individual ways to acquire and use energy efficiently. Thus, the phenotypic traits that while give an advantage to the individual in acquiring or saving energy (*e.g.* morphology or physiology) should be the drivers of its quality. The most obvious driver of these quality related traits is genetic, as every individual inherits different characteristics, thus different quality (Hunt et al. 2004). However, it is far from being the only driver of individual quality. For example, some studies focused on the effect of external conditions during offspring development on life-history traits and fitness at the adult age (Lindström 1999). When the conditions faced during development are similar for a lot of individuals, they can materialize in the population under the form of things such as cohort effect (differences in individual property such as fecundity depending on their birth year, Lindstrom and Kokko 2002). Conversely, when individuals face different conditions from each other (*e.g.* due to maternal effect, Walton & Hammond 1938), they can vary in quality through a different metabolism (Desai and Hales 1997), immunity (Saino et al. 1997) or secondary sexual characters (Birkhead et al. 1999).

b) Same quality, different strategies: trade-offs and individual variability

As pointed out by the same studies that recently tried to define the concept of quality, what we call individual quality could also simply be the expression of unmeasured trade-offs in energy allocation among other traits, thus becoming an indirect measure of individual "strategies" (Wilson and Nussey 2010). Trade-off is undoubtedly one of the core components of evolutionary and inter-individual variability concepts, as it arises from the simple observation that the quantity of energy available for an individual is by nature limited. Thus, when an individual is not able to acquire enough energy to fulfil all its needs, some life-history traits are favored among others and the available energy is allocated to them at the expense of other ones (Stearns 1992). One of the first energy allocation trade-off studied (and the most famous) is the cost of reproduction (Williams 1966, Stearns 1989) because it makes the bridge between individuals and population dynamics. In theory, the best quality individual would be able to live forever and produce quality offspring at all time. However, individuals are in practice not able to live indefinitely nor to breed successfully at all occasions. Therefore, the amount of energy allocated to one of these vital rates is mechanically going to diminish the amount of energy that can be allocated to the other, forcing the individuals to trade-off in the quantity ofenergy it will allocate to its own maintenance, its reproduction and eventually its growth. Thus, every individual has to establish "strategies" on what amount of energy is going to be allocated to each. At the inter-species scale, the most extreme strategy is to reduce the lifespan at one unique breeding event, during which the amount of energy dedicated to offspring production is maximized (*i.e.* semelparity, Cole 1954). Even among long-lived species, this slow-fast continuum exists and induces important variations in the amount of energy allocated to survival and breeding, resulting in very different longevities and clutch sizes for example (Stearns 1989). At the individual scale, these strategies can then also exist although in a lesser amplitude. For example in long-lived species, individuals can either invest an important amount of energy in offspring production with detrimental effects on their own lifespan and thus future breeding prospects, or conversely exhibit an important lifespan while investing less in each breeding (*Figure 6*). Different strategies may sometimes prove useful, but they could also be equivalent in terms of contribution to the population. Furthermore, the same strategy could be more or less efficient depending on the environmental conditions, which explain their diversity.

Figure 6: Individual strategies in life history

c) Quality, strategy... Or just lucky?

The last component of variability among individuals relies on the fact that every individual experiences slightly different environmental conditions during its life. Although life history has long been studied in a context where environment was assumed constant, this postulate has more recently proven to be at best imprecise (Tuljapurkar et al. 2009), at worse a fake marker of inherent inter-individual differences (Steiner and Tuljapurkar 2012). Indeed, environmental conditions vary in both space and time and at very different scales, from a few meters to thousands of kilometers and from a few minutes to years. For this reason, two (theoretical) identical individuals living in a slightly different place or at a slightly different period would still experience a different life history, given the variations and unpredictability (or stochasticity) of the environment they live in (*Figure 7*).

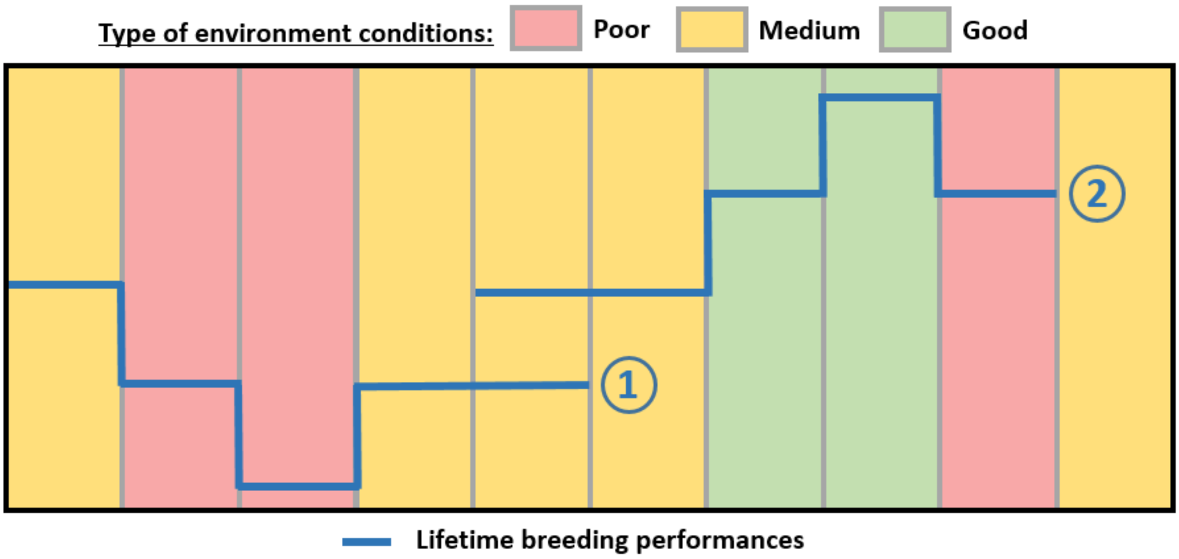


Figure 7: Effect of stochasticity on the life history of two theoretical identical individuals born at different times.

Environmental stochasticity can of course be the manifestation of many different factors including climate (temperature, precipitation...) as well as interactions with other species or even conspecifics. Individuals' response to these factors may be direct (*e.g.* cold temperature leading to poor reproduction) but also lagged in time (*e.g.* good conditions can allow energy storage that will help facing future adverse conditions should they occur, inducing carry-over effects). Thus, it is important that environmental stochasticity is taken into account and precisely assessed to truly understand and disentangle the diversity in life history that can occur in a population.

4. From individual back to population

a) Individual fitness as a measure of contribution to the population

The concept of fitness in evolutionary biology can be somewhat confusing as its meaning slightly evolved since its first introduction at the very beginning of Darwinian evolutionary theory (see *Citation below*). In its original Darwinian definition, fitness is simply a consequence of the intrinsic characteristics of individuals in juxtaposition with the environment (Ariew and Lewontin 2004). In other words, if an individual presents fitter traits in regard to the environment, its reproductive rates are expected to increase, ultimately changing its contribution to the population. While this concept is quite close from the one we currently use in modern evolution, the differences reside in the fact that fitness as seen by the Darwinian original definition only exists in the light of environment, from which it becomes the cause of differences in individual vital rates (*Figure 8*).

> *"This survival of the fittest, which I have here sought to express in mechanical terms, is that which Mr. Darwin has called 'natural selection', or the preservation of favored races in the struggle for life." (Spencer, 1864)*

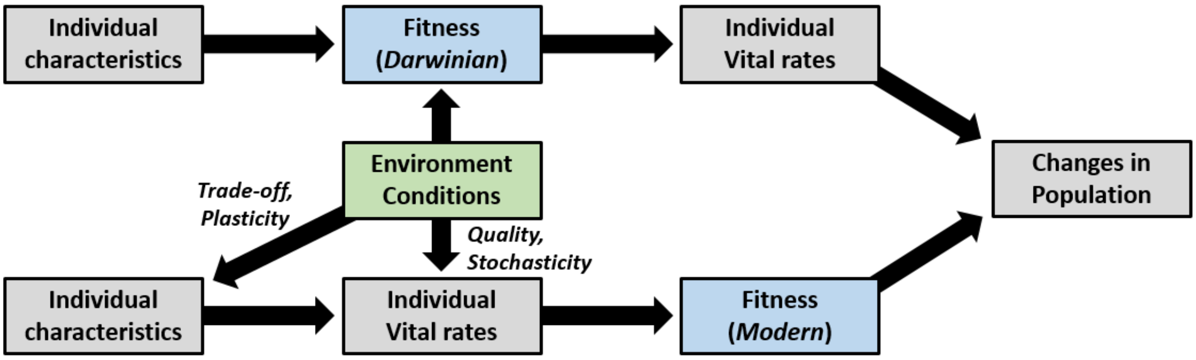


Figure 8: Differences between Darwinian and modern fitness definition (Adapted from Ariew and Lewontin 2004)

If we have to retain one lesson from spending so long on defining concepts such as individual quality and strategies, it is that environment is not the only driver of variations among individuals. Consequently, the modern definition of reproductive fitness evolved, now defining the fitness as a consequence of differences in individual vital rates rather than its cause. Even with this postulate, the current definition of fitness seems to still be lacking clarity, as its definition varies from “differences in viability and fecundity” to “the contribution to the next generation” and includes measures as diverse as lifetime reproductive success, expected lifetime reproductive success, reproductive rate, reproductive value, genotypic fitness or even population growth rates (De Jong 1994). In general, the problem behind the modern definition of fitness does not reside in our understanding of it, which is quite commonly accepted (*See citation above*), but in the way it is measured. Subsequently, many studies assessed selection gradients among individuals using components of fitness (*e.g.* offspring production, survival to maturity or copulatory success) rather than fitness itself. These components have the advantage of being relatively easy to measure, however they might not always reflect individual fitness.

> *“Fitness: Something everyone understands but no one can define precisely” (Stearns, 1976)*

This was true until 1996, when McGraw and Caswell developed a simple although very efficient method to assess what they called “individual fitness”. This method is based on the postulate that fitness is inherently a demographic concept, and can therefore be summed up as the “population growth rate of an individual”. In this case, an individual life is characterized by its propensity to survive and produce offspring at different discrete time steps of its life, analogously to a population being characterized by the average survival and fertility of each of its class age. In such conditions, an individual life can be represented by the same type of matrix as population projection, in which individual breeding success (divided by two as it takes two parents to produce one offspring) and survival at every time step (*i.e.* age) replace the usual class age average fertility and survival (*Figure 9*). Individual fitness is then defined as the dominant eigenvalue of the constructed matrix, analogously to the population asymptotic growth being the matrix dominant eigenvalue of population projection models. Rather than the individual breeding performances, this measure of fitness is the reflect of the genes’ transmission to the population. As such, individual breeding success is divided by two in the matrix projection as only half of an individual genome is transmitted to its offspring. Analogously, individual survival is considered here, contrary to measures such as lifetime reproductive success, as surviving one more year also equals transmitting your genome in the population for one more year.

$$\mathbf{A}_{\mathbf{pop.}} = \begin{pmatrix} \color{blue}{0.31} & \color{blue}{0.59} & \color{blue}{0.98} & \color{blue}{1.19} & \color{blue}{0.94} & \color{blue}{0.88} \\ \color{orange}{0.69} & 0 & 0 & 0 & 0 & 0 \\ 0 & \color{orange}{0.76} & 0 & 0 & 0 & 0 \\ 0 & 0 & \color{orange}{0.92} & 0 & 0 & 0 \\ 0 & 0 & 0 & \color{orange}{0.86} & 0 & 0 \\ 0 & 0 & 0 & 0 & \color{orange}{0.80} & 0 \end{pmatrix}$$

$$\mathbf{A}_{\mathbf{indiv.}} = \begin{pmatrix} \color{blue}{0} & \color{blue}{0} & \color{blue}{1.5} & \color{blue}{1} & \color{blue}{0} & \color{blue}{1} \\ \color{orange}{1} & 0 & 0 & 0 & 0 & 0 \\ 0 & \color{orange}{1} & 0 & 0 & 0 & 0 \\ 0 & 0 & \color{orange}{1} & 0 & 0 & 0 \\ 0 & 0 & 0 & \color{orange}{1} & 0 & 0 \\ 0 & 0 & 0 & 0 & \color{orange}{1} & 0 \end{pmatrix}$$

Figure 9: Population projection and individual fitness matrix modelling including class age or individual age breeding success (in blue) and survival (in yellow).
(Adapted from McGraw and Caswell 1992)

The main advantage of such a method resides in the fact that it sums-up the entirety of individual lives, and groups demographic parameters (*i.e.* longevity and fertility) into one integrative measure. However, this methodology (and others focusing on individual lifetime) requires to follow individuals during their entire lifetime, which may hinder its wide use. Furthermore, individual fitness as assessed by this method only makes sense when compared to other individuals' fitness (Dobson et al. 2020). Indeed, if fitness refers to the way individuals' genes propagate into the population, then it only makes sense if it is expressed as relative to others' genes propagation. For example, the same fitness value may reflect a poor contributor to the population in a healthy population and an over-contributor in a rapidly decreasing population (*i.e.* environmental perturbations), which has been addressed in several studies (*e.g.* Benton and Grant 2000, Sæther and Engen 2015).

Despite being difficult to use in practice, this method participated to revolutionize the use of fitness in evo-demographic studies, providing both an efficient tool and an unambiguous definition of individual fitness. In parallel, the concept of fitness has expanded and numerous interesting definitions and new concepts relying on individual fitness appeared. We could cite the inclusive fitness in which the contribution of an individual to the fitness of his family (*i.e.* partly common genes) is taken into account, especially in social species (Ferriere and Michod 2011, Dobson et al. 2012).

b) The evolutionary role of unequal contribution

Fitness can be summed-up as a measure of individual differential contribution to the population. As previously discussed, one and a half century of evolution sciences established that every individual is intrinsically different. Intuitively, we would thus be tempted to state that the most efficient individuals (*i.e.* the ones with the highest fitness) will produce more offspring sharing the same characteristics, thus quickly spreading their phenotype into the population. However, such a statement would be partially false. Indeed, if individuals with highest fitness will, by definition, produce more offspring than their conspecifics, the way their offspring will succeed and spread depends on many factors including, as seen earlier, trade-offs and environment. Besides, not all characteristics of an individual are expected to be transmitted to its offspring.

The propensity of a life history trait to be transmitted to the next generation is called heritability. While life-history traits are observed at the individual scale, the heritability of a trait is measured at the population level. It can be defined as the slope of the linear regression (if it exists) of the measurements of the character amongst offspring on the mean of the measurements of the trait for their two parents (Jacquard 1983). In other words, heritability defines the part of offspring values in a trait that can be predicted by those of the parents. Heritability is of course present in many physiological and morphological traits, but has also proven to be present in less intuitive traits such as behavior (Stirling et al. 2002). Most life-history traits have a more or less heritable component, depending on their type. For example, morphological traits are known to be very heritable, while behavioral traits depend much more on the environment encountered during life (Dochtermann et al. 2019). Some life history traits may also present very few to no heritability, in which case the variability in the trait among the population is entirely depending on other factors such as development and environment.

"Any variation which is not inherited is unimportant for us" (Darwin 1859)

Heritability must not be mixed with heredity, for two main reasons. First, heritability only exists in the light of variations. Thus, if a trait is fixed (*i.e.* no variations) in the population, it is by definition fully inherited, while at the same time not heritable. Second, heredity resides in the reliable transmission from one generation to the next as a matter of biology *(see Citation above*), and is therefore often associated with genetics, while heritability more easily includes very different concepts such as cultural learning (*i.e.* inclusive heritability, Danchin and Wagner 2010).

If higher fitness is the result of an overall advantage, then we would expect the traits with the highest positive impact on fitness to be quickly inherited and thus fixed in the population as they provide a selective advantage. However, it is actually quite the opposite. Indeed, according to Fisher's theorem of natural selection, the rate of change in mean fitness should equal the variance in fitness itself (Fisher 1930). In such conditions, populations are expected to reach an equilibrium under natural selection, where differences in fitness should approach zero (Gustafsson 1986). Therefore, the more a life-history trait is under selective pressure (for which the first condition is to be heritable), the less likely it is to exhibit variations in the population. The corollary of this is that variability in fitness among a population is expected to be mainly driven by traits that have a low heritability (Stirling et al. 2002), even when populations are not at equilibrium (Price and Schluter 1991).

Thus, while fitness is the main unit of measurement of individual capacity to propagate its genes in the population (thereby the main driver of natural selection and evolution processes), variability in fitness is also mainly driven by non-heritable life-history traits. This counterintuitive statement makes the link between life history and fitness even more complicated to clearly assess.

5. Filling the gap between inter-individual variability and fitness

a) Unravelling the integrative effects of quality, trade-offs and stochasticity

With these few pages, I described many concepts regarding variability among individuals for which the definition and the theory seem pretty well established. Furthermore, evidence of concepts such as individual quality, strategies in energy allocation or environmental stochasticity have all been studied and demonstrated in recent years (*e.g.* Beauplet et al. 2006, Komdeur 2006, Steiner et al. 2021). So where does my work try to add up on this fascinating subject that is variability among individuals?

Modern ecotoxicology studies (*i.e.* the study of pollutants on living organisms and ecosystems), often describe what they call a "cocktail effect" (Rizzati et al. 2016). Cocktail effect refers to the capacity of some pollutants known to individually affect organisms, to interact, when combined, either in antagonistic but mainly in synergetic interactions that ultimately affect organisms in very different ways and amplitudes that the simple sum of the effect of each pollutant. This cocktail effect is a much more realistic view of the effects of pollutants on organisms, as these pollutants are rarely encountered alone in nature, but it necessarily adds-up on previous findings regarding each of the pollutants separately.

If anything, the first part of my work is metaphorically the study of the cocktail effect of individual sources of variations on life history. Analogously to ecotoxicology, I aim at defining some drivers of interest, in my case life history traits, and assess their combined antagonistic and synergetic effects on the organisms, in my case life history and fitness. But in the same way that ecotoxicologists cannot study the thousands of pollutants that exist in nature together and tend to focus on some categories, thousands of physiological, morphological, behavioral and more life history traits cannot be monitored all at once.

As detailed earlier, the finite amount of energy available for each individual is at the core of its capacity to contribute to the population. Thus, I decided to focus my work on individual energy acquisition capacities (*i.e.* foraging performances) as well as the way they allocate this energy (*i.e.* breeding behavior). Apart for giving a very good overview of the energy allocation constraints faced by individuals, such traits can be assessed easily by long-term monitoring and with no to little invasive protocols. In the first part of this work, I aimed at reconstructing a large quantity of individual average life history traits along individuals' entire life, in order to build a complex integrative model in which these life history traits could affect fitness

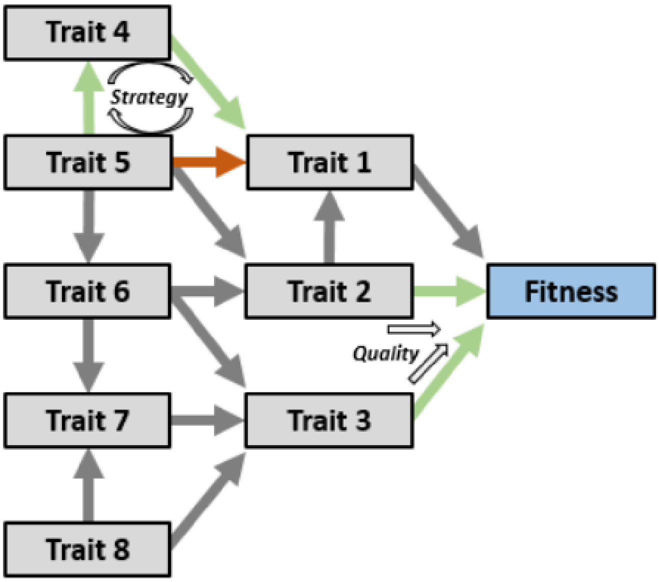


Figure 10: Modelling life history through different traits and their positive (green) and negative (red) interactions.

directly but also indirectly by interacting with other traits**.** In other words, my objective was to rebuild an entire individual life history using a convincing subsample of the thousands of traits than can affect the life on an individual. This modelling, which I will detail further along this manuscript, aimed at seeing the relative contribution of processes such as individual quality and energy allocation strategies. Indeed, following the concepts I previously detailed, higher quality individuals should display the highest fitness values, but also display high values in the large majority of the traits affecting fitness. Conversely, energy allocation strategies should also appear, for example if a trait has a direct negative effect on fitness but also increases another trait with a positive effect on fitness at the same time (*Figure 10*). Such model was expected to allow disentangling the relative importance of individual quality and energy allocation strategies in maximizing fitness. Furthermore, it ambitioned at taking environmental stochasticity into account, ultimately allowing to understand the relative importance of the three main sources of inter-individual variability described earlier in defining individual fitness.

b) From individual decision to life-history

Even if we are able to establish correlations between a life-history trait and individual fitness, the nature of this relation is often blurry. Indeed, a life history is composed of different traits that are often themselves the result of many consecutive individual decisions. The term “decision” could be debated, but here I supported the postulate that inter-individually variable characteristics such as where to forage (energy acquisition), if, where and when to breed or who to pair with (energy allocation to reproduction) can be viewed as individual decision making (McFarland 1977). While these decisions can be averaged at the individual lifetime and correlate it with overall individual performances, thus assessing the role of each trait in defining fitness, the processes through which such decisions ultimately affect the entire life of an individual remain unclear. For example, if it is easy to establish a relation between an individual breeding spot and its ultimate capacity to produce large amounts of offspring during its life, the small processes that hide behind this relation (*e.g.* protection from predators, abundance of food, absence of competition...) are often more complicated to establish and therefore remain hypothetical.

In the second part of this work, I aimed at assessing the effects of individual decisions at finer scale. To do so, I focused on the life history traits for which the effect on fitness is the most predominant, as defined in the first part. The main objective was to downscale the study of these traits at the breeding season level to see how their predominant effect on fitness can translate on the actual individual breeding capacity, and through which processes. More precisely, I aimed at establishing links between these traits, breeding success and intermediate factors such as the capacity to cope with environmental conditions, the modification of life cycles or the acquisition and use of energy.

c) The importance of early development in defining fitness

When we think about an individual life history, we often refer to its capacity to cope with adverse conditions or to adopt an efficient strategy. However, some of the traits that will affect an individual actually occur at a moment of their life where they have few to no control on their own capacity to maintain themselves. Early development (*i.e.* the period that spans from conception to developmental maturity, Henry and Ulijaszek 1996) is a very good example of this reality, as immature individuals mostly depend on their parents capacity to fulfil their needs in order to properly survive, maintain and develop. As life is unfair, the effect of development on individual’s capacity to breed and survive at later stages of its life are known to be important (*e.g.* in birds and mammals, Lindström 1999).

One last major part of my work thus aimed at understanding the role of parental care on defining individual life history. More precisely, my objective was to define the potential role of parameters such as growth rate, mass at fledging or growth irregularity on life history both at the breeding season level (*i.e.* capacity to breed, life cycle...) but also at the lifetime level, using the traits defined in the previous chapters. The main goal was to understand if the conditions faced during early-life could partly predict the capacity of an individual to perform as an adult and quantify the strength of this relation.

d) Choosing the right model to study inter-individual variability

Variability in energy acquisition/allocation trade-offs is expected to be mainly present in species with a relatively long lifespan. Indeed, while long-lived organisms have plenty of time to develop different history strategies such as maximizing survival by investing a limited amount of energy in breeding, or conversely maximizing offspring production in a shorter amount of life, short-lived organisms (*i.e.* in the most extreme case single breeding organisms) are way more constrained in the way they can maximize their fitness. Thus, while inter-individual variability is expected to be mainly driven by differences in individual quality and stochastic processes in shot-lived organisms, long-lived organisms are expected to rely more on energy allocation strategy. Therefore, highlighting the interaction of such processes in defining individual fitness is expected to be easier while focusing on long-lived species. However, long-lived species tend to be difficult to monitor over their entire lifespan, mainly because they simply live up to decades, but also because the longer the life, the harder the precise monitoring of life history.

Here, I was able to focus my work on a species that I would qualify as having the best of both worlds. Indeed, the little penguin (*Eudyptula minor*), as all penguins' species, is a very philopatric species (*i.e.* comes back at the same spot of the same colony all its life, Dann 1991), making it easier to monitor than species with important dispersion. Furthermore, although it displays a long-lived species strategy, the little penguin is by far the shortest-lived species of all penguin species (average lifespan of around 6 years, Dann et al. 2005), making it 1) easier to monitor for an entire life, 2) facing much more important pressure than very long-lived seabirds (*e.g.* Weimerskirch et al. 2001)

Apart from its position in an interesting sort of in between long-lived species type of strategy, the main interest of little penguins to study variability among individual resides in its very asynchronous breeding cycle that can extend up to almost eight months depending on the individual and the breeding season (see details in *Chapter 2*). This asynchrony in their breeding cycle is of particular interest, as the environmental conditions faced by early and late breeders are expected to be very different, affecting their breeding performances and the development of their offspring. Furthermore, their relatively short breeding cycle gives the opportunity to early enough birds to regularly attempt a second breeding event, implying important supplementary energy expenditures but also potentially a significant increase in offspring production. While little penguins tend to exhibit monogamous behavior, they also display high divorce rate probably associated with potential asynchrony in their post-winter arrival time.

While individual quality and energy allocation trade-offs should be observable in every species, the strength of their effect on individuals is probably very dependent on their life cycle. Indeed, species facing very important seasonal constraints (*e.g.* Antarctic species, Youngflesh et al. 2017) while it should display very small variability in their breeding timing. Similarly, species with very long generation times should display less inter-individual variability in some traits as it would be buffered on long periods (canalization hypothesis, Péron et al. 2016). In my case, the little penguin was an appropriate model, as it presents very few individual variability buffering features, that is to say high asynchrony, relatively short lifespan and small size.

Thus, I predicted that little penguins would display very important differences in their fitness, and expected to be able to observe the mechanisms through which this variability occurs. While differences in individual intrinsic quality would play an important role through processes such as differences in foraging performances, I also predicted that I would observe energy allocation trade-offs, some favoring a long-life with low breeding energy expense versus others investing a lot in breeding and second clutches. In general, exacerbated asynchrony, which is a very important specificity of this species, would be one of the most important drivers of lifetime fitness differences by having a ubiquitous effect on all the other life history traits. Indeed, while unfavourable phenology is not expected to directly affect individual capacities to perform, I predicted it to affect their foraging performances (through different conditions at sea), thus lowering their breeding success but also conducting to the production of poorer quality offspring, while exhausting the parents and inducing important carry-over effects. While I expected asynchrony to undoubtedly affect individual life as adults, it may also affect them much earlier as individuals growing later are expected to face poorer conditions, with probably very detrimental consequences on their quality and life history strategies as adults.

Chapter II: Methodology

Study species, study site and general methodology

1. Study site

This study was conducted at the world largest little penguin (*Eudyptula minor*) colony at Phillip Island, Victoria State, Australia (lat 38°15’S, lon 143°30’E). It consists of 32,000 to 40,000 breeding adults (Phillip Island Nature Park annual report 2022), in the Summerland peninsula, in the south-western part of the island (*Figure 11*).

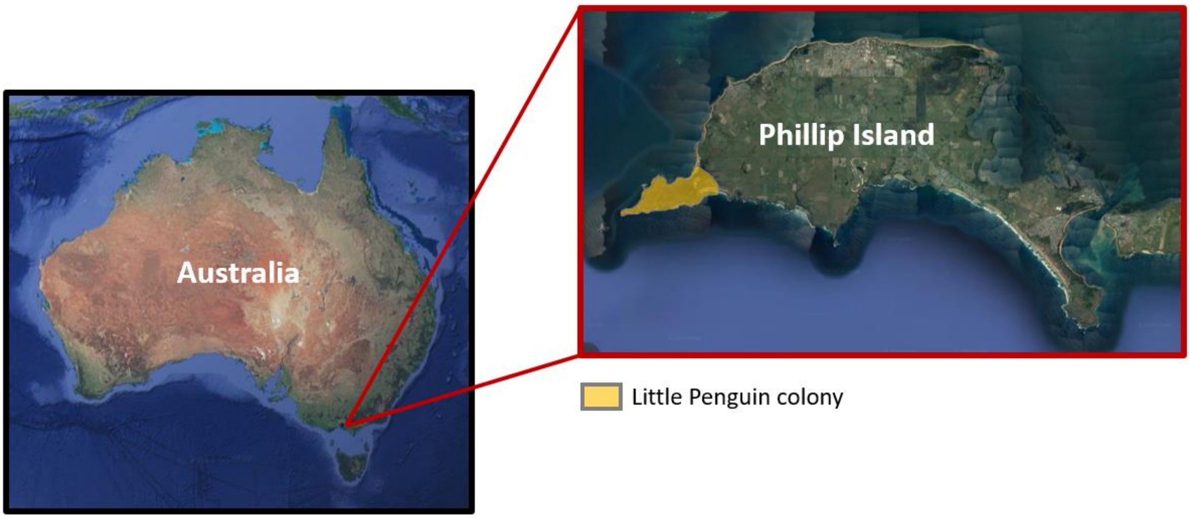


Figure 11: Location of the penguin colony on Phillip Island, Australia

The study site was the sub-colony called Penguin Parade ®, which is a popular tourist attraction visited by over half a million visitors per year. People are kept on boardwalks and stairs (*Figure 12*) to observe the daily arrival of penguins from the sea at dusk.

Figure 12: Penguin parade infrastructures on the beach

The study site contains around 100 artificial wooden box nests with a removable roof offering easy access to monitor penguins (*Figure 13*). These artificial nests are part of conservation measures to allow penguin nesting on previously degraded areas while providing a convenient monitoring tool for long-term studies without any impact on penguins survival and breeding success (Sutherland et al. 2014).

Figure 13: Two adults in a burrow (pre-laying, left) and one fledgling exploring around the nest (right)

2. Study species

The Little penguin is the smallest of all 18 penguin species and is endemic to Australia and New Zealand (Williams 1995). Like all penguins species, both parents participate in raising the chicks. Yet, little penguins exhibit a high divorce rate between breeding seasons (Reilly and Cullen 1981). Sexual maturity is reached at 3 years old, yet a high proportion of individuals tend to first breed at 2 or 4 years old.

Little penguins display a high variability in their life history. They are very asynchronous in their breeding timing that can occur between August and December, but can sometimes extend from May to February (Saraux 2011). Overall, the breeding seasons occurs as follows (as described in Chiaradia and Kerry 1999). The breeding season in itself is composed of a short courtship period, quickly followed by laying two eggs. The incubation of the eggs lasts 35 days. After hatching, the parents take intensive care of the chicks (guard period) for a period usually lasting from one week to one month, during which the two parents alternate on a daily basis between staying ashore with the chicks and foraging at sea. After these first few weeks, the parents start to leave the chicks alone ashore and go to forage at sea (during daytime; Chiaradia et al. 2007a) both at the same time. During this period that spans around 40 days, the shifts are usually still one or two days long (Chiaradia and Kerry 1999) but parents can sometimes leave for longer (up to 17 days) allowing the parents to replenish their own reserves (*Figure 14;* Chiaradia and Nisbet 2006, Saraux et al. 2011a). This asynchrony in the breeding timing coupled with a quite short breeding period compared to other penguin species allows some individuals to regularly attempt two different clutches per breeding season.

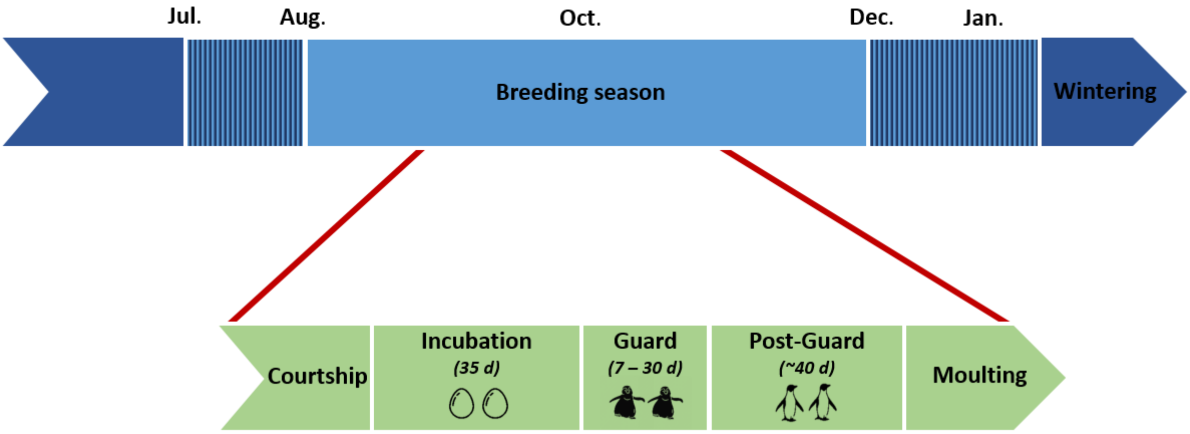


Figure 14: Little penguin life and breeding cycle

Apart from their breeding cycle, the little penguin also displays a very high variability in its lifespan. The Little penguin is considered as a long-lived species, however it displays relatively short lives compared to other seabird species (6.5 years in average, although largely skewed by juvenile survival as adults can reach up to 20 to 25 years; Dann et al., 2005).

3. Long-term monitoring

a) Individual detection and breeding monitoring


Figure 15: Automated Penguin Monitoring System

The little penguin population at Phillip Island has been monitored once every two weeks since 1968 (Reilly and Cullen 1981). A more frequent capture-mark-recapture monitoring has been running since 2000 on Penguin Parade ® site, which is the study site of this work. This long-term monitoring is a combination of an automated RFID monitoring (*Figure 15*) and frequent visits to the colony (3 times a week during the breeding season). Individual identification relies on the use of individual transponders implanted subcutaneously in each penguin either as chick just before fledging or when first encountered in the colony as adult (Chiaradia & Kerry 1999). This system allows an overall very efficient recapture rate, which we here assume to be of 100%.


Figure 16: Automated transponder reader

Besides, field patrols (3 times a week, from the entire span of the breeding season) permit to identify every individual encountered on the study site (*i.e.* in or near its nest) using manual transponder reader (*Figure 16*), allowing the assessment of its breeding status and success visually thus with limited disturbance, including their precise phenology (1 day gap). These field patrols also allow the monitoring of chick mass from the moment chicks are first left alone in the nest (*i.e.* end of guard) to limit disturbance. During the seventh week of growth, fledglings are also implanted with a transponder. Penguins are only sexed as adults when they return in the colony for breeding using bill length, as juvenile bill is not fully developed yet (Arnould et al. 2004).

b) Foraging performances at sea

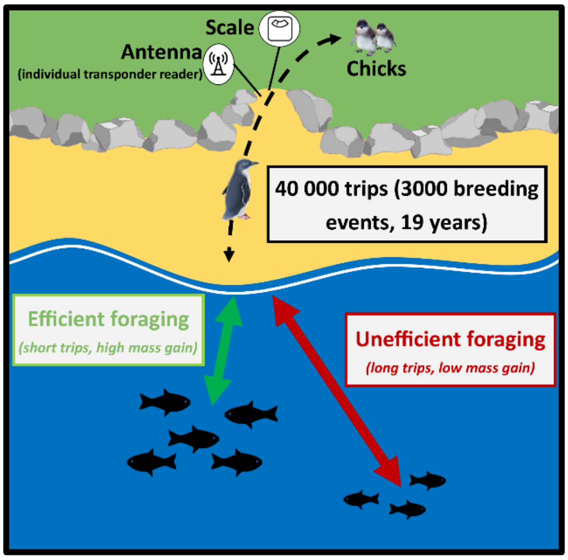


Figure 17: Foraging performances at sea based on automated monitoring system.

The study site has an Automated Penguin Monitoring System (APMS, *Figure 15*) including a couple of transponder readers located on the main penguin pathway between the colony and the sea (Chiaradia and Kerry 1999, *Figure 15*). This system allows a very precise monitoring of entrance/exit of the colony for all individuals. It is to be noted that even individuals not breeding or breeding on other parts of the colony can still be detected by the system. One of the automated transponder reader (accounting for about 75% of the passages) is itself coupled with a weighbridge that precisely records weights for each individual going in or out of the colony. These data have been used in the past (Saraux et al. 2011c) and in this work to infer foraging performances through the estimation of foraging trip duration and the mass gained during each trip (*Figure 17*). However, one of the two automated transponder reader present on the Penguin Parade ® (about 25% of the passages) is not coupled with a scale. Furthermore, in some rare cases some penguins may reach the colony by other paths, preventing its detection. For these reasons, when rebuilding individual foraging trips, only trips ranging from 1 to 17 days, penguin masses ranging from 700 to 1700g and penguin mass change ranging from -75 to 500g are considered valid (based on Salton et al. 2015, Saraux and Chiaradia 2022). Overall, I was able to rebuild around 50.000 foraging trips from half a thousand penguins over a 23 years period.

4. Rebuilding individual lives

Using this automated system, I was able to follow and extract information on individuals' attendance, body mass and foraging information over their lifetime. First, I assessed individual fitness using an adapted population projection matrix (Leslie 1945) as described by McGraw & Caswell (1996). Each individual's fitness was estimated as the dominant eigenvalue of an age-structured projection matrix, where the matrix is the size of the individual's lifespan, the first row is the number of chicks fledged per year divided by two (as only half of the genome is given by a single parent) and below the diagonal is yearly survival (1 until death). As such, individual fitness represents the asymptotic growth of an individual genotype through time. Regarding life history traits, my general methodology aimed at averaging the performances of an individual across its entire life in order to extract a single lifetime value. As an example, lifetime guard duration was assessed as the average length of guard period across the life on an individual for each of its breeding attempt (*Figure 18 A*). Regarding traits linked to foraging performances, the foraging trips were first averaged over the breeding season and then averaged over the entire lifetime, in order to give the same weight to each breeding attempt. For example, the individual mass gained at sea during chick rearing over a breeding season was assessed as the average mass gained at sea during each individual trip (*Figure 18 B*). Lifetime mass gained at sea was then assessed as the average of annual mass gains over lifetime to avoid biasing towards a year with more trips monitored. The construction of each life history trait used in this PhD is detailed in the next chapters.

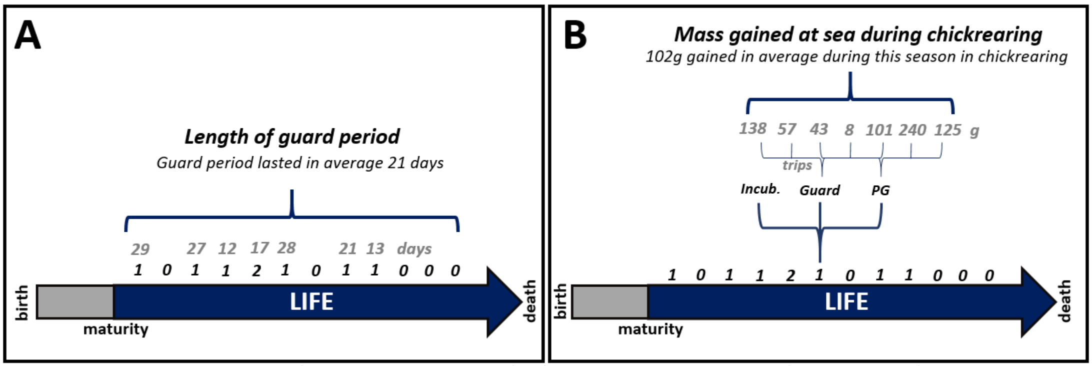


Figure 18: Example of the assessment of lifetime individual performances from annual performances (A) and from trip performances (B)

Because not all individuals used in this study were contemporaneous, I aimed at distinguishing processes such as strategy and/or individual quality from stochastic processes (i.e. "lucky" individuals experiencing excellent conditions throughout their life). Thus, in this work, I often used the individual performance relative to the population as a marker of individual variability rather than the absolute value. This relative values in individual lifetime trait was obtained by centring all values per year, that is to say subtracting each event's average annual population value from the individual value for each variable (residual values). As an example, the individual lifetime relative survival was assessed as the average of the individual relative yearly survival, that is to say the individual survival (*i.e.* binary) minus the yearly survival of the population (*Figure 19*). For variables available at the trip scale such as the relative mass gained at sea, the yearly relative survival was assessed in 3 steps as follows: 1) The relative mass gained of each trip was assessed as the mass gained by the individual minus the average mass gained by the population during the same year and at the same breeding stage. 2) The yearly relative mass gained was then defined as the average relative mass gain per trip. 3) Finally, the lifetime relative mass gain was assessed as the average of each season’s relative mass gain in order to give the same weight to each breeding event on lifetime performance (*Figure 19*). The detail of the construction of each relative life history trait used during this work is presented in the next chapters.

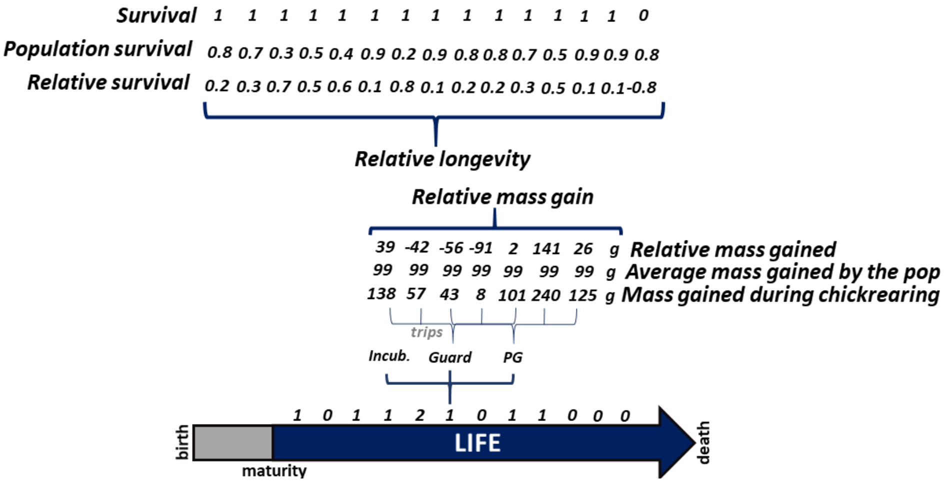


Figure 19: Example of the assessment of the lifetime individual performances relative to the population from annual performances and from trip performances.

Chapter III: Fitness drivers

Individual Quality, Energy Allocation and Stochasticity in Defining Fitness

<u>Modified from:</u>

Joly, N., A. Chiaradia, J.-Y. Georges, and C. Saraux. 2023. Unpacking the lifelong secrets of little penguins: individual quality, energy allocation, and stochasticity in defining fitness. Evolution:qpad126.

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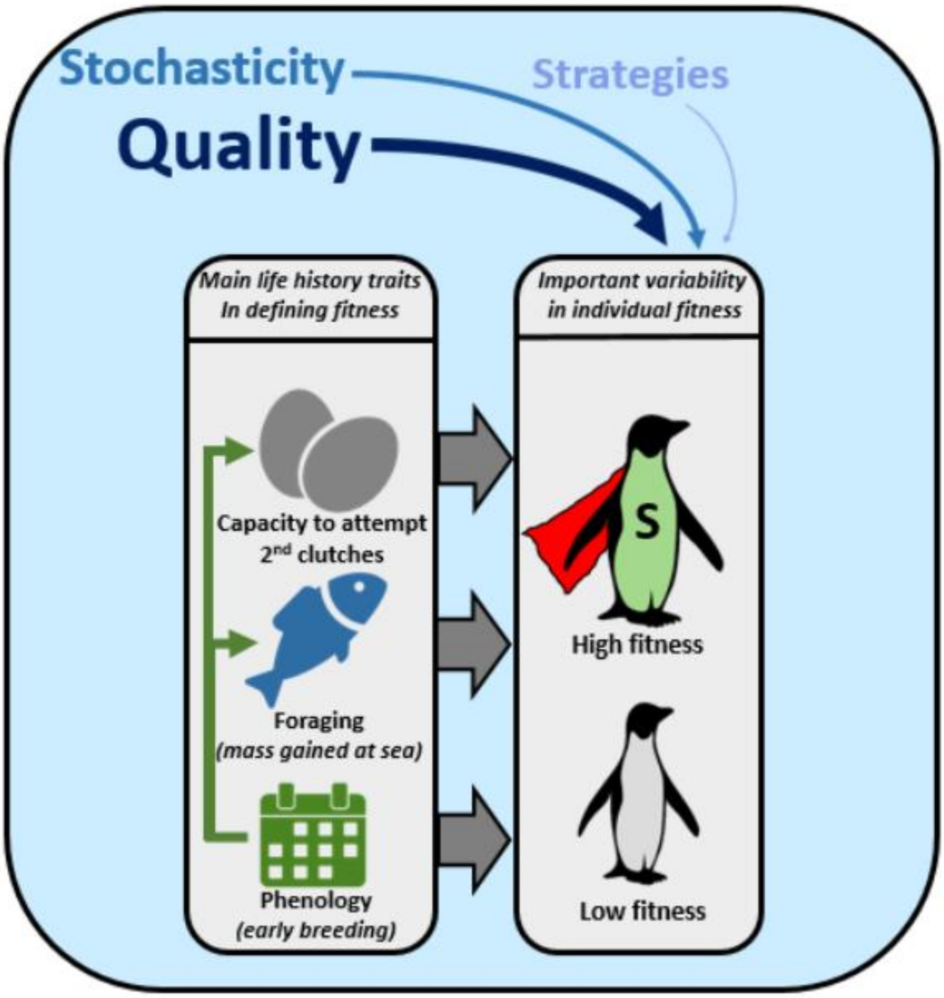
General context of the study:

Heterogeneity among individuals can arise from various processes (individual quality, energy allocation trade-offs and/or environmental stochasticity) but also through various pathways, that is to say many life-history traits and trajectories. In this first chapter, I aimed at overviewing the different life history traits for which I expected little penguins to display important differences and include them in a single structural equation model through which I could see how these traits interact with one another and ultimately affect individual fitness. The main goal of such study is to understand the relative importance of quality, strategies and stochasticity in defining fitness and disentangle the life history traits than will affect fitness the most in order to later focus my attention on them.

Graphical summary of the main results:



Abstract

While the heterogeneity among individuals of a population is more and more documented, questions on the paths through which it arises, particularly whether it is linked to fixed heterogeneity or chance alone, are still widely debated. Here, we tested how individual quality, energy allocation trade-offs and environmental stochasticity define individual fitness. To do so, we simultaneously investigated the contribution of 18 life-history traits to the fitness of breeding little penguins *(Eudyptula minor)*, using a structural equation model. Fitness was highly variable amongst the 162 birds monitored over their entire lifespan. It increased with the individual penguin's ability to increase i) the number of breeding events (*i.e.* living longer, breeding younger, breeding more often and producing more second clutches), and ii) the breeding success per event through increased foraging performances (*i.e.* mass gained at sea). While all three processes (stochasticity, individual quality and allocation trade-offs) affected fitness, inter-individual variability in fitness was mainly driven by individual quality, birds consistently breeding earlier in the season and displaying higher foraging efficiency exhibiting higher fitness. Why some birds consistently can perform better at sea and breed earlier remains a question to investigate to understand how selection applies to these traits.

Key words: *Fitness, individual heterogeneity, foraging, phenology, breeding ecology*

1. **Introduction**

Fitness is a measure of how an individual contributes to the population (De Jong 1994), which results from life-history traits such as survival and breeding success throughout an animal's lifespan (Stearns 1992; McGraw & Caswell, 1996). Yet, due to competing paths between survival and reproduction (Williams 1966), parents are expected to make trade-offs in relation to variations in benefits to their offspring and costs to themselves (Winkler 1987). An individual can thus maximise its fitness by producing as many healthy offspring (*i.e.* offspring that would themselves exhibit high survival and breeding success) as possible in its lifetime. In long-lived species especially, individuals are expected to maximise their breeding events (*i.e.* high longevity)while ensuring the highest number of offspring produced per breeding event (Maccoll and Hatchwell 2004).

Such heterogeneity in individual fitness is thought to result from the differences that individuals exhibit in their capacity to cope with environmental changes (Cam et al. 2002). While some individuals efficiently cope with adverse conditions, others have difficulties breeding and/or surviving (Grémillet & Boulinier, 2009; Reed et al., 2009). Thus, only a small proportion of individuals contribute to the majority of offspring production (Aubry et al., 2009), while others do not contribute at all.. This unequal contribution of individuals to the population can be a major driver of population demography (Jenouvrier et al. 2015).

However, part of the variability observed across individuals may also be explained by the fact that different individuals actually faced very different unpredictable conditions throughout their lives. While some individuals live in mainly favorable years, others may face unfavorable years all their lives (*i.e.* stochastic processes, Caswell, 2011; Steiner & Tuljapurkar, 2012).

Individual heterogeneity also depends on different allocation trade-offs in their life-history traits, which can be defined as different life-history "strategies" (Fay et al. 2022). In this case, fitness is increased due to a change in one trait but decreased by a second trait (Roff and

Fairbairn 2007). Although these processes are mainly visible at the species/population level, it may also vary among individuals of the same population. Skipping breeding events is a classic example of such strategy, as it will directly reduce individual fitness by removing a breeding event, but it might also increase it on the long-term by improving longevity due to lower breeding costs (Stearns 1989).

Apart from breeding success and longevity, fitness can depend on other life-history traits such as early development (Lindström 1999), phenology (Reed et al., 2009) or mating and foraging behaviors (Grémillet et al., 2016; Patrick & Weimerskirch, 2014), although their relative importance is rarely studied. The combination of the effects of such traits on fitness is difficult to assess, due to the complex interactions amongst them that may indirectly affect other traits, which may either compensate or amplify one another.

Here, we disentangled the different processes leading to individual heterogeneity in fitness such as intrinsic quality, strategies or environmental stochasticity by investigating simultaneously the combined effects of 18 life-history traits on lifetime fitness and in the little penguin (*Eudyptula minor*). The little penguin is a suitable model for this aim with regards to its relatively short life compared to other seabirds (6.5 years in average, up to around 20 to 25 years; Dann et al., 2005). It exhibits inter-individual variability in survival and breeding success, linked to many different breeding behaviors such as multiple clutches (1 or 2 clutches of two eggs) or skipped breeding events, high asynchrony in their breeding phenology, high divorce rate (up to 50%) and a high variability in their foraging efficiency and strategies at sea (Reilly and Cullen 1979, 1981, Chiaradia and Kerry 1999b, Ropert-Coudert et al. 2003, Saraux et al. 2011a, Pelletier et al. 2014, Joly et al. 2022).

Variability in individual quality in breeding is mainly driven by differences in their capacity to acquire and/or spare energy (Kahane Rapport et al. 2022). As reproduction is energetically costly, we expected both the energy stored over winter and foraging efficiency during breeding to play essential roles in explaining inter-individual variability in little penguin fitness. Further, because foraging success while breeding is often related to the match of the breeding period with prey abundance (Durant et al 2007), phenology was expected to affect foraging and breeding performances strongly (Joly et al, 2022; LeBohec et al, 2007; Regular et al, 2014). Reproducing earlier in the season might also give individuals access to better partners or nesting sites.

Besides differences in intrinsic individual quality, we also expected inter-individual heterogeneity to result from differences in energy allocation trade-offs among individuals. While breeding earlier in life or attempting two clutches per year could increase immediate breeding success but decrease longevity through earlier senescence (Zammuto 1986, Kim et al. 2011), skipping breeding events should decrease short-term breeding success but increase longevity (Le Bohec et al., 2007). Finally, the reproduction/maintenance trade-off (Williams 1966) could also be translated at the breeding season scale by looking at parameters such as the meal proportion given to chicks or the regularity of feeding (Weimerskirch, 1998).

To quantify the relative contribution of all these pathways to individual fitness, we built a structural equation model including all the traits mentioned above and their interactions, using a 19-year-long database of 162 individuals monitored throughout their entire life (including 87 for which we knew all 18 traits of interest). As individuals did not all live through the same years and some may have benefited or suffered from the conditions of the years they lived in, we ran a second model removing potential stochastic processes by expressing individual life-history traits relative to the other individuals living simultaneously. We expected the effects of most environment-depending variables, such as foraging or phenology, to be downscaled in amplitude.

2. **Methods**

a) Little penguins fitness and life-history traits

Fitness

Individual fitness was assessed using an adapted population projection matrix (Leslie 1945) as described by McGraw & Caswell (1996). Each individual's fitness was estimated as the dominant eigenvalue of an age-structured projection matrix, where the matrix is the size of the individual's lifespan, the first row is the number of chicks fledged per year divided by two (as only half of the genome is given by a single parent) and below the diagonal is yearly survival (1 until death). As such, individual fitness should represent the asymptotic growth of an individual genotype through time.

Breeding behavior and survival

Longevity was measured as the number of years between hatching and death. The number of breeding events was the number of times eggs were laid. The mean proportion of chicks fledged was estimated as the number of chicks fledged during life divided by the number of eggs laid. Age at 1st breeding was the age at first recorded laying. As some little penguins can lay a second clutch in the same season (Reilly and Cullen 1981), we assessed the proportion of 2nd clutch as the number of breeding seasons during which an individual attempted two clutches divided by the number of breeding seasons (*i.e* seasons with at least one laying event). We calculated the proportion of skipped breeding events as the number of seasons an adult penguin did not attempt breeding divided by the number of years between its first breeding attempt and its death.

Finally, the breeding cycle was separated into 3 stages: 1) the incubation period lasting for about 35 days, 2) the guard period (~2 weeks) when one parent stays with young chicks while the other forages at sea and 3) the post-guard period (5 to 8 weeks), when chicks are left alone during the day and parents return ashore at night to feed them (Chiaradia & Kerry 1999).

Mating behavior

We assessed the partner and nest changing proportion as the proportion of the breeding season during which an individual had a different partner/nest from the previous season. Only the first breeding event of each season (1st clutch) was considered.

Phenology

Phenology was investigated through the combination of two factors: i) personality: the average level of behavior through life and ii) plasticity: the penguin response to environmental variation as defined in (Dingemanse et al. 2010), Plasticity was calculated for each individual as the slope of the linear model between its laying dates and the timing of the annual decrease in chlorophyll concentration, which is known to affect little penguins phenology (Ramírez et al., 2021, Joly et al. 2022). Chlorophyll concentration data were extracted from MODIS/SeaWifs from the NASA (https://earthdata.nasa.gov/) dataset following Joly et al. 2022 (see *Supplementary Material S2*). The end of the chlorophyll peak was defined as the date at which 90% of the yearly cumulated daily chlorophyll was reached (Brody et al. 2013). Individual plasticity was then extracted from the following model:

Laying date ~ Chloro end * Individual + (1| year)

In this model, the date at which the chlorophyll peak ends (Chloro end) is the seasonal environmental cue to which penguins should react to assess the best moment to breed (Ramírez et al. 2016; Joly et al. 2022). While the penguin's laying date should be responsive to this variable, each individual is expected to respond with strong or weak strength (*i.e.* be more or less plastic). Here the model computes a slope per individual, *i.e.* the strength of the laying date shift in response to environmental cue shift, while considering the different years penguins lived in.

Body mass before breeding

Because body mass was not always recorded on the exact day of the laying date, body mass before breeding is the closest mass in a [-5,+5] days interval for males and a [-5,0] days interval for females (to avoid mass loss after egg-laying). Lifetime mass before breeding is as the mean of every breeding season's value.

Foraging performance during the breeding season

Adult foraging performance was based on trip duration and associated mass gain estimated through the APMS. Foraging trip duration was the number of days between "departure" and "arrival" dates (Chiaradia & Kerry, 1999). As most foraging trips lasted one day during guard (96% 1-d trips and 4% 2-d trips), trip duration was only investigated during incubation and post-guard. Trips longer than 17 days were considered as missing detections from the APMS and discarded (Saraux et al. 2016).

Adult body mass change was the mass change per foraging trip, calculated as the difference between a penguin's body mass after and before a given foraging trip. Only body mass changes ranging from [-75 to 500 g] during incubation and [0 to 600 g] during chick-rearing were considered in this study (see Salton *et al.* 2015 and Saraux & Chiaradia 2021). For trip duration and mass gain to be independent, mass gain was corrected for each breeding stage separately using residual values from the linear model [mass gain ~ trip duration] (Joly *et al.* 2022). Body mass gain during guard and post-guard trips were then scaled (*i.e.* standardised according to mean and standard deviation) by stage and grouped as mass gained during chick-rearing.

Lifetime foraging variables were assessed separately for different breeding stages (incubation and post-guard/chick-rearing) as the mean of each season's trip average to ensure that every season had the same weight in the final value, correcting for different numbers of trips.

Parental care

We built three investment variables to distinguish between energy allocated to chick growth and adults' survival. First, a chick-feeding irregularity was defined as the standard deviation of seasonal trip durations (post guard only). Because this variable was highly correlated to post-guard trip duration (*Supplementary Material S3*), we only kept chick feeding irregularity in our model.

Second, the proportion of meal mass delivered to the chicks was estimated during post-guard. Chick meal mass was calculated as the mass change difference between each "arrival" and the following "departure", as recorded by the APMS (Saraux et al. 2011a). Based on previous data, only meal masses ranging from [0 to 500 g] were considered to avoid unrealistic values (Chiaradia & Nisbet, 2006). The meal proportion given to chicks was then calculated as the chick meal mass divided by the mass change of the adult over the previous foraging trip. Note that the meal mass proportion given to chicks can be over 100%, if the adult entailed its own reserve while foraging for the chicks. Still, to avoid potential bias due to false negatives, proportions higher than the 95% interval around the mean proportion of food given to chicks [48%; 146%] were not considered.

As longer guard periods result in higher growth and fledging success due to longer intensive chick care (Chiaradia and Nisbet, 2006), lifetime guard length in days (mean over all breeding seasons) was also used as an index of reproductive effort. To avoid misinterpretation due to failed breedings, only guard lengths within a 95% interval around the mean (11-35 days) were kept.

b) Statistical analysis

We conducted two path models to examine the inter-individual variability of fitness. Path models are used to assess the relative strength of direct and indirect relations among variables (Wold, 1980; Wright, 1934, more details in *Supplementary Material S4)*. Structural equation modelling was computed using the partial least square path modelling method from `plspm 0.4.9` plspm function (Sanchez 2017, *more details in Supplementary Material S4*). Fitting model assumptions were checked following (Kline 2015) and are detailed in *Supplementary Material S5*. Overall, model validation was based on robust Satorra-Bentler corrected values (Hu and Bentler 1999) of RMSEA < 0.08, CFI > 0.90 and SRMR < 0.08, although small deviations from these values (< 0.02) were accepted due to our small sample size for such model (87 values). Direct relations between variables are presented with their 95% CI and associated p-value, while total effects of variables on fitness (*i.e.* sum of all direct and indirect effects of a given variable) are presented with their bootstrap estimated (n = 10000) 95% confidence interval around the mean and were considered significant when the 95% CI did not overlap 0. Lavaan grammar allows an input under the form of multiple linear relationships that have been included in the model as available in *Supplementary Material S6*.

Raw path analysis

The direct relationships tested in the path were defined a priori based on current knowledge and detailed in *Figure 20*. In general, foraging performances and investment in chicks were expected to affect breeding success positively, but an increased investment was also expected to negatively affect longevity. Mating behavior, phenology and the main life-history traits (age at first breeding, skipping reproduction events, etc.) were expected to importantly affect fitness through longevity.

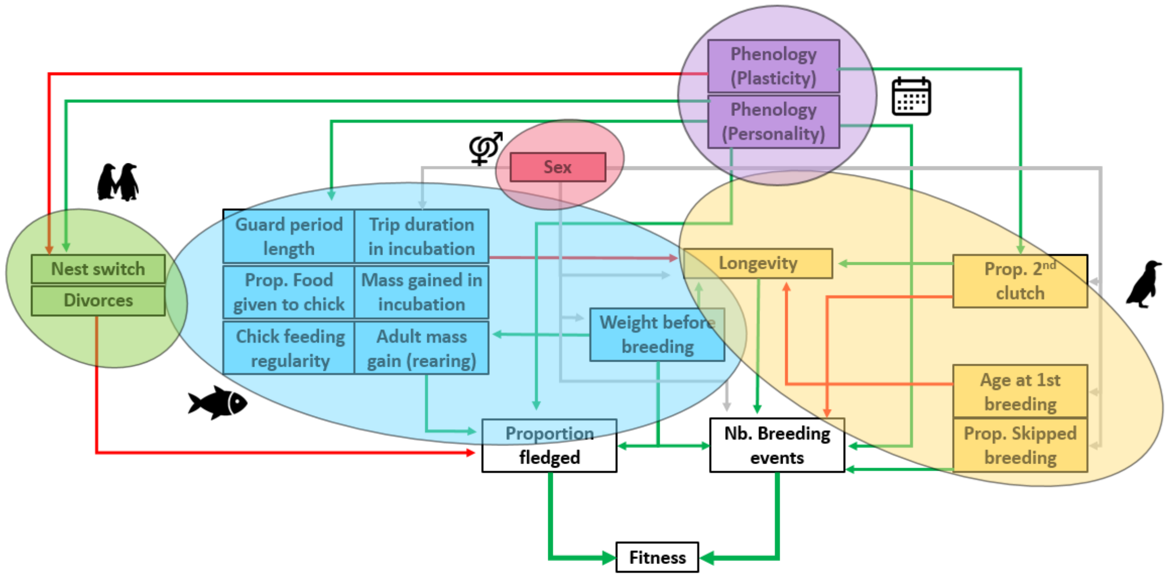


Figure 20: Theoretical path modelling including main expected relations among foraging (blue), chick investment (grey), breeding behavior and longevity (yellow), phenology (purple), mating behavior (green) and sex (red) as well as their effect on breeding success and fitness. Relationships expected to be negative are presented with red arrows while positive ones are presented with green arrows. For clarity purposes, instead of displaying all arrows, arrows pointing from/to a block composed of several variables were pooled into a single one representing the whole block.

Path analysis without year effect

Because individuals did not all live at the same time in our study, differences in fitness amongst individuals could translate to differences in individual quality or strategies, resulting from differences in environmental conditions over years (*i.e.* stochastic processes). To distinguish those individuals having winning strategy/high quality vs. the "lucky" ones experiencing excellent conditions throughout their life, we conducted a second path analysis including the same variables and relationships as the first path model, but for a correction applied to all variables to remove the effect of the different years. This was done by getting relative values per year, *i.e.* subtracting each event's average annual population value (*i.e.* average value of each individual) from the individual value for each variable. We distinguished three cases to accommodate different types of variables,: i) parameters measured once a year (*e.g.* the number of clutches, phenology personality, guard duration, proportion of chick fledged), for which we centered by removing the annual mean of the population to the annual individual value, ii) parameters estimated several times a year (*i.e* foraging trips and meal proportion given to chicks) for which we removed the annual mean of the population to all trip values before averaging the relative variable to get an annual value and iii) parameters originally estimated once across an individual's life (*e.g.* longevity, pair switch and nest infidelity), decomposed in a series of 0 or 1 each year to which the population mean was subtracted. Examples of cases ii and iii can be found in *Supplementary Material S7*. All corrected annual values were then averaged over the individual's life. Phenology plasticity was estimated as the slope of the same relationship as before, albeit on yearly-centered laying dates instead of raw laying dates. Only fitness, the number of breeding events (for which we wanted to understand how they were affected by relative variables) as well as sex and age at 1st breeding were not corrected for. The path analysis was then conducted as detailed in *3.1*.

3. <u>Results</u>

a) <u>Fitness and life-history traits</u>

<u>Individual fitness</u>

Individual fitness was assessed for 162 breeding individuals that laid at least one egg and were monitored from birth to death (*Figure 21)*. Among them, 27 individuals (17%) failed to fledge a single chick during their life (5.4 ± 3.9 SD years), resulting in a 0 fitness. However, 135 individuals (83%) produced at least one chick during their life (9.3 ± 4.3 years). Among them, 14 individuals (9%) had a fitness of less than one, meaning they only produced one chick during their life. A total of 24 individuals (15%) had a fitness of exactly one, meaning they fledged two chicks in their life. Most individuals (97 penguins, *i.e.* 60%) had a fitness above one (1.27 ± 0.11 on average), *i.e.*, they fledged more than two chicks (10.1 ± 5.5 chicks in average).

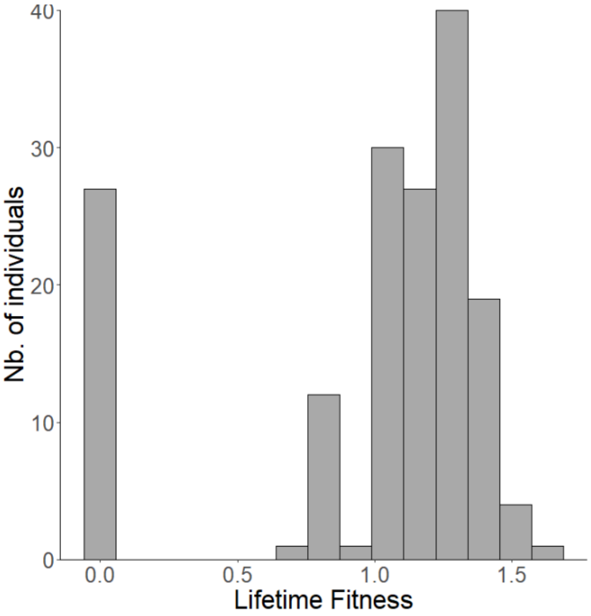


Figure 21: Individual fitness histogram for all 162 mature little penguins known for their entire life.

<u>*Life-history traits*</u>

The distribution of life-history traits highlights inter-individual variability *(Figure 22)*. Individuals that reached maturity most commonly died at the age of 5, while the average longevity remained much higher (8.6 ± 4.5 years). Around 38% of individuals never attempted to lay a 2nd clutch, and 37% never skipped any breeding seasons during their lives. Conversely, 14% of individuals missed breeding seasons and 34% produced a 2nd clutch more than half of the time.

Age at 1st breeding attempt (laying) was 3 years old most of the time (60%), but was also regularly 2 or 4 years old, and rarely at 1 (n=5) or above 4 years old (n=6). The mating behaviors (partner or nest changes from one season to the next) varied from individual to individual, from no change during their life to every season changes.

Guard period length was variable, from 11 to 34 days, but it was, on average, around 20 days long (19.5 ± 3.5 days). Phenology was highly unsynchronised, the time from the earliest and latest breeders of a given season being almost half a year (177 days, from day 194 to day 349), although the average laying date was day 282 ± 23 (mid-October).

The plasticity in phenology in response to the peak of chlorophyll concentration was again very variable among individuals. Still, most individuals (90%) advanced breeding when the end of the chlorophyll peak occurred earlier and only a few displayed the opposite relationship of delaying breeding. On average, individuals bred 3 days earlier (3.1 ± 3.9) for each day the end of the chlorophyll peak ended earlier, although some displayed a much stronger response, advancing reproduction by 10 days per day of shift in the bloom end.

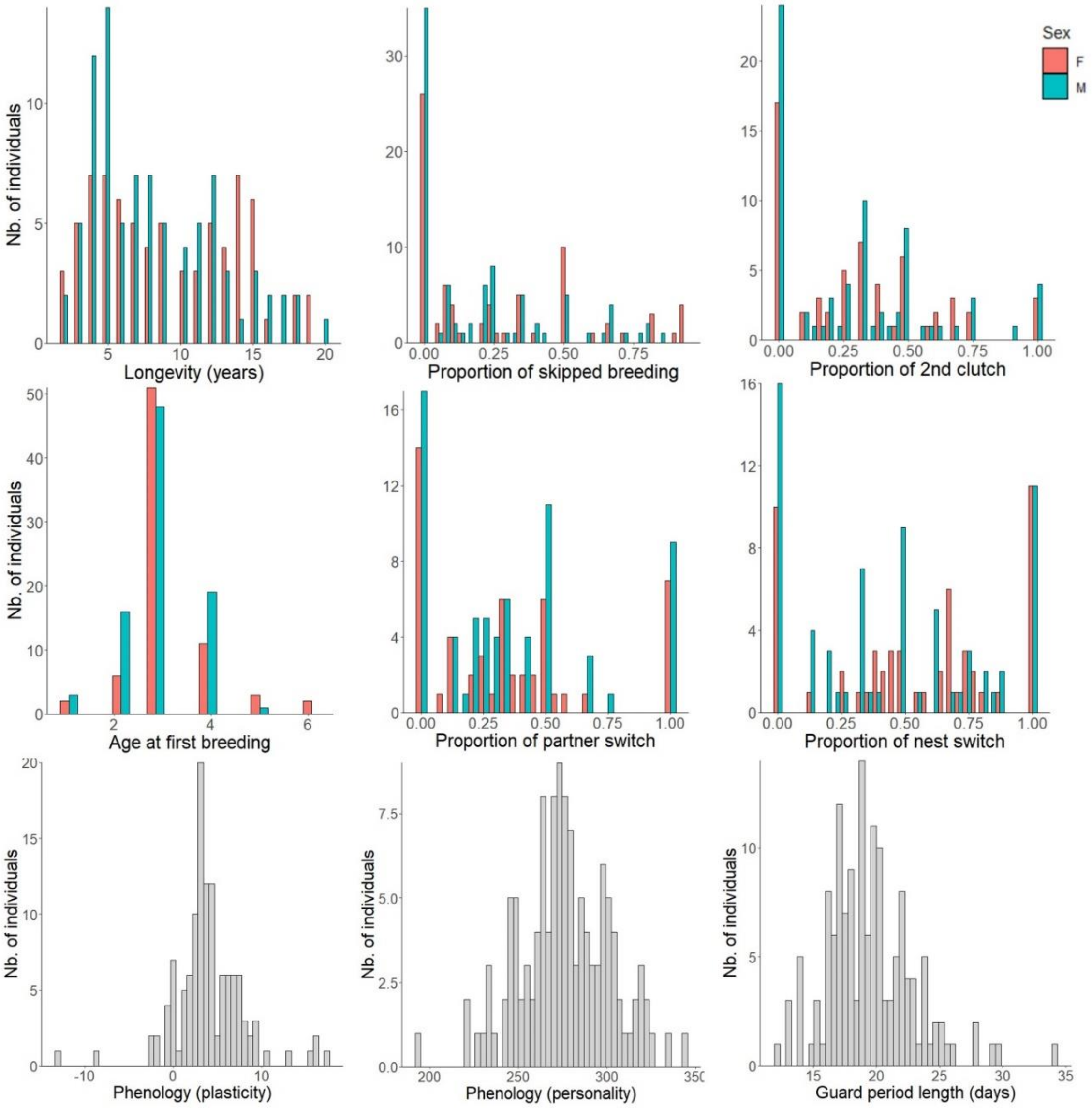


Figure 22: Histograms of life-history traits associated to survival, breeding and mating behavior and phenology (skipped breeding, 2nd clutches, age at 1st breeding, partner/nest switch and personality and plasticity in phenology) and longevity of 162 mature little penguins known for their entire life depending on their sex when applicable (males are represented by blue bars and females by red ones). Because all traits could not always been estimated, the sample size varies for each histogram.

b) Direct relationships between traits

The first path analysis (chi-square < 0.001, CFI = 0.91, RMSEA = 0.082, SRMR = 0.078), has been conducted on 87 individuals (breeding at least twice) for which the 18 variables included in the model were available. Outcomes are presented in *Figure 23*. Details are in *Supplementary material S8*.

The proportion of chicks fledged and the number of breeding events both had a strong effect of similar strength on individual fitness (0.63 and 0.51 respectively, $p < 0.001$, $R^2 = 0.659$) although being poorly correlated with each other (Pearson's $R^2 = 0.18$, *Supplementary Material S9*). Number of breeding events strongly depended on individual longevity (relative estimate of 0.83, CI95% [0.76; 0.90], $p < 0.001$). Breeding events also benefited from a higher proportion of 2nd clutches (rel. est. = 0.27 [0.20; 0.34], $p < 0.001$), while it was negatively affected by older age at 1st breeding (rel. est. = -0.21 [-0.27; -0.15], $p < 0.001$) and skipped breeding seasons (rel. est. = -0.27 [-0.37; -0.19], $p < 0.001$). These four variables (longevity, 2nd clutches, 1st breeding, skipped breeding) explained 96% of the variability in the number of breeding events (plspm $R^2 = 0.964$).

Foraging and investment in the chicks affected breeding success through mass gained at sea and chick feeding, although the results were not statistically significant. Individuals gaining more mass at sea during chick-rearing tended to fledge more chicks per breeding event (rel. est. = 0.22 [-0.04; 0.48], $p = 0.089$). Conversely, individuals that managed to provide a higher proportion of the meal mass to their chicks exhibited a lower proportion of chicks fledged (rel. est. = -0.25 [-0.56; 0.00], $p = 0.057$).

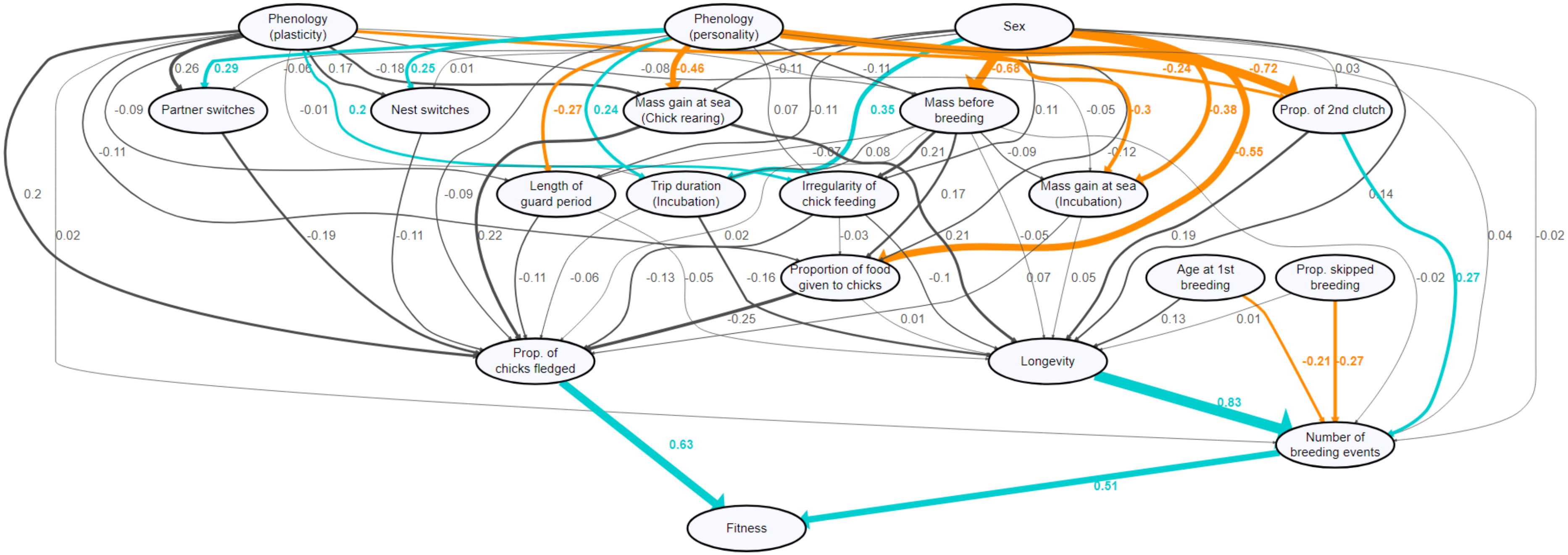


Figure 23: Path modelling of the relation between fitness and 18 different life-history traits (light grey nodes). Numbers correspond to relative estimates of partial least square path model. Arrows and numbers colours indicate the positive/negative (blue/orange) sign of the relation when it was considered significant (bootstrap IC95% (n = 10000) does not include 0). Grey arrows and numbers correspond to non-significant relations.

Average phenology (personality) had broad effects on several parameters. Earlier breeding was linked with a higher proportion of 2nd clutches (rel. est. = 0.71 [0.59; 0.81], $p < 0.001$) and higher mass gained at sea during chick-rearing (rel. est. = 0.46 [0.26; 0.64], $p < 0.001$) and tended to result in shorter foraging trips during incubation ($p = 0.011$), longer guard periods ($p = 0.005$) and lower partner switch ($p = 0.003$) and nest switch ($p = 0.017$). Conversely, plasticity in phenology only affected the proportion of 2nd clutches (rel. est. = -0.24 [-0.38; -0.06], $p = 0.003$). Phenology (and sex) explained respectively 53% and 24% of the variability in proportion of 2nd clutches and mass gain during chick-rearing (plspm $R^2 = 0.526$ and 0.238).

Mating behavior (partner and nest switches) had small to no effects on breeding success. And while other variables such as sex significantly affected some life-history traits (mainly linked to foraging), these effects did not impact breeding success and fitness. Females were for instance, lighter before breeding and gave less food to the chicks in proportion compared to males (full stats $p < 0.001$), without any consequences on the number of breeding events or the proportion of chicks fledged.

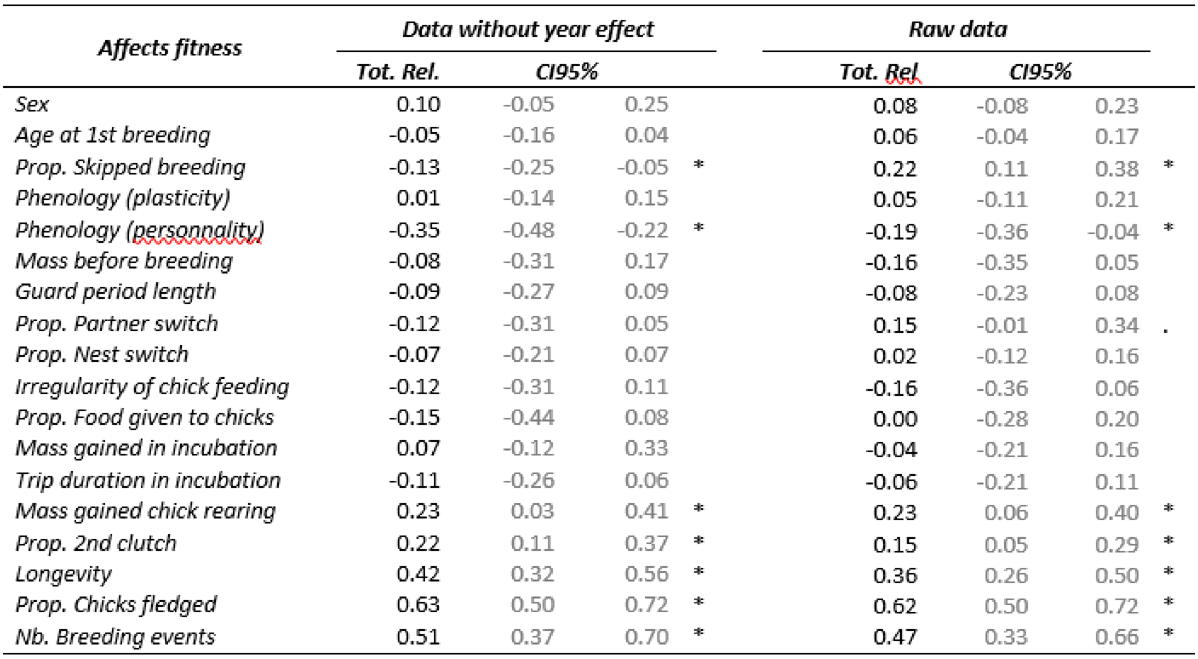
The second path analysis (chi-square < 0.001, CFI = 0.88, RMSEA = 0.092, SRMR = 0.078) presented the same model as in *Figure 23*, but data were corrected by year to only account for inter-individual differences rather than differences due to individuals living in different years. In most cases, relationships were similar to what was found with raw data and presented above, albeit some changes in effect strength and a few rare occasions, where the relationships changed (*see Supplementary Material S10 & S11*).

c) Overall effect on fitness

Variables' total effects on fitness are the combination of their direct and indirect effects through other variables (*Table 1*). First, penguins' fitness was directly affected by the proportion of chicks fledged, and number of breeding events (total effects = direct effects presented above).

Longevity also significantly affected fitness (0.42 CI95% [0.32; 0.56]) through an increased number of breeding events. Regarding indirect variables, the penguin fitness increased when individuals skipped fewer breeding seasons (rel. est. = -0.13 [-0.25; -0.05]) and conducted more 2nd clutches (rel. est. = 0.22 [0.11; 0.37]). In terms of foraging, individuals gaining more mass at sea during chick-rearing also exhibited higher fitness (rel. est. = 0.23 [0.03; 0.41]). Finally, early breeding had the strongest and most beneficial total effect on fitness, with a strength almost as important as breeding success and longevity (rel. est. = -0.35 [-0.48; -0.22]). No other studied variables affected fitness, despite a significant direct effect on chick-fledging or the number of breeding events for some of them (such as the proportion of mass gained given to chicks or plasticity in phenology, *Figure 23*) as other indirect effects partly compensated it.

Table 1: Total effect (sum of direct and indirect) of 18 different life-history traits on fitness either using raw data or transformed data to remove stochastic year effect. "Tot. rel." stands for the total relative estimates of partial least square path model. 95% Confidence Interval bootstrap (n = 10,000) are given. Significant relationships (i.e. CI95% not intersecting 0) are indicated by stars.



Affects fitness	*Data without year effect*				*Raw data*			
	Tot. Rel.	*CI95%*			*Tot. Rel*	*CI95%*		
Sex	0.10	-0.05	0.25		0.08	-0.08	0.23	
Age at 1st breeding	-0.05	-0.16	0.04		0.06	-0.04	0.17	
Prop. Skipped breeding	-0.13	-0.25	-0.05	*	0.22	0.11	0.38	*
Phenology (plasticity)	0.01	-0.14	0.15		0.05	-0.11	0.21	
Phenology (personnality)	-0.35	-0.48	-0.22	*	-0.19	-0.36	-0.04	*
Mass before breeding	-0.08	-0.31	0.17		-0.16	-0.35	0.05	
Guard period length	-0.09	-0.27	0.09		-0.08	-0.23	0.08	
Prop. Partner switch	-0.12	-0.31	0.05		0.15	-0.01	0.34	.
Prop. Nest switch	-0.07	-0.21	0.07		0.02	-0.12	0.16	
Irregularity of chick feeding	-0.12	-0.31	0.11		-0.16	-0.36	0.06	
Prop. Food given to chicks	-0.15	-0.44	0.08		0.00	-0.28	0.20	
Mass gained in incubation	0.07	-0.12	0.33		-0.04	-0.21	0.16	
Trip duration in incubation	-0.11	-0.26	0.06		-0.06	-0.21	0.11	
Mass gained chick rearing	0.23	0.03	0.41	*	0.23	0.06	0.40	*
Prop. 2nd clutch	0.22	0.11	0.37	*	0.15	0.05	0.29	*
Longevity	0.42	0.32	0.56	*	0.36	0.26	0.50	*
Prop. Chicks fledged	0.63	0.50	0.72	*	0.62	0.50	0.72	*
Nb. Breeding events	0.51	0.37	0.70	*	0.47	0.33	0.66	*

Once stochastic processes and year effects were removed from our variables (*Table 1*), the results of the new path analyses were highly consistent with those of the first model on raw data. Indeed, the variables that significantly affected fitness were strictly the same in both analyses. Further, the effect sizes of the proportion of chicks fledged, the number of breeding events, longevity and mass gained during chick-rearing remained similar between both analyses (although slightly decreased for longevity, rel. est = 0.36 [0.26; 0.50]). Nevertheless, some interesting differences also appeared. The effects of 2nd clutches and earlier breeding, while still significantly positive, were notably decreased in amplitude once the year effects were removed. More surprisingly, one relationship changed. While missing breeding seasons had an adverse impact on fitness before, here (*i.e.* after removing the year effect), it showed positive effects (rel. est. = 0.22 [0.11; 0.38]). Finally, switching partners had an overall positive (although non-significant) effect on fitness (rel. est. = 0.15 [-0.01; 0.34]).

4. Discussion

Fitness as an evolutionary concept refers to the overall genetic contribution of an individual to its population (De Jong 1994). The fact that some individuals disproportionately contribute to the population implies that others display a much less critical contribution (Aubry et al. 2009b). This variability in individual contribution to their population is vital to understanding population demography, especially in climate change (Grémillet and Boulinier 2009a, Jenouvrier et al. 2015). In this study, little penguins reached the end of life with very different fitness , either not contributing to the population (16%), making one chick (9%), contributing just enough to propagate their genes into the next generation (exactly 2 chicks, 15%) or over-contributing (> 2 chicks, 60%). While these differences in individual fitness may be explained by many different factors (Naves et al., 2006; Patrick & Weimerskirch, 2014; Reed et al., 2009), their relative contribution has rarely, if ever been assessed.

We showed that although stochastic processes explained part of the variability, fitness was mainly due to different individual capacities to multiply the number of their breeding attempts. In general, increased breeding attempts were achieved by living longer, laying more second clutches, skipping fewer breeding events, while fledging proportion was mainly driven by foraging efficiency. Besides those variables, the average phenology of an individual appeared to be one of the main contributors to its fitness due to very indirect but ubiquitous effects on many different life-history traits.

Lifetime fitness depends on the individual's capacity to maximise its survival, as longer life may lead to multiple breeding events (Stearns 1976) and on its capacity to efficiently fledge chicks at each breeding event (Brommer et al. 1998, Maccoll and Hatchwell 2004). In long-lived species such as seabirds, individuals are expected to favor survival over breeding success when trading-off energy allocation, as the number of future breeding prospects is important (Goodman, 1974; Stearns, 1992), so longevity is often expected to be the main component of individual fitness. Here, the number of breeding events and the proportion of fledged chicks had a similarly important effect on the variability in individual fitness. These results imply that both long-lived and short-lived strategies are somewhat equivalent at the individual lifetime scale for this species. Yet, this is not unexpected as little penguins are one of the shortest-lived seabirds, placing them at an intermediate position on the short-lived / long-lived species gradient, implying that the costs of a failed breeding event tends to have a more important impact on fitness than for species with much longer lifespan. Indeed, longevity is known to drive fitness through factors such as gained experience in long-lived species (*e.g.* albatrosses, Aubry et al. 2011). However, such interests of surviving might be less important in shorter-lived species where decreased performances tend to happen after only a few breeding events (Saraux et al. 2022).

Here, the number of breeding events still depended on longevity, but was also affected by the number of skipped breeding seasons, the proportion of 2nd clutches and the age at first breeding. The variability in these three parameters is a well-known trade-off between survival and breeding (*i.e* balance of allocation to breeding or self-maintenance, Le Bohec et al. 2007, Dobson and Jouventin 2010). While skipping a breeding event (season or 2nd clutch) decreases the immediate offspring production, it simultaneously reduces the costs of reproduction and increases the number of potential future breeding events (Desprez et al. 2018). The same trade-off applies for later age at 1st breeding (Aubry et al. 2009b), as starting to breed at an older age tends to decrease an individual overall number of breeding events but also allows individuals to delay the energetic costs of reproduction to optimum ages in their foraging and chick provisioning performance (Krüger 2005, Aubry et al. 2009a, Limmer and Becker 2009, Saraux and Chiaradia 2021). However, in this study we showed that no significant increase in longevity was associated with an increased number of skipped breeding events, leading to a significant detrimental effect of missed breeding events on individual fitness. Thus, if skipping breeding events to maximise longevity may be a good strategy in very long-lived species (Jenouvrier et al. 2005), this may not be true in relatively shorter-lived species such as the little penguin.

Regarding age at 1st breeding, there was no significant effect on fitness, although it led to slightly fewer breeding events. This may be explained by the lack of variability in age at 1st breeding in little penguins (*i.e* between 2 and 4 years old in almost all cases) and that the breeding success of young individuals is lower than older ones (Saraux & Chiaradia 2021). Thus, adding one failed breeding event might not affect lifelong fitness.

Finally, the balance between maintenance and reproduction can also be perceived at finer scales within breeding seasons. Higher parental investment should increase breeding success but decrease a parent's body condition and future success (Storey et al. 2017). This was investigated through 3 parameters in our study: the duration parents could maintain the intensive care guard period, the regularity of chick feeding and the proportion of the captured food allocated to the chicks. Yet, none of this affected fitness and their effects on either side of the energy balance were not significant either. This may be because individuals rarely overreach while favoring their own body reserves (Saraux et al. 2011c) to avoid decreased longevity. On the other hand, a decreased parental investment may be partly compensated by the partner, as little penguins exhibit unequal parental investment (Saraux et al. 2011a). Interestingly, we found no sex-specific strategies that directly affected fitness, while it is known to affect survival in many birds taxa (Liker and Székely 2005). Zhang et al (2015) also showed that although common terns exhibit sex-specific recruitment and survival, these effects did not translate to reproductive value.

Beyond energy allocation trade-offs, fitness should depend on an individual's quality (Coulson and Porter 1985, Bolton 1991, Blomqvist et al. 1997). Individual quality defines the capacity of an individual to maximise its life-history traits simultaneously and is often perceived through positive correlations between traits (Wilson and Nussey 2010, Vedder and Bouwhuis 2018), *e.g.* individuals reproducing better also surviving better.

Mass gained at sea during chick-rearing positively affected both longevity and breeding success (in lines with previous studies: Berlincourt & Arnould, 2015; Chiaradia & Kerry, 1999; Saraux et al., 2016), which indicates that an individual capacity to acquire energy (*i.e.* foraging efficiency) might be a major driver of individual quality (Lescroël et al. 2009, 2010).

Certain traits may not directly affect breeding success, but instead affect other life-history traits, thus reaching fitness through their capacity to influence various other traits rather than by the strength of a single effect. We established the strong positive impact of early phenology on fitness due to the cumulative sum of small effects on different parameters. We showed that earlier breeding was associated with varying behaviors of breeding, mainly significantly increasing 2nd clutch events, consistent with Reed et al. (2013). Earlier breeding was also important in affecting foraging and chick provisioning through increased mass gain at sea, decreased trip duration, or increased length of chick guard. If early phenology is so important for little penguins as seem to be the case for most seabirds (Keogan et al. 2018), one can wonder why individuals do not all breed early and why this is species so asynchronous. Evidence shows that individual breeding may start when reaching an energetic threshold (*i.e.* carry-over effect of wintering; Robinson et al., 2005; Salton et al., 2015). Thus, some individuals may delay their breeding until they reach this threshold (the required duration could then depend again on individuals' capacity to acquire energy or in their reproductive investment in the previous season for instance). While the shift in seabird breeding timing is often described as the result of individuals exhibiting plastic phenology to match with environment cycles (Frederiksen et al., 2004; Keogan et al., 2018; Reed et al., 2009), few significant effects of plasticity in phenology were found in this study. Likely, the overall population switch in phenology to cope with environmental shifts is so strong that it hides the inter-individual compound of this variability.

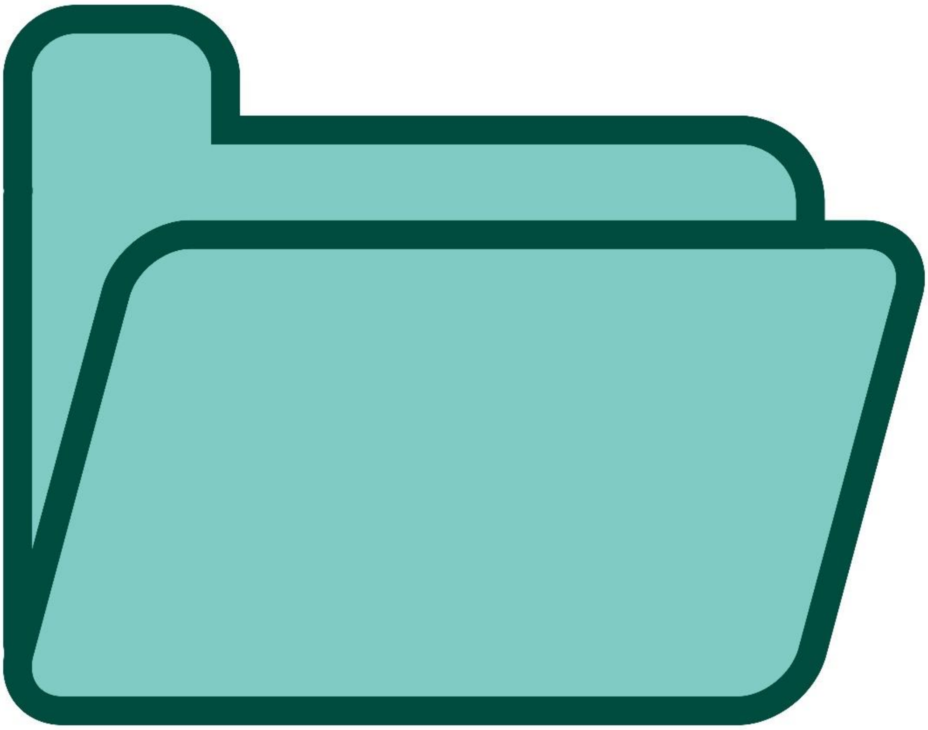
The role of stochastic processes in inter-individual variability is subject to much debate (Caswell 2011, Steiner and Tuljapurkar 2012, Davison et al. 2019). Individuals may perform better because of their quality or because they live in favorable conditions. We compared our results with those of a second model minimising stochastic processes by looking at individual performances relative to the population living in the same year. Based on our results, we argue that although stochastic processes tend to exacerbate individual variability; life-history traits were never entirely driven by unpredictable events while presenting no individual variation in the capacity to face the event. Some individuals lived in better years of earlier breeding and higher foraging performances, increasing their fitness. However, these processes did not explain the significant part of inter-individual variability. This is not surprising as relatively long-lived species using a partly capital breeding strategy should have a higher capacity to buffer environmental changes (Morris et al. 2008, Stephens et al. 2009). However, it implies that even processes that are strongly driven by overall population shifts and inherent variability (*i.e.* independently from the environment), such as phenology (Youngflesh et al. 2018, Keogan et al. 2018), include some inter-individual variability in the trait(*i.e* breeding earlier in the case of phenology). Whether this might have a genetic basis (heritability, (Dobson et al. 2017) or derive from early-life conditions (environmental and maternal effects, (Hamel et al. 2009) or other processes will need to be further investigated.

Conclusion

Using a 20-year dataset from 162 little penguins, we constructed a detailed map showing the different paths these iconic penguins take to lifetime fitness. Individual variability in life-history traits seemed to depend primarily on individual quality and secondarily on different trade-off strategies. Although energy allocation trade-offs are expected to mediate the effect of individual quality, our study demonstrates that they may not compensate for high intrinsic differences among individuals (Kim et al. 2011). We also showed that penguins' individual quality mainly relied on efficient foraging and early phenology, which are highly dependent on the environment (Joly et al. 2022), raising major questions about population demography in the context of rapid environmental changes.

Chapter III : Fitness

Supplementary Material



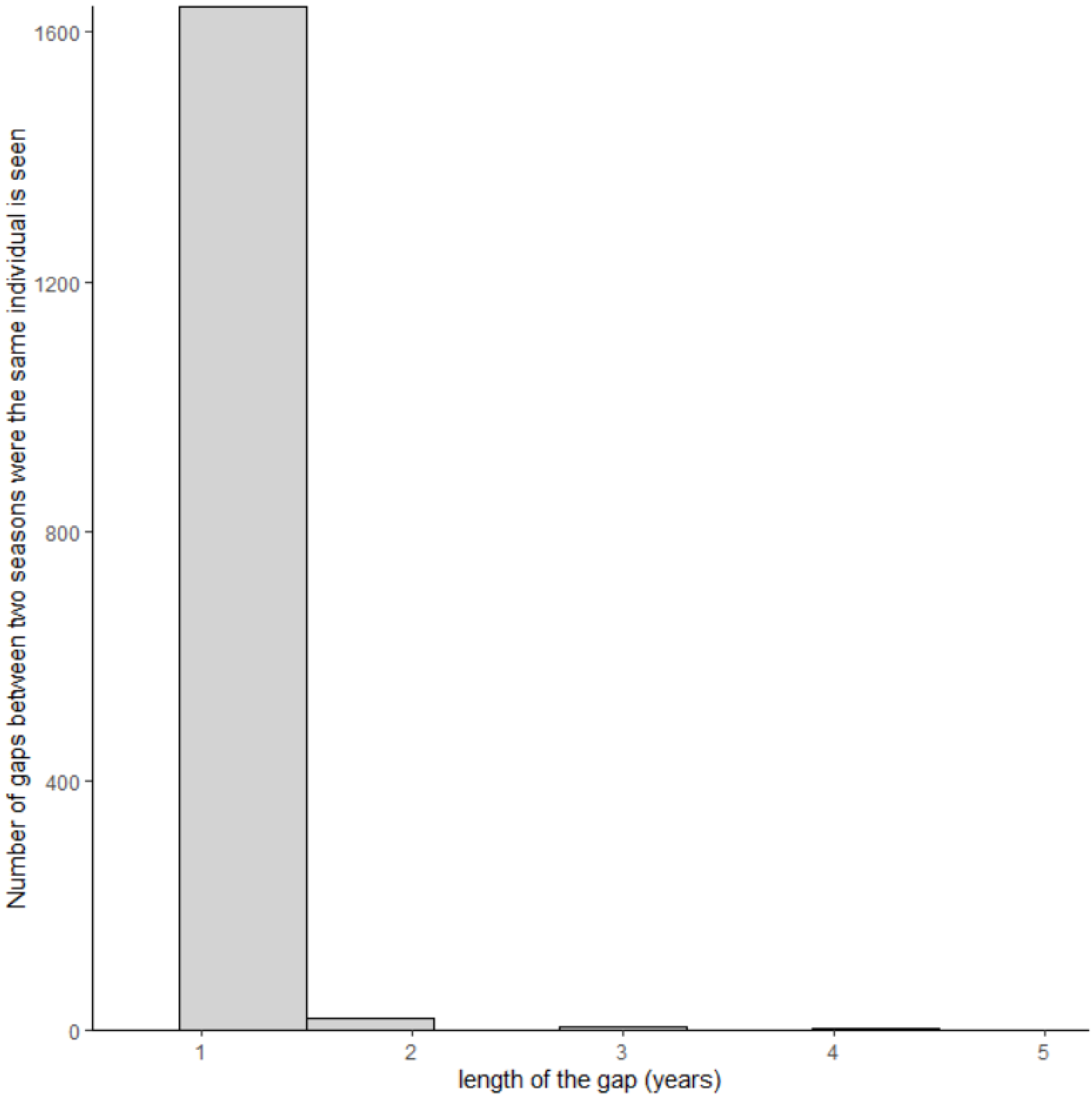


Figure S1: *Frequency of the gaps between two detection of an individual on the penguin automatic monitoring system in years. In almost all cases, individual is either seen every year or never seen again.*

Text S2: Chlorophyll random resampling method (*Figure S1*)

Chlorophyll-a concentration (Chla) was gathered from MODIS and SeaWiFS datasets to cover the entire study period. Raw data were truncated to a maximum value of 1.6µg/l to avoid abnormal high values of Chla at coastal pixels due to turbidity (*i.e.* the 99% quantile, coherent with Gibbs et al. 1986). Because data were not available in each pixel (due to cloud cover), random subsampling was performed on both datasets to assess the minimum number of pixels necessary to obtain unbiased daily means (*i.e.* deviation smaller than 5%, Figure S1).

To assess days with a sufficient number of gridded values to obtain an unbiased daily average, random subsamplings were performed separately for MODIS and SeaWiFS. Every day with more than 2,000 gridded values has been randomly resampled 10,000 times, from which we assessed the number of times were subsampling was significantly different from the daily average. More precisely, a subsampling was considered different from the daily average when mean(subsampling) > or < mean(daily gridded data) ± 5%. The minimum number of values to consider to assess an unbiased daily average is then defined as the lowest value were resampling is different from the daily average less than 5% of the time (all resampled days combined).

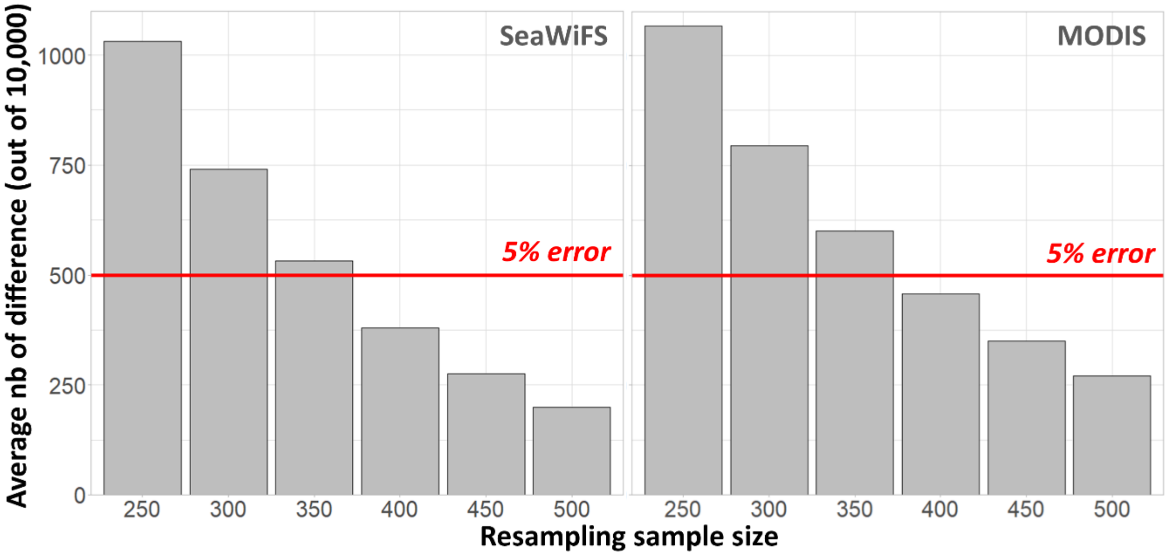


Figure S2: [Chla] Resampling method. *Average number of differences between full day data and random subsamplings of the day (5% difference with full day data) out of 10,000 random resamplings. Number of difference is tested for every day with more than 2000 gridded values. Minimum number of values to assess daily average is considered as the lowest sample size with less than 5% error (red line) = 400 daily values.*

Biased daily means due to too few pixels were then removed (1341 out of 3304 days for SeaWiFS and 1348 out of 6250 days for MODIS). SeaWiFS and MODIS daily time series were then merged based on their significant correlation over the 2002-2010 common period (Pearson's r = 0.56) and previous studies (Zhang et al. 2006). When MODIS and SeaWiFS data were available for the same day, only MODIS data were retained (due to a more precise grid).

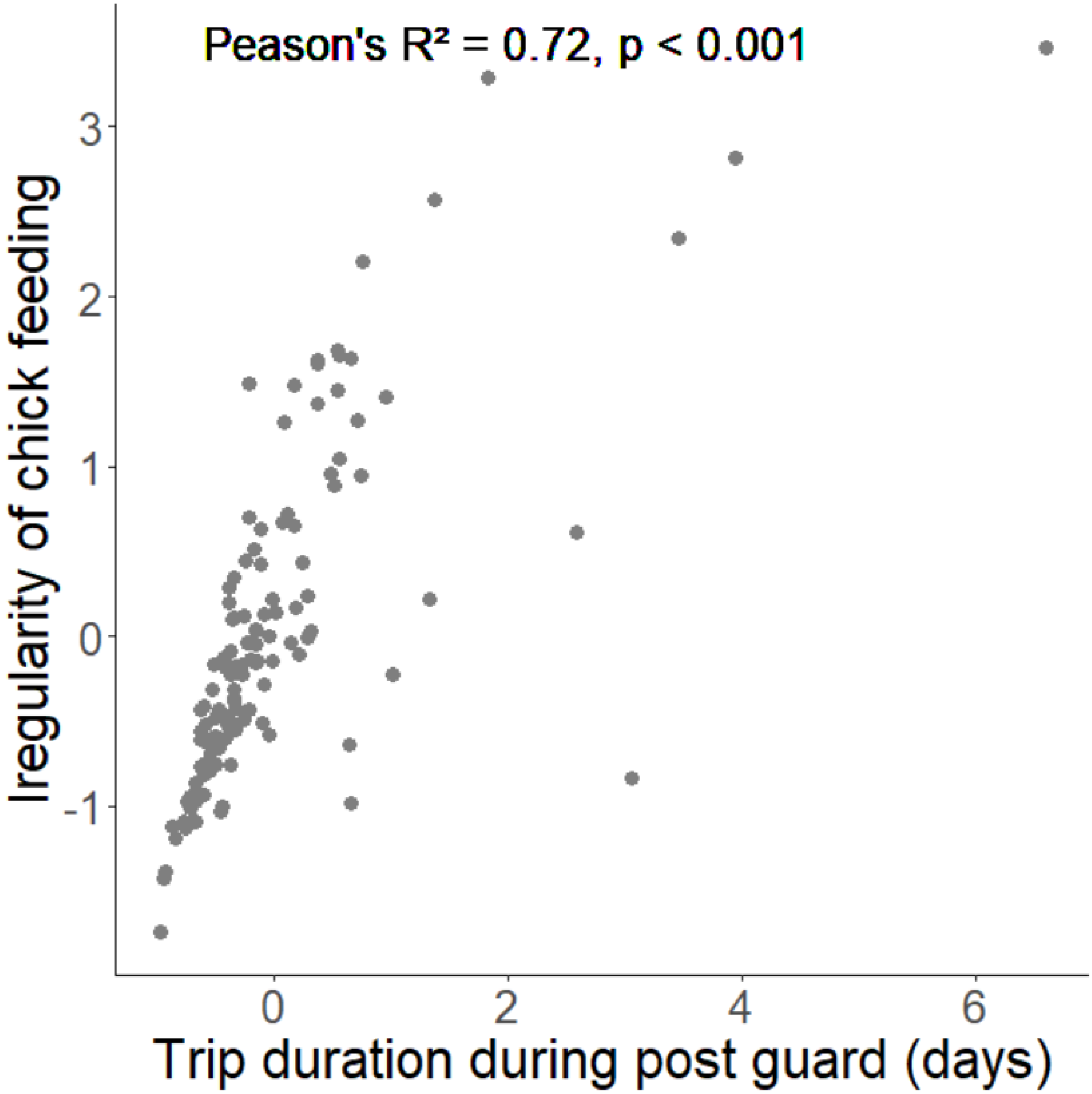


Figure S3: *Correlation between individual lifetime average trip duration and irregularity of chick feeding.*

Text S4: Path analysis and partial least square path modelling description

It is challenging to apply traditional statistical approaches such as multiple linear regressions to a multitude of indicators that are not independent and that may contain different or even conflicting signals and non-linear patterns (Cotter et al., 2009; Petitgas and Poulard, 2009). Path analysis is a statistical approach based on structural equation models, used to explore and quantify the direct and indirect relationships among multiple variables in a complex system. While it was originally developed for phylogenetic theoretical modelling (Wright 1918, 1921, 1922) it is now commonly used in various fields, including psychology (Werts & Linn 1970), sociology (Land 1969) and economics (Sonis & Hewings 1998). More recently, it has been used in ecology to investigate multiple causal relationships (Fan et al. 2016). The basic idea behind path models is that the complexity within a system can be modeled through a relational network among variables. Causal relations are built a priori in the model based on hypotheses and prior knowledge. Variables are represented as nodes that are connected to each other by directional links, called paths (Lleras 2005). Each of these paths is associated to an estimate depicting the relative strength of each relation. The effect of one variable on another is then the resultant sum of the direct effect (path coefficient) and indirect effects which describe the influence of the variable by taking an indirect path, *i.e.* through other variables. As such, path models allow to examine complex models with multiple variables simultaneously, providing a comprehensive understanding of the interconnections between variables. Partial least square (PLS) path modelling is one of the several existing structural equation modelling methods, and aims at finding latent factors or components that explain the maximum covariance between the predictor variables and the response variables (Sanchez et al 2013). In these models, PLS path models are formally defined by two sets of linear equations: the measurement model (also called the outer model) and the structural model (also called the inner model). The measurement model specifies the relations between a construct, *i.e.* the latent variable and its observed indicators (also called manifest variables, Wold 1980), whereas the structural model specifies the relationships between the constructs (Henseler 2017)

Text S5: Path analysis assumption method

Structural equation modelling was computed using the partial least square path modelling method from `plspm 0.4.9` plspm function (Sanchez 2017). Potential model bad fit between the hypothesised model and the observed data was verified by computing the model using maximum likelihood structural equation model with Satorra-Bentler scaling corrected statistic from `lavaan 0.6.9` sem function, following Evermann & Tate (2016) and Hu & Bentler (1999) recommendations. Structural equation model chi-square, RMSEA, CFI and SRMR are systematically reported (Kline 2015), although chi-square was not considered in our model validation due to its great sensitivity to sample size. Threshold values of model validation are RMSEA < 0.08, CFI > 0.90 and SRMR < 0.08 (Kline 2015), although small deviations from these values were accepted due to our small sample size (87 values). Path models using maximum likelihood method should not violate the assumption of normality. To check for that, we conducted separate linear models (one per relation written in path modelling) and graphically checked normality of their residuals. Partial least square path modelling method is however not resting on any distributional assumptions (Sanchez 2017).

Text S6: Path analysis model details with lavaan grammar

Fitness ~ Prop. Chicks fledged + Breeding events

Breeding events ~ Longevity + Phenology (pers.) + Phenology (plast) +Prop. 2nd clutch + Skipped breeding +Age t 1st breeding + Weight before breeding + Sex

Prop. Chicks fledged ~ Prop. Nest switch + Phenology (pers) + Phenology (plast) + Prop. Partner switch + Prop. Food to chicks + Irregularity of chick feeding + Mass gained at sea (rearing) + Trip duration (incub.) + Mass gained at sea (incub.) +Weight before breeding + Guard length

Longevity ~ Prop. Food to chicks + Irregularity of chick feeding + Weight before breeding + Mass gained at sea (rearing) + Trip duration (incub.) + Mass gained at sea (incub.) + Age t 1st breeding + Prop. 2nd clutch + Skipped breeding + Guard length+ Sex

Prop. 2nd clutch ~ Phenology (pers.) + Phenology (plast.) + Sex

Mass gained at sea (rearing) ~ Phenology (pers.) + Phenology (plast.) + Sex

Trip duration (incub.) ~ Phenology (plast.) + Phenology (pers.) + Weight before breeding + Sex

Mass gained at sea (incub.) ~ Phenology (plast.) + Phenology (pers.) + Weight before breeding + Sex

Prop. Food to chicks ~ Phenology (pers.) + Phenology (plast.) + Weight before breeding + Sex

Irregularity of chick feeding ~ Phenology (plast.) +Phenology (pers.) + Weight before breeding + Sex

Prop. Nest switch ~ Phenology (plast.) +Phenology (pers.) + Sex

Prop. Partner switch ~ Phenology (plast.) +Phenology (pers.) + Sex

Guard length ~ Phenology (plast.) + Phenology (pers.) + Weight before breeding + Sex

Weight before breeding ~ Phenology (plast.) + Phenology (pers.) + Sex

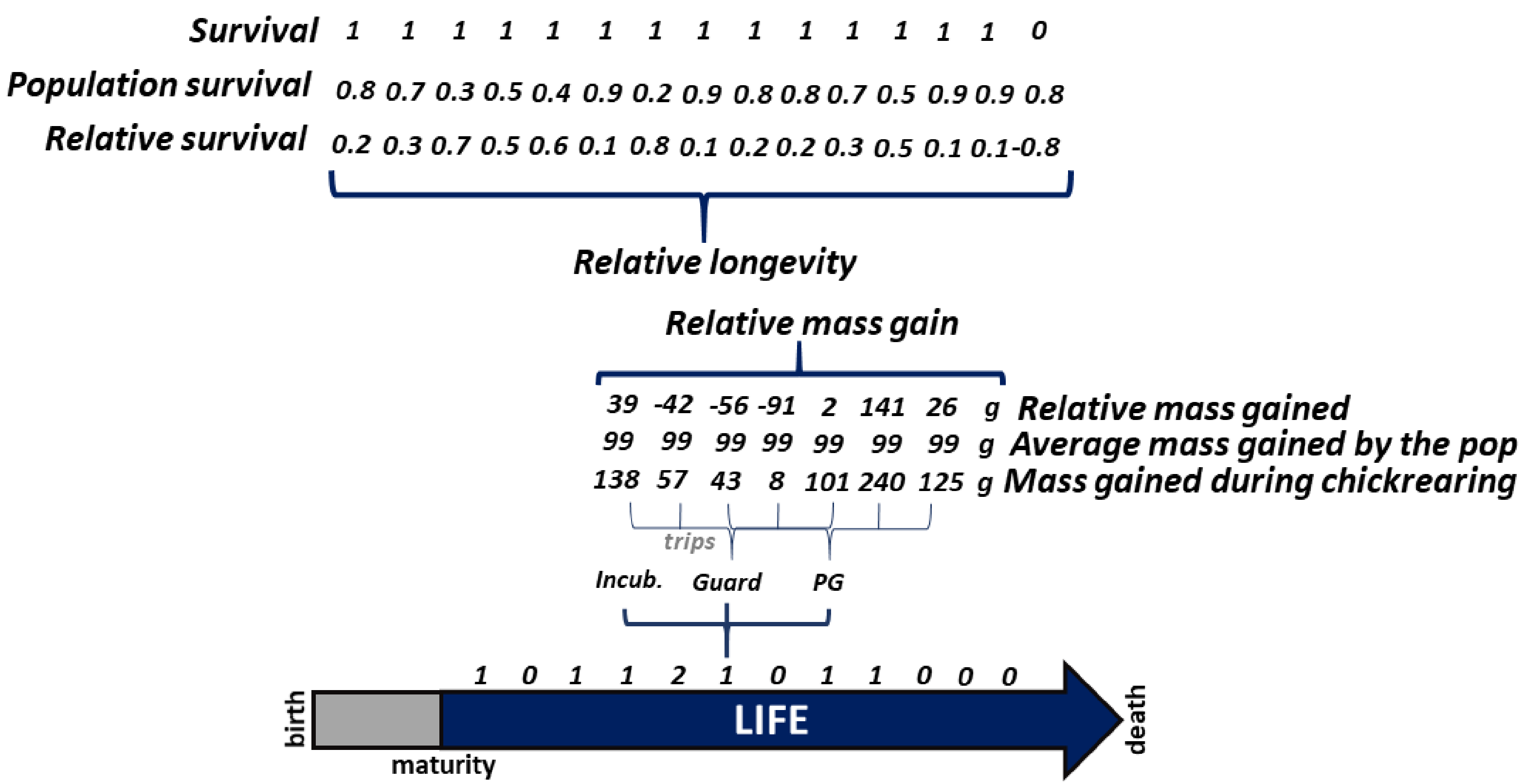


Figure S7: *Methods to build variables independently from year effects, i.e. within year centering through 2 examples: (A) longevity and (B) mass gained during chick rearing. Individual relative longevity is assessed as yearly survival (1 until death year where 0) from which yearly population survival is subtracted (proportion of individuals that did not die each year) to get individual annual relative survival. Relative longevity is then obtained by averaging relative survival over life. Relative mass gained during chick-rearing is assessed at the trip scale by subtracting the population yearly average mass gain to each individual trip's mass. Seasonal relative mass gain is then obtained by averaging trips relative mass gain by season, from which lifetime relative mass gain is assessed as the average of all breeding seasons' annual relative mass gain.*

Table S8: *Details of Partial least square path modelling estimates for all raw data direct relationships, including real estimate, bootstrap average estimate (n = 10,000), standard error and 95% upper and lower confidence intervals.*

	Estimate	**Bootstrap**	**Std.Error**	**Perc.025**	**Perc.975**
Sex -> Weight before breeding	-0.6759	-0.6725	0.0578	-0.7745	-0.5506
Sex -> Guard length	-0.1072	-0.1028	0.1315	-0.3529	0.1447
Sex -> Prop. partner switch	-0.0605	-0.0563	0.1018	-0.2491	0.1455
Sex -> Prop. nest switch	0.0148	0.0248	0.1024	-0.1730	0.2208
Sex -> Irregularity of chick feeding	0.1106	0.0975	0.1267	-0.1736	0.3243
Sex -> Prop. Food to chick	-0.5465	-0.5477	0.1060	-0.7552	-0.3364
Sex -> Mass gained at sea (incub.)	-0.3817	-0.3738	0.1427	-0.6434	-0.0942
Sex -> Trip duration (incub.)	0.3524	0.3680	0.1435	0.0976	0.6612
Sex -> Mass gained at sea (rearing)	-0.1137	-0.1164	0.0952	-0.3006	0.0690
Sex -> Prop.2nd.clutch	0.0251	0.0231	0.0767	-0.1184	0.1767
Sex -> Longevity	0.1355	0.1308	0.2061	-0.2442	0.5507
Sex -> Breeding events	-0.0184	-0.0146	0.0277	-0.0661	0.0421
Age at 1st breeding -> Longevity	0.1345	0.1338	0.1055	-0.0794	0.3376
Age at 1st breeding -> Breeding events	-0.2137	-0.2125	0.0299	-0.2718	-0.1539
Skipped breeding -> Longevity	0.0106	0.0060	0.1081	-0.2179	0.2329
Skipped breeding -> Breeding events	-0.2720	-0.2720	0.0456	-0.3599	-0.1879
Phenology (plast.) -> Weight before breeding	-0.0785	-0.0757	0.0889	-0.2378	0.1168
Phenology (plast.) -> Guard length	-0.0941	-0.0919	0.1007	-0.2827	0.1100
Phenology (plast.) -> Prop. partner switch	0.2637	0.2602	0.1317	-0.0076	0.5004
Phenology (plast.) -> Prop. nest switch	0.1738	0.1710	0.1216	-0.0675	0.3971
Phenology (plast.) -> Irregularity of chick feeding	0.1999	0.1924	0.0871	0.0214	0.3562
Phenology (plast.) -> Prop. Food to chick	-0.1135	-0.1080	0.0752	-0.2486	0.0481
Phenology (plast.) -> Mass gained at sea (incub.)	-0.0517	-0.0539	0.0827	-0.2173	0.1055
Phenology (plast.) -> Trip duration (incub.)	-0.0116	-0.0141	0.0964	-0.1837	0.1803
Phenology (plast.) -> Mass gained at sea (rearing)	-0.1771	-0.1802	0.0978	-0.3631	0.0131
Phenology (plast.) -> Prop.2nd.clutch	-0.2387	-0.2316	0.0773	-0.3787	-0.0763
Phenology (plast.) -> Prop. of chicks fledged	0.2040	0.2201	0.1193	-0.0057	0.4606
Phenology (plast.) -> Breeding events	0.0178	0.0149	0.0279	-0.0345	0.0746
Phenology (pers.) -> Weight before breeding	-0.1090	-0.1098	0.0785	-0.2658	0.0445
Phenology (pers.) -> Guard length	-0.2693	-0.2640	0.1094	-0.4676	-0.0492
Phenology (pers.) -> Prop. partner switch	0.2875	0.2849	0.0926	0.1051	0.4618
Phenology (pers.) -> Prop. nest switch	0.2493	0.2413	0.1101	0.0243	0.4444
Phenology (pers.) -> Irregularity of chick feeding	0.0653	0.0641	0.1196	-0.1708	0.2939
Phenology (pers.) -> Prop. Food to chick	-0.1182	-0.1090	0.1090	-0.3156	0.1029
Phenology (pers.) -> Mass gained at sea (incub.)	-0.3030	-0.2975	0.1239	-0.5194	-0.0451
Phenology (pers.) -> Trip duration (incub.)	0.2447	0.2385	0.0908	0.0685	0.4052
Phenology (pers.) -> Mass gained at sea (rearing)	-0.4593	-0.4659	0.1003	-0.6630	-0.2668
Phenology (pers.) -> Prop.2nd.clutch	-0.7167	-0.7140	0.0580	-0.8164	-0.5845
Phenology (pers.) -> Prop. of chicks fledged	-0.0911	-0.0849	0.1187	-0.3177	0.1523
Phenology (pers.) -> Breeding events	0.0448	0.0428	0.0300	-0.0166	0.1042
Weight before breeding -> Guard length	-0.0677	-0.0643	0.1400	-0.3376	0.2131

Weight before breeding -> Irregularity of chick feeding	0.2138	0.1939	0.1813	-0.1992	0.5291
Weight before breeding -> Prop. Food to chick	0.1708	0.1797	0.1253	-0.0554	0.4248
Weight before breeding -> Mass gained at sea (incub.)	-0.0865	-0.0795	0.1693	-0.4018	0.2600
Weight before breeding -> Trip duration (incub.)	0.0835	0.0924	0.1106	-0.1175	0.3228
Weight before breeding -> Longevity	-0.0525	-0.0510	0.1583	-0.3552	0.2796
Weight before breeding -> Prop. of chicks fledged	0.0200	0.0362	0.1457	-0.2364	0.3488
Weight before breeding -> Breeding events	-0.0183	-0.0151	0.0318	-0.0741	0.0505
Guard length -> Longevity	-0.0491	-0.0544	0.1044	-0.2696	0.1385
Guard length -> Prop. of chicks fledged	-0.1146	-0.1044	0.1073	-0.2985	0.1026
Prop. partner switch -> Prop. of chicks fledged	-0.1860	-0.1935	0.1461	-0.4807	0.0940
Prop. nest switch -> Prop. of chicks fledged	-0.1069	-0.1117	0.1142	-0.3415	0.1101
Irregularity of chick feeding -> Prop. Food to chick	-0.0275	-0.0240	0.1254	-0.2587	0.2011
Irregularity of chick feeding -> Longevity	-0.0995	-0.0762	0.1082	-0.2751	0.1613
Irregularity of chick feeding -> Prop. of chicks fledged	-0.1299	-0.1174	0.1391	-0.3793	0.1613
Prop. Food to chick -> Longevity	0.0141	0.0013	0.1619	-0.3196	0.2913
Prop. Food to chick -> Prop. of chicks fledged	-0.2472	-0.2730	0.1413	-0.5609	-0.0022
Mass gained at sea (incub.) -> Longevity	0.0511	0.0742	0.1092	-0.1389	0.2849
Mass gained at sea (incub.) -> Prop. of chicks fledged	0.0692	0.0876	0.1423	-0.1918	0.3718
Trip duration (incub.) -> Longevity	-0.1638	-0.1566	0.1095	-0.3596	0.0635
Trip duration (incub.) -> Prop. of chicks fledged	-0.0646	-0.0518	0.1130	-0.2907	0.1588
Mass gained at sea (rearing) -> Longevity	0.2069	0.2034	0.1134	-0.0328	0.4118
Mass gained at sea (rearing) -> Prop. of chicks fledged	0.2248	0.2201	0.1317	-0.0373	0.4681
Prop.2nd.clutch -> Longevity	0.1880	0.2039	0.1206	-0.0357	0.4373
Prop.2nd.clutch -> Breeding events	0.2658	0.2673	0.0376	0.1957	0.3466
Longevity -> Breeding events	0.8333	0.8335	0.0370	0.7575	0.9053
Prop. of chicks fledged -> Fitness	0.6268	0.6271	0.0599	0.4982	0.7273
Breeding events -> Fitness	0.5052	0.5259	0.0862	0.3784	0.6998

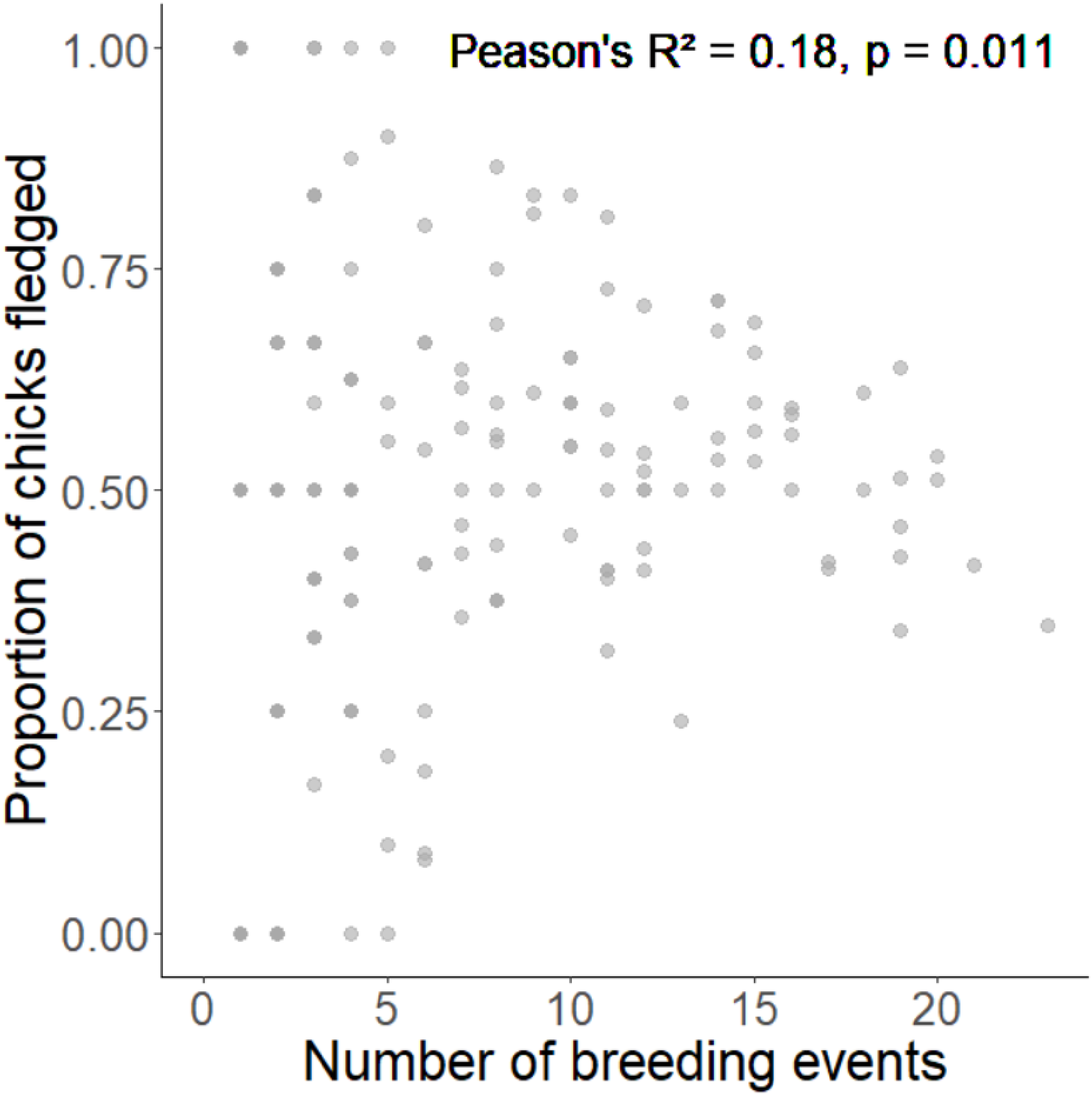


Figure S9: *Correlation between number of breeding events during life and proportion of chicks fledged (out of number of eggs layed) per breeding event .*

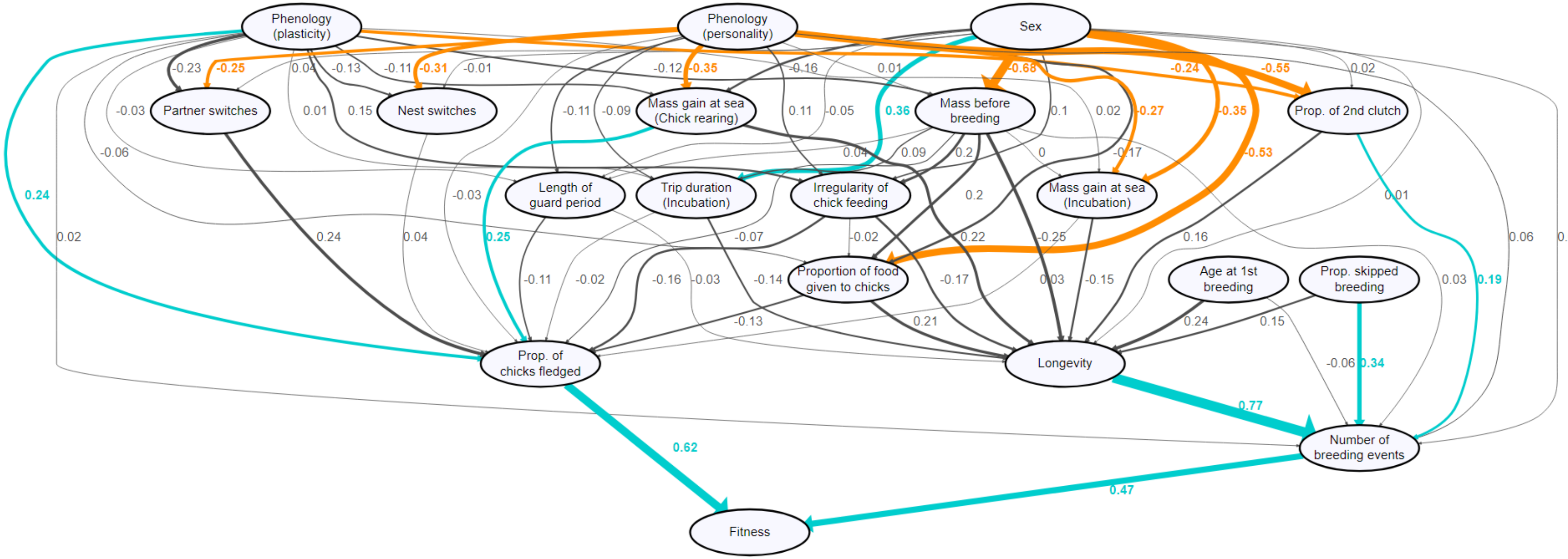


Figure S10: *Path modelling of the relation between fitness and 18 different life-history traits (light grey nodes) for which the effects of year have been removed. Numbers correspond to relative estimates of partial least square path model. Arrows and numbers colours indicate the positive/negative (green/red) sigh of the relationship when the latter is considered significant (bootstrap IC95% (n = 10,000) does not include 0). Grey arrows and numbers correspond to non-significant relations.*

Table S11: *Details of Partial least square path modelling estimates for all data without stochastic variability (year effect) direct relationships, including real estimate, bootstrap average estimate (n = 10,000), standard error and 95% upper and lower confidence intervals.*

	Original	**Mean.Boot**	**Std.Error**	**perc.025**	**perc.975**
Binary.sex -> Weight.before.breeding	-0.6779	-0.6794	0.0566	-0.7801	-0.5595
Binary.sex -> Guard.length	-0.0549	-0.0540	0.1266	-0.2940	0.2134
Binary.sex -> Divorces	0.0375	0.0369	0.1016	-0.1640	0.2311
Binary.sex -> Switch.nest	-0.0090	-0.0134	0.1014	-0.2023	0.1841
Binary.sex -> Chick.feed.ireg	0.1047	0.0913	0.1246	-0.1688	0.3110
Binary.sex -> Chick.feed.prop	-0.5310	-0.5335	0.0976	-0.7171	-0.3350
Binary.sex -> Mass.Incub	-0.3451	-0.3378	0.1310	-0.5868	-0.0753
Binary.sex -> Dur.Incub	0.3577	0.3695	0.1413	0.0816	0.6378
Binary.sex -> Pooled.mass.chickrear	-0.1563	-0.1669	0.0973	-0.3677	0.0199
Binary.sex -> Prop.2nd.clutch	0.0199	0.0203	0.0888	-0.1475	0.2024
Binary.sex -> Longevity	0.0085	-0.0047	0.1804	-0.3966	0.3325
Binary.sex -> Breeding.events	0.0326	0.0362	0.0650	-0.0846	0.1731
First.repro -> Longevity	0.2359	0.2383	0.1203	-0.0116	0.4653
First.repro -> Breeding.events	-0.0588	-0.0583	0.0470	-0.1558	0.0318
Skip.breed -> Longevity	0.1532	0.1569	0.1201	-0.0896	0.3921
Skip.breed -> Breeding.events	0.3413	0.3383	0.0603	0.2172	0.4536
Phenology.plast -> Weight.before.breeding	-0.1248	-0.1245	0.0873	-0.2805	0.0547
Phenology.plast -> Guard.length	-0.0315	-0.0304	0.1005	-0.2230	0.1709
Phenology.plast -> Divorces	-0.2315	-0.2294	0.1277	-0.4705	0.0080
Phenology.plast -> Switch.nest	-0.1314	-0.1325	0.1265	-0.3750	0.1248
Phenology.plast -> Chick.feed.ireg	0.1531	0.1450	0.0918	-0.0474	0.3007
Phenology.plast -> Chick.feed.prop	-0.0588	-0.0483	0.0753	-0.1955	0.0950
Phenology.plast -> Mass.Incub	0.0162	0.0152	0.0865	-0.1596	0.1866
Phenology.plast -> Dur.Incub	0.0068	0.0055	0.1117	-0.1955	0.2385
Phenology.plast -> Pooled.mass.chickrear	-0.1136	-0.1164	0.1003	-0.3083	0.0757
Phenology.plast -> Prop.2nd.clutch	-0.2447	-0.2441	0.0832	-0.3998	-0.0763
Phenology.plast -> Prop.fledged	0.2380	0.2508	0.1238	0.0074	0.4989
Phenology.plast -> Breeding.events	0.0197	0.0193	0.0556	-0.0852	0.1297
Phenology.pers -> Weight.before.breeding	0.0134	0.0065	0.0958	-0.1830	0.1962
Phenology.pers -> Guard.length	-0.1122	-0.1103	0.0993	-0.2855	0.0890
Phenology.pers -> Divorces	-0.2525	-0.2492	0.1174	-0.4726	-0.0086
Phenology.pers -> Switch.nest	-0.3089	-0.3006	0.1133	-0.5018	-0.0431
Phenology.pers -> Chick.feed.ireg	0.1090	0.1165	0.1266	-0.1208	0.3527
Phenology.pers -> Chick.feed.prop	-0.1707	-0.1671	0.1183	-0.3936	0.0736
Phenology.pers -> Mass.Incub	-0.2687	-0.2590	0.1143	-0.4783	-0.0295
Phenology.pers -> Dur.Incub	-0.0927	-0.0974	0.0880	-0.2654	0.0649
Phenology.pers -> Pooled.mass.chickrear	-0.3535	-0.3611	0.0967	-0.5425	-0.1680
Phenology.pers -> Prop.2nd.clutch	-0.5460	-0.5420	0.0835	-0.6978	-0.3659
Phenology.pers -> Prop.fledged	-0.0268	-0.0444	0.1332	-0.3031	0.2219

Phenology.pers -> Breeding.events	0.0649	0.0641	0.0507	-0.0269	0.1639
Weight.before.breeding -> Guard.length	0.0415	0.0441	0.1287	-0.2084	0.2858
Weight.before.breeding -> Chick.feed.ireg	0.1998	0.1869	0.1773	-0.1835	0.5049
Weight.before.breeding -> Chick.feed.prop	0.2031	0.2065	0.1227	-0.0401	0.4366
Weight.before.breeding -> Mass.Incub	0.0046	0.0049	0.1617	-0.3041	0.3396
Weight.before.breeding -> Dur.Incub	0.0886	0.0909	0.1134	-0.1411	0.3041
Weight.before.breeding -> Longevity	-0.2516	-0.2375	0.1732	-0.5767	0.1091
Weight.before.breeding -> Prop.fledged	-0.0692	-0.0583	0.1320	-0.3162	0.1913
Weight.before.breeding -> Breeding.events	0.0340	0.0416	0.0745	-0.0959	0.1907
Guard.length -> Longevity	-0.0322	-0.0405	0.1219	-0.2699	0.1852
Guard.length -> Prop.fledged	-0.1098	-0.0975	0.1096	-0.3112	0.1125
Divorces -> Prop.fledged	0.2393	0.2446	0.1454	-0.0423	0.5333
Switch.nest -> Prop.fledged	0.0364	0.0277	0.1171	-0.2089	0.2454
Chick.feed.ireg -> Chick.feed.prop	-0.0193	-0.0100	0.1286	-0.2586	0.2245
Chick.feed.ireg -> Longevity	-0.1703	-0.1566	0.1082	-0.3561	0.0672
Chick.feed.ireg -> Prop.fledged	-0.1638	-0.1420	0.1434	-0.4096	0.1289
Chick.feed.prop -> Longevity	0.2141	0.1809	0.1578	-0.1621	0.4641
Chick.feed.prop -> Prop.fledged	-0.1292	-0.1552	0.1431	-0.4464	0.1117
Mass.Incub -> Longevity	-0.1489	-0.1288	0.1126	-0.3405	0.1117
Mass.Incub -> Prop.fledged	0.0255	0.0385	0.1256	-0.2071	0.2839
Dur.Incub -> Longevity	-0.1375	-0.1232	0.1252	-0.3677	0.1369
Dur.Incub -> Prop.fledged	-0.0196	-0.0135	0.1117	-0.2326	0.2272
Pooled.mass.chickrear -> Longevity	0.2198	0.2068	0.1223	-0.0450	0.4432
Pooled.mass.chickrear -> Prop.fledged	0.2484	0.2436	0.1208	-0.0073	0.4732
Prop.2nd.clutch -> Longevity	0.1569	0.1711	0.1172	-0.0520	0.4120
Prop.2nd.clutch -> Breeding.events	0.1911	0.1940	0.0518	0.0929	0.2916
Longevity -> Breeding.events	0.7666	0.7745	0.0461	0.6807	0.8682
Prop.fledged -> Fitness	0.6243	0.6263	0.0548	0.5073	0.7186
Breeding.events -> Fitness	0.4723	0.4910	0.0877	0.3351	0.6596

Chapter IV: Phenology

Individual variability in phenology: Causes and consequences on breeding

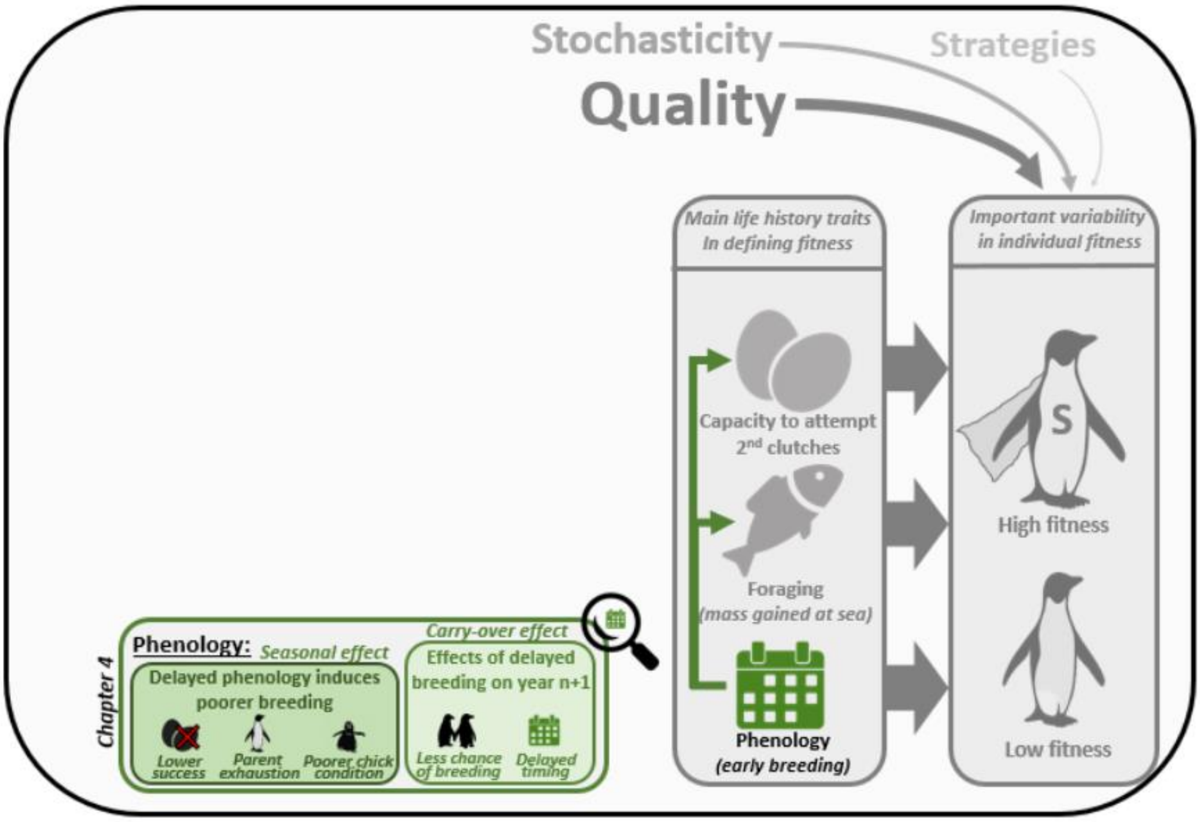
Modified from:

Joly, N.B., A. Chiaradia, J.-Y. Georges, and C. Saraux. Individual variability in the phenology of an asynchronous penguin: causes and consequences on breeding. In review for Oecologia.

General context of the study:

In the previous chapter, I highlighted individual phenology, and more precisely the capacity of an individual to always breed earlier than others, as the major life history trait defining individual fitness. This variability came from the very ubiquitous effect of phenology, driving many other traits such as foraging efficiency and the capacity to breed multiple times. In this study, my aim was to understand the effect of phenology at finer scale, that is to say looking at breeding events individually rather than at the lifetime scale, in order to understand the different processes through which phenology ultimately affected individual capacity to breed.

Graphical summary of the main results:



Abstract

Phenology is a major component of animals' breeding, as they need to adjust their breeding timing to match optimal environmental conditions. While the effects of shifting phenology are well-studied on populations, few studies emphasise its ecological causes and consequences at the inter-individual level. Using a 20-year monitoring of more than 2500 breeding events from ~500 breeding little penguins (*Eudyptula minor*), a very asynchronous seabird, we investigated the consequences of late breeding on present and next breeding events. We found that individuals breeding later had reduced breeding success, lighter chicks at fledging, lower probability of laying a second clutch, and decreased parents' post-breeding body condition. Importantly, we found important cycling effects where delayed breeding during a given year led to significantly later laying date, breeding success and lower chance of breeding during the next season, suggesting potential carry-over effects from one season to the next. To further understand the causes of such variability in phenology while earlier breeding is associated with better individual fitness, we aimed at assessing intrinsic differences among individuals. We showed that the heterogeneity in breeding timing was partly fixed, the laying date being a significantly repeatable behavior (17%), asking for more studies on heritability or early-development effects. This large-scale study highlights the combined roles of carry-over effects and intrinsic differences on individual phenology, with important implications on breeding capacity through life.

Key words: *Breeding timing, early-life, repeatability, life-history, fitness*

1. **Introduction**

The link between animal phenology and breeding outputs is known to be mainly caused by a variability in the amount of energy available in the environment through match/mismatch with food resources (Durant et al. 2007, Hipfner 2008, Regular et al. 2014). These potential mismatches are themselves driven by variations in the environment (Grémillet and Boulinier 2009b), making phenology a particularly responsive trait to environment variability (Visser et al. 2004, Reed et al. 2009a) and trends such as the ones recently observed with climate change (Parmesan and Yohe 2003, Poloczanska et al. 2013, Cohen et al. 2018)

While the effects of phenology at the population level are well described, very few studies emphasise its importance in terms of inter-individual variability on animal breeding cycle. Yet, inter-individual variability is known to be an important ecological driver of breeding success and fitness (Gordo et al. 2013, Gilsenan et al. 2020, Joly et al. 2023). It consists of a combination of differences in individual plasticity (*i.e* strength of individual response to environmental variations) and individual repeatability (*i.e* consistent behavior across time) (Reed et al. 2009a, Dingemanse et al. 2010, Lourenço et al. 2015, Gilsenan et al. 2020). Individual capacity to cope with shifts in environmental conditions is not uniform, which leads to important differences in the breeding timing among individuals of a same population (Reed et al. 2009a). Further, traits such as breeding timing are also expected to be partly consistent during individual life, which might be explained by the trait being genetically transmitted (heritable behavior; (Stirling et al. 2002) or due to the phenotypic value of the trait depending on conditions during development and growth (Lindström 1999, Monaghan 2007).

Inter-individual variability in phenology thus implies that some individuals will better match the optimum environmental conditions (*e.g.* prey availability) than others. In long-lived species such as seabirds, individuals tend to favor their own survival and maintenance over offspring when facing unfavorable environmental conditions to maximise future breeding events (Goodman, 1974; Stearns, 1992). Thus, phenological mismatch with prey availability should directly affect individual breeding output through detrimental breeding decisions favoring adult survival over offspring's (*e.g.* nest desertion or reduced clutch size; Stearns 1989, Chastel et al. 1995) or through less energy allocated to offspring development (Watanuki et al. 2009). Still, life-history strategies also vary within a population among individuals, so that even in long-lived species, some individuals may avoid these reduced breeding outputs by allocating significant amounts of energy to offspring, in which case they may face post-breeding exhaustion (Shultz et al. 2009). In this case, carry-over effects may occur from one breeding season to the next (Harrison et al. 2013). For instance, individuals may take more time and have a slower recovery, potentially affecting their future breeding events (Harrison et al. 2011).

Here we focused on the breeding phenology of the world's largest little penguin (*Eudyptula minor*) colony at Phillip Island, Australia. Little penguin phenology is especially interesting because of their particularly asynchronous breeding timing (4 to 6 months between earliest and latest birds; Reilly and Cullen 1981). Their breeding cycle also allows them to regularly attempt more than one breeding event per season (Reilly and Cullen 1981), further increasing the breeding season duration range. In addition to being asynchronous, this colony of little penguins exhibited a quick and strong shift in its breeding timing during the last decades (Cullen et al. 2009), due to changes in marine conditions and prey distribution in the area (Ridgway 2007, Last et al. 2011). Such important variations in little penguin phenology have been recently shown to largely explain little penguin foraging success at the population scale (Joly et al 2022) as well as individual lifetime fitness (Joly et al. 2023).

Using a long-term monitoring of around 2500 breeding events from more than 500 penguins across 20 years, we first assessed whether the variability in phenology resulted from fixed versus dynamic heterogeneity by testing how repeatable breeding timing was among individuals. While little penguin phenology changes importantly from year to year as a response to the environment (Joly et al. 2022), we still expected part of the variability in laying to be repeatable, with some birds breeding consistently earlier than others, once the year effect is removed.

Second, we aimed to understand the paths through which delayed phenology affects penguin reproduction. As an increased delay is thought to increase the mismatch with preys (Reed et al. 2009a), thus inducing poorer foraging (Joly et al. 2022), we expected later breeding to be associated with lighter and slower chick growth and deteriorated breeding outputs (*e.g*. breeding success, number of breeding events). We expected delayed breeding adults and invest less energy in parental care (*e.g.*, shorter guard period) associated with lower breeding success (Chiaradia and Kerry 1999a), smaller chicks at fledging and fewer second clutches attempted in an effort not to lose weight during breeding.

Finally, we investigated the carry-over effects of late breeding and the consequences of a bad breeding season on the next one. We expected that late breeding would induce poor post-breeding conditions (Salton et al. 2015, Fayet et al. 2016) that would themselves delay the next breeding event, creating a cycle in which phenology would constantly delay. Regarding demography, late breeding (and associated poor post-breeding conditions) should decrease the likeliness of breeding during the next breeding event. Penguins that still attempted breeding should display lower breeding success (Shoji et al. 2015) and less chance of trying a second clutch. However, skipping a breeding event (*i.e.* skipping breeding season or not attempting a second clutch) might help break the negative cycle by allowing a better post-breeding recovery, inducing an earlier breeding the following year (Shoji et al. 2015).

2. Methods

a) Little penguins breeding traits

Breeding events

A penguin breeding event was considered as soon as an egg was laid in the nest. Penguin breeding timing was defined as the date of egg laying. The laying date reflects both the population variability in phenology across breeding seasons and the asynchrony among individuals during each breeding season. As we wanted to disentangle these two processes, we assessed a relative laying date for each breeding event, defined as the laying date of the individual minus the average laying date of the population on a given season (in days).

Despite little penguins laying two eggs per clutch, here a clutch was considered successful as long as at least one chick fledged, making breeding success a binary variable. Breeding events were considered second clutches if they were the second time an individual laid eggs within the same season, whether the first clutch was successful or not.

Adult body conditions

Adult body mass at the beginning of the breeding season was defined as the closest recorded mass from the laying date (APMS) entering the colony in a five days interval before the laying date. Adult body mass at the end of breeding was considered the closest recorded mass from chick fledging (APMS) of a parent leaving the colony for five days after fledging. Relative penguin mass change during breeding was considered as the quantity of mass gained or lost during the breeding event (mass at the end minus mass at laying) divided by the individual start mass (mass at laying) to account for variability in individual size. In many cases, mass at the beginning (70%) and/or end (62%) of the breeding season was unknown due to lack of detection in this restrained period. However, we decided to favor accurate mass rather than expand the period of detection.

Chick growth and care

Chick growth was defined by the mass at fledging (the last recorded mass in the colony) and the length of the guard period, as longer guard periods result in higher growth and fledging success due to longer parental care (Chiaradia and Nisbet, 2006).

b) Statistical analysis

All analyses were performed using R 3.5.1 and RStudio 1.1.456. Data significance was accepted with an error threshold of 5%. Results are presented as means ± standard errors (SE). Whenever running a linear model (or linear mixed model, LMM), the normality of the residuals was tested using density plots and q-q plots. When more than one explanatory variable was included as a fixed effect in a model, the best model was selected according to Akaike's Information Criterium (AIC) unless otherwise specified. When the difference in AIC was lower than 2, the most parsimonious model (*i.e.* the one with the least variables) was retained (Burnham & Anderson 2004).

Repeatability of penguin phenology and associated causes

Repeatability of laying date across individuals was assessed using `rptR 0.9.22` package (*REP = Laying Date ~ (1 | Individual)*). The potential effect of sex or age on repeatability was also assessed (*REP = Laying Date ~ Sex and/or Age + (1 | Individual)*). Repeatability was considered to be significantly different from zero based on 95% confidence interval.

Effect of phenology on current and future breeding events

We assessed the effect of individual laying date on breeding outputs using generalised linear mixed models from lme4 1.1-19 package. Because little penguins exhibit bi-parental care, breeding success and chick growth condition (guard length and age/mass at fledging) were estimated per pair and models were run at the pair level with the breeding season as a random variable and the clutch number in interaction with laying date as fixed effects. However, because divorce rates are quite high in this species (Simpson et al. in prep), the probability of performing a second clutch or the effect on the next breeding season was assessed at the individual rather than the pair scale and individual and age were added to the breeding season as random variables while the effect of laying date was tested in interaction with sex, as males and females could display different reaction norms. Similarly, the effect of laying date on the adult condition (mass change during breeding) was assessed at the individual level with individual, age and breeding season as random variables and the interaction of sex and clutch number (as adult condition is expected to be overall lower and effect of timing stronger in the second clutch). For binary variables, *i.e.* breeding success and probability of second clutch, binomial GLMMs were performed, while LMMs were performed for adult and chick growth conditions. When looking at the effect of the laying date on the next breeding season, only the first laying date (*i.e.* start of breeding period) was considered in the case of multiple clutches, as subsequent laying should depend on previous overall breeding timing rather than on previous second clutch

Link between current breeding conditions and next laying

Effect of previous breeding season conditions such as mass at the end of breeding, guard length, chick mass and age at fledging on the next laying date was also tested using LMM with random effect of the breeding season, age and sex. Different models were used to test these parameters individually in order to avoid significant loss of data points due to missing chicks and adult mass information.

To test for a potential recovery effect from skipping breeding, we assessed the difference in relative laying date between two subsequent breeding seasons. We then looked for a potentially significant difference between the group of individuals breeding twice in a row and those that skipped a breeding event between two breeding events using a linear model, including the random effect of the breeding season and individual ID and age.

3. Results

Penguins breeding seasons generally spanned from the end of July to mid-December (around 5 months, *Supplementary S1*) with many variations across years, and extreme breeding cases were observed from June to early February. Regarding intra-season variability, most individuals tended to breed in a two month interval before and after the population average (*Supplementary S2*), although some breeding events occurred more than 100 days before or after the population average (more than six months between the very first and very last event).

a) Consistency in phenology at the individual level

We assessed repeatability of individual laying date across life using an increasingly detailed model to account for some other factors inducing variability in penguin phenology. The repeatability of individual laying date was of 9% ($R = 0.094 \pm 0.018$ SE, $N = 388$, $n = 2215$, $p < 0.001$) when taking nothing else into account. When accounting for the individual age as a random variable, individual repeatability in laying date went up to 17% ($R = 0.166 \pm 0.021$, $p < 0.001$). Further adding the effect of sex into the model did not affect repeatability ($R = 0.167 \pm 0.022$, $p < 0.001$).

b) Effect of breeding timing on current and next breeding seasons

Effects of laying date were tested using both raw and relative laying dates (*i.e.* laying date relative to the population average during the current season). As both analyses tended to display very similar results and amplitude, only the effects of raw laying dates are presented below. More information on relative laying dates are available in *Supplementary Material S3*.

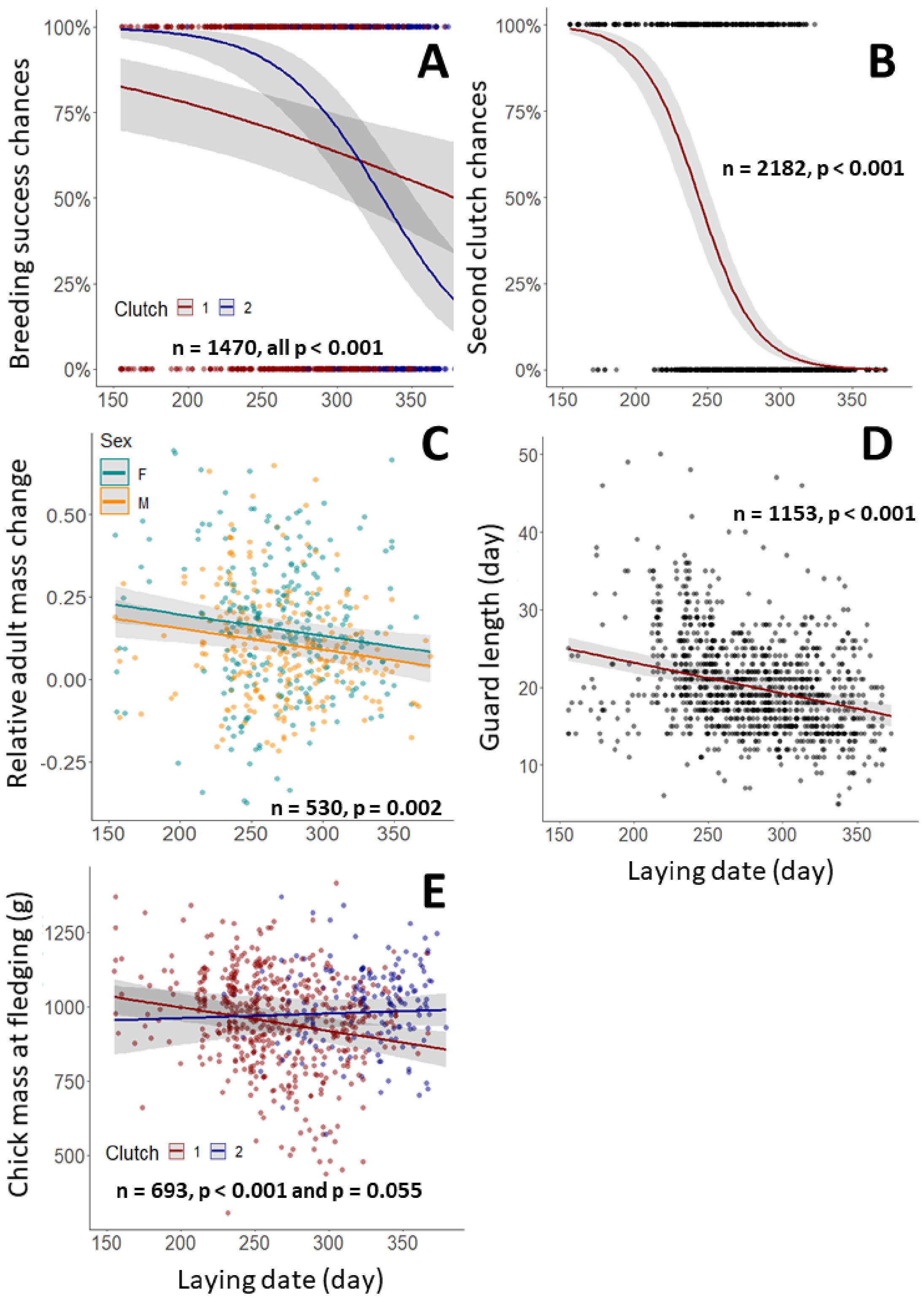


Figure 24: Breeding parameters of little penguins based on their laying date with linear mixed model or generalized additive model (red curve) ± SE (grey area). Blue curve (A, E) represents second clutches, and orange/light blue curves (C) represents differences between sexes. Sample sizes as well as p-values (for first and second clutches when relevant) are presented.

<u>*Breeding timing effect on the current breeding season*</u>

Regarding breeding output, later breeding was associated with a strong decrease in breeding success, even stronger during second clutches (binomial GLMM, n = 1470, N = 272, p < 0.001, *Figure 24 A and 25 A*). Regarding chick care, later breeding timing was associated with shorter guards (*i.e.* intensive chick care, -0.03 ± 0.00 days of guard per day of delay, LMM, n = 1153, N = 252, p < 0.001, *Figure 24 D and 25 B*). Later breeding was also associated with lower chick mass at fledging during first clutches (-0.8 ± 0.2 g per day of delay, LMM, n = 693, N = 182, p < 0.001, *Figure 24 E and 25 B*) but not for second clutches (*i.e.* significant clutch interaction, p = 0.014 with no significant effect of laying date on second clutches masses at fledging, 0.15 ± 0.38 g per day of delay, p = 0.055).

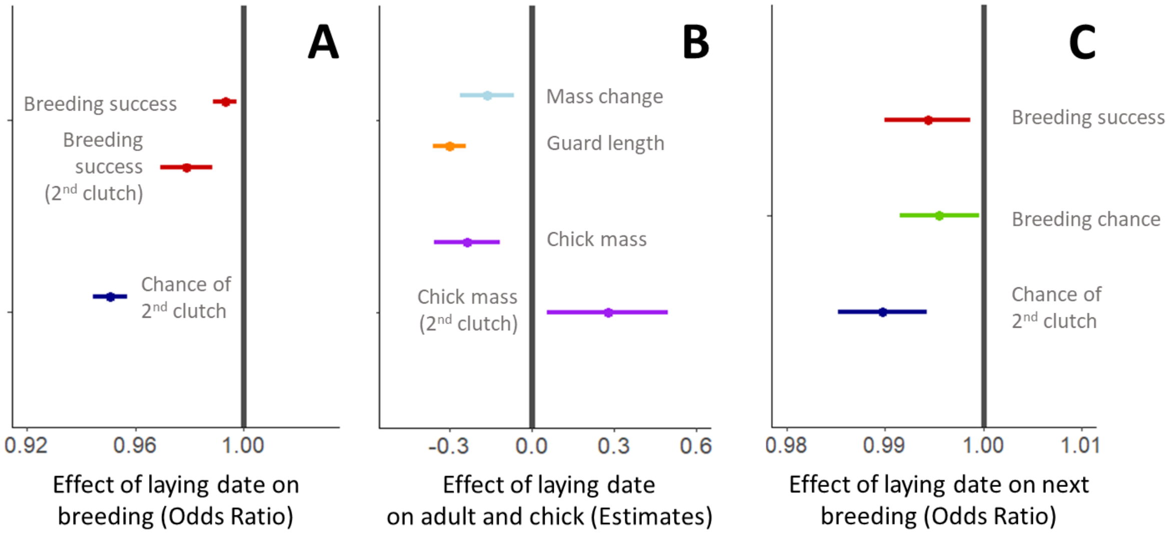


Figure 25: Breeding effects on little penguin breeding (i.e breeding success and second clutch, A), mass loss (B) and chick caring (i.e. guard length and weight of chicks at fledging, B) and breeding next season (i.e. chance of breeding, chance of second clutch and breeding success, C) including odds ratio for breeding (binomial GLMM) and estimates of scaled variables for others (GLMM) and CI95%.

Delayed breeding also had important effects on the adult condition during the season. Later laying date was indeed associated with more significant mass loss during the breeding season with no interaction of sex (although different intercept, p = 0.019) or clutch (-0.08% mass at the end of the season per day of delay, LMM, n = 530, N = 196, p < 0.002, *Figure 25*

C) and adults were way less susceptible to attempt second clutches no matter the sex (-5.1% chance to do a second clutch per day of delay, GLMM, n = 2182, N = 466, p < 0.001, *Figure 24 B and 25 A*).

Delayed effect of breeding timing on future seasons

On top of affecting the current breeding season performances, delayed breeding was also associated with lower breeding performances during the next season (*Figure 26*, no effect of sex). Later laying was associated with fewer chances of breeding the next season (excluding dead penguins, -0.4% chance to breed the following year per day of delay, GLMM, n = 1927, N = 423, p = 0.029, *Figure 26 A and 25 C*). When penguins still bred on the following season, their breeding success was lower (GLMM, n = 1600, N = 353, p < 0.001, *Figure 26 C and 25 C*), and they had much less chance to attempt a second clutch (-1.0% chance per day of delay, GLMM, n = 1600, N = 353, p = 0.012, *Figure 26 B and 25 C*). Once again, relative laying date affected the next breeding season in the same way and with a similar amplitude to the raw laying date (see *Supplementary Material S4* for more details).

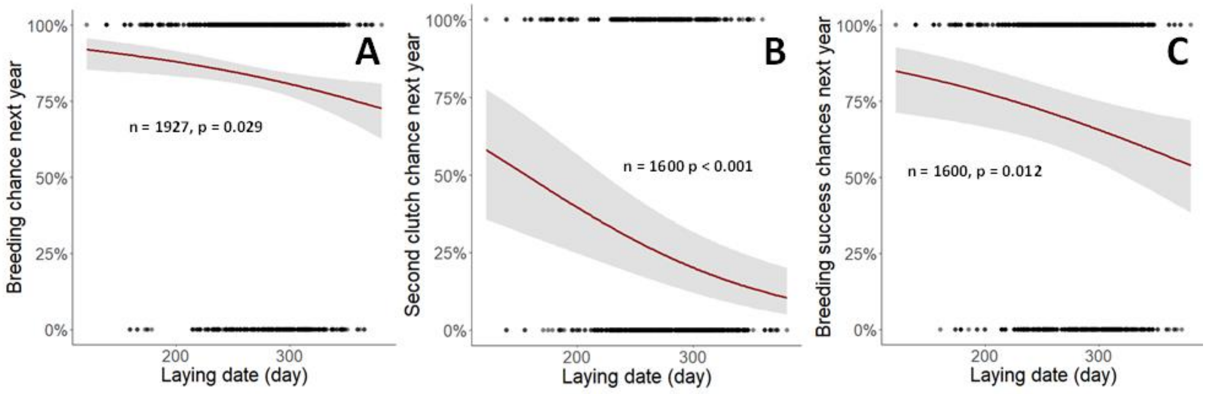


Figure 26: Breeding chances (first and second clutch) and breeding success of little penguins based on their laying date on previous season with linear mixed model (red curve) ± SE (grey area).

c) Cycling effect of the previous breeding season on phenology

The penguins' laying date was related to the conditions faced during the previous breeding season. Precisely, penguins were more likely to breed later when they already bred late (or ended breeding late as both variable were strongly correlated, Pearson's correlation = 0.91) during the previous season (0.14 ± 0.02 day later per day of delay on previous season, LMM, $n = 1595$, $N = 352$, $p < 0.001$, *Figure 27 A*). Regarding the carry-over effect of chick care, penguins were more likely to breed late when they had longest guard periods on previous season (0.42 ± 0.15 day later per day of guard, LMM, $n = 1283$, $N = 316$, $p = 0.004$, *Figure 27 B*) and when they fledged lighter chicks (0.01 ± 0.01 day later per gram, LMM, $n = 765$, $N = 260$, $p = 0.038$, *Figure 27 C),* although not when they reduced parental care duration by fledging chicks at a younger age (LMM, $p = 0.66$). Penguin laying date was also affected by their overall body condition at the end of the previous breeding season (0.02 ± 0.01 day later per gram less at the end of the season, LMM, $n = 702$, $N = 212$, $p = 0.023$, *Figure 27 D*) but was interestingly not depending on the amount of mass lost during the previous breeding season (LMM, $p = 0.25$, $n = 331$, $N = 143$).

Regarding the potential effect of skipping a breeding event, individuals that missed previous breeding did not breed earlier than others (LMM, $p = 0.64$, $n = 1745$, $N = 422$) and did not advance their relative breeding timing (*i.e.* number of days gained compared to previous season) during the next event more than the ones that did not skip (LMM, $p = 0.62$, $n = 1381$, $N = 320$). It is important to notice that out of the 1576 non-first breeding events, only 95 followed a skipped event (6.0%), making it a rare occurrence that is more complex to study.

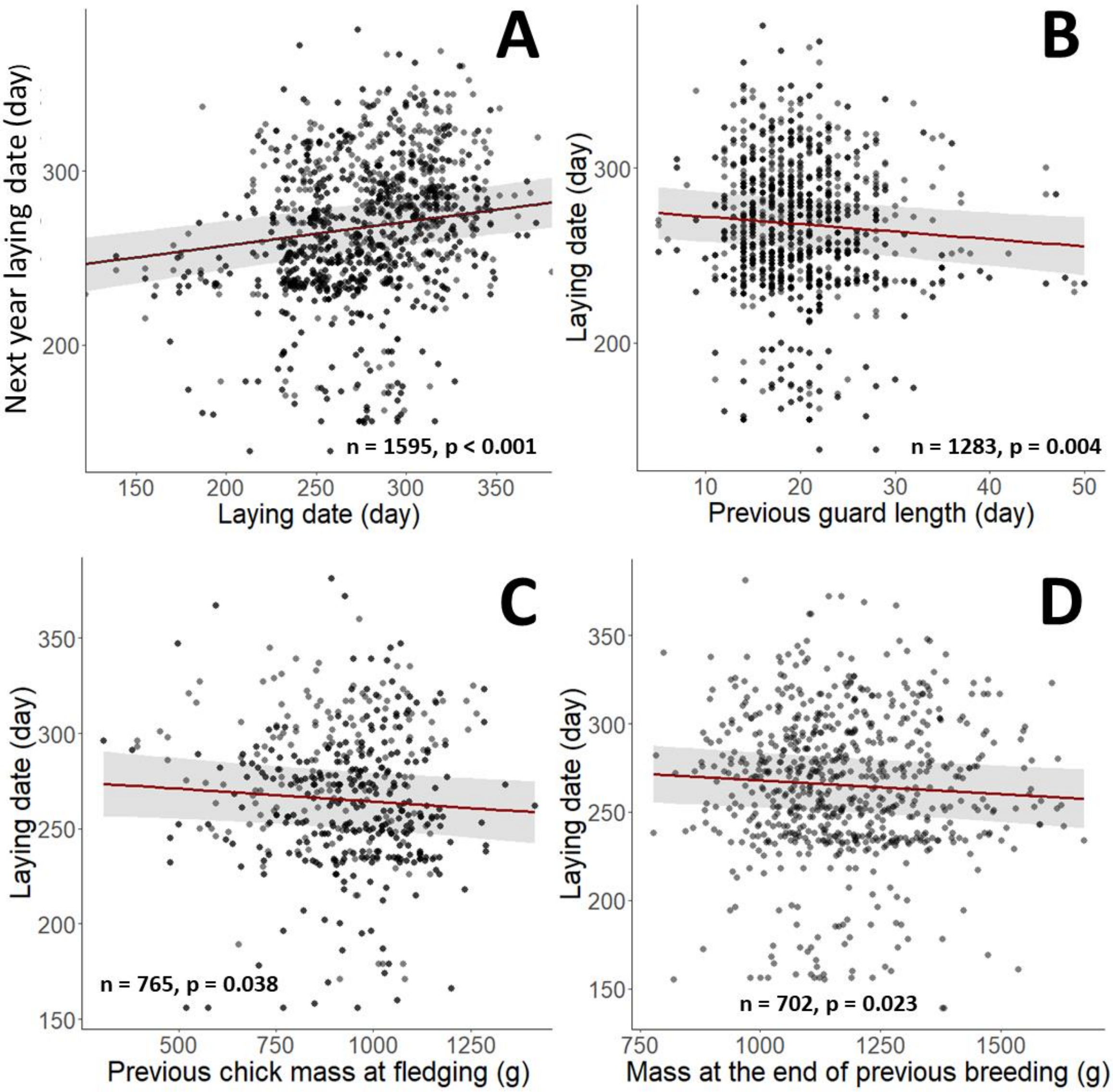


Figure 27: Laying date of little penguins based on previous season laying date, adult post-breeding condition and average mass of chick fledging with linear mixed model (red curve) ± SE (grey area).

4. Discussion

By studying more than 2500 breeding events from more than 500 individuals across 20 years, we assessed the breeding consequences of delayed phenology at the individual level using little penguins as a model. Trade-off between maximizing immediate breeding outputs and saving energy for breeding events is known to be one of the main driver of breeding decisions in long-lived species (Stearns 1989). Here, we demonstrated the central role of breeding cycle in individual life-history strategies as phenology could affect not only current but also future breeding seasons through important carry-over effects.

The importance of individual breeding timing on reproductive outputs is well documented in seabirds, including lower breeding success (Reed et al. 2009a, Ramírez et al. 2016) or clutch size (Moe et al. 2009). The link between late phenology and consecutive deteriorated breeding is mainly the result of a mismatch with the available resources during chick-rearing (Hipfner 2008, Shultz et al. 2009), inducing an increased foraging effort (Regular et al. 2014). However, the path through which current and future success are affected by low resource availability (*i.e.* poor chick development and parents' exhaustion; Regular et al. 2014) are very often assumed and rarely tested due to the difficulty of gathering this type of data. Here, we were able to test the effect of inter-individual variability in breeding phenology on breeding output and on breeder body condition and offspring development.

Overall, we confirmed that later breeding was associated with a significant decrease in subsequent breeding success (Regular et al. 2014, Ramírez et al. 2016), which was even more visible for the second breeding attempt within a season. Even when breeding was successful, we highlighted that late breeding led to lighter chicks at fledging, although not related to younger age. This suggests that late breeding is probably associated with fewer resources available in the environment during chick-rearing (Hipfner 2008, Shultz et al. 2009), which was already showed to affect little penguins' breeding success (Joly et al. 2022). While little penguins' breeding success and even lifetime fitness (Joly et al. 2023) have been shown to depend for an important part on individual capacity to fledge chicks, these results suggest that breeding timing effects on fitness could be even stronger when taking into account chick survival after fledging as chick mass at fledging is expected to affect birds' post-fledging survival (Coulson and Porter 1985, Krementz et al. 1989, Magrath 1991).

While we showed an immediate effect of late breeding on chick body condition at fledging, long-lived species are expected to be able to easily buffer a poor breeding events at the lifetime scale by allocating more energy to their future breeding (Stearns 1989). Here, we found that late breeding not only affected chick growth but also affected the parent body condition throughout the breeding season (*i.e* higher mass loss during breeding). Late breeding is thus more likely to imply adult deteriorated body condition while breeding, probably through a decreased food availability (Monaghan 2007, Koyama et al. 2021). This deterioration may trigger a reduced investment in the chicks (Martins and Wright 1993, Saraux et al. 2011c), including complete nest abandonment (Groscolas et al. 2008, Spée et al. 2010), to favor breeder survival (Williams 1966, Stearns 1992), which is likely to partly explain the low breeding success of late breeders.

Suppose late breeding is constantly associated with unfavorable breeding. In that case, questions remain on why some birds still tend to breed late during their life. The most likely hypothesis is that lower body conditions at the end of breeding is expected to increase post-breeding resting time, inducing important carry-over effects on subsequent breeding (Fayet et al. 2016). Indeed, birds facing strong carry-over effects are expected to adjust their breeding timing on the following season to increase pre-breeding energy intake (Hennin et al. 2016, Gatt et al. 2021). Evidence of a multiannual relation between individual phenology and breeding output could therefore be the mark of a cycling effect where breeding conditions affect subsequent breeding timing, affecting following breeding conditions.

Here, we found a clear link between late breeding on one breeding season and subsequent breeding season, including lower breeding success (Shoji et al. 2015) and significantly less chance of attempting a breeding event (first or second). While inter-individual variability in breeding timing was already known to affect direct breeding outputs (Reed et al. 2009a), these results suggest that its effect at the lifetime scale might be even more important through an interannual impact on fitness. Furthermore, we highlighted that delayed laying date tended to induce later timing for the next breeding event, confirming this multi-annual effect (Fayet et al. 2016). In our case, delayed laying was associated with lower mass at the end of previous breeding, which confirms the hypothesis that seabirds need to reach a certain body condition threshold to start breeding (Chastel et al. 1995b, Robinson et al. 2005b, Sorensen et al. 2009). Interestingly, the subsequent laying date was not affected by the mass lost during breeding but only by the body mass after breeding. This could be because penguins starting breeding with higher body mass can invest more in their chicks, thus losing more mass than others while still remaining in good body condition. Although little penguins are expected to be mainly income breeders, this study (as well as others, (Salton et al. 2015)) shows that the capital breeding dimension should not be neglected, as often showed in migrating birds (Graña Grilli et al. 2018, Steenweg et al. 2022).

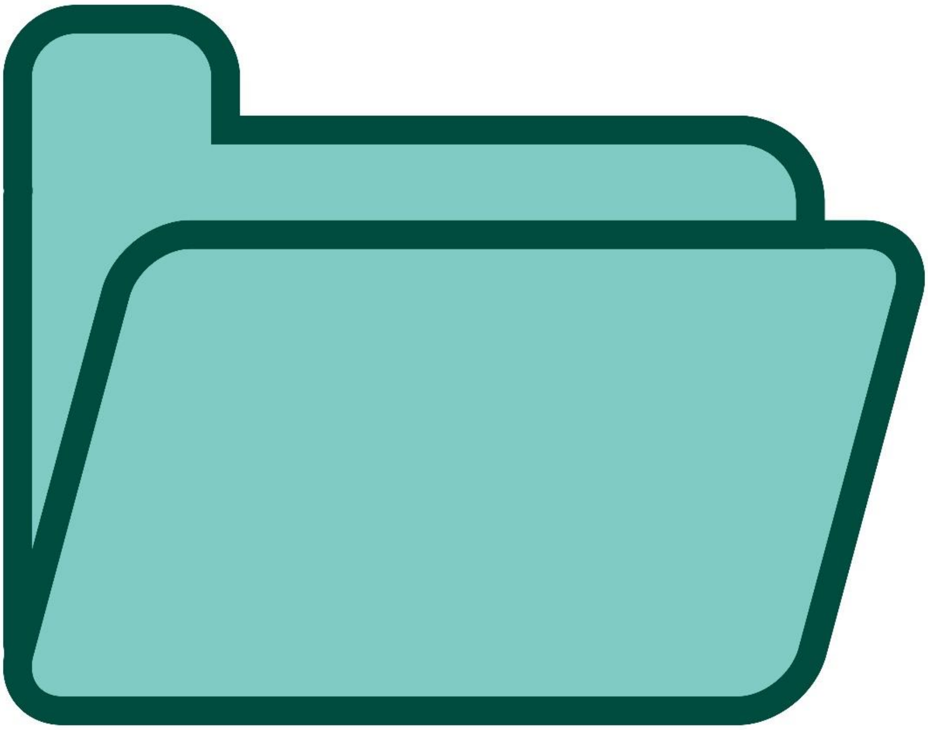
With those results, we confirmed the carry-over effects to be a major driver of the variability in seabirds' phenology (Shoji et al. 2015, Fayet et al. 2016) at the inter-individual scale. However, individuals could theoretically break this vicious cycle by skipping a breeding event, giving them more time to replenish energy and start a new one. Here, we found no effect of a skipped breeding event on subsequent breeding timing (including no significant advance of relative breeding timing) or the capacity to counterbalance carry-over effects, which was a sporadic event. This is consistent with previous studies arguing that skipped breeding events are more the reflection of poor individual quality (Cam et al. 1998) than a valuable strategy to cope with carry-over effects (Reed et al. 2015).

While conditions faced during previous breeding events are a major driver of inter-individual differences in success and fitness (Harrison et al. 2011, O'Connor et al. 2014), it cannot be the only cause of these differences as it is mainly relevant for experienced breeders. Another reason that may explain a part of the difference in penguins' phenology is the fixed heterogeneity arising from intrinsic individual differences (Cam et al. 2016). These intrinsic differences can lead to important differences in individual quality (*i.e.* inter-individual differences in performances through life, Lescroël et al. 2009). Here, we found that many individuals tended to breed earlier than others even if they produced larger chicks on previous event (*i.e.* invested in breeding) in the previous year. This suggests that some individuals may perform well without facing important carry-over effects because of their intrinsic good quality (Joly et al. 2023).

A good way to approximate consistency (*i.e.* intrinsic differences) among individual behavioral traits is to assess the trait repeatability (Bell et al. 2009, Carlson and Tetzlaff 2020). Here, we found that around 17% of the individual laying date was repeatable, which is quite consistent with previous studies on other seabirds' species (Sydeman and Eddy 1995, Fayet et al. 2016, Dobson et al. 2017). Consistent inter-individual differences due to genetic (Dochtermann et al. 2019) or early-life conditions (Lindström 1999, Lee et al. 2012) may thus explain an important part of the variability in their laying dates, including their first breeding experiences.

Chapter IV: Phenology

Supplementary Material



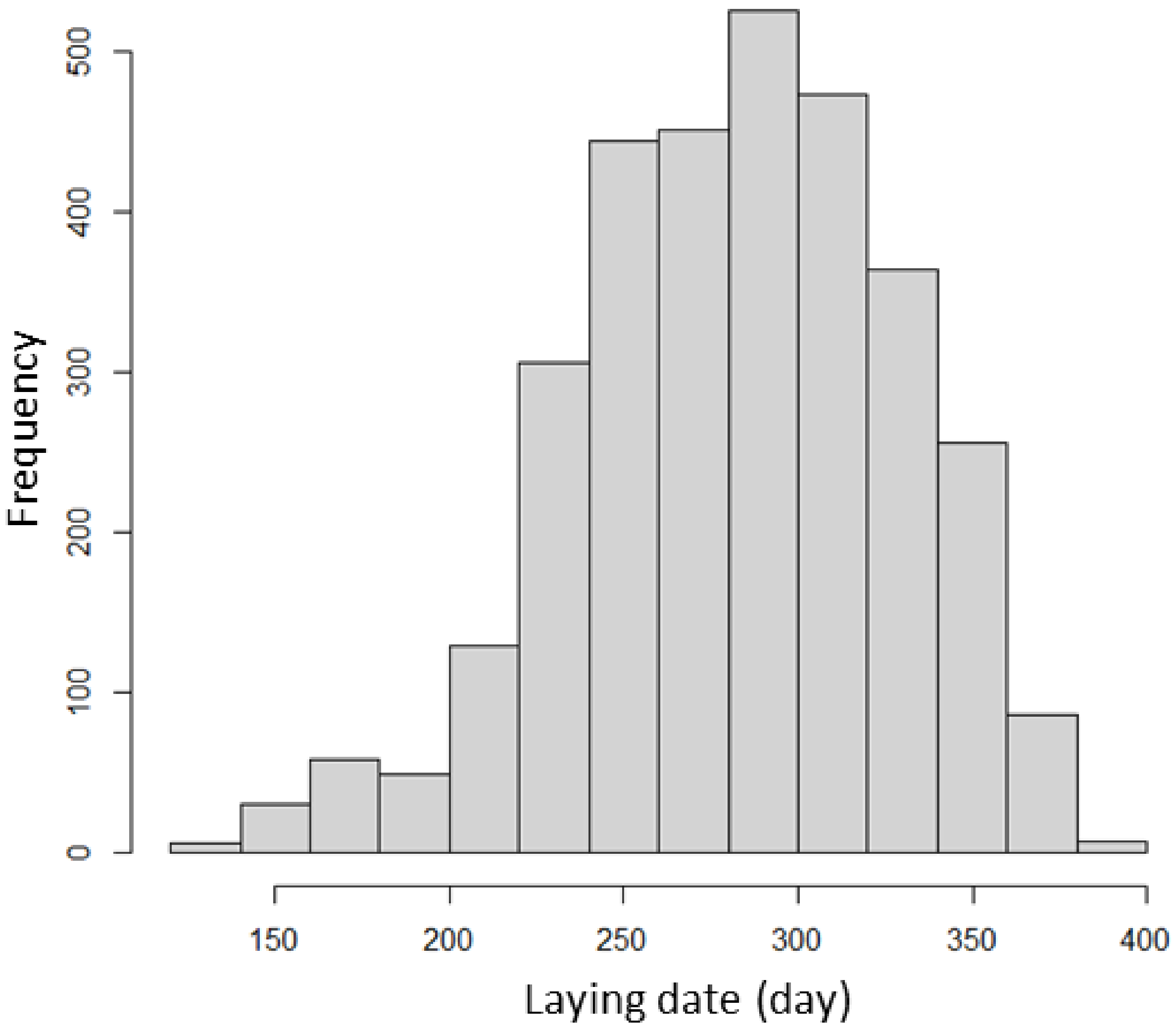


Figure S1: *Frequency of penguins laying date in day of the year from 2000 to 2020*

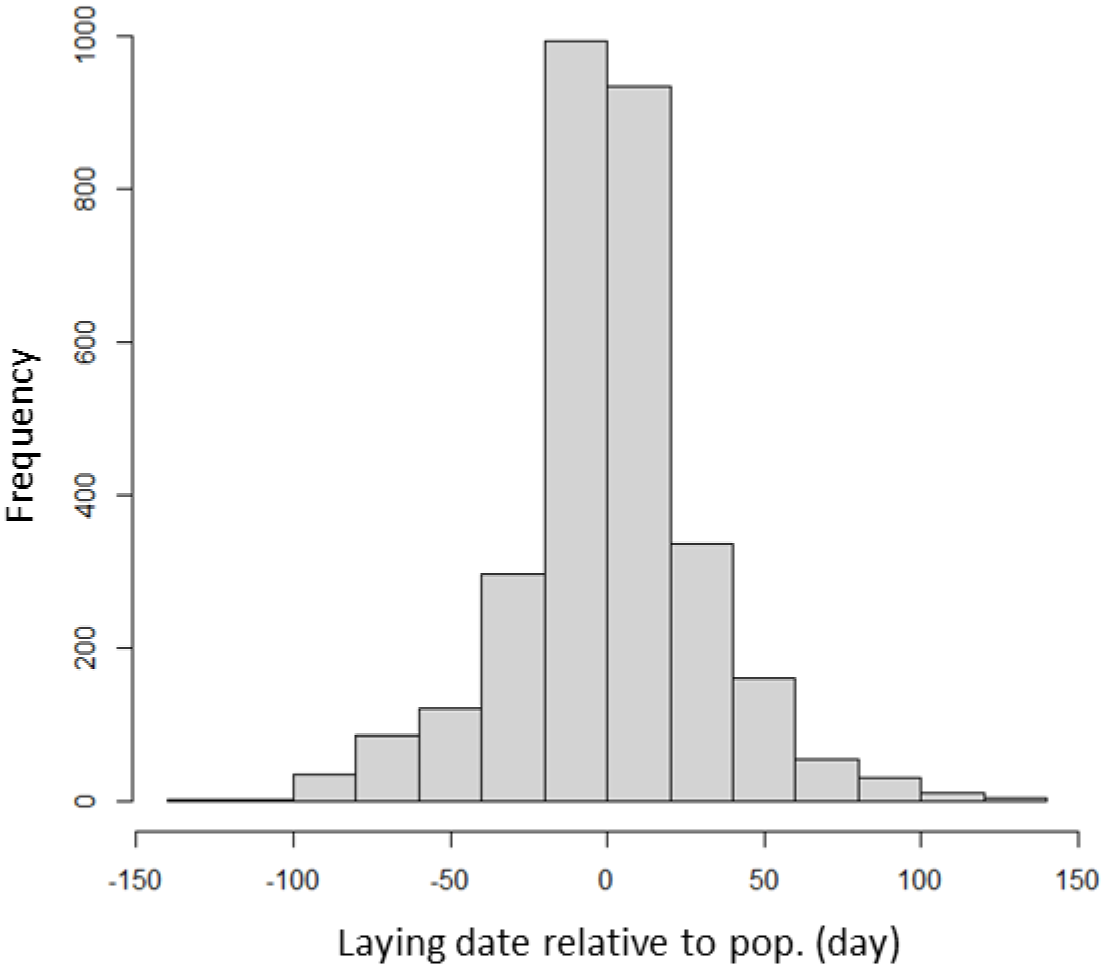


Figure S2: *Frequency of penguins relative laying date in day of the year from 2000 to 2020*

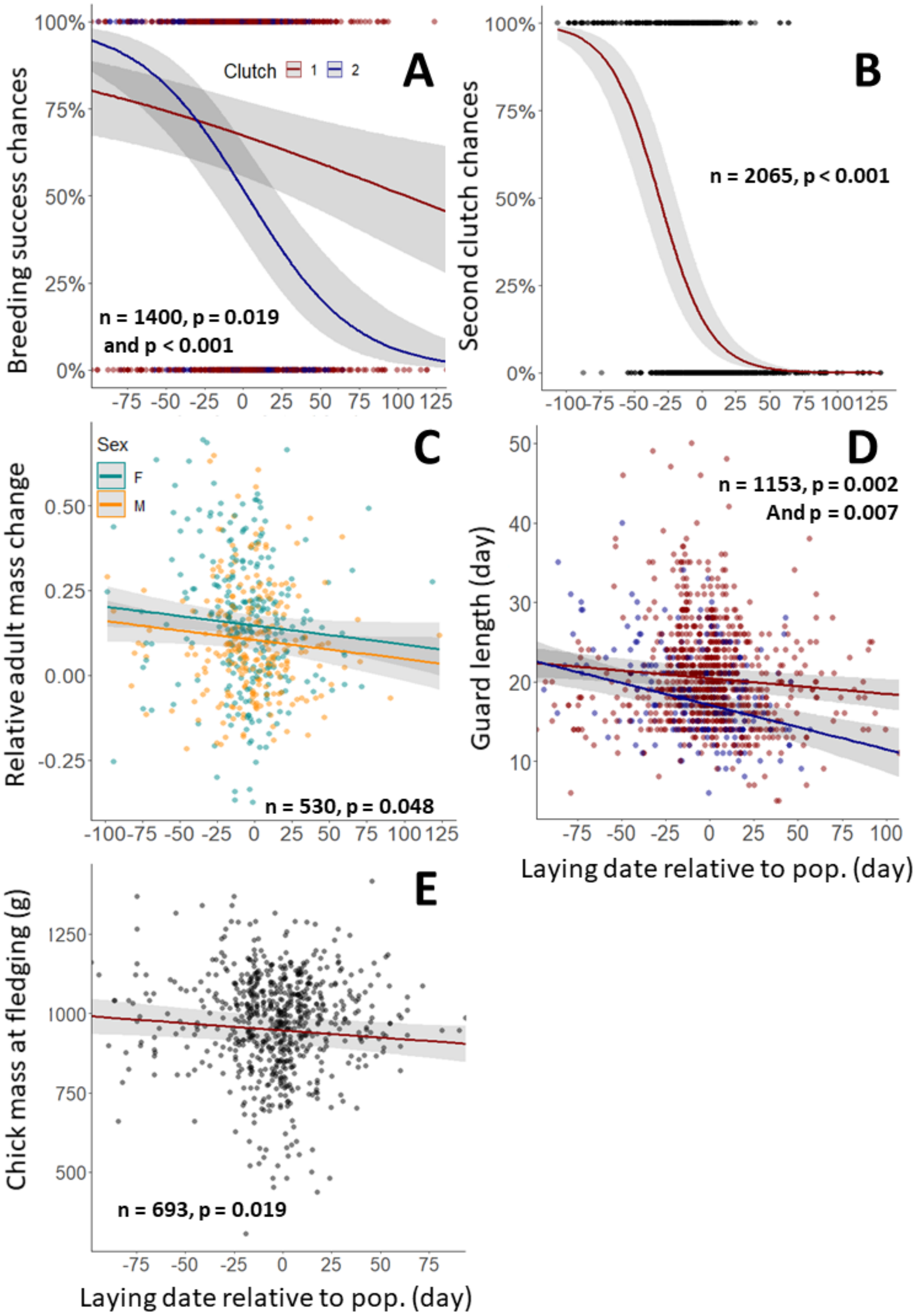


Figure S3: *Breeding parameters of little penguins based on their relative laying date with linear mixed model or generalized additive model (red curve) ± SE (grey area). Blue curve (A, E) represents second clutches, and orange/light blue curves (C) represents differences between sexes. Sample sizes points as well as p-values (for first and second clutches when relevant) are presented.*

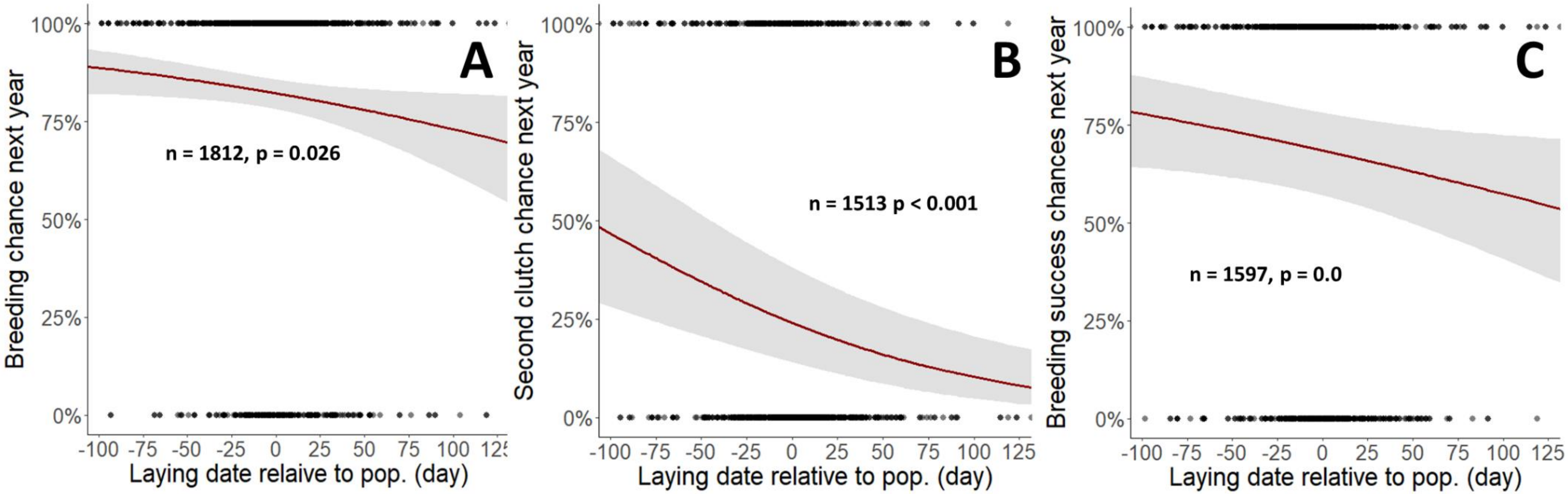


Figure S4: *Breeding chances (first and second clutch) and breeding success of little penguins based on their relative laying date on previous season with linear mixed model (red curve) ± SE (grey area).*

Chapter V: Foraging

Foraging performances: a matter of phenology and stochasticity

Modified from:

Joly, N. B., A. Chiaradia, J.-Y. Georges, and C. Saraux. 2022. Environmental effects on foraging performance in little penguins: a matter of phenology and short-term variability. Marine Ecology Progress Series 692:151–168.

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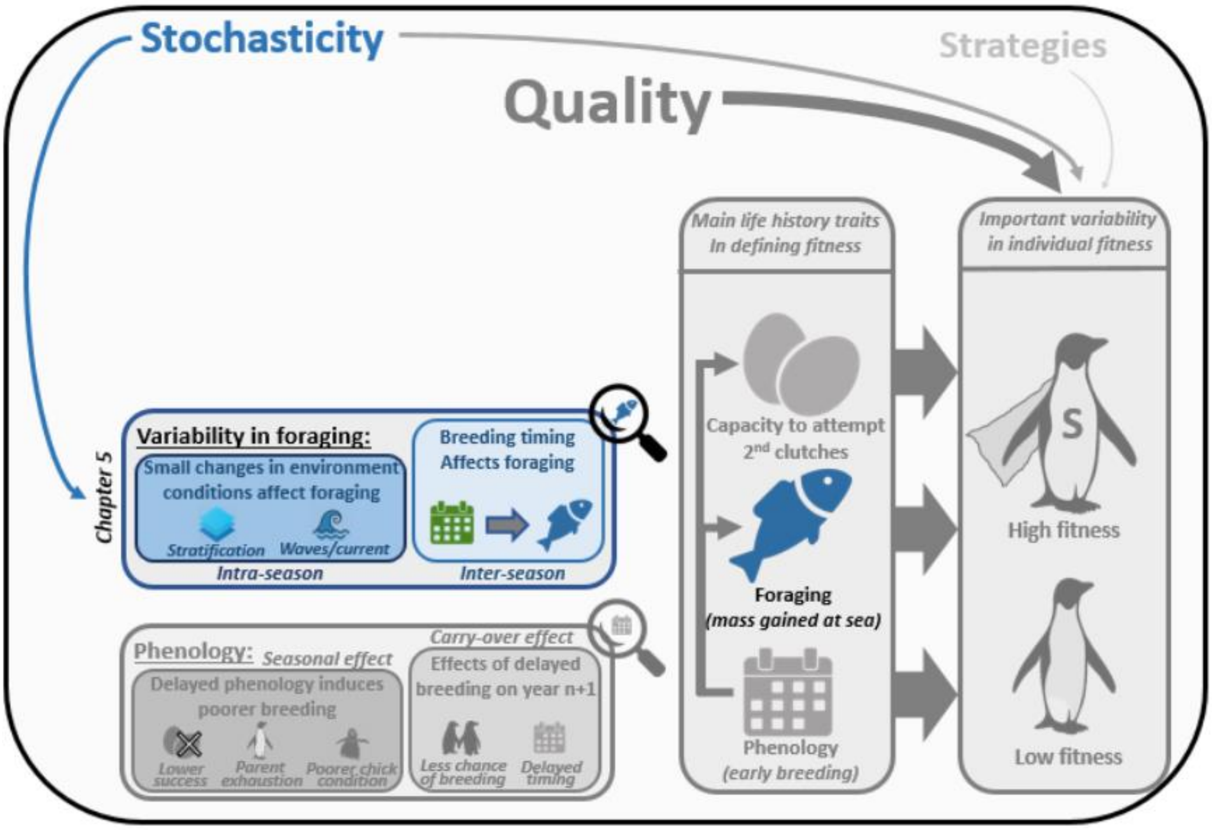
General context of the study:

In the third chapter, I highlight the foraging performances, and especially the capacity to acquire food during chick rearing, as an important driver of inter-individual variability in fitness. In this chapter, I aim at understanding the variability that exists in foraging performances at different time scales (variability across trips, intra seasonal variations and inter-annual variations) to understand how breeding phenology and foraging performances are linked. Furthermore, I assess the role of environment in creating variations in foraging performances in order to discover the potential role of stochasticity at different time scales.

Graphical summary of the main results:



Abstract

Foraging provides an integrative view of the effects of environmental variability on marine top predators, as it results from both direct effects through increased energetic costs at sea and indirect effects through modification of prey accessibility. Using a 19-year automated monitoring system of ~400 individuals (> 45,000 foraging trips), we investigated short-term and interannual variability in foraging performances (trip duration and mass gain) of the little penguin (*Eudyptula minor*), an inshore seabird living in a climate change hotspot. We found marked but variable seasonal patterns in foraging performances with clear optimum periods but no decrease along the breeding season. Although foraging was less variable at the inter-annual scale, we highlighted three groups of low, average and good annual foraging performances. Overall annual performances were affected mainly by late chick-rearing, and low performances during this stage were associated with significantly lower breeding success. To understand how the environment might explain such variability, we further studied simultaneously the effect of variable that may affect penguins foraging directly through energy costs at sea (currents, waves and tides) and indirectly through modifications of prey availability (primary production and vertical stratification). Although foraging performances are often thought to mainly depend on prey accessibility, lower foraging performances were mostly associated with increased waves and currents and only secondarily with a decreased and shallower stratification, showing the primary role of parameters directly affecting seabirds costs at sea. Finally, a good synchrony between birds' phenology and primary production cycles explained inter-annual foraging performances, highlighting the importance of phenology.

Key words: *Climate variation, breeding ecology, breeding success, little penguin, match/mismatch, stratification, waves, currents*

1. Introduction

Marine top predators such as seabirds are good indicators of environmental changes, as they integrate direct and indirect effects of the environment through lower trophic levels of the ecosystem (Parrish and Zador 2003, Piatt et al. 2007). For instance, seabird energetics can be directly affected by wind regime (Spear and Ainley 1997, Mateos and Arroyo 2011) but also indirectly by prey availability (Piatt and Anderson 1996, Romano et al. 2006). An efficient way to study environment-driven changes in marine ecosystems is thus to assess seabirds' foraging performances, as they should reflect both energetic costs at sea (Mullers et al. 2009, Collins et al. 2020) and prey availability (Cairns 1988, Grémillet et al. 2004).

The environment is expected to affect seabirds' foraging (thus survival, breeding and ultimately population dynamic, Baird 1990) differently depending on the time scale considered, especially during breeding when biological constraints due to parental care are maximal. Prey availability, which is very constraining for central place foragers (Hunt 1999; Burke & Montevecchi 2009), could be modified by short-term (days/weeks) changes in spatial (vertical/horizontal) prey distribution due to environmental variations. Indeed, prey are neither randomly nor uniformly distributed in time and space but rather aggregate until a specific density in favorable areas (Fauchald 2009). These favorable areas are created by ocean vertical and horizontal structuration including fronts, eddies, upwellings or water column stratification (Spear et al. 2001, Charrassin and Bost 2001). At a medium temporal scale (several weeks/months), prey availability changes according to seasonal cycles (especially so in temperate and polar environments). Seabird foraging performances should thus be optimal when they best match maximum prey availability (Regular et al. 2014). However, this optimum period may also shift in time when a population predation range is limited, leading to local prey depletion throughout the breeding season (Ashmole 1963, Birt et al. 1987, Lewis et al. 2001). At even larger time scales, inter-annual variability can affect i) prey phenology and therefore shift the optimum period between successive years (Watanuki et al. 2009), ii) prey recruitment with delayed effect on prey abundance during the following seasons (Biela et al. 2019), and/or iii) prey quality (*e.g*. energetic composition) through different productivity levels (Wanless et al. 2005).

In such complex marine ecosystems, little penguins (*Eudyptula minor*) is an appropriate model to study the integrated effects of climate on the marine food web. Due to their limited diving capacities (around 65m, (Ropert-Coudert et al. 2006) and restricted foraging range (Collins et al. 1999) little penguins are strong central place foragers during breeding (*i.e.* when adults have to feed their chicks regularly; Reilly and Cullen 1981, Chiaradia et al. 2007). Their small size also leads to high metabolic rates and limited energy storage capacity (as should be in small animal species, Schmidt-Nielsen and Knut 1984), making them particularly sensitive to short-term environmental variability. Moreover, the little penguin has a long and asynchronous breeding season (Reilly & Cullen 1981), meaning that environmental conditions may differ between but also within individuals across the season depending on their breeding timing.

Little penguins have been suggested to be sensitive to any change in local prey abundance, distribution as well as diversity (Chiaradia *et al.* 2003, 2016). As such, they should be affected by any environmental parameter affecting prey. This species is for instance known to rely on vertical stratification to improve hunting (Ropert-Coudert *et al.* 2009a; Pelletier *et al.* 2012), as prey tend to aggregate around the thermocline (Hansen *et al.* 2001). Yet, direct effects of climate on their energy expenditure at sea for instance should not be discarded, as shown with the effect of currents and tides in a close related species, the Magellanic penguin (*Spheniscus magellanicus*, Raya Rey *et al.* 2010). While stronger winds, for instance, are known to be detrimental for little penguin foraging performances (Saraux *et al.* 2016), the underlying mechanisms (increased energetic costs due to swell or decreased efficiency due to more dispersed prey associated with a lower vertical stratification) remains to be investigated. Finally, large scale decadal oscillations such as ENSO, which can outperform local climate parameters impacts on life-history traits (Hallett et al. 2004, Stenseth and Mysterud 2005), may also affect little penguin foraging (Berlincourt and Arnould 2015).

In this study, we examined how little penguins' foraging performances varied through time according to the environment (swell, currents, tides, wind, thermocline and decadal oscillations) at the world’s largest colony for this species at Phillip Island, Australia. Using an automated penguin monitoring system deployed continuously over 19 years, we compiled a unique dataset of foraging performances (*i.e.* foraging trip duration and associated mass gain) across a wide range of environmental conditions (≥ 45,000 trips). First, we investigated little penguin foraging performance variability at different timescales (within- and among breeding years) with fine-scale temporal resolution. In particular, within year, we tested whether foraging performances decreased throughout the year, as would be expected in case of substantial local prey depletion, or instead reached an optimum during the breeding season (as should be during a temporal match with maximal prey availability). Among years, we tested differences in overall foraging performances and their potential links with annual breeding success.

Second, we investigated how foraging performances responded to the environment at different time scales: i) on the short-term, *i.e.* environmental conditions varying from one trip to another, ii) the seasonal scale, and iii) the inter-annual scale. Because the environment is known to be multifactorial, we simultaneously studied the effects of all environmental parameters known (thermocline, wind, primary production), or suspected (waves, currents, tides, oscillations: AAO & ENSO) to affect little penguin foraging success. By doing so, we expected to partition the variance in foraging performances between different environment-driven processes. In particular, we expected foraging performances to be affected both directly through energetic costs at sea (*e.g.* currents, waves) and indirectly through prey availability (vertical stratification, primary production). Further, we predicted very different effects and relative importance of these parameters depending on the time scale considered. While short-term unfavorable conditions should be driven by environmental variables known to increase energetic costs and decrease prey accessibility, inter-annual differences in foraging performances should depend on ecosystem productivity and temporal match with prey (*i.e.* phenology). A single variable could even have opposite effects depending on the time scale considered. For example, wind and current speed are expected to instantaneously increase swimming and foraging costs while decreasing vertical stratification (Raya Rey *et al.* 2010; Saraux *et al.* 2016), whereas they should improve water mixing and thus enhance primary production in the longer run, favoring the entire food web (Marra 1980).

2. Methods

a) Foraging performances

Foraging trip duration was calculated as the number of days between sequential recordings of a "departure" and an "arrival", considering little penguins leave the site before sunrise and return after sunset (Chiaradia & Kerry 1999). As foraging duration was one day long in the vast majority of guard trips (96% 1-d trips and 4% 2-d trips), variability in trip duration was only investigated during incubation and post-guard. Trips longer than 17 days were considered as missing detections and discarded (Saraux *et al.* 2016).

Body mass gain was defined as the amount of mass change per foraging trip and was calculated as the difference between a penguin’s body mass after and before a given foraging trip. Only body mass ranging from 700 to 1700g and body mass change ranging from [-75 to 500 g] during incubation and [0 to 600 g] during chick-rearing were considered (based on Salton *et al.* 2015 and Saraux & Chiaradia 2021). For our two measures of performances (trip duration and mass gain) to be independent from each other, mass gain was corrected as follow (Saraux

& Chiaradia 2021): 1) in incubation when it increased with trip duration (LM, $p < 0.001$), we used residual values from the linear model [mass gain ~ trip duration], 2) in guard when trip duration is almost invariant, we only subtracted the overall population average mass gain (283.5 g) to the trip mass gain (so as to be centered on 0, as in the other stages), 3) in post-guard when mass gain was better explained by the binary short/long trip variable (Saraux *et al.* 2011) than by actual trip duration, we used the residuals of the linear model [mass gain ~ short/long].

b) Environmental data

Environmental parameters

All data handling was performed using R 3.5.1 and ncdf4 1.17 package for NetCDF files opening and shaping. Water column temperature, chlorophyll concentration, wave height, current speed, wind speed, tides and decadal oscillations (AAO & ENSO) were gathered from different online databases as detailed in *Table 2*. Water column temperature was used to construct several thermocline variables (presence, depth and intensity) using an innovative method, as unequal depth segments and coastal pixels (with very shallow depths) prevented the use of classically used ones (Fiedler 2010) in this study. Briefly, we estimated temperature gradients between each consecutive depths ($\frac{\Delta T}{\Delta Depth}$) and then looked for changes in these gradients along depths using breakpoints (see *Supplementary material Figure S2* for details). The segment of the highest gradient was identified as the thermocline. The depth of the thermocline was defined as the top of this segment. The intensity of the thermocline was the mean |temperature gradient| within this segment. The thermocline was assessed as present in a pixel when its intensity was higher than 0.02°C/m (based on slope breakpoints in the thermocline depth/gradient relationship), and its depth shallower than 70m (*i.e.* reachable for little penguins)

Table 2: Summary table of the studied environmental parameters with their temporal and spatial resolutions, their types and origins.

	Obtained from	Specificity	Temporal resolution	Spatial resolution	Type	Data processing	
						in each pixel	in time series
Water column T° (Thermocline)	Copernicus (https://marine.copernicus.eu)	Two datasets (reanalysis up to 2019, then analysis)	daily	0.083°, 27 depths (from 0.5 to 220 m)	Satellite observations + models		
[Chla]	NASA (https://earthdata.nasa.gov/)	MODIS satellite before 2002 and SeaWiFS satellite from 2002 to 2019	daily	9km (SeaWiFS) and 4km (MODIS)	Satellite observations	To avoid unconsistent data, only values under 1.6µg/l were kept *(i.e. the 99% quantile, coherent with Gibbs et al. 1986)*	Biased daily means (too few pixels due to cloud cover) removed based on random subsampling (1341 out of 3304 days for SeaWiFS and 1348 out of 6250 days for MODIS, Sup. mat. Fig. S1).
Wave height	Copernicus (https://marine.copernicus.eu)	Two datasets (reanalysis up to 2019, then analysis)	daily	0.083° grid	Satellite observations + models		
Current speed	Copernicus (https://marine.copernicus.eu)	Two datasets (reanalysis up to 2019, then analysis)	daily	0.083°, 20 depths (from 0.5 to 65 m)	Satellite observations + models	Current speed was computed as the square root of the sum of the squared norms of u and v vectors.	
Wind speed	Remote Sensing Systems Research Company (http://www.remss.com/)		daily	0.25° grid	Satellite observations + models (CCMP)	Wind speed was computed as the square root of the sum of the squared norms of u and v vectors.	
Shore water level (Tides)	Australian Bureau of Meteorology (http://www.bom.gov.au/)		hourly	13 km from the site (Stony point station)	Direct measures		
AAO	NOAA (https://psl.noaa.gov/data/climateindices/list/)		monthly		measures		
ENSO	NOAA (https://psl.noaa.gov/data/climateindices/list/)		monthly (15th to 15th)		measures		

Water level (tides) data were available as hourly values, from which we assessed the water level (m) at both penguins departure at sea and arrival on land (*i.e.* the periods during which tides are expected to affect penguins' swimming energetic costs

Finally, wind speed is known to affect little penguins at sea (Saraux et al. 2016) but is not expected to directly affect foraging (non-flying seabirds), but rather through other variables (waves, currents, stratification). Therefore, it was included in this study only to assess its correlation with other variables for which we had strong predictions (see *Supplementary material Figure S3 & Figure S4*) to understand the paths through which wind affected foraging.

Building time series of environmental variables

To build time series, data coming from more than one dataset (*e.g.* MODIS/SeaWifs) were merged as specified in *Table 2*. Daily time series were built for all parameters (apart from decadal oscillations for which data was available as monthly values) by averaging gridded data, except for thermocline presence that was defined as daily proportion of pixels where the thermocline was deemed present in the area. The area used to extract environmental parameters (140 to 148° E, 38.2 to 41° S, approx. 120,000 km2, *Figure 28*) was much larger than the known little penguin foraging areas to account for oceanographic processes occurring outside of the foraging area but which can still be influential (*e.g.* phytoplankton bloom). However, some other parameters might be more local, affecting little penguins' foraging directly at the locations penguins travel or forage (*e.g.* currents, waves, stratification). To assess the sensitivity of the time series to the chosen area, we compared two different time series averaged over either the entire large area (red rectangle) or a smaller one corresponding to foraging grounds only (yellow rectangle, Sánchez et al. 2018). No significant differences were observed (see *Supplementary material Figure S6*), so that results were considered unbiased by the area and are only presented over the largest one.

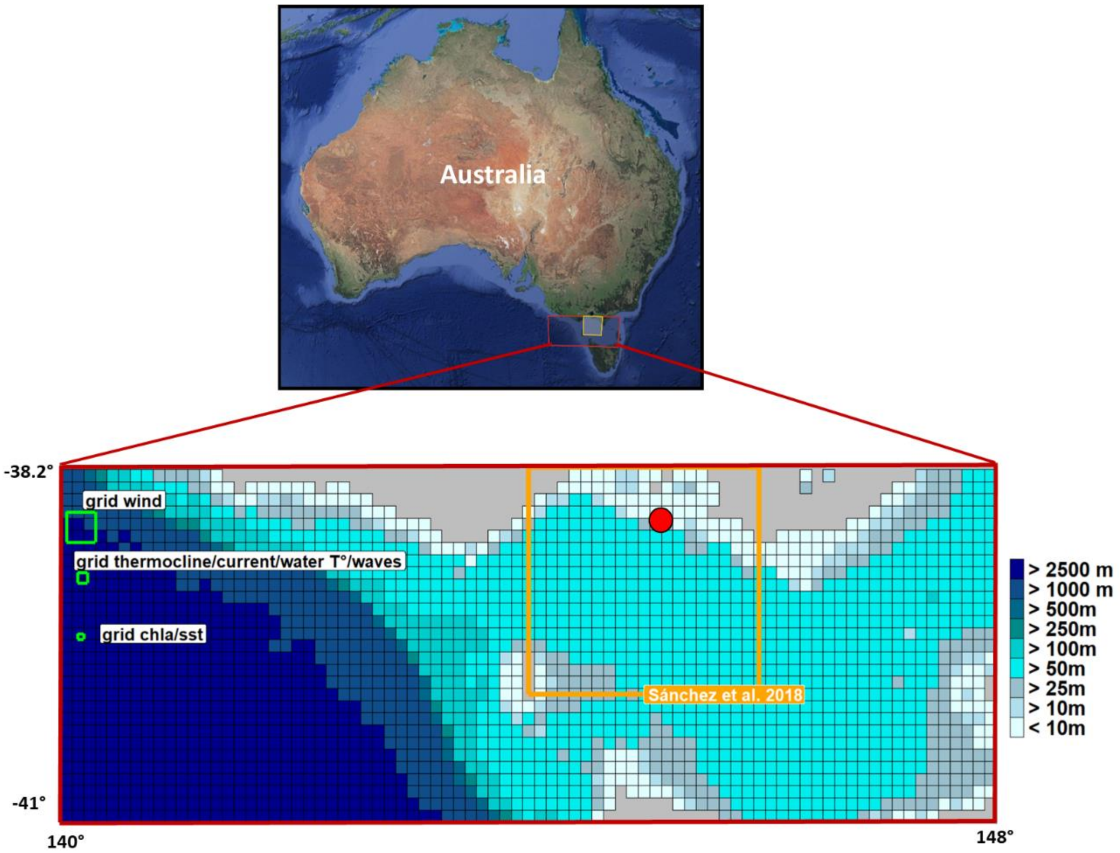


Figure 28: Study area: colony (red dot) and marine area considered for the analyses of environmental variables (red rectangle). The lower panel shows a close-up of the marine study area with bathymetry indicated in shades of blue, known LP foraging areas (yellow rectangle, Sanchez et al. 2018) and the different spatial resolutions used for the climatic variables (green squares).

A seasonal time series was then built by extracting the seasonal signal from the above-described daily time series (except for tides, which do not present strong seasonal patterns). The seasonal signal was computed as the average value of each week among years to assess medium-term environmental patterns. Anomalies from this seasonal signal were estimated as the daily value minus the corresponding weekly seasonal signal and represented short-term patterns. This method was compared with others using additive or multiplicative time series decomposition and gave very similar results (see *Supplementary material Figure S7*).

Finally, a last time series was created for inter-annual comparisons. It was composed of yearly environment variable anomalies (averaged over the breeding season: from the first to the last breeding day of each season), annual oscillation indices (ENSO & AAO, from April to

March) and annual phytoplankton bloom beginning and end dates (dates at which 10 and 90%, respectively, of the annual cumulated daily Chla were reached, Brody et al. 2013).

c) <u>Analyses and statistics</u>

All analyses were performed using R 3.5.1 and RStudio 1.1.456. Data significance was accepted with an error threshold of 5%. Results are presented as means ± standard errors (SE). Whenever running a linear model (or linear mixed model, LMM), normality of the residuals was tested using density plots and q-q plots. When more than one explanatory variable was included as a fixed effect in a model, the best model was selected according to backward stepwise selection based on Akaike's Information Criterium (AIC) starting from the full model, unless otherwise specified. When the difference in AIC was lower than 2, the most parsimonious model (*i.e.* the one with the least variables) was retained (Burnham and Anderson 2004).

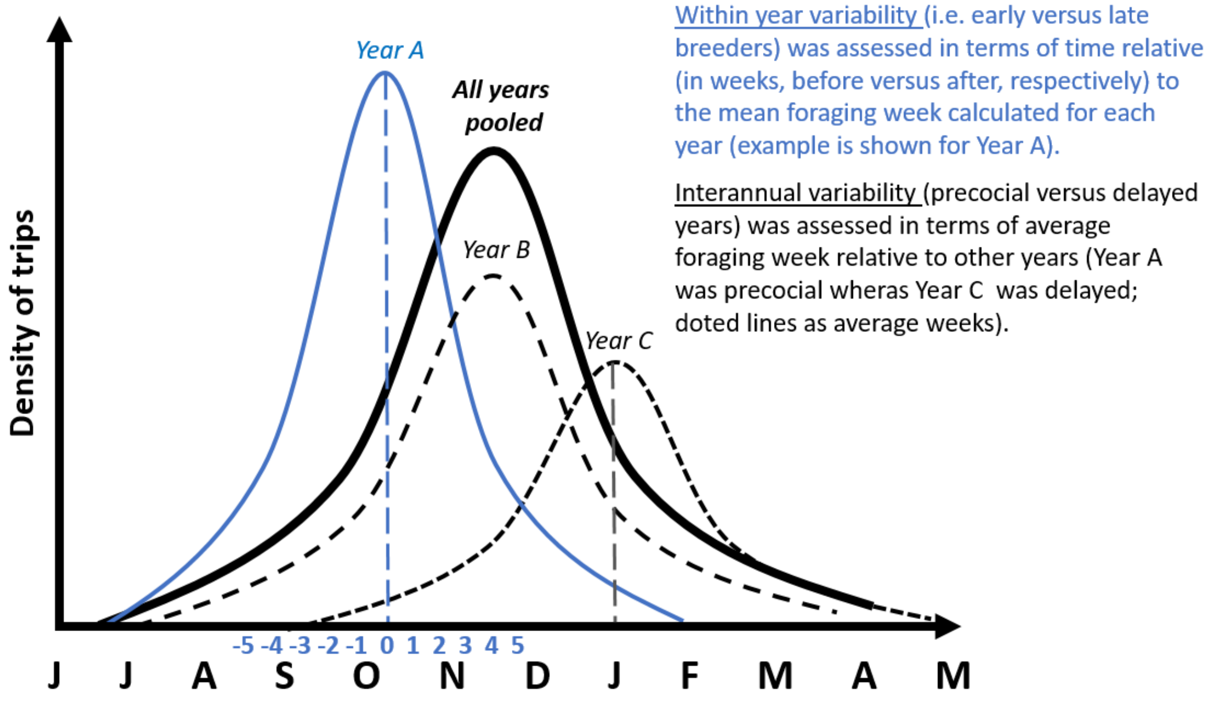
<u>Seasonal patterns in foraging performances</u>

Trip duration and associated mass gain were averaged per calendar week to assess seasonal patterns in foraging performances throughout the year. Generalized Additive Models from `mgcv 1.8-33` (*GAM = Mass gain or Trip duration ~ smooth{week}*) were then run for each breeding stage separately. However, an early week could result from two different processes: individual foraging early in the year or an overall early year. To disentangle between the two and assess the variability of seasonal patterns among different years, we computed the average foraging week of each breeding year and the relative week of each trip (*i.e* the week value of each trip minus the average week of the season, *Figure 29*).

Effects of average week (overall timing, rather early or delayed years compared to others), relative week (timing of each week within the season) and their interaction were assessed using the following Generalized Additive Mixed Models:

GAMM = Mass gain or Trip duration ~ smooth{relative week} + smooth{average week} + tensor product{average week, relative week}

We added individual ID as random effect for both foraging parameters as well as a random effect of chick age for trip duration and adult sex for mass gain (based on preliminary variance analysis, see *Supplementary material TableS1*).



Within year variability (i.e. early versus late breeders) was assessed in terms of time relative (in weeks, before versus after, respectively) to the mean foraging week calculated for each year (example is shown for Year A).

Interannual variability (precocial versus delayed years) was assessed in terms of average foraging week relative to other years (Year A was precocial wheras Year C was delayed; doted lines as average weeks).

Figure 29: Schematic view of within year (early vs late breeders) and interannual (precocious vs. delayed years) breeding timing variability assessment.

Inter-annual differences in foraging and link with breeding success

To categorize years based on their overall foraging performances (*e.g.* low, average, high), we used a clustering analysis performed using k-means method and `kmeans` function from `stats 3.6-2`. For each breeding stage as well as the whole season, the optimal number of clusters was assessed by running the kmeans function 1000 times for each cluster number from 1 to 10. Both within- and among-clusters square sum of distances were then computed for all cluster numbers, and the strongest break in slope for these two parameters was used to define the optimum number of clusters.

Finally, we investigated whether years of contrasted foraging performances resulted in different breeding success and whether this applied for each breeding stage and the whole year. To do so, we tested for differences in annual breeding success between above-defined clusters using Kruskal-Wallis followed by Post-Hoc Dunn tests.

Effects of short-term environmental variation on foraging

We assessed the link between environmental parameters and trip duration and associated mass gain on the short-term (*i.e.* at the trip scale) using linear mixed models for each breeding stage separately (as effects were expected to differ due to very different constraints among breeding stages). Daily parameter anomalies and seasonal signals were averaged per foraging trip, except for tides (closest hourly water level measure) and used as explanative variables in the models. Effects on mass gain were tested using LMM with random effects of year, individual and sex, while effects on trip duration were tested using GLMM with Poisson distribution and random effects of year, individual and chick age (based on preliminary variance analysis, *Supplementary material TableS1*). Variance Inflation Factors (VIF) were estimated on full models, including all variable anomalies and seasonal signals. Variables with the highest VIF were then sequentially removed until no variable had VIF > 3 to avoid collinearity issues (Zuur et al. 2010).

Effects of inter-annual climate variability and breeding timing on foraging

To test for the relation between the environment and foraging performances at the inter-annual scale, we computed linear models explaining annual means of either mass gain or trip duration by yearly means of environmental anomalies averaged over the breeding season (except for tides that were expected to present no inter-annual differences) as well as annual ENSO and AAO indices. Considering the small sample size (n=19 years) compared to the number of explanative variables tested, we decided to run separate linear models for each explanatory variable (lm = mass gain or trip duration ~ environmental variable).

Finally, we studied the effect of phenology and tested for the effect of match or mismatch between foraging and optimal conditions (as inferred by chlorophyll a). Because the bloom of primary production occurs mainly during winter in this zone (*i.e.* finishing in spring, Kämpf and Kavi 2017) while little penguins breed in spring/summer, we assessed penguin foraging and primary production synchrony as the yearly average week of foraging minus the bloom end week. The link between this synchrony and foraging performances was assessed using GAMs on annual mass gain and trip duration separately.

3. Results

a) Variability in foraging performances

Over all individuals (N = 399) and years (N=19), foraging trips (n = 45,363) lasted on average (mean ± SE) 3.21 ± 0.03 days in incubation (n = 7,075), 1.09 ± 0.00 days in guard (n = 11,767) and 1.40 ± 0.01 days in post guard (n = 26,521), ranging from one to 17 days. Relative mass gain (*i.e* mass gain corrected according to trip duration) was estimated for 28,633 trips (63%) and varied from -394 to +352g. Due to the significance of breeding stage on foraging performances (*Supplementary material TableS1*), further analyses were run separately per breeding stage.

Seasonal patterns in foraging performances

Except for relative mass gain during incubation (GAM, p= 0.32, n= 29 weeks, *Figure 30 C*), little penguins' foraging performances presented non-linear changes within a season in all breeding stages (*Figure 30*). All four GAMs showed a similar optimal period of foraging (*i.e.*

shorter trips and higher mass gains) in October (weeks 40-42). Foraging performances also seemed to re-increase for the latest trips in the season with shorter trips in January (week 55) for incubation and shorter trips with higher mass gains in March (week 63) for post-guard.

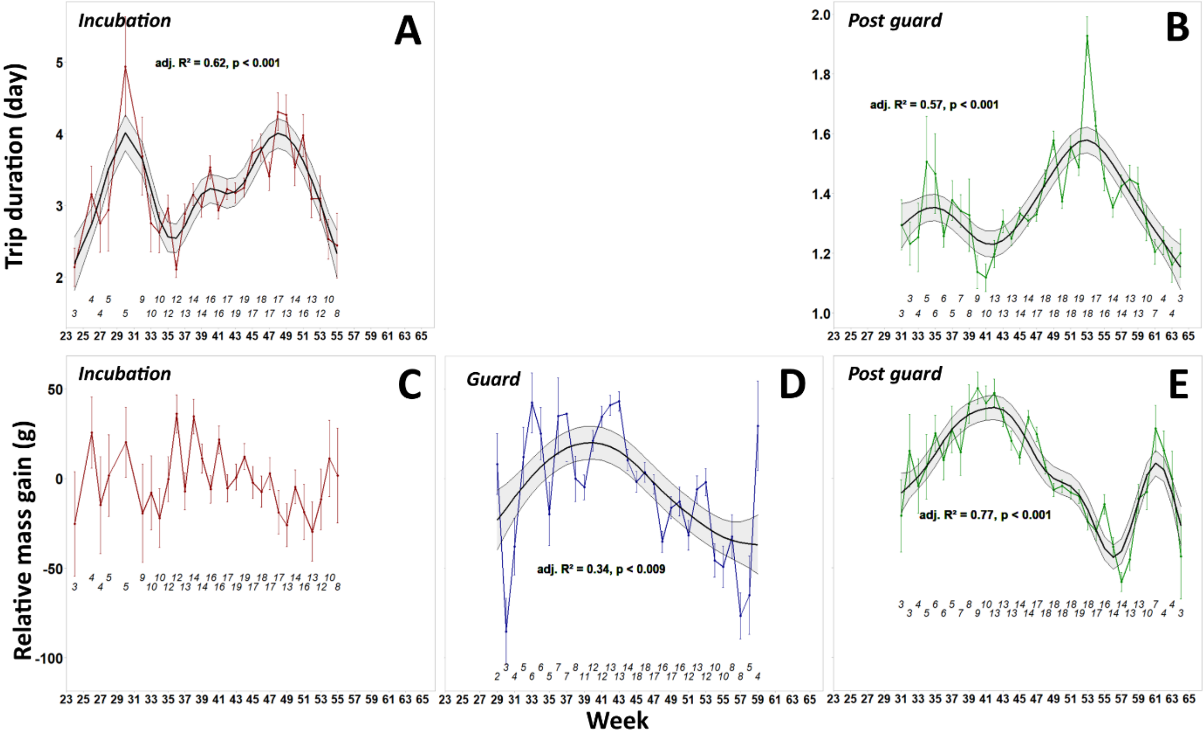


Figure 30: Weekly mean ± SE relative mass gain and trip duration in incubation (red), guard (blue) and post-guard (green). The prediction (black curve) and standard error (grey area) of the GAM are superimposed when week was significant. Italic numbers at the bottom of each panel indicate the number of years per breeding week.

Interaction between phenology and foraging performances patterns

To assess how the above-described optimum patterns were affected by differences in overall years timing, further analyses considered the effects of average year week (inter-annual variability, *i.e.* precocious versus delayed breeding year) and week relative to average year week (within-year variability, *i.e.* early versus late within the year, see *Figure 29* for more details). Both average and relative weeks had a significant effect on penguins trip duration during incubation and post guard, as did their interaction (GAMMs, n = 5,705 and 21,604, all $p < 0.001$), suggesting that the intra-annual pattern in foraging performances varied depending on the year overall timing (*i.e.* precocious or delayed years). Penguins conducted shorter trips just before mid-year (relative weeks -5 to 0) during incubation and post guard and at the end of incubation. While this remained true regardless of the year timing (*Figure 31 A and B*), the effect was much more pronounced during delayed years than in precocious years.

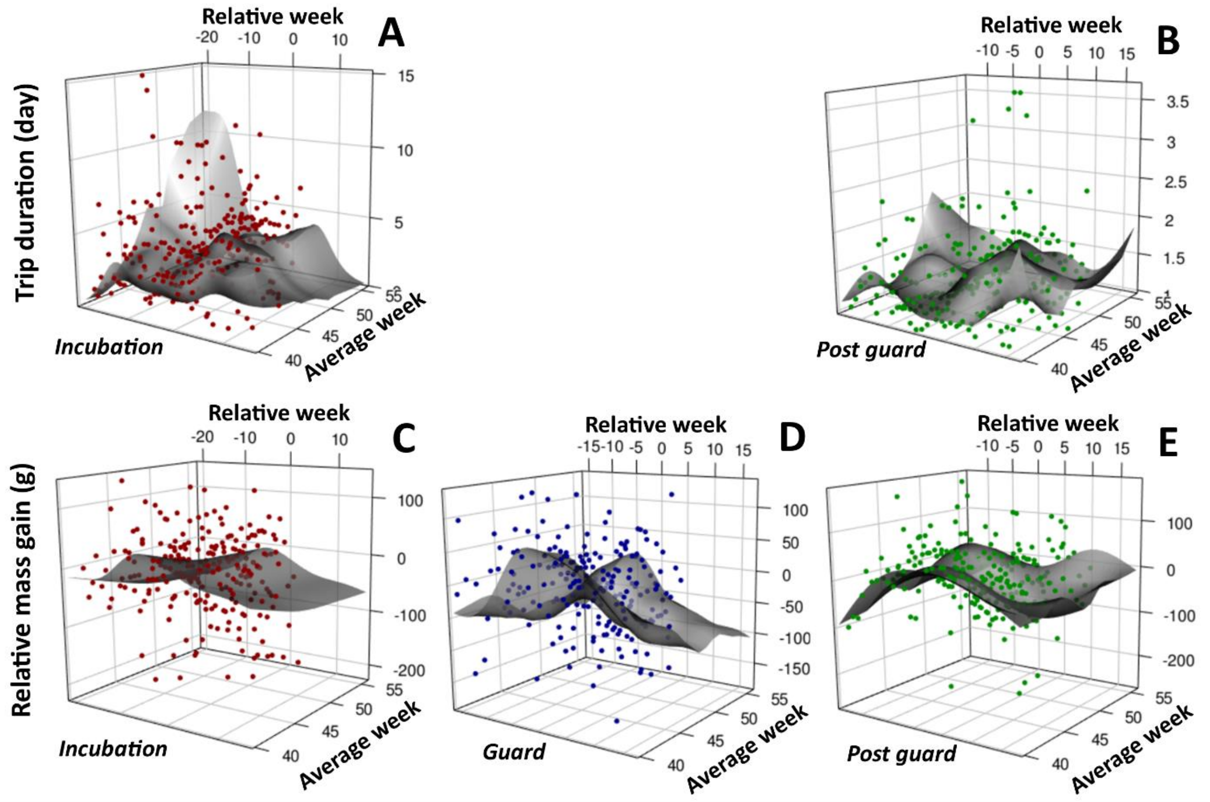


Figure 31: Average mass gain and trip duration depending on average week and/or relative week in incubation (red), guard (blue) and post-guard (green). The prediction by the GAM with average week, relative week and their interaction (but for panel C where the interaction was not significant) is represented by the grey surface.

During incubation, penguins' relative mass gain was related to both average year week and relative week, yet the interaction was not significant (GAMM, n = 3,422, $p < 0.001$ for single effects and 0.378 for their interaction). Their mass gain was significantly lower during delayed years *(Figure 31 C)* and was very similar early and late within the year, but slightly higher in early mid-year (relative weeks from -10 to 0). During guard, the relative mass gain was affected by relative week and its interaction with the average week (GAMM, n = 6,367, $p < 0.001$ for relative week and interaction, $p = 0.171$ for the average week). Penguins' mass gain followed a clear optimum pattern with a peak during early mid-year weeks (relative week around -10 to 0, *Figure 31 D*). However, this was very important in precocious and delayed years but less so in average years. Finally, mass gain in post guard was affected by the average week and its interaction with the relative week (GAMM, n = 13,874, $p < 0.001$). Overall, as for guard, the mass gain was lower when breeding year timing was average than for precocious and delayed years (*Figure 31 E)*. While individuals' mass gain was higher in mid-year for early years, it was the opposite in delayed years, when mass gain was higher early or late in the year.

Inter-annual differences in foraging parameters

Based on the combination of little penguins' trip duration and mass gain (or just mass gain in guard), three distinct clusters, hereafter named years of low, average and high foraging performances, were defined for each breeding stage (and for the entire breeding season with all 3 breeding stages pooled, *Figure 32 A, C, E, G*). Apart from incubation, clusters reflected real differences in quality, with both foraging parameters varying together (*e.g.* clusters of high foraging were characterized by high mass gain and short trips, *Figure 32 C, E, G*). During incubation, however, clusters also reflected different strategies, one cluster being characterized by average mass gain but very long trips while another one displayed the exact opposite (*i.e.* average trip duration but low mass gain, *Figure 32 A*).

Some years were associated with the same foraging performances cluster for all three breeding stages (*e.g.* 2001 and 2015 being defined as low and high foraging years, respectively). However, most of the years consisted of breeding stages belonging to different foraging performances (*e.g.* 2018 was a composite of high performances during incubation but low performances during guard and post-guard).

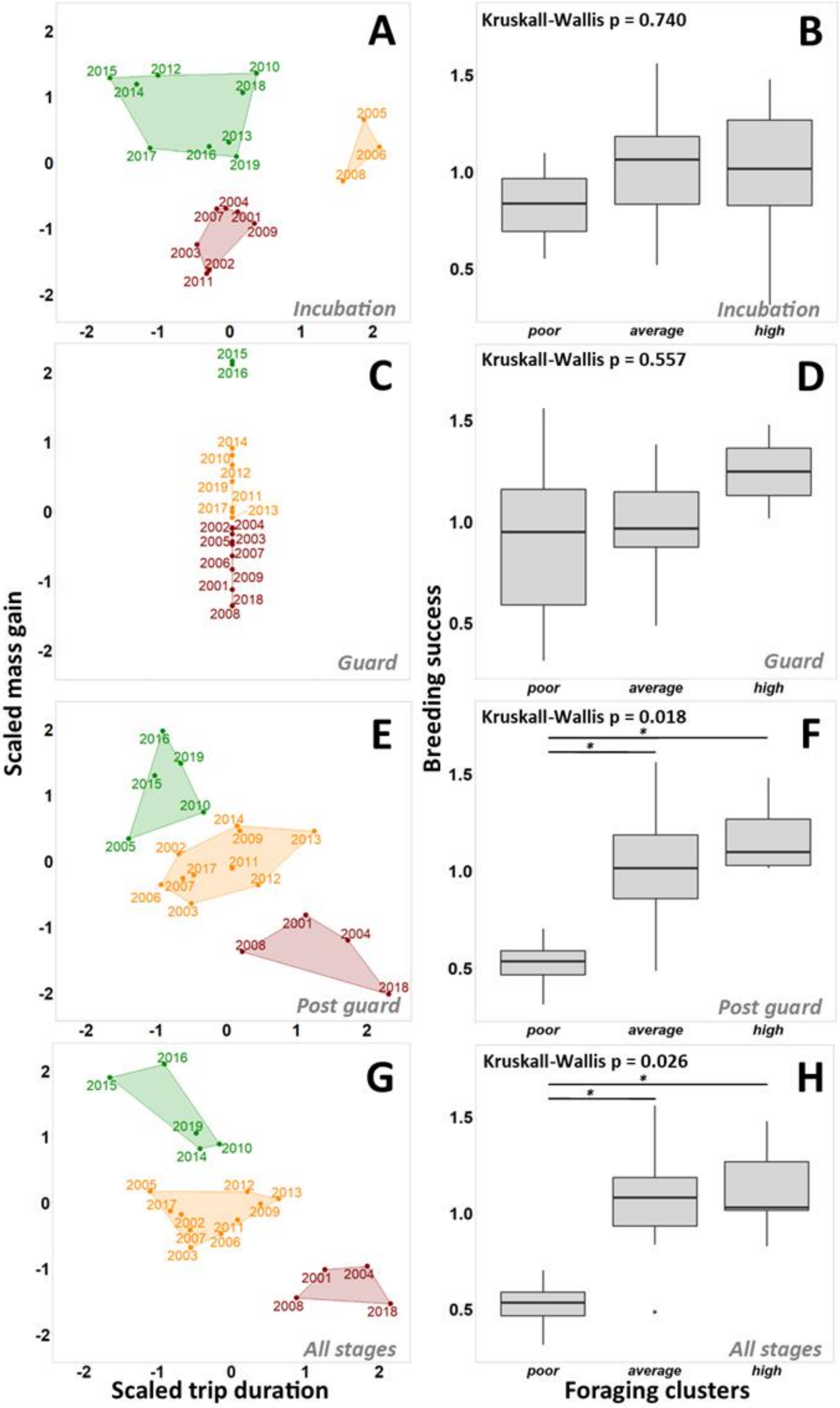


Figure 32: Annual foraging performances grouped by kmeans clustering (A,C,E,G, nstart = 1000) based on both scaled trip duration and mass gain (only based on mass gain for guard). For each breeding stage as well as for all stages pooled, years were clustered in three groups of poor (in red), average (in orange) and high (green) foraging performances. Breeding success (nb. of chicks fledged per breeding event) is compared between clusters (B,D,F,H). Stars represent significant differences according to Dunn (holm adj.) post-hoc test.

Breeding success

Penguins' breeding success tended to increase with foraging performances for each breeding stage (*Figure 32, B, D, F and H).* Yet, differences in breeding success among categories of foraging performances were only significant during post-guard (Kruskal-Wallis, p = 0.018) or when pooling all stages together (p = 0.026). During these periods, breeding success in years of low foraging performances was about half that of breeding success in years of average and high performances (Post-hoc Dunn tests, *Figure 32 F*).

b) Environment variability and foraging performances

Short term effects of the environment on foraging

Although both environmental anomalies and seasonal signals were run together to explain short-term effects of the environment on foraging performances (*Figure 33*), only the effect of the anomalies are described here. Indeed, seasonal signals were quite correlated, so that several variables had to be removed to avoid collinearity problems, making the results harder to interpret. A detailed description of seasonal signals as well as model outputs can be found in *Supplementary material TableS2 to TableS6*.

All studied environmental variables affected foraging performances at some point, although some were always present while others specifically affected certain breeding stages or foraging parameters (either only mass gain or trip duration). Waves had the most consistent effect on foraging, higher wave heights resulting in penguins simultaneously gaining less mass and making longer trips (LMM, $p < 0.001$ in all cases, not tested in incubation because of high VIF caused by correlation with current speed). The current speed also had numerous effects on foraging but with less consistency. Indeed, increased current speed had a negative effect on individuals mass gain during incubation (LMM, p = 0.002), but conducted to shorter trips during that same stage (p = 0.002) and had a positive effect on the mass gain during guard (p < 0.001).

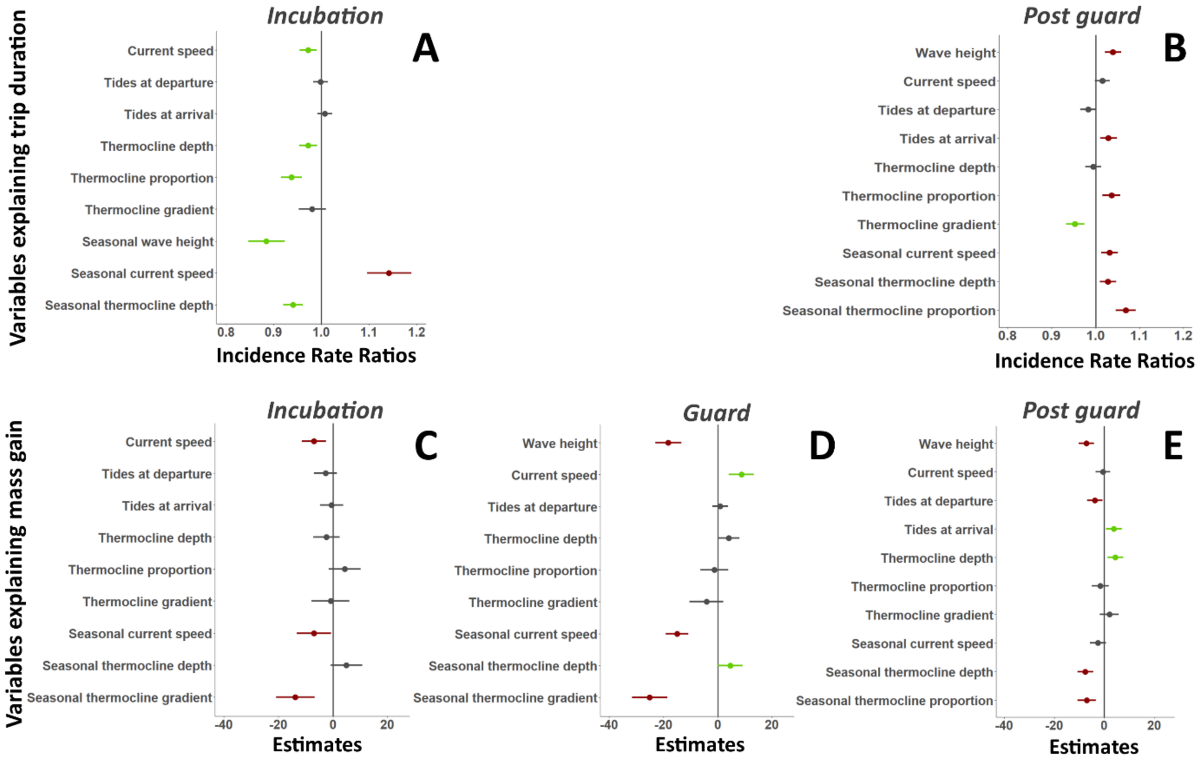


Figure 33: Environmental effects on foraging trip duration (top panels A & B) and relative mass gain (bottom panels C, D & E) for each breeding stage. Estimates and 95% confidence intervals from LMMs explaining mass gain and incidence rate ratios and 95% confidence intervals from GLMM (Poisson distribution) are presented. Significant effects are presented in color (red for significant detrimental effect, i.e. lower mass gain or longer trips) and green for significant positive effect), while non-significant effects are presented in grey. Some variables were removed from the full models due to important VIF.

Vertical stratification had a more contrasted influence on penguins' foraging performances as it had no effects on mass gain but for a positive effect of thermocline depth in post-guard (p = 0.004). However, when looking at trip duration, deeper and more extensively spread thermocline conducted to significantly shorter trips during incubation (p = 0.004 and p < 0.001, *Figure 33 A*). By contrast, penguins made significantly shorter post-guard trips when thermocline was stronger but spread less extensively (LMM, p < 0.001 in all cases, *Figure 33 B*).

Finally, tide effects were only detected during post guard (*Figure 33 B & E*) and had opposite effects on mass gain and trip duration. Penguins going at sea at high tides had lower mass gain and tended to perform shorter trips (LMM, p = 0.019 and 0.071), whereas the opposite occurred when they returned on land (p = 0.017 and 0.002).

Annual effects of the environment on foraging

Little penguins' annual mass gain and trip duration were not significantly related to annual oscillation index (ENSO & AAO) nor current speed, wave height, thermocline proportion, gradient or depth anomalies (LM, p > 0.1 in all cases). However, trips were significantly shorter when Chlorophyll concentration anomalies were higher during the breeding season (LM: 0.24±0.10 days shorter per 0.1µg/l more Chla, p = 0.034).

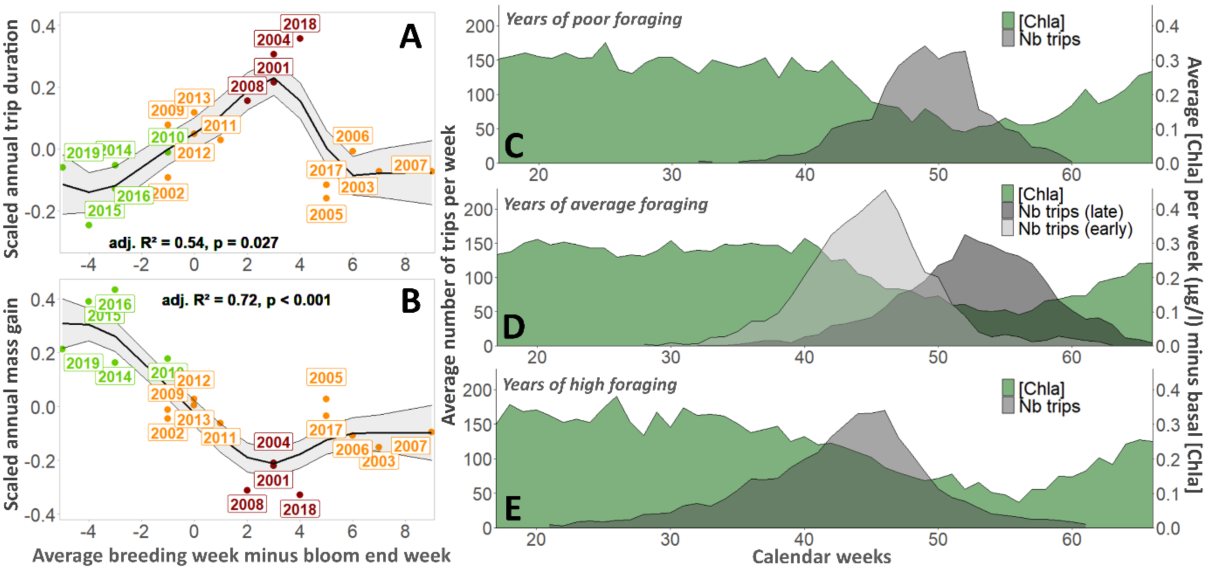


Figure 34: Effect of synchrony between foraging and primary production on annual mass gain and trip duration (A & B), with generalized additive model (black curve) ± SE (grey area). Points are colored according to established high (green), average (orange) and poor (red) foraging clusters. Weekly average Chla concentration (dark green) and trip density (grey) during the year are presented for each of the 3 clusters (C, D & E). Trip density in the average foraging cluster (D) is split in two different categories based on breeding timing: early breeding (2002, 2009, 2011, 2012 and 2013 in light grey) and very late breeding (2003, 2005, 2006, 2007 and 2014 in grey) based on A & B.

Furthermore, penguins' foraging performances were associated with the synchrony between their breeding timing (*i.e.* average foraging week) and the spring decrease in primary production, hereafter called winter bloom end (*Figure 34 A & B*, GAMM, $p < 0.001$ for mass gain and $p = 0.027$ for the trip duration). More precisely, years were optimal in terms of foraging when the average foraging week happened around one month before the winter bloom end, and minimal when the average week happened one month after (*Figure 34*). Extremely delayed seasons (average breeding week 5 to 7 weeks after winter bloom end) had intermediate foraging performances, potentially due to higher synchrony with the start of the next winter bloom at the end of summer (*Figure 34 A, B & D)*. Years of low foraging performances were mainly characterized by delayed breeding (*Figure 34 C*) while years of high foraging were characterized by precocious breeding (*Figure 34 E*).

4. Discussion

We assessed the variability in little penguins' foraging performances both within and among years, and investigated how they respond to climate and oceanography conditions. Based on trip duration and mass gain of 399 little penguins over 19 breeding seasons and 45,363 trips, we showed that their foraging during breeding varied both within and among years. Some periods were frequently more favorable within the year than others, *i.e.* birds conducting shorter trips and gaining more mass. We further identified groups of low, average and good foraging years at the inter-annual scale, which seemed to drive the annual breeding success. Finally, we integratively studied different climatic and oceanographic variables from which we highlighted the primary importance of variables thought to affect foraging directly (*i.e.* through increased costs while swimming or diving: waves and currents), as well as the secondary role of variables affecting foraging indirectly (*i.e.* through a modification of prey distribution affecting travelled distances or capture efficiency: vertical stratification). At the interannual scale, we showed the dominant role of phenology and match with primary production cycles in foraging performances variability.

Variability at the trip scale

Sudden and short environmental variations can affect seabirds' foraging behavior and efficiency (Raya Rey et al. 2010, Dehnhard et al. 2013, Osborne et al. 2020). In little penguins, changes in foraging had been previously associated with changes in vertical stratification (Pelletier et al. 2012) and wind speed (Saraux et al. 2016). However, if wind is energetically costly during foraging in flying seabirds (Amélineau et al. 2014, Elliott et al. 2014, Tarroux et al. 2016), the question remained on the mechanism through which wind could affect non-flying seabirds such as little penguins. Wind may affect vertical stratification and water mixing (Klein and Coste 1984, Warrach 1998) potentially modifying prey distribution (Sanvicente-Añorve et al. 2007) but also increase wave height and surface currents (Mao and Heron 2008, Young et al. 2011) making swimming conditions at sea more difficult. Here, we found strong correlations between daily wind speed and current speed and wave height, but weak correlations with vertical stratification (thermocline intensity and proportion, see Supplementary material). Furthermore, wave height and current speed had the strongest and most consistent detrimental effects on foraging trip duration. We argue that wind speed effects previously highlighted on non-flying seabirds (Dehnhard et al. 2013, Saraux et al. 2016) might be primarily mediated through waves and currents (energy spent) rather than by increased water mixing (prey accessibility). This pattern suggests that non-flying seabirds face adverse foraging conditions while commuting during strong wind days, similar if not even worse compared to flying birds (*e.g.* compared to positive effects of increased wind speed on foraging in albatrosses, Weimerskirch et al. 2012).

Based on previous work on Magellanic penguins, we also expected little penguins to be affected by tidal cycles when commuting from land to sea (Wilson et al. 2001, Raya Rey et al. 2010). However, effects of tides were only significant during post-guard, when higher water levels on the way back to land resulted in longer trips but higher mass gain (mass gain was conversely lower when the water level increased when departing to sea). These unexpected results might suggest that tidal effects are a matter of prey accessibility rather than unfavorable commuting conditions (as for Adélie penguin, Oliver et al. 2013), through fish and zooplankton migrations (Gibson 2003), known to enhance very nearshore seabird foraging (Holm and Burger 2002). However, tidal effects on little penguin foraging would need further investigations to better understand their underlying processes.

The presence of a vertical stratification also affected little penguin foraging performances, following previous studies (Ropert-Coudert et al. 2009, Pelletier et al. 2012). Overall, stronger thermocline allowed shorter trips in post-guard, which is coherent as more stratified waters should enhance fish aggregation (Hansen et al. 2001) with benefits for seabirds (Kokubun et al. 2010, Pelletier et al. 2012). Thermocline proportion also had positive effects during incubation but was detrimental during post-guard. One explanation may be that during incubation (*i.e* early in the season) thermocline is not well established (average of 42% thermocline in the area during incubation trips), so that more extensively present thermocline should lead to more extended areas of prey aggregation and foraging grounds. Conversely, during post-guard, once thermocline is well established (average of 76% thermocline in the area per trip), a further increase in thermocline area presence might reflect an uniformly distributed physical barrier and the absence of horizontal prey aggregation areas (*e.g.* fronts, Spear et al. 2001). Deeper thermocline generally had positive effects on little penguins foraging performances (no negative effects expected in such shallow waters) which might result from higher prey aggregation at deeper stratification (Spear et al. 2001) or from a decrease in energy costs in deep dives compared to shallow ones (Wilson et al. 1992).

Seasonal patterns of variability in foraging

Variations in seabird foraging performances along a breeding season are usually thought to be either mainly driven by local prey depletion (Ashmole 1963, Birt et al. 1987, Lewis et al. 2001) or by a match with maximum prey availability (Durant et al. 2007, Regular et al. 2014). In case of prey depletion, foraging performances are expected to linearly decrease during the breeding season, while a match/mismatch with prey availability is expected to create optimum shaped foraging performances, the optimum being the moment when foraging birds encounter maximum prey availability. Here, we found established optimum patterns (optimum around 1/3rd of the season), when mass gain was maximal and foraging trips were the shortest. Conversely, we found no decrease of foraging performances along the season, confirming previous suggestions that prey depletion would not explain the foraging pattern of deep-divers such as the little penguin because of their use of three-dimensional foraging areas (Chiaradia et al. 2007b). This suggests that little penguin foraging performances at the season scale are much more dependent on the match with their prey than on potential prey depletion in their limited foraging area.

As optimum foraging performances were characterized by shorter trips and higher mass gain at the same time even for birds at different breeding stages, our results also suggest that foraging variability is driven by external (environmental) conditions rather than by intrinsic (behavioral) plasticity, where one parameter could be traded-off with the other (Paiva et al. 2010, Saraux et al. 2011).

Variability at the inter-annual scale

According to the seasonal optimums in foraging performances highlighted above, phenology should play an important role in foraging variability, as previously suggested (Chambers 2004, Chiaradia and Nisbet 2006, Cullen et al. 2009, Ramírez et al. 2016). Maximizing foraging performances should thus depend on the population overall timing (four months difference between the earliest and latest years in breeding onset) and the individual breeding onset within the season. Here, we demonstrated the duality between intra- and inter-annual breeding timing by assessing the interaction between these two timescales. We showed that the best time-window to forage (*i.e.* optimum prey availability) differed from the start to just past the middle of the breeding season depending on how early the overall season was.

Despite this critical role of phenology, no link between overall breeding season foraging performances and oceanographic variables (stratification, wave and current regime) could be established. This disconnection is predictable as inter-annual environmental variability of marine ecosystems is multifactorial (Grémillet and Boulinier 2009b, Sydeman et al. 2012, Quillfeldt and Masello 2013) and composed of fluctuating parameters that are not easily integrated at larger time scales. However, we showed that years when phenology better-matched winter high primary production (maximum occurring during fall and winter in the region, Kämpf et al. 2004) resulted in higher foraging performances. Years of high foraging performances were consistently precocious years during which most trips occurred before the spring decrease in primary production while years considered low were delayed by around a month. If temporal match with prey availability is a driver of seabirds foraging and breeding success (Hipfner 2008, Regular et al. 2014), few studies directly established a relation with primary production. One reason might be that seasonal variations in marine productivity of most temperate areas are driven by temperature and photoperiod (Nicklisch et al. 2008), which are also the primary triggers of birds breeding (Mickelson et al. 1991, Dawson 2008). Therefore, it is unlikely that temporal mismatches happen between these two phenomena. This is not the case in the Bass Strait region, where primary production is driven by winter nutrient intakes (Gibbs et al. 1986) so that the environmental cues for penguins might be more challenging to detect. Primary production, however, may not affect prey demography at the year scale (although very important at multiannual scale, beyond the scope of our study, Capuzzo et al. 2018), but is arguably affecting prey quality (junk-food hypothesis, Wanless et al. 2005, Österblom et al. 2008), presence and accessibility (Bost et al. 2009). Therefore, the central hypothesis explaining the role of mismatch with primary production on little penguins foraging may be its essential function on prey quality (size and body condition) and spatial distribution. The most delayed breeding seasons (5 to 9 weeks after the spring decrease in primary production) had higher foraging performances than those delayed by only 2 to 4 weeks. This supports the hypothesis of prey quality/accessibility importance, very late years being delayed enough to potentially benefit from an increased prey quality/accessibility via the return of high primary production in the fall. This is also coherent with the recent discovery that some experienced individuals of this very same population tended to breed a second time in fall, correlated with the return of high primary production (Ramírez et al. 2021).

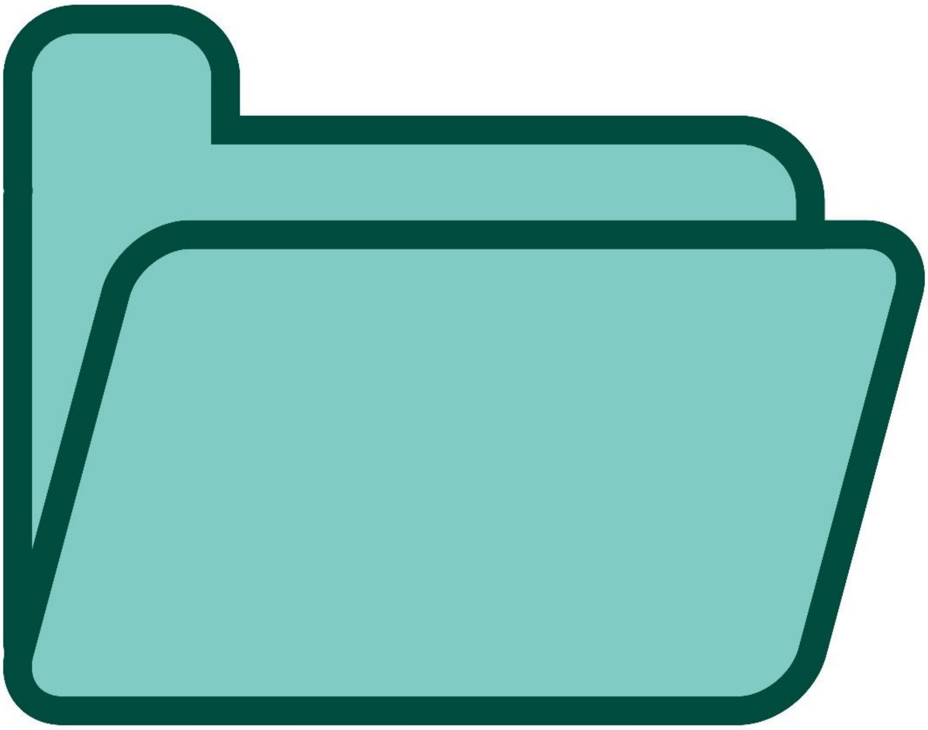
The primary role of a match with prey could be the critical element to understand the link between annual foraging performances and breeding success (Shultz et al. 2009, Regular et al. 2014). Here, we established a significant relationship between breeding success and annual foraging performances, confirming previous findings in this species (Chiaradia and Nisbet 2006). This link mainly relies on the foraging conditions during post-guard, a long and very constrained breeding stage (Reilly and Cullen 1981). Differences in breeding success were only significant between years of low foraging performances and other ones, suggesting that the relationship between breeding success and foraging may not be linear but rather only occur below a threshold under which foraging is too inefficient to allow successful breeding (Cury et al. 2011, Guillemette et al. 2018).

Conclusion

Little penguin foraging varied at very different time scales with contrasted environmental contexts. We showed that changes in little penguin phenology were significantly affecting their breeding success through foraging, which may become even more critical in a context of climate change where seabirds phenology has changed dramatically all around the world (Wanless et al. 2009, Sydeman and Bograd 2009). We also highlighted significant concurrent effects of waves and currents (possibly driven by wind) and, to a lesser extent, vertical stratification on seabirds foraging at shorter time scales. Although the effect of these variables on breeding success is not as clearly established yet, they may have increasing importance in the future as waves and currents are globally expected to increase in intensity due to climate change (Young et al. 2011, Capotondi et al. 2012).

Chapter V: Foraging

Supplementary Material



Text S1: Chlorophyll random resampling method (*Figure S1*)

Chlorophyll-a concentration (Chla) was gathered from MODIS and SeaWiFS datasets to cover the entire study period. Raw data were truncated to a maximum value of 1.6µg/l to avoid abnormal high values of Chla at coastal pixels due to turbidity (*i.e.* the 99% quantile, coherent with Gibbs et al. 1986). Because data were not available in each pixel (due to cloud cover), random subsampling was performed on both datasets to assess the minimum number of pixels necessary to obtain unbiased daily means (*i.e.* deviation smaller than 5%, Figure S1).

To assess days with a sufficient number of gridded values to obtain an unbiased daily average, random subsamplings were performed separately for MODIS and SeaWiFS. Every day with more than 2,000 gridded values has been randomly resampled 10,000 times, from which we assessed the number of times were subsampling was significantly different from the daily average. More precisely, a subsampling was considered different from the daily average when mean(subsampling) > or < mean(daily gridded data) ± 5%. The minimum number of values to consider to assess an unbiased daily average is then defined as the lowest value were resampling is different from the daily average less than 5% of the time (all resampled days combined).

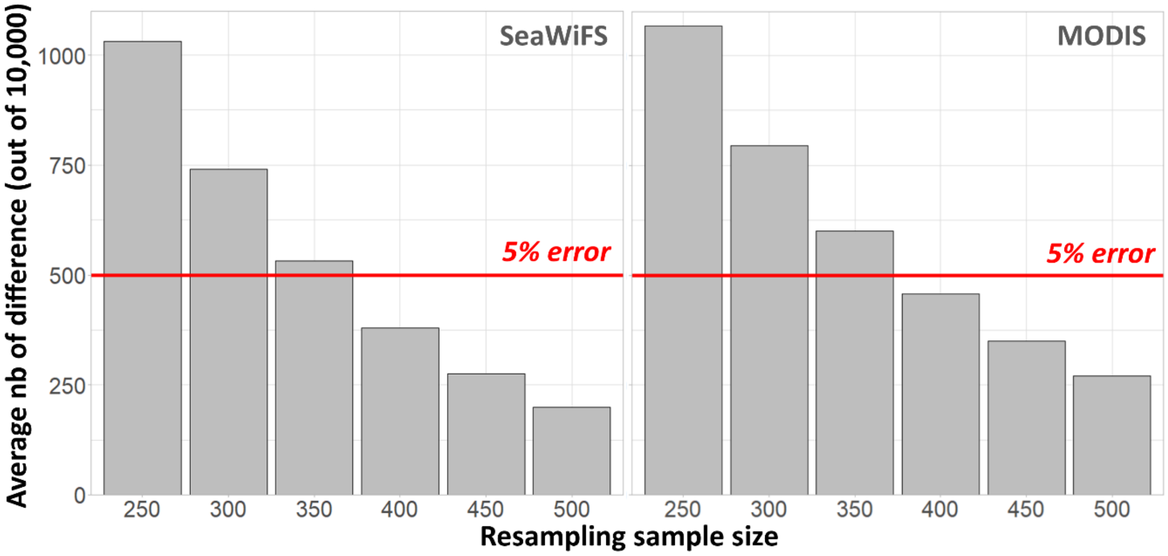


Figure S1: [Chla] Resampling method. *Average number of differences between full day data and random subsamplings of the day (5% difference with full day data) out of 10,000 random resamplings. Number of difference is tested for every day with more than 2000 gridded values. Minimum number of values to assess daily average is considered as the lowest sample size with less than 5% error (red line) = 400 daily values.*

Biased daily means due to too few pixels were then removed (1341 out of 3304 days for SeaWiFS and 1348 out of 6250 days for MODIS). SeaWiFS and MODIS daily time series were then merged based on their significant correlation over the 2002-2010 common period (Pearson's r = 0.56) and previous studies (Zhang et al. 2006). When MODIS and SeaWiFS data were available for the same day, only MODIS data were retained (due to a more precise grid).

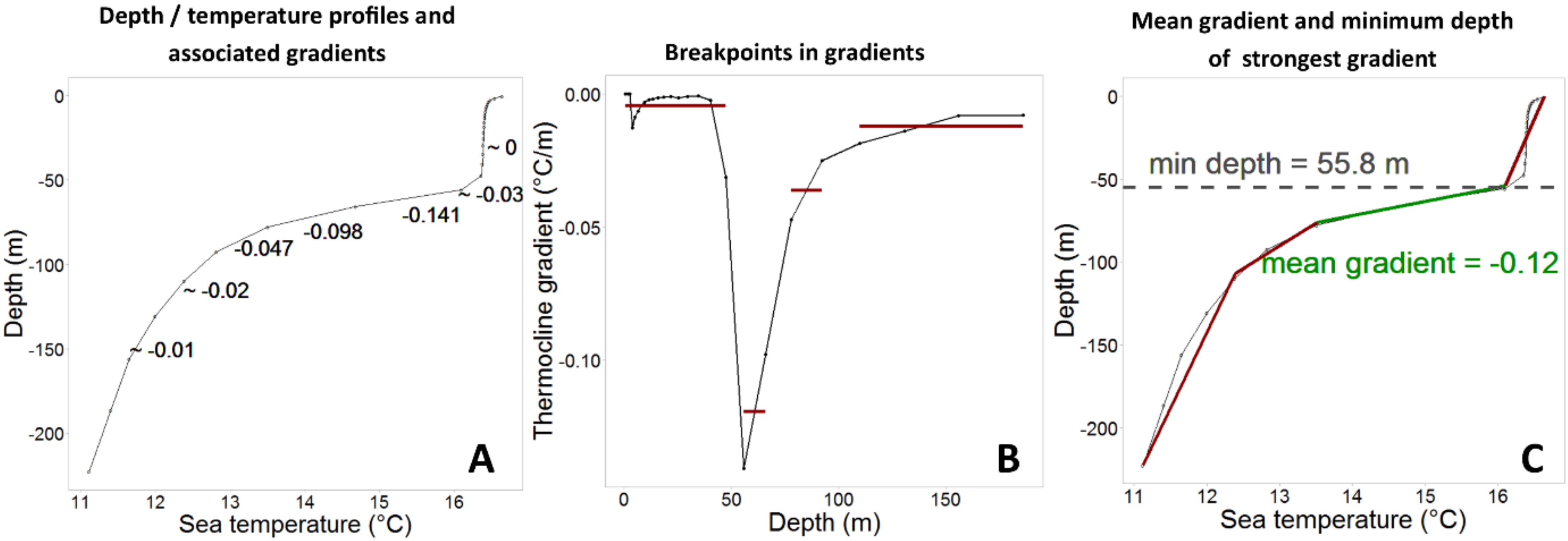
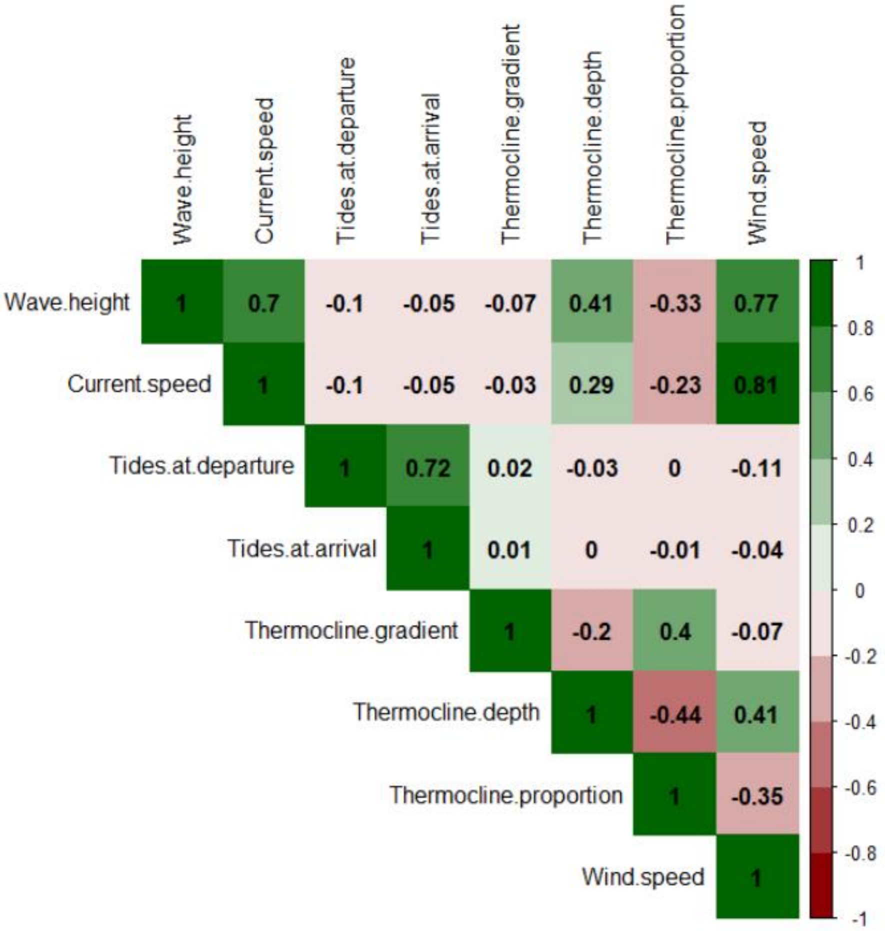


Figure S2: Thermocline detection. *Thermocline profile example (2002-04-10, 142.08 E – 39.33 S). Temperature gradients (shown in A) are defined as the temperature difference between each available depth. Breakpoints in temperature gradients depending on depth are assessed using breakpoints function from package strucchange 1.5-2, from which different segments are defined (red lines in B). Thermocline gradient is then computed as the mean gradient of the segment with stronger temperature gradient (green in C) and thermocline depth as the shallower point of this same segment (dashed grey line in C).*



	Wave.height	Current.speed	Tides.at.departure	Tides.at.arrival	Thermocline.gradient	Thermocline.depth	Thermocline.proportion	Wind.speed
Wave.height	1	0.7	-0.1	-0.05	-0.07	0.41	-0.33	0.77
Current.speed		1	-0.1	-0.05	-0.03	0.29	-0.23	0.81
Tides.at.departure			1	0.72	0.02	-0.03	0	-0.11
Tides.at.arrival				1	0.01	0	-0.01	-0.04
Thermocline.gradient					1	-0.2	0.4	-0.07
Thermocline.depth						1	-0.44	0.41
Thermocline.proportion							1	-0.35
Wind.speed								1

Figure S3: Correlations of daily environmental variables. *Pairwise correlations between daily anomalies (corrected by seasonal signal, except for tides) in different environmental variables including all the ones tested in linear models (wave height, current speed, tides and thermocline depth, gradient and proportion) and wind speed.*

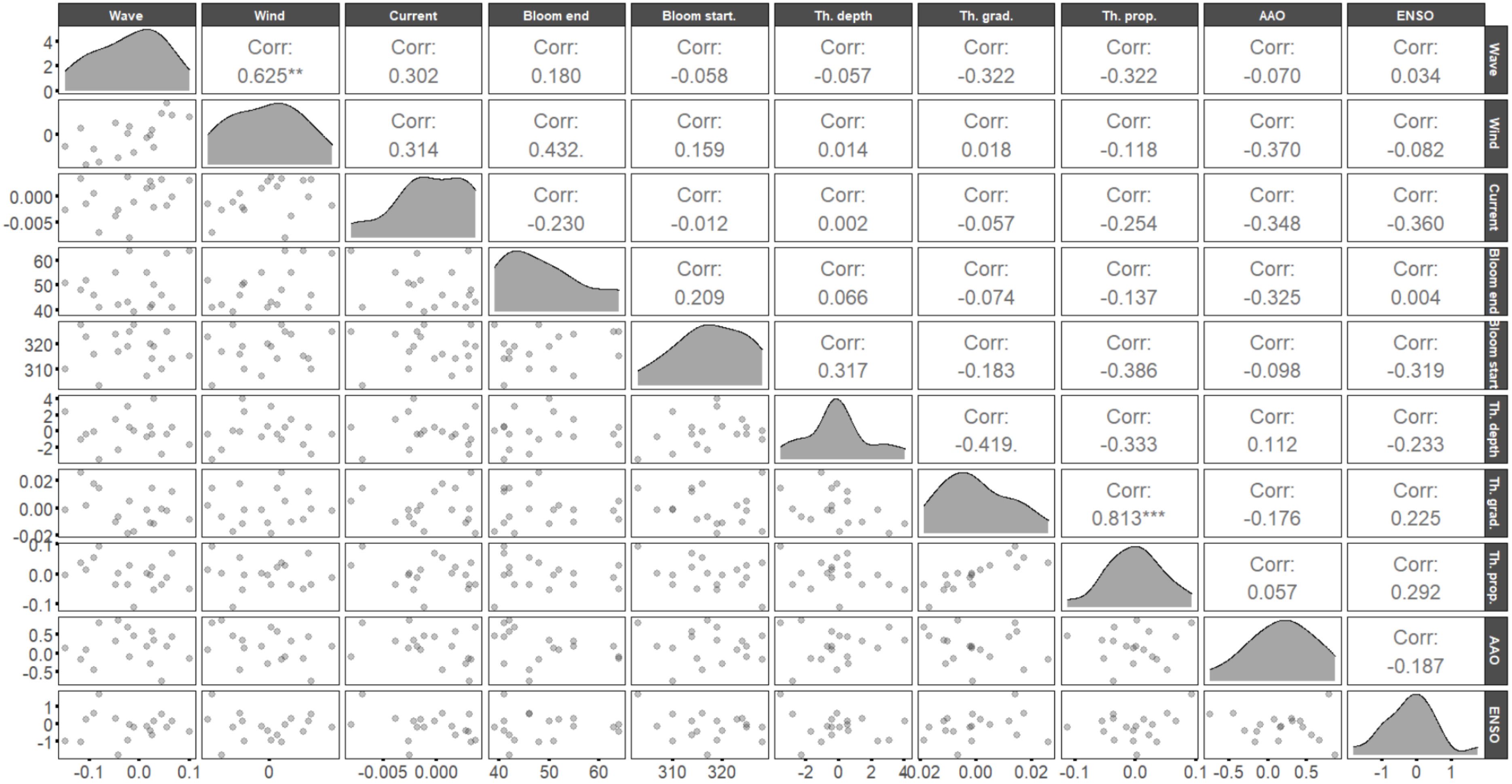


Figure S4: Correlations of annual environmental variables. *Pairwise correlations and scatterplots of annual averaged anomalies (corrected by seasonal signal) in different environmental variables including wave height (m), current speed (m/s), bloom start and end dates, thermocline depth (m), thermocline gradient (°C/m), thermocline proportion and wind speed*

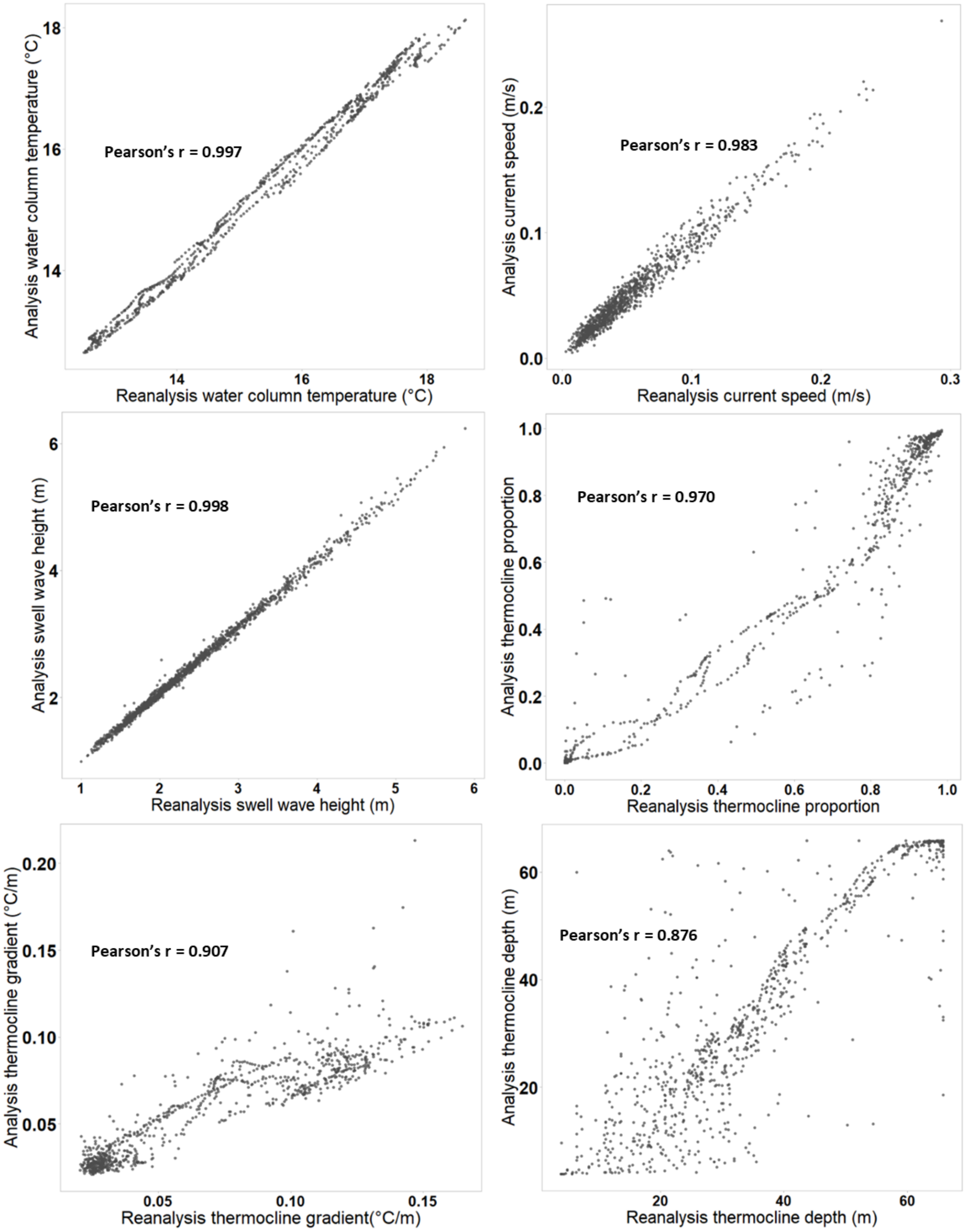


Figure S5: Correlations between environmental *daily values obtained from the* ***analysis and reanalysis datasets (Copernicus)*** *based on the common period of availability (from July 2018 to the end of 2018).*

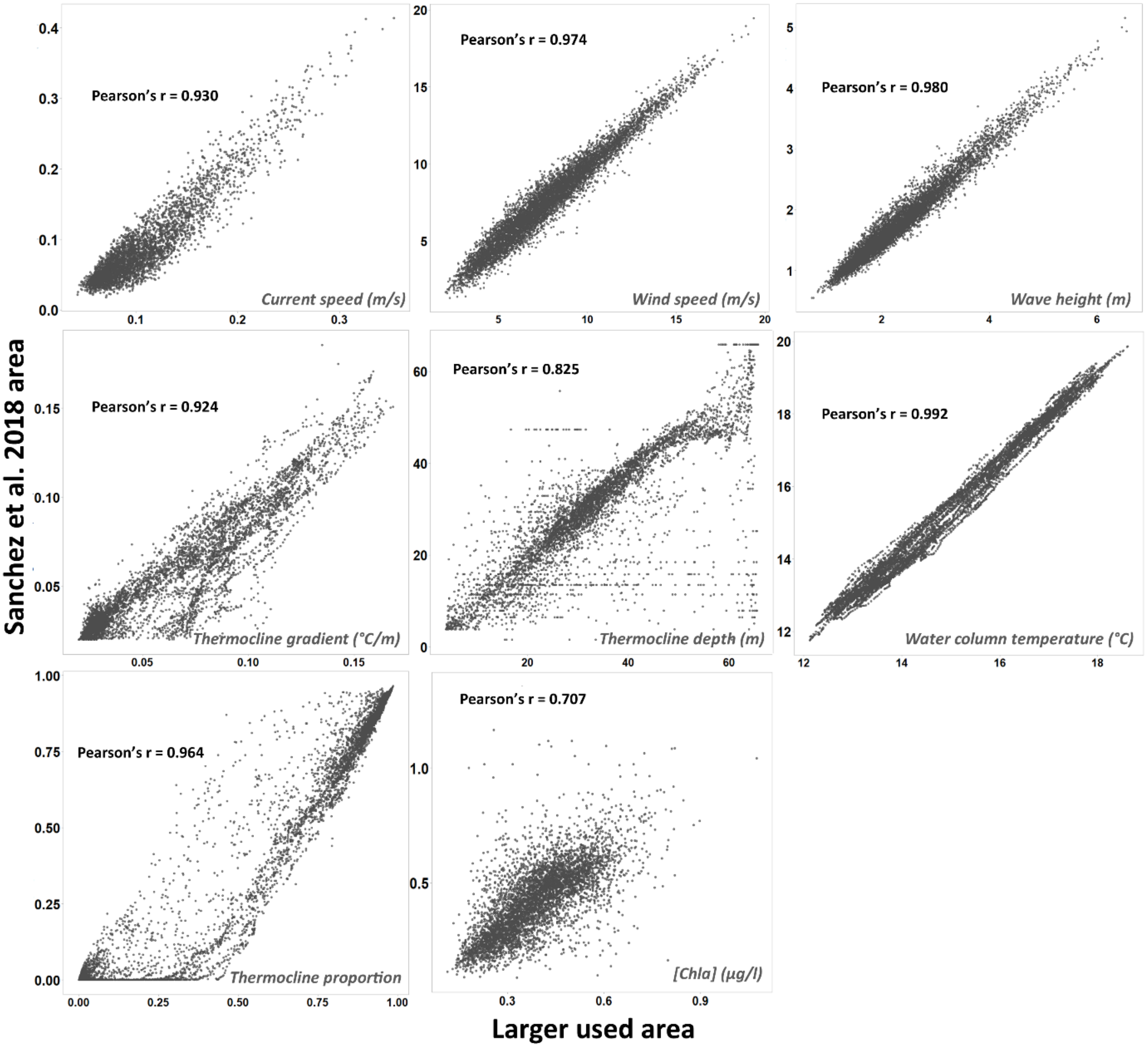
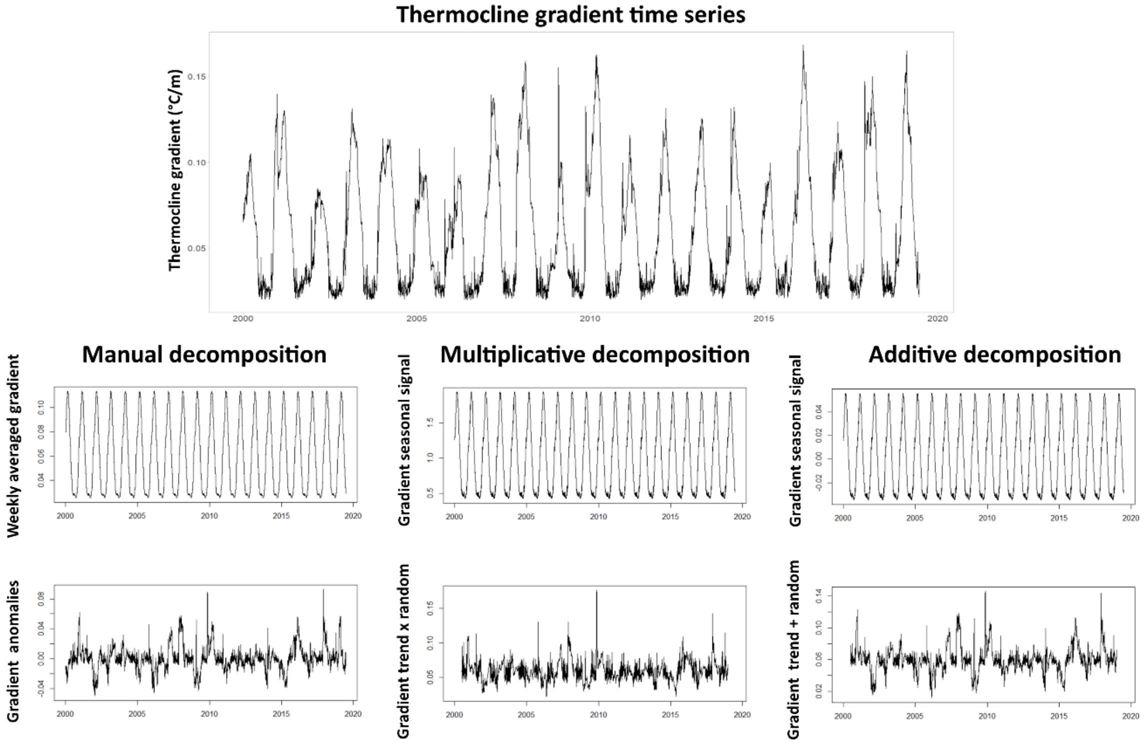


__Figure S6: Correlations between environmental daily values averaged over a known foraging area established by Sanchez et al. 2018__ (144 to 146° E, 38.2 to 40° S) and a larger area including most of the Bass Strait as well as the continental slope (140 to 148° E, 38.2 to 41° S) for every gridded environmental variable.

Decomposition methods comparison in a strongly seasonal variable (Thermocline gradient)



Decomposition methods comparison in a weakly seasonal variable (Wave height)

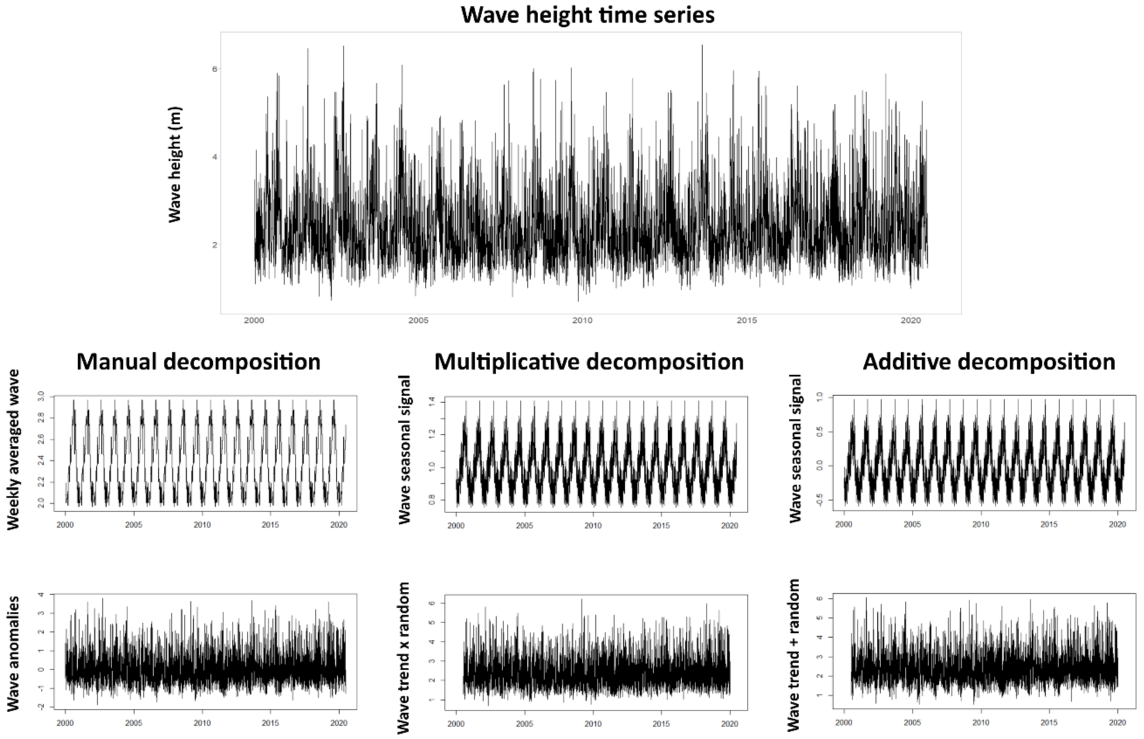


***Figure S7: Comparison of different methods for time series decomposition** into seasonal signal and anomalies from daily time series in both strongly (Thermocline gradient) and weakly seasonal (Wave height) variables. Manual decomposition is achieved by assessing both average value of each calendar week (seasonal signal) and daily values minus average value of the corresponding week (anomalies). Additive and multiplicative decomposition methods are done using the decompose function from R package stats 4.0.3*

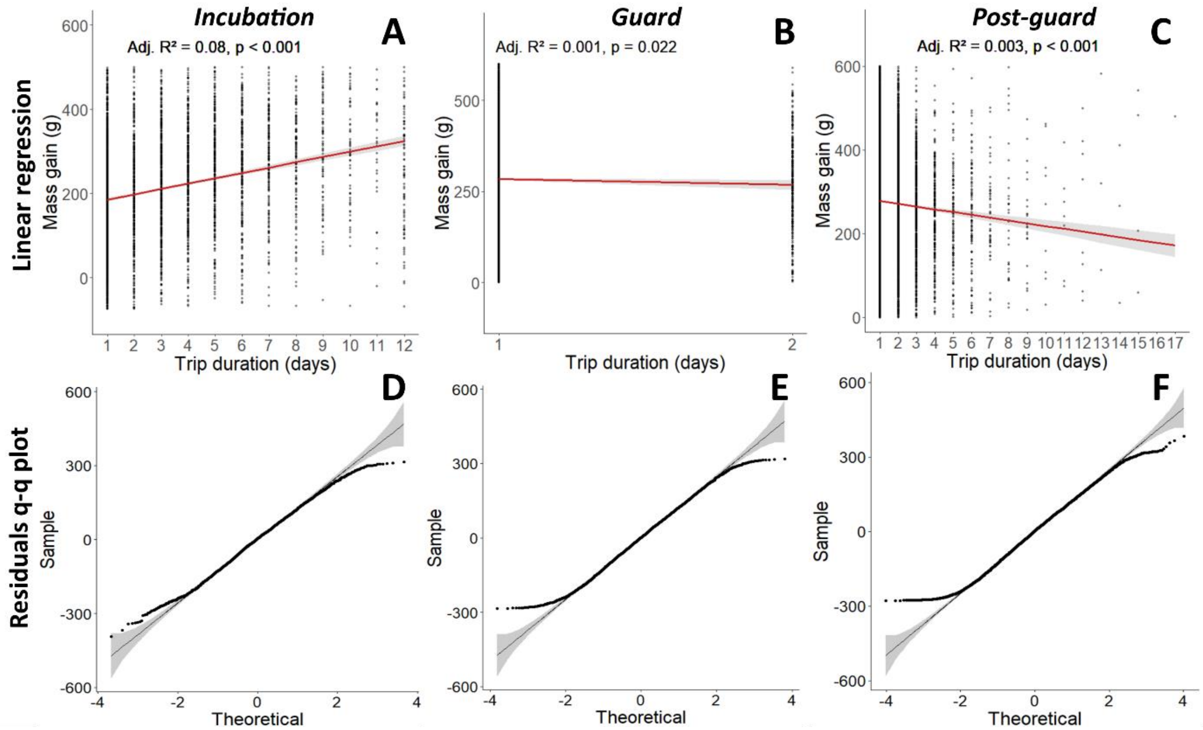


Figure S8: Mass gained per trip depending on trip duration in days (A to C) with associated linear regressions (red lines), R² and p-values. Residuals of these regressions (that have further been used as mass gain corrected by trip duration) are displayed under the form of a q-q plot in panels D to F.

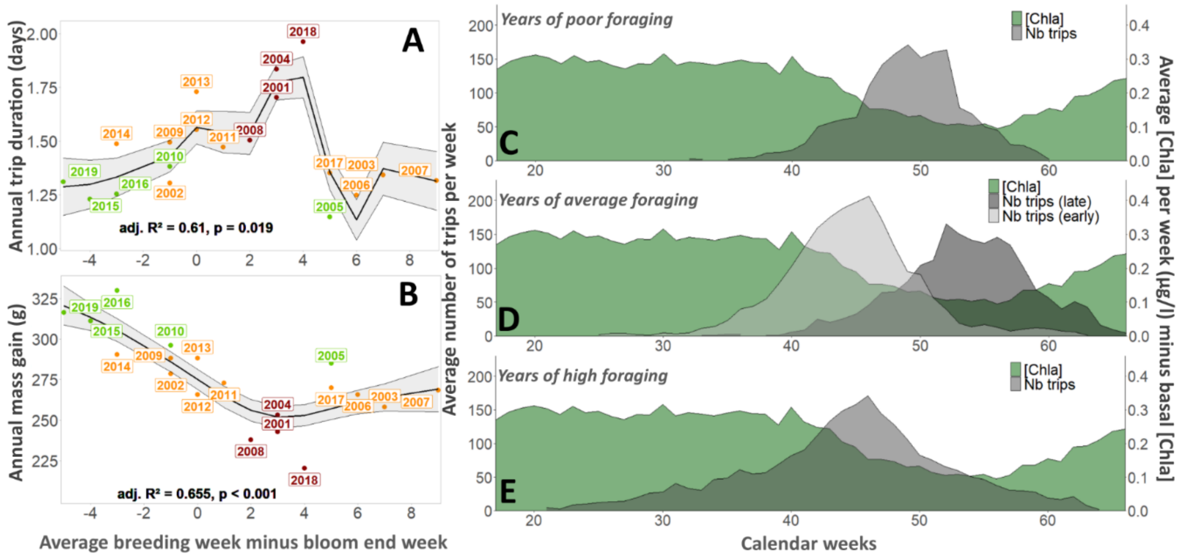


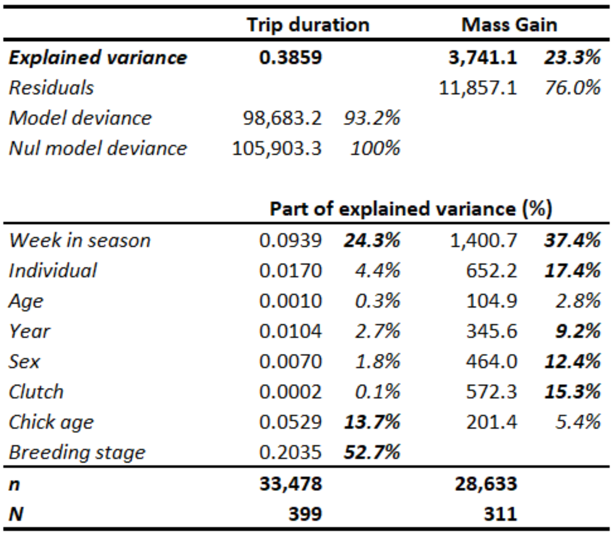
Figure S9: Effect of synchrony between post-guard foraging and primary production on annual mass gain and trip duration (A & B), with generalised additive model (black curve) ± SE (grey area). Points are colored according to established high (green), average (orange) and poor (red) foraging clusters. Weekly average Chla concentration (dark green) and trip density (grey) during the year are presented for each of the 3 clusters (C, D & E). Trip density in the average foraging cluster (D) is split in two different categories based on breeding timing: early breeding (2002, 2009, 2011, 2012 and 2013 in light grey) and very late breeding (2003, 2005, 2006, 2007 and 2014 in grey) based on A & B.

Text S2: Partition of variance in foraging performances (*Table S1*)

Individuals age was assessed assuming first seen as adults (not tagged as chicks) were 3-yr old (mean age of first breeding). Sex was assessed using bill depth measurements (Arnould et al. 2004) and confirmed with male and female pairing data. Chick age was determined as the difference in days between the hatching date and the parent departure from the colony before every trip; thus negative age values correspond to the number of days before hatching.

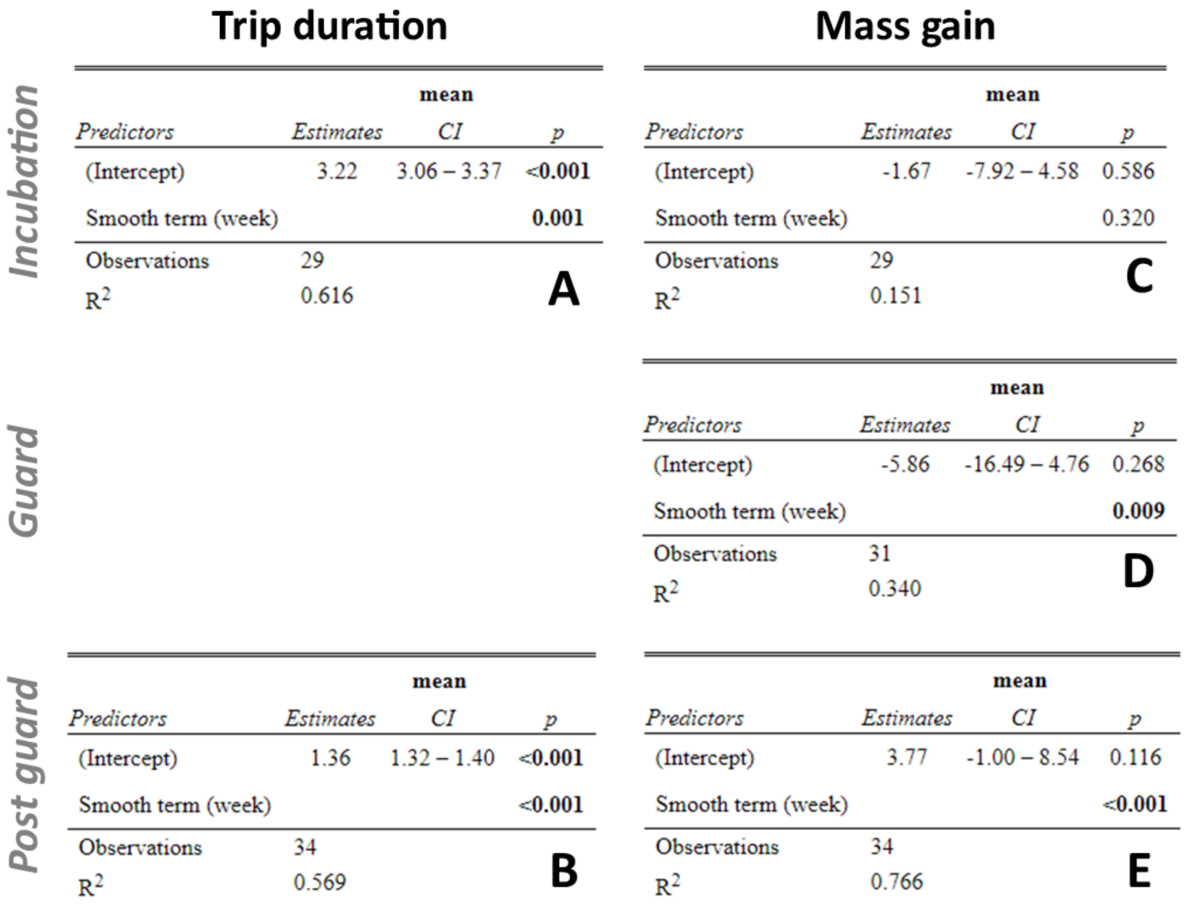
Mixed models in *Table S1* included temporal factors (years and weeks of the year), endogenous factors (identity, sex, age and clutch) and breeding factors (breeding stage and chick age) and explained respectively 6.8% of the trip duration model deviance compared to null model (GLMM with Poisson distribution) and 23.3% of the mass gain model variance (LMM). Variations in foraging duration and mass gain were mainly due to the week of the year (that explained respectively 24% and 37% of the explained variance). Changes among years also accounted for 3% and 9% of trip duration and mass gain variance, respectively. Temporal factors apart, trip duration was mainly explained by the breeding stage (around 53%) and the age of the chick (around 14%), while mass gain variation was mainly due to the clutch (15%) as well as differences among individuals (17%) and sexes (12%).

TableS3: Variance in foraging performances depending on different factors (n = number of trips, N = number of individuals)



	Trip duration		**Mass Gain**	
Explained variance	**0.3859**		**3,741.1**	***23.3%***
Residuals			11,857.1	*76.0%*
Model deviance	98,683.2	*93.2%*		
Nul model deviance	105,903.3	*100%*		
	Part of explained variance (%)			
Week in season	0.0939	***24.3%***	1,400.7	***37.4%***
Individual	0.0170	*4.4%*	652.2	***17.4%***
Age	0.0010	*0.3%*	104.9	*2.8%*
Year	0.0104	*2.7%*	345.6	***9.2%***
Sex	0.0070	*1.8%*	464.0	***12.4%***
Clutch	0.0002	*0.1%*	572.3	***15.3%***
Chick age	0.0529	***13.7%***	201.4	*5.4%*
Breeding stage	0.2035	***52.7%***		
n	**33,478**		**28,633**	
N	**399**		**311**	

TableS2: Generalized Additive Models estimates (and confidence intervals) for the effects of week of the year signals on trip duration and mass gain during incubation, guard and post guard Significant effects are presented with a bold p-value. CI = 95% Confidence Interval around mean.



Trip duration

Mass gain

Incubation

A

Predictors	*Estimates*	**mean** *CI*	*p*
(Intercept)	3.22	3.06 – 3.37	**<0.001**
Smooth term (week)			**0.001**
Observations	29		
R^2	0.616		

C

Predictors	*Estimates*	**mean** *CI*	*p*
(Intercept)	-1.67	-7.92 – 4.58	0.586
Smooth term (week)			0.320
Observations	29		
R^2	0.151		

Guard

D

Predictors	*Estimates*	**mean** *CI*	*p*
(Intercept)	-5.86	-16.49 – 4.76	0.268
Smooth term (week)			**0.009**
Observations	31		
R^2	0.340		

Post guard

B

Predictors	*Estimates*	**mean** *CI*	*p*
(Intercept)	1.36	1.32 – 1.40	**<0.001**
Smooth term (week)			**<0.001**
Observations	34		
R^2	0.569		

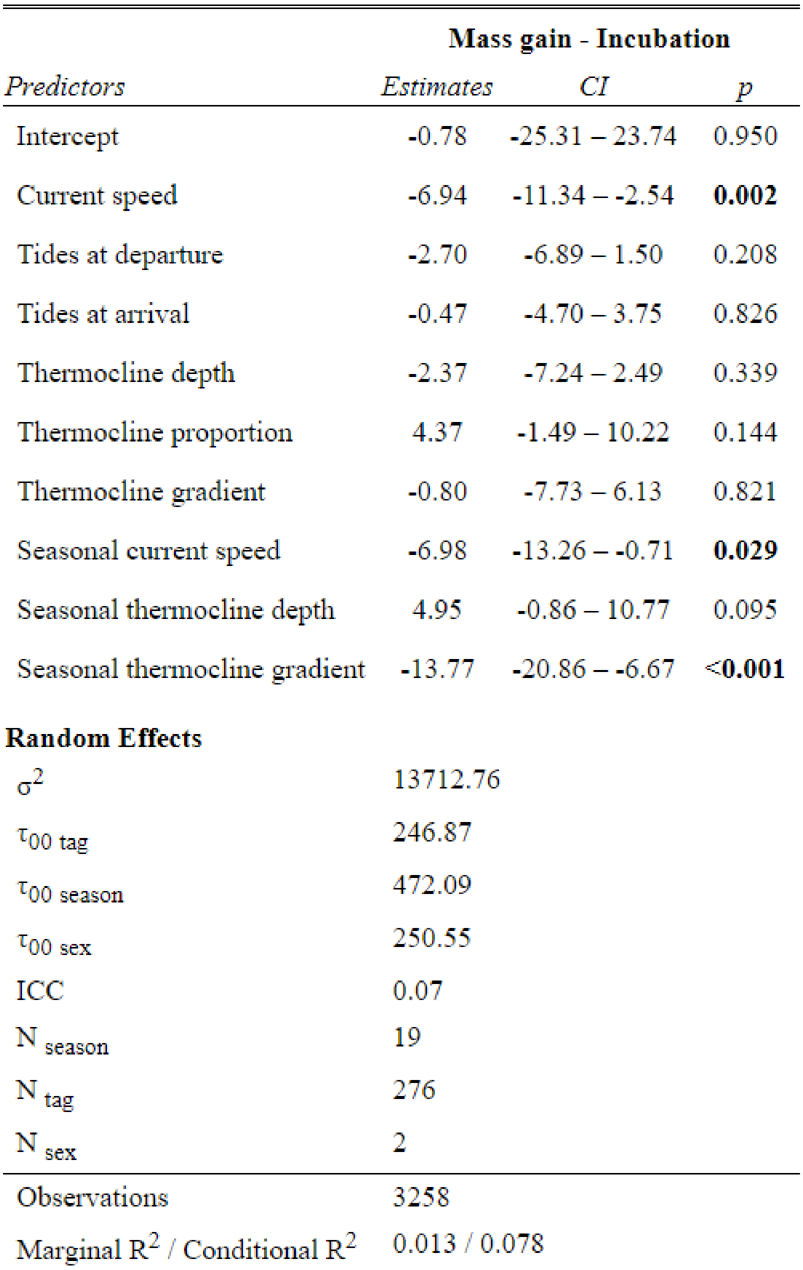
E

Predictors	*Estimates*	**mean** *CI*	*p*
(Intercept)	3.77	-1.00 – 8.54	0.116
Smooth term (week)			**<0.001**
Observations	34		
R^2	0.766		

Text S3: Detailed description of seasonal environmental effects on foraging and mixed model outputs (*TableS3, TableS4, TableS5 TableS6 & TableS7.*)

Regarding the effects of seasonal environmental signal, current speed had a constant negative effect on foraging performances, indicating that at periods of the year when the current is stronger, foraging performances decreased. Mass gain decreased by -81.3±37.3g per 0.1 m/s quicker current in incubation and -219.3±30.4 in guard (LMM, $p = 0.029$ & $p < 0.001$, although not significant in post guard, $p = 0.130$), trip duration conversely increased by 0.59±0.24 days per 0.1m/s quicker current in incubation and 1.54±0.24 days in post guard (GLMM, $p < 0.001$). Deeper and more present (higher proportion) thermocline also had a very detrimental effect on foraging trips during post guard (LMM, 1.9±0.4g less, and GLMM: 0.01 days longer per meter of thermocline depth, LMM: -3.0±0.8g less, GLMM: 0.29±0.05 days per 10% point more thermocline, $p = 0.002$ for post guard trip duration, otherwise $p < 0.001$, *Figure 5 A & B*). However, thermocline depth had a positive effect on trip duration in incubation (GLMM: 0.02±0.00 days shorter per meter of thermocline depth, $p < 0.001$) and on mass gain in guard (1.4±0.7g per meter of thermocline depth, $p = 0.046$). Finally, an increase of thermocline gradient also had a negative effect on foraging, although only tested for mass gain during incubation and guard due to high VIF (LMM, $p < 0.001$).

TableS3: Linear Mixed Model estimates (and confidence intervals CI) for the effects of seasonal environmental signals and environmental anomalies on mass gain during incubation with random effects of individual (tag), season and sex. All explanative variables were scaled so that estimates can be compared. Significant effects are presented with a bold p-value. σ^2 = within-group variance, τ_{00} = among-group variance, ICC = intra-class correlation coefficient.

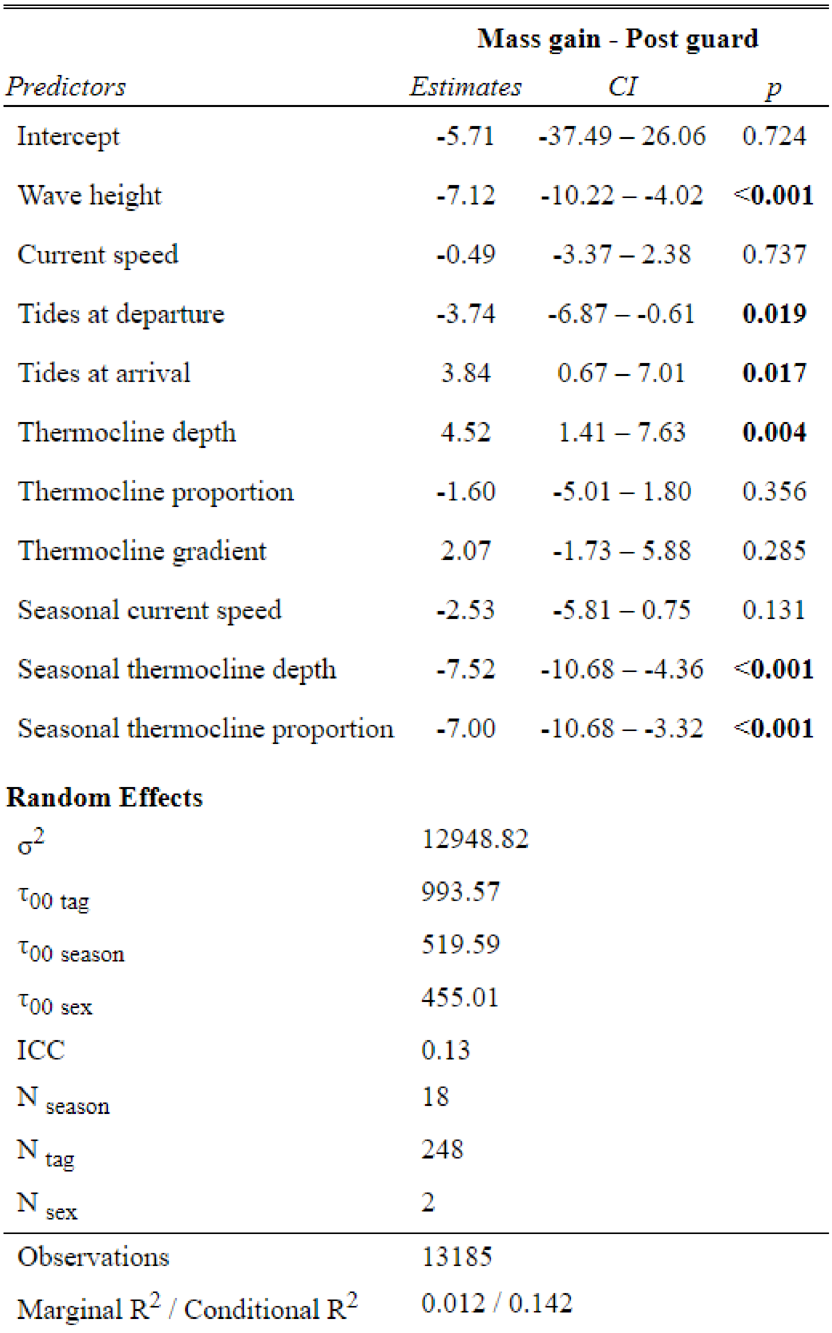


	Mass gain - Incubation		
Predictors	*Estimates*	*CI*	*p*
Intercept	-0.78	-25.31 – 23.74	0.950
Current speed	-6.94	-11.34 – -2.54	**0.002**
Tides at departure	-2.70	-6.89 – 1.50	0.208
Tides at arrival	-0.47	-4.70 – 3.75	0.826
Thermocline depth	-2.37	-7.24 – 2.49	0.339
Thermocline proportion	4.37	-1.49 – 10.22	0.144
Thermocline gradient	-0.80	-7.73 – 6.13	0.821
Seasonal current speed	-6.98	-13.26 – -0.71	**0.029**
Seasonal thermocline depth	4.95	-0.86 – 10.77	0.095
Seasonal thermocline gradient	-13.77	-20.86 – -6.67	**<0.001**
Random Effects			
σ^2	13712.76		
τ_{00} tag	246.87		
τ_{00} season	472.09		
τ_{00} sex	250.55		
ICC	0.07		
N_{season}	19		
N_{tag}	276		
N_{sex}	2		
Observations	3258		
Marginal R^2 / Conditional R^2	0.013 / 0.078		

Table S4: Linear Mixed Model estimates (and confidence intervals CI) for the effects of seasonal environmental signals and environmental anomalies on mass gain during guard with random effects of individual (tag), season and sex. All explanative variables were scaled so that estimates can be compared. Significant effects are presented with a bold p-value. σ^2 = within-group variance, τ_{00} = among-group variance, ICC = intra-class correlation coefficient

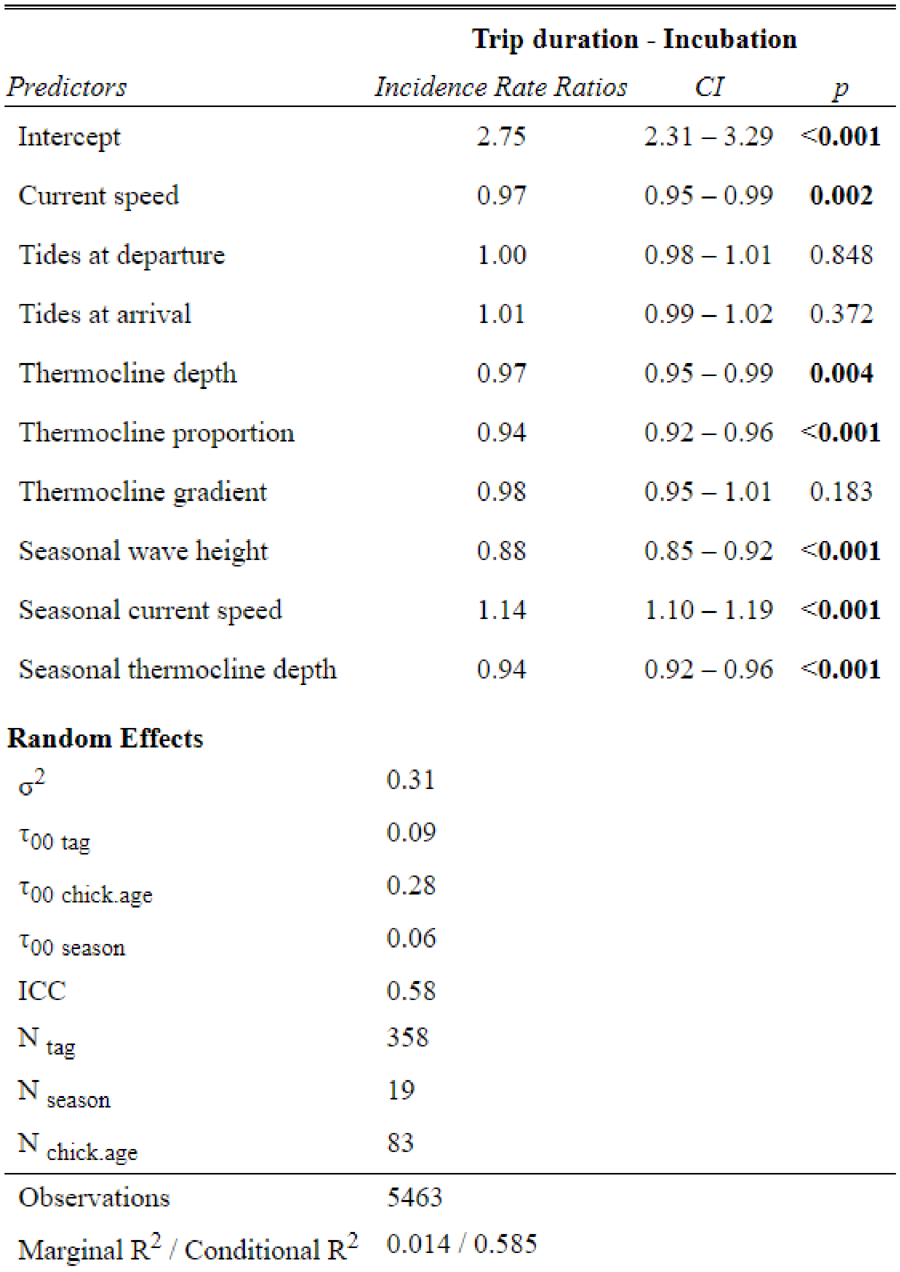
	Mass gain - Guard		
Predictors	*Estimates*	*CI*	*p*
Intercept	-5.27	-35.76 – 25.22	0.735
Wave height	-18.18	-23.02 – -13.34	**<0.001**
Current speed	8.73	4.13 – 13.34	**<0.001**
Tides at departure	0.98	-1.87 – 3.82	0.502
Thermocline depth	4.01	-0.02 – 8.04	0.051
Thermocline proportion	-1.21	-6.32 – 3.90	0.643
Thermocline gradient	-4.16	-10.31 – 2.00	0.186
Seasonal current speed	-14.90	-19.07 – -10.73	**<0.001**
Seasonal thermocline depth	4.68	0.08 – 9.27	**0.046**
Seasonal thermocline gradient	-25.06	-31.59 – -18.53	**<0.001**
Random Effects			
σ^2	12293.99		
τ_{00} tag	827.28		
τ_{00} season	1324.31		
τ_{00} sex	323.55		
ICC	0.17		
N_{season}	18		
N_{tag}	261		
N_{sex}	2		
Observations	5984		
Marginal R^2 / Conditional R^2	0.036 / 0.198		

TableS5: Linear Mixed Model estimates (and confidence intervals CI) for the effects of seasonal environmental signals and environmental anomalies on mass gain during post guard with random effects of individual (tag), season and sex. All explanative variables were scaled so that estimates can be compared. Significant effects are presented with a bold p-value. σ^2 = within-group variance, τ_{00} = among-group variance, ICC = intra-class correlation coefficient.



	Mass gain - Post guard		
Predictors	*Estimates*	*CI*	*p*
Intercept	-5.71	-37.49 – 26.06	0.724
Wave height	-7.12	-10.22 – -4.02	**<0.001**
Current speed	-0.49	-3.37 – 2.38	0.737
Tides at departure	-3.74	-6.87 – -0.61	**0.019**
Tides at arrival	3.84	0.67 – 7.01	**0.017**
Thermocline depth	4.52	1.41 – 7.63	**0.004**
Thermocline proportion	-1.60	-5.01 – 1.80	0.356
Thermocline gradient	2.07	-1.73 – 5.88	0.285
Seasonal current speed	-2.53	-5.81 – 0.75	0.131
Seasonal thermocline depth	-7.52	-10.68 – -4.36	**<0.001**
Seasonal thermocline proportion	-7.00	-10.68 – -3.32	**<0.001**
Random Effects			
σ^2	12948.82		
τ_{00} tag	993.57		
τ_{00} season	519.59		
τ_{00} sex	455.01		
ICC	0.13		
N_{season}	18		
N_{tag}	248		
N_{sex}	2		
Observations	13185		
Marginal R^2 / Conditional R^2	0.012 / 0.142		

TableS7: Linear Mixed Model estimates (and confidence intervals CI) for the effects of seasonal environmental signals and environmental anomalies on trip duration during post guard with random effects of individual (tag), season and chick age. All explanative variables were scaled so that estimates can be compared. Significant effects are presented with a bold p-value. σ^2 *= within-group variance,* τ_{00} *= among-group variance, ICC = intra-class correlation coefficient.*



	Trip duration - Incubation		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Intercept	2.75	2.31 – 3.29	**<0.001**
Current speed	0.97	0.95 – 0.99	**0.002**
Tides at departure	1.00	0.98 – 1.01	0.848
Tides at arrival	1.01	0.99 – 1.02	0.372
Thermocline depth	0.97	0.95 – 0.99	**0.004**
Thermocline proportion	0.94	0.92 – 0.96	**<0.001**
Thermocline gradient	0.98	0.95 – 1.01	0.183
Seasonal wave height	0.88	0.85 – 0.92	**<0.001**
Seasonal current speed	1.14	1.10 – 1.19	**<0.001**
Seasonal thermocline depth	0.94	0.92 – 0.96	**<0.001**
Random Effects			
σ^2	0.31		
$\tau_{00\ tag}$	0.09		
$\tau_{00\ chick.age}$	0.28		
$\tau_{00\ season}$	0.06		
ICC	0.58		
N_{tag}	358		
N_{season}	19		
$N_{chick.age}$	83		
Observations	5463		
Marginal R^2 / Conditional R^2	0.014 / 0.585		

TableS7: Linear Mixed Model estimates (and confidence intervals CI) for the effects of seasonal environmental signals and environmental anomalies on trip duration during post guard with random effects of individual (tag), season and chick age. All explanative variables were scaled so that estimates can be compared. Significant effects are presented with a bold p-value. σ^2 = within-group variance, τ_{00} = among-group variance, ICC = intra-class correlation coefficient.

	Trip duration - Post guard		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
Intercept	1.46	1.36 – 1.56	**<0.001**
Wave height	1.04	1.02 – 1.06	**<0.001**
Current speed	1.02	1.00 – 1.03	0.067
Tides at departure	0.98	0.97 – 1.00	0.071
Tides at arrival	1.03	1.01 – 1.05	**0.002**
Thermocline depth	0.99	0.98 – 1.01	0.556
Thermocline proportion	1.04	1.02 – 1.06	**<0.001**
Thermocline gradient	0.95	0.93 – 0.97	**<0.001**
Seasonal current speed	1.03	1.01 – 1.05	**0.001**
Seasonal thermocline depth	1.03	1.01 – 1.05	**0.003**
Seasonal thermocline proportion	1.07	1.05 – 1.09	**<0.001**
Random Effects			
σ^2	0.52		
τ_{00} tag	0.01		
τ_{00} chick.age	0.00		
τ_{00} season	0.02		
ICC	0.05		
N_{tag}	321		
N_{season}	18		
$N_{chick.age}$	88		
Observations	20544		
Marginal R^2 / Conditional R^2	0.016 / 0.070		

Chapter VI: Early-life

Early-life as a predictor of life history trajectories and fitness

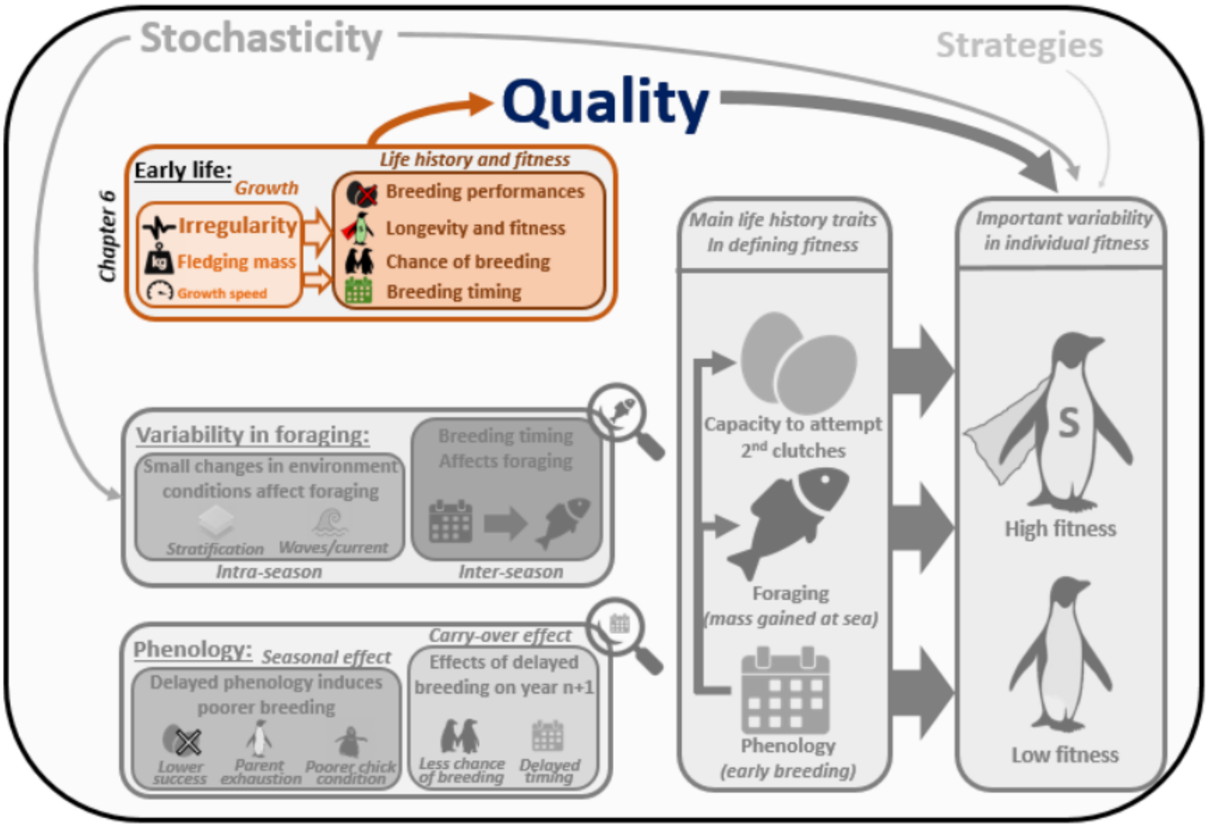
Modified from:

Joly, N. B., J. Wintz, A. Chiaradia, J.-Y. Georges, C. Lemonnier, and C. Saraux. Grown to be alive: Conditions faced during early-life can predict adult life history and fitness in little penguins. In prep.

General context of the study:

Early-life is known to have a major effect on individual quality and life history. While it has been importantly studied in mammals, the impact of deteriorated development on individual quality and fitness is hardly studied in long-lived seabirds. In this last study, I aim at understanding how growth conditions, cohort effects or birth phenology can efficiently predict life history trajectories and breeding outcomes, thus individual quality. Such results would give me important insights on the amount of variability among individuals that can be simply explained by the very beginning of their life.

Graphical summary of the main results:



Abstract

Heterogeneity in individual life-history trajectories and fitness is thought to be greatly affected by the conditions faced during early-life. In particular, juvenile survival and recruitment are known to depend for an important part on individual growth speed and condition at fledging. However, information on the effects of a deteriorated growth on individual lifetime performances remain scarce, especially in long-lived species. Here, we monitored 42 different little penguins (*Eudyptula minor*) during growth and as adults (around 300 breeding events), including 25 individuals known from birth to death, and investigated the consequences of growth conditions on breeding performances both at the breeding season and at the lifetime scale. We found the irregularity of growth to be by far the best predictor of bad performances as an adult, as it negatively affected individual life history (*i.e.* tendency to skip breeding events, later age at recruitment, delayed breeding cycle) with important consequences on individual fitness and breeding outputs. Interestingly, the growth parameters known to be good predictors of juvenile survival and recruitment (*i.e.* growth speed and weight at fledging) turned out to be quite poor predictors of lifetime fitness, although weight at fledging seemed to be associated with shorter lifespan. This suggests that the conditions faced during early-life may have even more important and complex effect on individuals’ life-history strategies, affecting both juvenile survival and breeding performances as adults but through different pathways and with different consequences. This study is, to our knowledge, one on the first to establish a direct link between early-life, life-history trajectories and fitness in long-lived species.

Key words: *Early-life, Cohort effect, Silver spoon, Growth, Irregularity, Fitness*

1. Introduction

Although populations are fundamental units of study in ecology and evolutionary biology, and are often considered relatively homogenous, they are actually constituted of individuals with very different capacities to breed and/or survive (Stearns 1992), ultimately affecting their capacity to transmit their genes into the population (McGraw and Caswell 1996). These differences are often defined as the result of different energy-allocation trade-offs (Stearns 1989), that is to say an increased or maintained energy allocation in one trait which results in a decrease in the energy allocated to one or several other traits. As this unequal allocation can greatly vary from one individual to the other, they are often referred to as life-history "strategies" (Fay et al. 2022).

These differences in energy allocation trade-offs can however not explain the entirety of the variability that exist across individuals in a population. Indeed, individuals also display differences in their intrinsic quality (Lescroël et al. 2009), that is to say their capacity to maximise their fitness related traits beyond trade-offs (Wilson and Nussey 2010, Vedder and Bouwhuis 2018). In that case, the differences observed are mostly independent of individuals but are rather defined long before individual independence, during early-life. The most obvious of these factors is genetic, as individuals inherit many morphological, physiological and even behavioral characteristics from their parents (Dochtermann et al. 2019). However, many studies also highlighted the seemingly important role of conditions faced during early development on adult capacities and health at adult age, whether it is during embryo development (Stier et al. 2020) or during postnatal care (Lindström 1999, Lee et al. 2012).

Early-life conditions after birth are primarily depending on the environment that can affect development either directly (*e.g.* warm temperatures, Andreasson et al. 2020) or indirectly through a decreased parental investment and capacities (Thierry et al. 2013). In such suboptimal environmental conditions, juvenile growth is expected to be slowed down as energy supplied by the parents will be reduced, often inducing a lower mass at independence with potential consequences on their survival (Naef-Daenzer et al. 2001) but also on their life-history as adults (*e.g.* senescence, brood size or age at first reproduction; Haywood and Perrins 1997, Péron et al. 2010, Spagopoulou et al. 2020). If they happen to be compensated by periods of rapid growth, these events are still expected to affect individual long-term performances as compensatory growth is known to induce important costs carried on to adult life (Metcalfe and Monaghan 2001). Furthermore, irregular growth, whether it is compensated or not, has been shown to be a very important driver of reproductive investment and lifespan (Inness and Metcalfe 2008).

In the case of an environment with important interannual variations, offspring are expected to display strong differences in their growth, thus in their life history, based on the year they were born in, called the cohort effect (Wooller et al. 1992). Conversely, in an environment with relatively stable conditions from year to year but displaying important seasonal variations, offspring conditions and survival could be more influenced by parent breeding timing within the breeding season itself (Ortega et al. 2022).

Although very important, the effects of early-life and development on adult life history is rarely integrated over an entire individual lifespan , especially regarding long-lived species, and often focuses on life-history traits such as juvenile survival and recruitment age (Noguera et al. 2011, Watson et al. 2015, Payo-Payo et al. 2016). Here, we sought to understand how individual life history and intrinsic quality at the lifetime scale, including fitness, could be explained by the conditions faced during their early-life.

Using the world's largest little penguin (*Eudyptula minor*) colony as a model, we were able to monitor 39 individuals (more than 250 breeding events), including 25 known from birth to death. Little penguins are known to exhibit a particularly strong asynchrony both among and across season (4 to 6 months between earliest and latest birds; Reilly and Cullen 1981), which is of great interest to disentangle the scale at which environment experiences during early-life will affect life-history the most (*i.e.* intra-annual variations due to parents phenology versus inter-annual processes such as cohort effects). As little penguins' feeding shifts are also very short compared to other seabirds, their foraging performances at sea (thus chick growth) cannot be buffered much and are easily affected by short variations in environmental conditions (Joly et al. 2022).

Using this long-term monitoring, we first aimed at understanding the link between the life-history traits that are known to influence penguins' fitness the most at the scale of the breeding season (*i.e.* breeding success, survival, second breeding attempts, phenology and foraging performances; Joly et al. 2023) and their early-life growth conditions (*i.e.* weight at fledging, linear growth speed, growth irregularity and guard length, Wintz et al. in prep.) . We expected the regularity of chick feeding (as well as the length of the guard period, characterised by very regular feeding of the chicks) to best explain performances at the breeding season scale (Inness and Metcalfe 2008). Conversely, although weight at fledging and growth speed are known to be good predictors of juvenile survival, we expected them to have less effect on adult life history due to potential long-term antagonistic effects (*e.g.* quicker development can decrease longevity; Cooper and Kruuk 2018). Little penguins being very asynchronous, we also expected to detect potential cohort effect or strong effect of birth date on life history at the breeding event scale.

Second, we focused on 25 birds for which we were able to monitor their growth and their life as breeders until their death, and for which we could thus assess their fitness and life history including potential reproductive improvement and senescence processes (Rebke et al. 2010). In this part, we aimed at establishing a relation between individual performances at the lifetime scale, including fitness and breeding outputs, and growth conditions. Once again, we expected growth irregularity to be the main driver of individual lifetime performances, but we also expected weight at fledging to potentially negatively affect individual longevity through a decreased lifespan.

2. Methods

a) Little penguins’ life-history traits and growth

Life-history at breeding season scale

Breeding success was established for each breeding event (*i.e.* clutch), successful breeding being reached if at least one offspring fledged. Post breeding survival was simply assessed depending on whether or not the individual was seen again during next breeding event, as the probability of not detecting an alive individual for more than one season is close to zero (*Supplementary material S1*).

Three other life-history traits were considered based on their known major effect on little penguins’ fitness (Joly et al. 2023), namely laying date, second breeding attempt within a season (second clutch) and foraging performances at sea. All three of these variables were considered relatively to the population, in order to display the individual performance compared to its conspecifics rather than an effect of differences in annual environmental conditions. Yearly relative laying date was defined as the laying date in days minus the average population laying date this season. Similarly, relative second clutch attempt was defined as binary second clutch attempt per breeding year minus the proportion of second clutches attempted in the population this season. Foraging efficiency was defined for each foraging trip as the mass gained at sea (corrected by trip length, see Joly et al. 2022) minus the average amount of mass gained by the population during the same breeding stage this season, then averaged over the entire season (Joly et al. 2022, 2023).

Life-history at lifetime scale

Life history traits at the lifetime scale were estimated as the lifetime average of annual values in each of the trait. Most traits were tested relatively to the population as we aimed at testing the relative individual performance compared to its conspecifics rather than the effect of environment. Relative lifetime traits (*i.e.* proportion of chicks fledged, survival, proportion of skipped breeding, and laying date but not including foraging because of too small sample size (N = 15)) were estimated from the annual values of each trait minus the yearly average value of the population in the same trait, averaged on the entire life. The effect of growth on lifetime phenology (*i.e.* laying date) was tested on both relative and non-relative values as we expected growth to potentially affect individual general life cycle as well as its capacity to breed at the same time as its conspecifics.

Individual lifetime fitness was assessed as the dominant eigenvalue of an age-structured projection matrix, where the matrix is the size of the individual's lifespan, the first row is the number of chicks fledged per year divided by two (as only half of the genome is given by a single parent) and below the diagonal is yearly survival (1 until death). As such, individual fitness should represent the asymptotic growth of an individual genotype through time, as described by McGraw & Caswell (1996). In order to be coherent with the existing literature that often uses the lifetime reproductive success (LRS) rather than fitness as an indicator of individual lifetime performances, we also assessed it as the total number of offspring fledged during life.

Growth and early-life

Chick growth curves were built as mass change according to age. Because measurements were not performed at the same chick age for all individuals (in particular the start of the monitoring depended on the parents' departure at sea for post-guard), growth curves were analyzed through discrete parameters rather than functional analyses, following Wintz et al.'s in prep. methodology. Only growth curves with more than six measurement points were retained to have sufficient data. Five parameters were extracted out of these growth curves based on their known importance in defining the little penguins' growth phenotype (Wintz et al. in prep.) and for which we had the strongest predictions that they could affect lifetime performances based on literature. First, the linear growth speed was estimated as the mass change (in g/days) of the steepest linear growth period, defined as the segment of the smoothed individual growth curve with the largest positive derivative (fastest growth period). Second, the end of guard period and defined as the first and last recorded measures, and the weight at fledging was defined as the mass at the last recorded measure. Finally, the growth irregularity was established as the sum of the absolute deviations from the smoothed growth curves. All these methods are defined in more details in Wintz et al. in prep.

b) Statistical analysis

All analyses were performed using R 3.5.1 and RStudio 1.1.456. Data significance was accepted with an error threshold of 5%. Results are presented as means ± standard errors (SE). Whenever running a linear model (or linear mixed model, LMM), the normality of the residuals was checked using density plots and q-q plots. When more than one explanatory variable was included as a fixed effect in a model, the best model was selected according to Akaike's Information Criterium (AIC) doing stepwise selection starting from the full model unless otherwise specified. When the difference in AIC was lower than 2, the most parsimonious model (*i.e.* the one with the least variables) was retained (Burnham & Anderson 2004).

Variance in breeding performances explained by early-life

We first aimed at getting an overview of the amount of variability in performances (*i.e.* breeding success, breeder's survival, second clutch attempt, relative phenology and relative foraging efficiency based on Joly et al. 2023) that could be explained by growth (*i.e.* linear growth speed, guard length, growth irregularity and weight at fledging), conditions at birth (year and date of birth) as well as endogenous (individual identity, sex and age) and breeding decisions (current laying date and number of clutch). To do so, we used linear mixed modelling (LMM) for relative phenology as well as relative foraging efficiency and generalized linear mixed modelling (GLMM) with binomial distribution for binary variables (breeding success, breeder's survival and second clutch attempt) using the `lme4 1.1-27` package, where all aforementioned explanative variables were only included as random effects. To do so, continuous variables were included in the model as categorical variables including 5 groups corresponding to categories based on 20% quantile.

Effect of early-life on annual performances

In order to understand the relation between breeding performances and the growth and conditions at birth, we performed respectively LMMs and GLMMs with binomial distribution on each of the five breeding performances variables to test for the effect of growth, cohort effect and birth phenology. To avoid overfitting, we applied two rules to these models based on the previous variance quantification models. First, only endogenous or breeding decision variable that explained part of the variability in the breeding performance variable of interest, as well as individual identity by default, were added as a random variable in the model. Second, explanative variables were excluded from the model if they did not explain any variance in the model. However, as growth variables are expected to be somewhat covariable (See

Supplementary material S2), all five growth variables were included as fixed effect in the model if one of them explained variance. Model selection was then performed as described earlier.

Effect of early-life on lifetime performances

In order to see if relationship between growth and breeding performances could be visible on individual lifetime performances, we used a pool of 25 individuals for which we both monitored the growth and the entire life until death. We then assessed the link between individuals' life-history (longevity, proportion of skipped breeding, phenology and foraging) or breeding outputs (fitness, LRS and proportion of chick fledged) and early-life using LMMs always including individual sex as a random factor as well as individual longevity for breeding outputs, in order to take into account processes such as learning and senescence.

3. **Results**

a) Variability in life history explained by early-life

The total amount of variance explained by our model including binary variables (*i.e.* breeder's survival, breeding success and second clutch) is unknown due to the construction of models. However, the amount of explained variance in breeder's survival was obviously importantly related to age (36%) but was also interestingly highly driven by differences during early-life, namely the hatching timing (37%) and age at fledging (27%). Conversely, breeding success was mainly driven by endogenous and breeding factors (age, breeding season, laying date, clutch) but was also affected by growth, namely irregularity and growth speed (3% each). Detailed results are presented in *Table 3*.

Between the two relative life-history traits studied for which we could assess the unexplained variance, we managed to explain an important but variable amount of the variation in the annual relative foraging at sea (34%) and relative laying date (26%). Although relative laying date was quite poorly explained in our model, the majority of the variability explained was due to early-life, namely irregularity (6.4%) as well as individual age (7.1%). Regarding foraging, early-life also explained an important part of the variance, including 7.8% for the year of birth, 9.9% for the weight at fledging and 1.5% for guard length, but is also depended on individual age, sex and laying date (2.4%, 9.9% and 3.0% respectively).

Table 4: Quantity of explained variance in relative (to population) life-history traits at the breeding event scale explained by different seasonal, individual, early-life and growth parameters. Quantity of variance explained by each parameter is defined by a linear mixed model including all parameter as random variables. Percentage of variance explained by each parameters is defined by the amount of variance explained by each parameter relatively to the total amount of variance (explained + unexplained). Number of breeding events (n) and individuals (N) are given.

	Binary						***Relative***			
	Breeders' survival		**Breeding success**		**Second clutch**		**Laying date**		**Foraging**	
Individual	0.0000	*(0%)*	0.0000	*(0%)*	0.0000	*(0%)*	0.00	*(0%)*	0	*(0%)*
Age	0.5004	*(31.14%)*	0.2863	*(11.89%)*	0.0000	*(0%)*	51.78	*(6.72%)*	0.0186	*(9.03%)*
Sex	0.0000	*(0%)*	NA	NA	NA	NA	NA	NA	0.0042	*(2.04%)*
Laying date	0.0000	*(0%)*	1.3407	*(55.66%)*	2.9033	*(94.33%)*	NA	NA	0.0053	*(2.57%)*
Second clutch	0.0065	*(0.4%)*	0.5557	*(23.07%)*	NA	NA	NA	NA	0	*(0%)*
Year of birth	0.0000	*(0%)*	0.0000	*(0%)*	0.0000	*(0%)*	0.00	*(0%)*	0.0280	*(13.59%)*
Hatching date	1.1000	*(68.45%)*	0.0000	*(0%)*	0.0157	*(0.51%)*	0.00	*(0%)*	0	*(0%)*
Growth irregularity	0.0000	*(0%)*	0.2148	*(8.92%)*	0.0000	*(0%)*	42.93	*(5.57%)*	0	*(0%)*
Linear growth speed	0.0000	*(0%)*	0.0000	*(0%)*	0.0532	*(1.73%)*	25.19	*(3.27%)*	0.0247	*(11.99%)*
Weight at fledging	0.0000	*(0%)*	0.0112	*(0.46%)*	0.0000	*(0%)*	10.72	*(1.39%)*	0	*(0%)*
Guard length	0.0000	*(0%)*	0.0000	*(0%)*	0.1055	*(3.43%)*	0.00	*(0%)*	0.0002	*(0.1%)*
Unexplained (residual)							639.80	*(83.05%)*	0.125	*(60.68%)*
Total	1.6069		2.4087		3.0777		770.42		0.206	
n	**204**		**212**		**214**		**279**		**155**	
N	**38**		**39**		**39**		**39**		**23**	

b) Early-life effect on life history at the breeding event scale

Regarding breeding capacities, we found that penguins that grew more regularly during their early-life had an overall much higher chance of breeding successfully (from > 75% of successful breeding for the most regular birds to almost 25% for the least regular, GLMM, N = 42 n = 216, p = 0.011, length of guard and irregularity retained by model selection, *Figure 35 A*). Individuals who benefited from better care during early-life (*i.e.* longer guard) also displayed much higher chances of making a second clutch (from around 15% for the ones that faced the shortest guards (14-day) up to 50% from the ones that beneficiated from the longest guards (28 days), GLMM, N = 42, n = 216 p = 0.016, length of guard retained by model selection *Figure 35 B*).

When focusing on the effect of growth on penguins’ capacity to forage, we found that individual that left at sea heavier as fledglings also displayed a better foraging efficiency (*i.e.* more mass gained at sea relatively to conspecifics, LMM, N = 26, n = 184, p < 0.001, weight at fledging retained by model selection *Figure 35 C*). No link could be established between early-life and phenology at the breeding season scale, either regarding individual laying date or regarding laying date relative to conspecifics based on model selection.

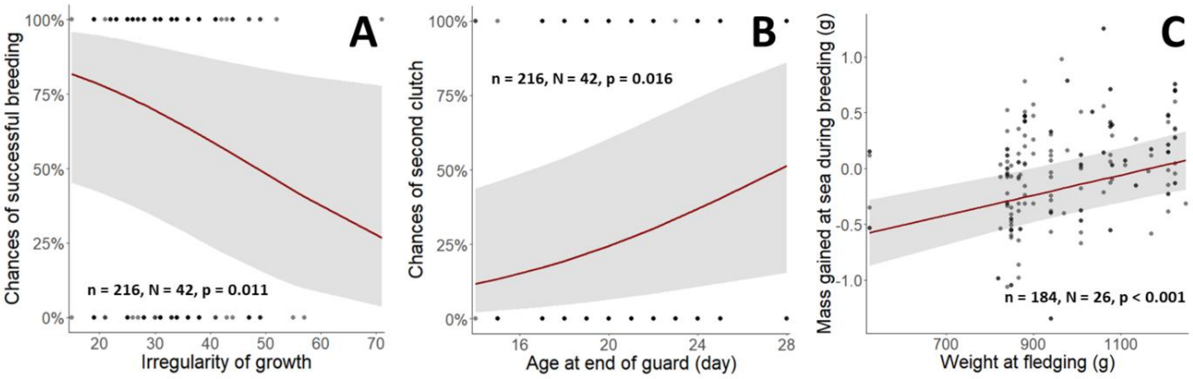


Figure 35: Chances of breeding success (A), chances of making a second clutch (B) and amount of mass gained at sea relative to population (C) depending on growth variables (irregularity of growth, age at the end of guard and weight at fledging) as defined by the models, including linear regression (red line) and standard deviation of the regression (grey area). Number of individuals (n) and p-values of regression are given.

c) Early-life effect on life history at the lifetime scale

Chick growth irregularity had a ubiquitous effect on life-history traits and outcomes at the lifetime scale, as it was the only selected variable in five different models based on model selection. Precisely, more pronounced irregularity in growth was associated with a significant decrease in fitness, relative proportion of chicks fledged during life, relative proportion of skipped breeding during life (LMs, p < 0.05, n = 25; *Figure 36 A to C),* an increase in average laying date (LMM with random effect of longevity, p = 0.017, n = 25; *Figure 36 D*). However no effect of irregularity on continuous age at maturity was established (Poisson GLMM with random effect of sex, n = 37, p = 0.184).

Surprisingly, weight at fledging was associated with a significant decrease in relative adult survival (p = 0.037, n = 25, *Figure 36 E*), although influenced by an extremely low value (p = 0.12 without). No significant effect of growth during early-life could be established on lifetime reproductive success (model selection retained birth date and growth irregularity, LMs, respectively p = 0.084 and 0.077, p = 25), absolute laying date (growth irregularity retained, LM, p = 0.071, n = 25) and foraging (null model selected).

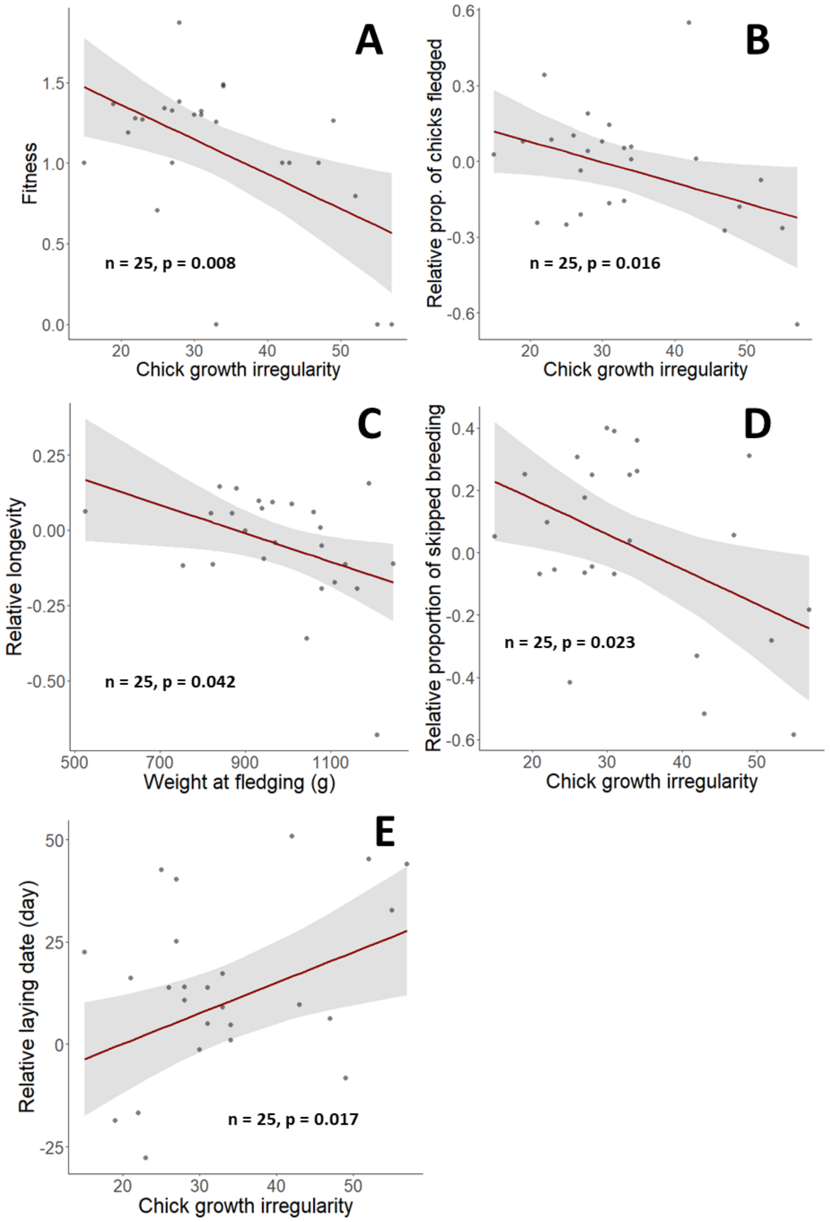


Figure 36: Relative life-history and outcomes at lifetime scale depending on growth as chick (irregularity: A,B,D,E and weight at fledging: C) including linear regression (red line) and standard deviation of the regression (grey area). Number of individuals (n) and p-values of regression are given.

4. Discussion

By studying 200 breeding events of around 40 little penguins across 20 years, including 25 individuals known from birth do death, we were able to highlight the link between adult lifetime performances and life history trajectories and the conditions faced during growth. While growth conditions were already known to be a major driver of population dynamics through juvenile survival and recruitment in long-lived species (*e.g.* Fay et al. 2015, 2017), we demonstrate here that the effects of unfavorable growth conditions can actually affect individuals in longer-term with important effect on their breeding outputs over their entire life. Here, by studying different growth parameters along with birth date, we were able to test for both cohort and growth effects and pinpoint the most relevant drivers of life history. While several growth factors seemed to affect individual capacities as an adult, irregularity in growth was by far the most ubiquitous parameter in predicting individuals' life-history and fitness.

Overall, we expected growth conditions to be quite ubiquitous but also quite low predictors of individual breeding performances, life history and fitness. Indeed, while conditions faced during development should impact the entire life of an individual (*i.e.* fixed heterogeneity), they are intended to be much less important than more direct factors (*i.e.* dynamic heterogeneity) such as climate (Jenouvrier et al. 2005, Sandvik and Einar Erikstad 2008), food availability (Oro et al. 2004, Furness 2007) or phenology (Reed et al. 2009a, Joly et al. 2023). Here however, we managed to explain an important part of the variance in some life-history traits by growth only, including more than 10% of individual laying date relative to conspecifics and up to around 26% of the total variance in relative foraging (12% by growth conditions and 14% by birth year). Furthermore, we expected the variables describing external conditions at birth (*i.e.* year of birth and birth date) to be good of variance in breeding performances. Indeed, inter-individual variability in life-history and breeding capacities due to variations in annual environmental conditions (*i.e.* cohort effects) or to delayed phenology are well described in the literature (Reed et al. 2009a, Fay et al. 2018). However, they were overall less good predictors of breeding capacities and life history traits than growth itself, at the exception of survival for which hatching date and relative foraging explained the most variance.

Chick weight at fledging is often used in seabirds as the main indicator of the parental investment and quality of the produced offspring (*e.g.* Weimerskirch et al. 2001, Hipfner 2008), as it is both relatively easy to measure and quite informative on the overall conditions of the chick at the time of independence. While weight at fledging has proven to be a good predictor of juvenile survival and recruitment (*e.g.* Becker and Bradley 2007, Morrison et al. 2009, Jenouvrier et al. 2018), studies struggle to identify its potential effect on adult life history and breeding performances (Visser and Verboven 1999, Ancona and Drummond 2013). Here, we were not able to establish strong correlations between weight at fledging and individual performances as an adult either. This suggests that, although a good predictor of juvenile life-history, including in little penguins (Reilly and Cullen 1982), its longer-term effects might be less obvious as individuals with insufficient mass face selection pressure either prior to fledging or during post-fledging period (Braasch et al. 2009), thus never reaching breeding age. However, we were able to establish a link between mass at fledging and the relative foraging performances at sea during breeding, which may reflect an advantage of heavy individuals, less subject to starvation, in their important early days of learning foraging skills (Riotte-Lambert and Weimerskirch 2013). These effects of mass at fledging on foraging performances were not visible when looking at individual entire life in our case, which may suggests that such effects could be mainly important during the first breeding years but buffered at the lifetime scale. Conversely, effects of early-life could be harder to detect because poor quality individuals may only breed once or twice, thus get diluted at the breeding event scale, while they would conversely drive an important part of the variability among individuals at the lifetime scale. However, long-term effects of mass at fledging were still visible in our case as it affected individual relative longevity, although importantly driven by a single point. This may be an evidence of the potentially detrimental effect of important growth (*i.e.* silver spoon effect, Cooper and Kruuk 2018) on individual ageing processes (Spagopoulou et al. 2020, Payo-Payo et al. 2023). Overall, weight at fledging seemed to be a quite poor predictor of individual breeding performances but still provided useful information on individual life history through learning and ageing capacities.

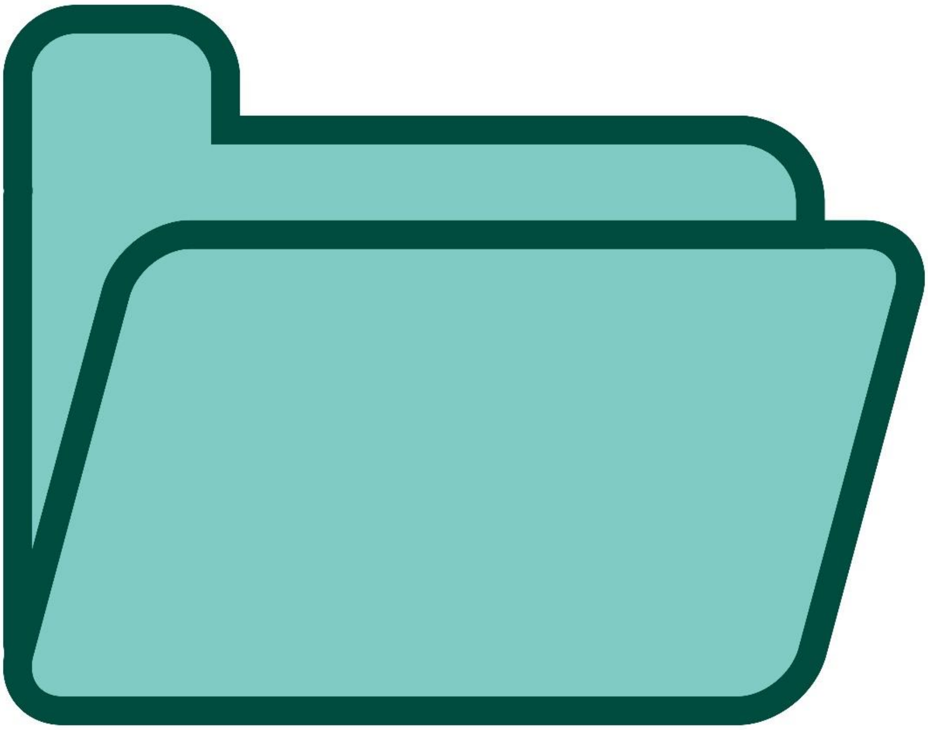
In our case, the best predictor of life history and breeding output was growth irregularity, as it efficiently predicted individual chances of breeding successfully, and mainly affected the individual age at recruitment, phenology and tendency to skip breeding events with important consequences on lifetime breeding outputs including fitness and proportion of chicks fledged. Feeding regularity is known to be an important driver of breeding success in seabirds (Weimerskirch 1998, Saraux et al. 2011c), and relation between irregularity of growth and life history has been demonstrated in birds (Inness and Metcalfe 2008). This relation is thought to be driven by numerous physiological factors such as a telomere attrition or increased oxidative stress (Noguera and Velando 2021, Sirman et al. 2023). While the physiological effects of irregular and compensatory growth are well known, their consequences on individual as an adult can rarely be documented in the wild. Here, we show for the first time to our knowledge a direct link between an individual growth and its breeding outcomes at the lifetime scale (*i.e.* fitness) through variability in life history strategies. More precisely, individuals with more irregular growth displayed lower fitness because of their incapacity to fledge chicks efficiently but also because they tended to start breeding at later age with a delayed breeding phenology. This is very consistent with previous studies highlighting breeding cycle as one of the main driver of fitness in little penguins (Joly et al. 2023) and unravels a real continuum from conditions faced in early-life to lifetime performances.

Although growth irregularity explained the most important part of the effect of early-life conditions on life history, we still detected some other though minor effects. The capacity of individuals to perform second clutches during one breeding season was importantly linked with longer guard periods (*i.e.* intensive parental care) during development, precisely more than twice as much chance for a doubled guard length. Guard is the most intensive chick care period in little penguins, during which the parents only perform one day trips to feed the chicks several time a day (Chiaradia and Kerry 1999). Therefore, guard length is of primary importance in this species and is actually known to reflect individual growth speed during the first days/weeks (Chiaradia and Nisbet 2006), meaning that this period might be critical in defining some of the life history strategies in little penguin, including double brooding. However, similarly to weight at fledging, the effect we observed at the breeding season scale was not translated at the individual lifetime scale, which once again suggests that guard length, thus early growth speed and regularity, is actually affecting pre and post-fledging juvenile survival (Merilä and Svensson 1997) as well as young breeder life history while being buffered at the lifetime scale by other processes such as senescence (Péron et al. 2010), individual strategies (Stearns 1989) or simply environmental stochasticity (Steiner et al. 2021).

Conclusion

Using the full life of 25 individuals and 200 little penguins' breeding events, we aimed at unravelling the existing continuum between conditions faced during early-life and individuals' capacities as adults. Indeed, while the link between development and early adult life has been very well established in the past (*e.g.* Merilä and Svensson 1997, Braasch et al. 2009), the potential longer-term effects of poor development have most of the times been limited to hypothesis in long-lived species due to the difficulty of inferring entire life histories. Here, we were able to point that detrimental growth conditions, and mainly irregularity of growth, show to be an efficient predictor of individual life history and breeding performances over individuals' entire life. Interestingly, the growth variables that are known to be excellent predictors of juvenile survival and recruitment such as chick growth speed and weight at fledging (Merilä and Svensson 1997, Morrison et al. 2009, Jenouvrier et al. 2018) were, in our case, poor to null predictors of individual lifetime performances. This suggests that poor growth conditions may actually affect individuals' life twice with different causes and consequences, first by reducing their ability to survive as young adults, then by decreasing their breeding performances at adult age, with sometimes antagonistic effects (*e.g.* increased weight at fledging increases post-fledging survival and recruitment but seems to have a detrimental effect on individual longevity when restricting to individuals that reached maturity).

Supplementary Material



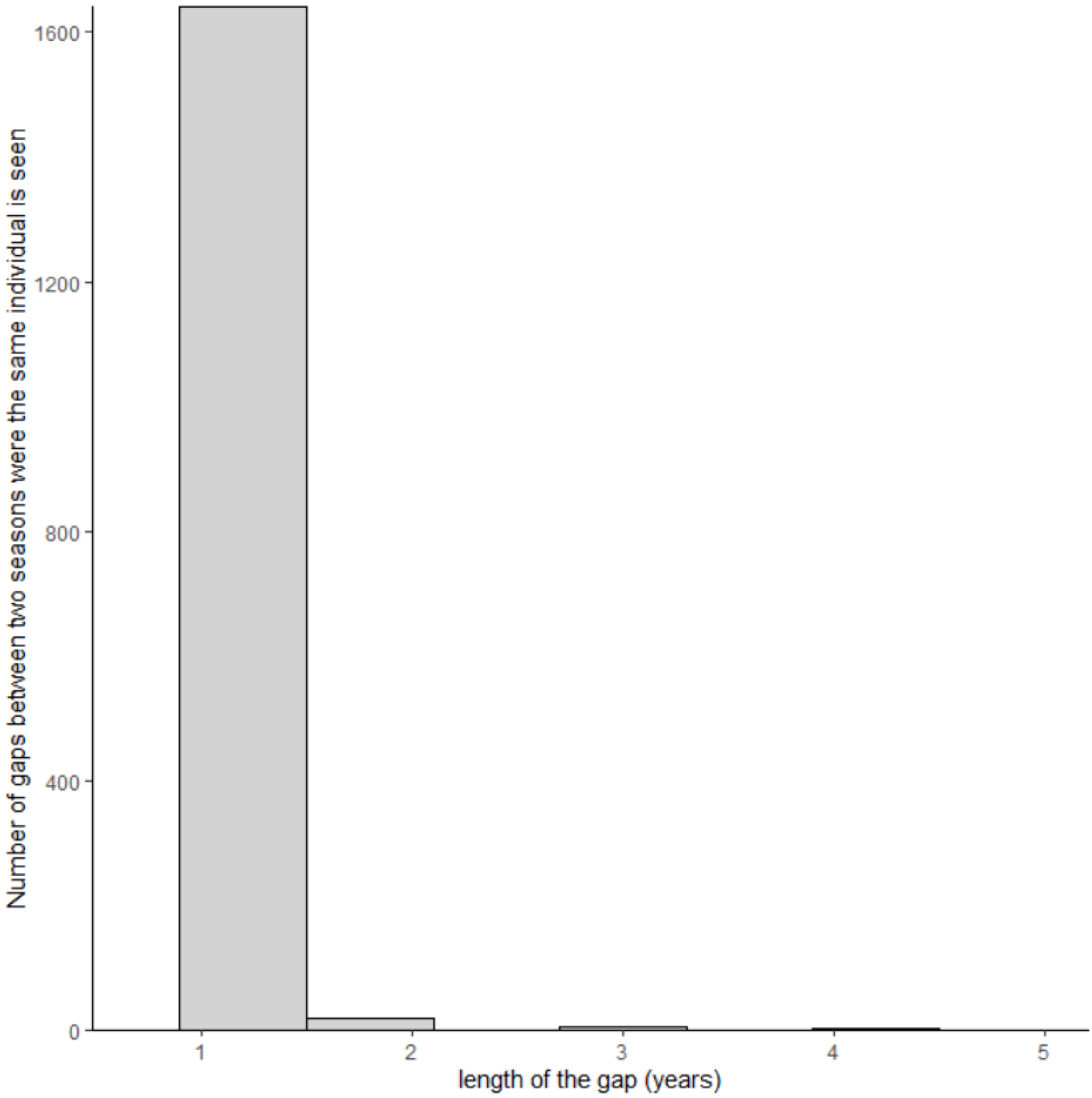


Figure S1: *Frequency of the gaps between two detection of an individual on the penguin automatic monitoring system in years. In almost all cases, individual is either seen every year or never seen again.*

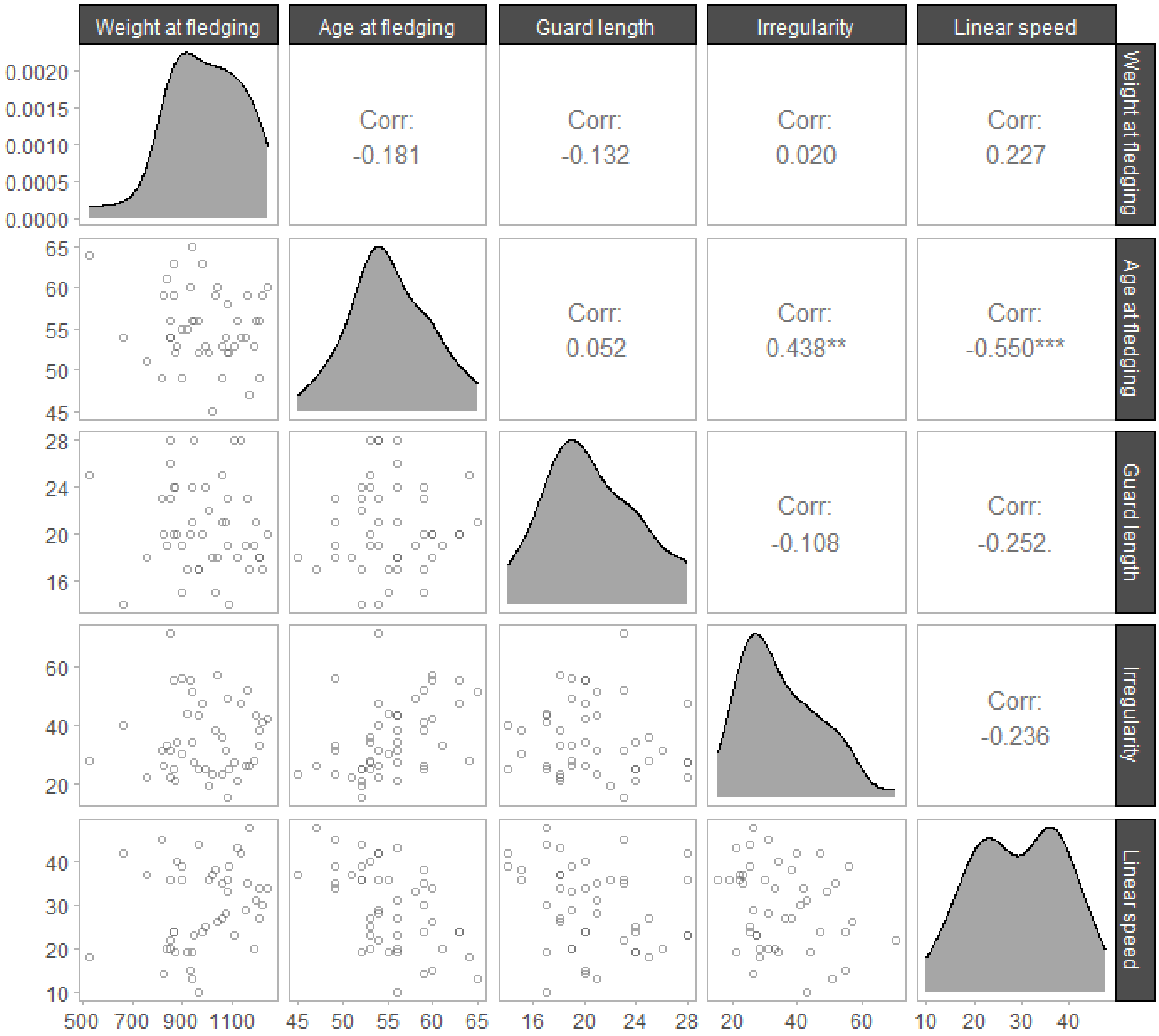


Figure S4: *Correlations of growth variables including weight at fledging (g), age at the end of guard and at fledging (day), linear growth speed (g/day) and growth irregularity.*

Chapter VII: Discussion

A story of life history trajectories and fitness

1. **Summary of the main results**

The aim of this work was to quantify the variability in lifetime performances that could exist among individuals in a little penguin population and understand how these variations were related to individual quality, energy allocation strategies or stochastic processes. By using a very complete dataset including more than 500 penguins (more than 150 of them being known for their entire life) during around 3000 breeding events and 45.000 foraging trips, I wanted to obtain enough information to encompass the complexity of the conditions faced during the life of an individual, as well as the diversity of their responses. The main results of this work are summed up in the *Figure 37*.

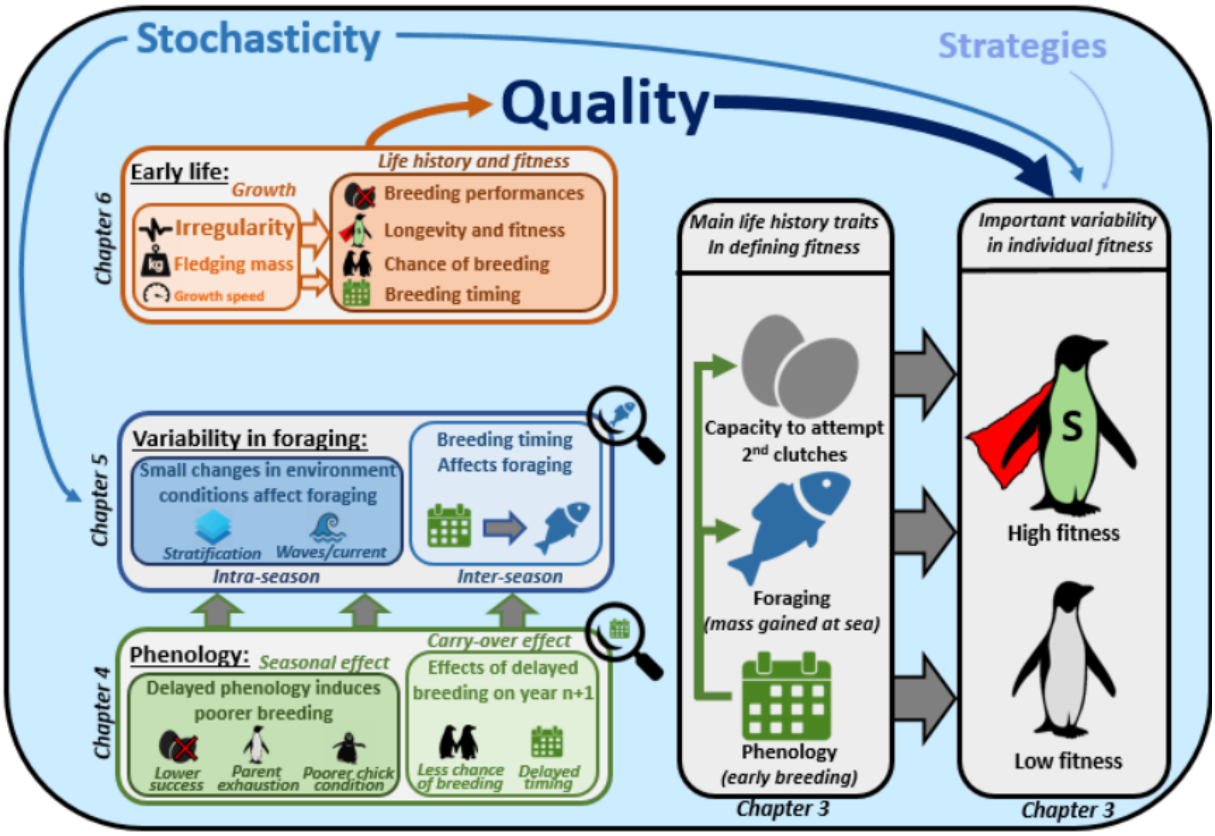


Figure 37: Summary of the main results of this work

Overall, we found an important variability in the fitness displayed by little penguins, including a large quantity of individuals with null fitness and a few overachievers. This variability in fitness depended on individuals' capacity to breed efficiently (numerous breeding events and high breeding success) and have an important lifespan.

In general, individuals that displayed higher fitness seemed to be able to maximize their allocation in most of the traits of interest (*e.g.* no cost of reproduction but a positive covariation of mean annual breeding success and longevity), meaning that individual quality rather than energy allocation strategies was the main driver of the variation among individuals. Individual quality often resides in their capacity to acquire energy, which we confirmed here as efficient foragers exhibited higher fitness. More surprisingly, individuals that performed better during their lifetime mainly displayed a capacity to breed early in the season. These differences in lifetime performances induced by phenology could be explained by direct effect on breeding performances both immediate and delayed through important carry over effects from one season to the next. Additionally, phenology had indirect effects on lifetime breeding performances and fitness, via effects on among others, individual capacity to perform multiple breeding events per year and foraging performances.

If fitness has proven to be strongly affected by traits such as foraging performances and phenology, one can wonder why individuals displaying poor capacities in these traits still exist in the population. Here, we were able to show that an important part of these differences does not depend on individual life history trajectories during its life but is actually fixed and can be explained by conditions faced during early-life through our analysis of growth trajectories.

While environmental stochasticity did not erase the variability in fitness and life history, it still had an important effect on the amplitude of the variability among individuals. Stochasticity was particularly visible when looking at foraging efficiency, as little penguins were very sensitive to small-scale temporal changes in environmental conditions.

2. Quality, strategies, stochasticity or all at once in defining fitness?

While differences among individuals are known to depend on individual quality, energy allocation strategies and stochastic events, knowledge is lacking on the relative contribution of these processes on individual lifetime performances. Variability among individuals has long been assumed to be a manifestation of evolutionary processes, but recent research tend to demonstrate the low heritability of fitness components and the importance of environmental stochasticity in defining the amplitude of fitness variations in a population (Tuljapurkar et al. 2009, Steiner and Tuljapurkar 2012). These studies emphasized how stochasticity could actually lead to overestimating or falsely detecting the effect of evolution processes while looking at the variance in life history trajectories. Furthermore, one could argue that, as energy allocation trade-off is the principal driver of differences in life history across species (Stearns 1989), its contribution on the variations that exist among individuals in a species should also be of primary importance, following a biological continuum.

In this work, we focused our analysis on the variability in the life history of individuals but also and mainly on the deviation of each individual life history from the average "life history" of the population at a given time. Doing so, we were able to assess the performances of each individual relative to its conspecifics at the same time, to obtain a measure of relative lifetime performances. While imperfect because of the limited amount of individuals monitored preventing us from finer scale comparisons (*e.g.* looking at performances relatively to conspecifics of the same class age or sex, as those can have a significant effect on performances, Forslund and Pärt 1995, Angelier et al. 2007), this methodology still gave us a good approximation of individual performances relative to others, removing environmental stochasticity from the equation.

Demonstration of individual quality in seabirds is not new, and often relies on positive covariation between longevity and breeding success (*e.g.* Lescroël et al. 2009, Fay et al. 2018), differences in energy acquisition (*i.e.* foraging performances, *e.g.* Lescroël et al. 2020) or even in energy expenditure (Kahane-Rapport et al. 2022). Here, we also found a strong covariation between individual longevity, lifetime breeding performances and lifetime foraging efficiency

(*Chapter 3 and 5*), showing the importance of individual quality in defining fitness. While quality seemed to be the main explanatory factor of fitness in our case, the drivers of this quality were sometimes surprising. Indeed, while foraging performances or multiple brooding where importantly affected by individual quality (*i.e.* covariated), the trait that had the most importance in our case was individual phenology (*Chapter 4*). Once again, the importance of phenology in defining seabirds' breeding performances is not new, but is thought to depend on individual capacity to synchronize with the most favorable environmental conditions (Reed et al. 2009). Here however, individual fitness was not influenced by its capacity to be flexible in its breeding timing (*i.e.* detect environmental cues) but rather on its capacity to be constantly earlier than its conspecifics (*Chapter 4*). While this is quite unexpected, it suggests that in our case breeding early is consistenlty favorable in terms of environmental conditions. Indeed, in the study region, high primary production tend to occur during winter and exhibit a strong decrease at spring (Gibbs et al. 1986). We showed that overall breeding timing of the population in regard to this primary production decrease is stongly related to their breeding success (see *Chapter 5*), indicating that earlier breeding is always the most favorable choice in terms of food availability. Thus, if breeding timing is not only driven by the most favorable breeding conditions (in which case all individuals would start to breed before the end of the primary production bloom), it may also be importantly triggered by body conditions treshold (*i.e.* recovery capacities from last breeding or carry-over effect; Salton et al. 2015, *Chapter 4*), explaining the disproportionnate effect of individual quality on phenology. Moreover, little penguins have been shown to express a strong variabilty in their phenology and foraging efficiency across their lives, associated with changes in their breeding success (*i.e.* due to learning and senescence processes, Saraux and Chiaradia 2021). This suggest a very important effect of individual lifespan on their overall lifetime breeding outcomes, as individuals experiencing too short lifespan may never reach sufficient experience to display favorable breeding timing and foraging performances.

While we established a major role of individual quality in defining variability across individuals, we were able to establish very few energy allocation strategies processes as strong marker of individual fitness. In particular, we expected individual longevity to be negatively correlated with their annual breeding success (Williams 1966), implying that individuals would trade-off their energy investiment between breeding and their own survival. Following the same principle, we also expected to describe important trade-offs in skipped breeding events, as described in several studies (*i.e.* cost of reproduction; *e.g.* Dobson and Jouventin 2010, Cubaynes et al. 2010). However, to our surprise, we actually found a strong positive link between individual longevity and breeding success, and few to no effect of skipping breeding events on fitness, implying that variability in individual life history was actually driven by individual quality rather than strategies. Even though we highlighted the important role of carry-over effect in defining individuals' breeding phenology, thus lifetime performances, skipping breeding events was seeminlgy not a good strategy in stopping the vicious cycle of delayed breeding and exhaustion (*Chapter 3 and 4*). While this has proven to be an efficient strategy in long-lived birds (see above) and in long-lived species in general (*e.g.* amphibians and turtles; Rivalan et al. 2005, Cayuela et al. 2014), little penguins may display such a short lifespan compared to other long-lived species (Reilly and Cullen 1981) than the cost of skipping one breeding event is too high to be an efficient strategy.

If little penguins display little to no efficient strategy to cope with unfavorable breeding conditions, stochasticity in the conditions faced during their life should be one of the main compound of inter-individual variability in lifetime performances (Tuljapurkar et al. 2009, Steiner and Tuljapurkar 2012). Here, we mainly focused our work on understanding and quantifying the potential inter-individual differences in quality and/or energy allocation trade-offs. In this context, we aimed at accounting for environmental stochasticity rather than directly study its effect. However, I believe this work still provides interesting insights on the role of environmental variability and stochasticity in defining individual lifetime performances.

While this work focuses on individuals that sometimes experienced completely different lives (*i.e.* lived in different years), We were never able to establish a predominant effect of environmental stochasticity on lifetime performances, although we definitely noticed small differences in the amplitude of variability across individuals depending on stochastic processes (see *Chapter 3*). While it shows that environmental stochasticity plays a role in defining individual overall life history, it also highlights how little such changes can be in the light of processes like individual intrinsic quality. To discuss it in the same terms I used to introduce the concept of stochasticity in the first chapter of this work, while differences definitely exist in the conditions faced by individuals across their life (*Figure 37, individuals 1 and 2*), these differences proved to never be strong enough to overpass the scale of intrinsic differences among individuals (*Figure 37, individuals 1 and 3*).

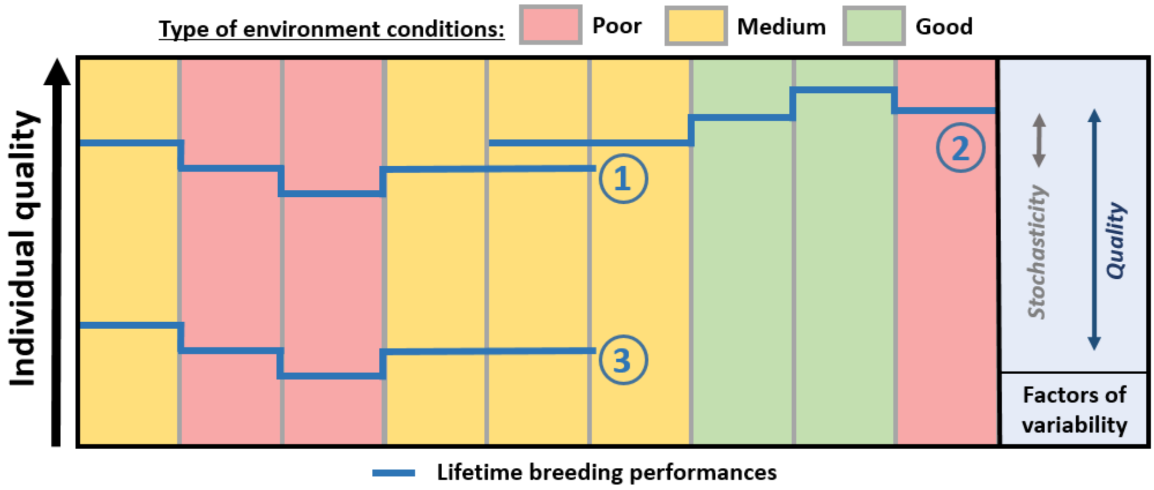


Figure 38: Effect of stochasticity compared to individual quality on the life history of two theoretical identical individuals born at different times.

However, we need to be careful with such conclusion when we take into account the relatively short span of this study compared to the speed of environmental and biological processes. Indeed, although little penguins are relatively short-lived species (Reilly and Cullen

1979), allowing us to compare individuals with sometimes few to no overlap in the periods they lived in, we still compared individuals that lived in quite similar conditions. Furthermore, on land conditions in this population are also very specific as they breed in artificial burrows and in close proximity with human presence. While these conservation measures are known to have a slightly positive effect on the overall performances of this penguin population (Sutherland et al. 2014), they may in the same time limit some stochastic events such as predation events (Hentati-Sundberg et al. 2021).

In any case, although it does not act as a primary driver of fitness, stochasticity definitely reinforces the relationships between the variability in individual life-history trajectories and their fitness. Therefore, stochasticity can be considered as a catalyser of already existing individual differences (*i.e.* more constraints would exacerbate already existing differences in individual quality; Saraux et al. 2011, Jenouvrier et al. 2015). Conversely, we could expect very good environmental conditions to act as a buffer of individual variability (*e.g.* if food availability is particularly high then the intra and inter specific competition should be decreased, allowing even poorer foragers to feed; Lewis et al. 2001).

Although stochasticity might be of lesser importance compared to processes such as individual quality in explaining long-lived species lifetime performances, it may still play an important role at smaller timescales. In such an asynchronous species, individuals may for example face very different conditions only because they started breeding at a different time of the year (Hipfner 2008, Reed et al. 2009a). In *Chapter 4 and 5*, we were able to establish the link between foraging performances and breeding timing and show how this decrease in foraging performances with time was related to poorer food availability and environmental conditions during the season. These results showed how stochastic processes can affect individuals breeding capacity from one year to another. Although stochasticity in itself is not driving lifetime performances, poor conditions at the season scale can definitely participate in triggering other processes such as increased carry-over effects (*Chapter 4*). At even smaller timescale, we were able to highlight the major importance of stochastic processes in defining individual foraging trip. These effects were probably particularly strong in our study model because of its low buffering capacities due to its size (Schmidt-Nielsen 1984), relatively short lifespan and life cycle (Reilly and Cullen 1981) and would probably be buffered more easily in other species (e.g. Albatrosses; Weimerskirch et al. 2001). However, it still provided evidence of the potential effect of very small differences in conditions faced by individual on their performances.

Overall, while individual quality and energy allocation trade-offs are supposedly the two main processes inducing differences in individuals' life history trajectories and lifetime breeding performances, quality may become of increasing importance compared to strategies in species with shorter lifespan, thus more constraint in the short time they have to make the most of. While stochastic processes also play a role in defining individual life history and fitness, they do not seem to be the main drivers of differences across individuals, but rather a catalyser of the existing intrinsic differences and an accelerator of selection processes (Lenormand et al. 2009).

3. Perspective on the fatality of life history trajectories

In the previous parts of this general discussion, I defined the overall individual quality as the main driver of fitness and energy allocation strategies as well as stochasticity as a conversely relatively poor predictor of lifetime performances. Although individual quality can somewhat vary through life (*e.g.* with age with improvement and senescence processes; McCleery et al. 2008), it is expected to be mainly driven by either genetic bases (Hunt et al. 2004) and/or development conditions (Hamel et al. 2009). Therefore, an important part of their life history trajectories is actually probably already decided during or even before their early-life. Testing this hypothesis, that has been importantly studied in long-lived mammals (*e.g.* Douhard et al. 2014, Plard et al. 2015, Pigeon et al. 2017), but has hardly been demonstrated in long-lived birds (Cam and Aubry 2011) due to the complexity of gathering such information, was one of the aim of this work (*Chapter 6*). We were able to demonstrate how individual quality, life history strategies and lifetime performances were importantly driven by conditions faced during growth. This highlights the fatalist part of individual life history trajectories. While we intuitively could argue that lifetime breeding outputs depend on so many factors faced during individual life that they can then only be encompassed while looking at the individual entire life, such results tend to actually describe the life of an individual as a continuum in which the starting point is also deciding for the majority of the entire race until death.

Here, we were able to describe the role of growth in defining individual life history and fitness. However, this is only half of the story regarding the early causes of inter-individual variability. Indeed, while conditions faced during early-life importantly affect life history strategies, individual inherited characteristics are also expected to play an important role on their overall quality as an adult (Hunt et al. 2004). In this work, we were unable to test the amount of individual quality that could be explained by genetic factors. While quality inheritance could explain a part of the observed differences in individual growth (*Chapter 6*), it is very likely that it will also explain an important part of the differences we observe among individuals and for now are unable to explain. Thus, assessing the heritability of some life-history traits is, in my opinion, one of the next big step following this work, as it will allow to precisely quantify the amount of variance in fitness that can be explained by inheritance and growth (*i.e.* completely independent from individual capacities as an adult).

Even though they raise up unanswered questions about the potential heritability of individual quality, such results give very interesting insights on the fatality of individual life history trajectories, potentially mainly driven by processes occurring at a very young age. While it is a really depressing thought, it also brings new perspectives in assessing and understanding the different paths followed by individuals during their life.

4. General conclusion

In general, this work aimed at unravelling the relative contribution of intrinsic quality, energy allocation trade-offs and stochastic processes in defining the life history and fitness of individuals, in a species known for displaying important differences in life history trajectories (*e.g.* asynchrony, longevity, divorce rate, foraging; Chiaradia & Kerry, 1999; Pelletier et al., 2014; Reilly & Cullen, 1979, 1981; Ropert-Coudert et al., 2003; Saraux, Chiaradia, et al., 2011). We were able to highlight the preponderant role of individual quality to describe the variance in the continuum of lifetime performances in a population, and tried to understand the fine scale processes behind the most important life history traits (foraging and phenology). While I discussed the potential reasons for which the role of strategies and stochasticity were hardly distinguishable in our case, I also emphasized the major role of early-life in defining individual quality, thus lifetime performances, implying a somewhat fatalist dimension of life history theory.

While this work is not necessarily applicable to other systems that would display very different life histories (*e.g.* albatrosses that are very long-lived and for which senescence processes could play a much higher role; Fay et al. 2018) or much more important environmental constraints (*e.g.* Antarctic penguin species; Forcada and Trathan 2009), to only mention relatively close systems, it provides important insights on the diversity of individuals constituting a population. Such diversity involves important differences in the way individuals contribute to their population, and therefore necessarily plays a disproportionate role in evolutionary processes and populations/species resilience. Thus, such concepts are of primary importance in understanding the dynamics of populations and predicting their changes, especially in a context of rapid climate change, although they are very often overlooked. In future research projects, I will aim at developing population models centered around individuals in order to further develop our understanding of variability among individuals and their consequences.

Chapter VIII: Limits

Taking a step back:

Critical view of this work

1. Measurement of fitness

If fitness is the measure of an individual relative genetic contribution to the population, then the most important, although often unexplored because complicated to assess, driver of fitness is not the amount of offspring produced but their quality. In such conditions, the breeding success might prove to be a somewhat biased predictor of lifetime contribution to population by giving an overestimated importance to the quantity of offspring produced while overlooking quality. This fact alone is, in my opinion, one of the main limits of this work, that resides in the way we defined individual quality and fitness. Indeed, our fitness measurement was based on both individual survival and breeding success at fledging.

> *"Clutch size has been evolved through natural selection to correspond with the largest number of young for which the parents can on the average find enough food." (Lack 1954)*

While the number of offspring at independence is the most commonly used predictor of individual lifetime performance (*e.g.* Patrick and Weimerskirch 2014, Zhang et al. 2015), it has been shown that the link between fitness and breeding success is actually not so straightforward (Dobson et al. 2020) and that fitness could be predicted more accurately by looking for example at the fledgling survival at first year or even at recruitment (*Figure 39;* Viblanc et al. 2022). This is especially true as the trade-off

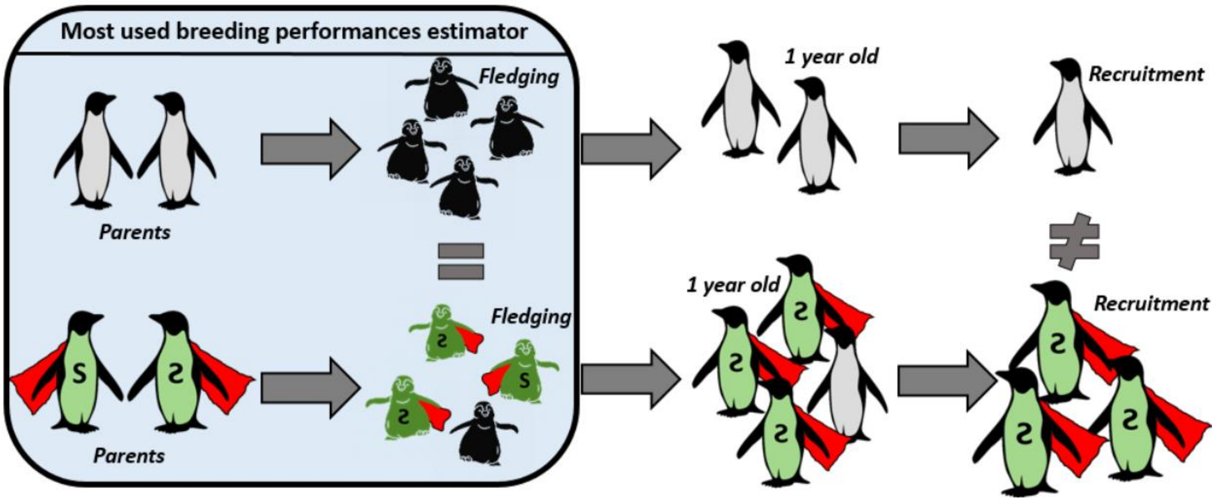


Figure 39: Potential bias in using breeding success as the main indicator of breeding performances.

between offspring quantity and quality, which has been studied through the prism of clutch size since the middle of the 20th century (*See citation above*), can lead to strategies in which individuals maximize the number of offspring produced during their life while investing little energy in their development. This is expected to induce poor quality offspring that will exhibit poor survival and breeding success, thus leading to an overestimated fitness of the parents if using the breeding success as a proxy. Following this reasoning, individual fitness can never be precisely assessed, as its theoretical measurement actually relies on the performances of thousands of generations (in theory an infinity) of individuals. However, it would be of great interest, although probably difficult, to use the same approach as we used in this work but defining fitness with longer-term metrics of offspring capacity to contribute to the population, such as the survival at recruitment, and understand how such fitness assessment decisions can lead to mixing individual quality with what we could call a R strategy (*See citation*, Pianka 1970).

> *"We can visualize an r-K continuum, and a particular organism's position along it. The r-endpoint represents the quantitative extreme-a perfect ecologic vacuum, with no density effects and no competition. Under this situation, the optimal strategy is to put all possible matter and energy into reproduction, with the smallest practicable amount into each individual offspring, and to produce as many total progeny as possible. Hence r-selection leads to high productivity. The K-endpoint represents the qualitative extreme-density effects are maximal and the environment is saturated with organisms. Competition is keen and the optimal strategy is to channel all available matter and energy into maintenance and the production of a few extremely fit offspring."* (Pianka 1970)

In models such as the little penguin, assessing a fitness value that reflects individual real contribution to the population is seemingly of particular importance. Indeed, in this species, most of the offspring die before reaching their first year (around 85%, Sidhu et al. 2007). In such case, most breeding pair that successfully fledged chick(s) will actually not increase at all their contribution to the population, as their offspring will never reach breeding age. Thus, survival at one year is already seemingly a much better predictor of individual fitness that fledging success in our case. However, this measure of juvenile survival is still probably insufficient to encompass the complexity of individual genetic contribution. Indeed, in this work, we demonstrated that an important part of the individuals recruiting still did not manage to contribute to the population (*Chapter 3*). Furthermore, we demonstrated a strong effect of growth conditions on life history and fitness as an adult (*Chapter 5*). This highlights how, even when offspring overpass the first selection filter of juvenile survival, their contribution to the population might be very different, and so the fitness of their parents.

2. Inheritance and fitness

The presence of important variability in individual quality does not necessarily result from evolutionary processes. Indeed, for evolutionary processes to arise on a set of traits, they need to be both under selection and heritable (Falconer and Mackay 1996). The “under selection” requirement is met as soon as we observe individual quality, as quality itself results in a strong correlation between a set of traits and individual fitness (Wilson and Nussey 2010). However, individual quality does not necessarily induces heritability, and traits that affect fitness are actually quite conversely often poorly heritable (Stirling et al. 2002). In this work, we were not able to directly assess the heritability of the traits linked to quality, mainly because such assessment often requires genotypic data and/or pedigree information (Zhu and Zhou 2020), which are difficult to obtain in long-lived species due to their important generation time. Thus we could not conclude about the importance of genetic and inheritance in defining individual fitness. However, this work already allowed us to gather clues regarding the potential partial inheritance of certain traits. Indeed, we were able to establish a significant repeatability in the individual phenology, especially for such behavioral trait (see *Chapter 4;* Bell et al. 2009). While repeatability of a trait across the life of an individual does not necessarily involve its inheritance, it usually sets the upper limit of heritability and can thus be used as a first interpretation tool to assess the potential heritability of certain life history traits (Dohm 2002). This perspective provides an interesting follow-up question to this work, as assessing the heritable part of the variance in major life history traits, or simply the correlation that may exist between parent and offspring quality, may answer questions about the part of individual quality that is actually inherited. In other words, what part of individual quality is actually contributing to an individual fitness through the quality of its offspring.

3. Extreme versus average individuals in understanding life-history

During this work, I define individual quality as the main driver of fitness in the population. But does it necessarily mean that energy allocation trade-offs are of limited importance compared to individual quality when looking at each individual contribution to the population? Well, this is probably depending on the scale at which we want to assess this contribution.

Inter-individual variability that exists in the population can be importatly driven by the most extremes individuals, those individuals being either of very poor or very high lifetime performances. Individuals displaying very poor lifetime performances are expected to be the ones struggling the most in acquiring energy, thus allocating it mainly to their self maintenance (Stearns 1989, Charlesworth 1994; *Figure 40*) with very few capacities to develop energy allocation strategies. Conversely, very high performances individuals are expexted to be the ones with the best energy acquisition capacities, and are therefore in capacity to allocate important quantities of energy to most of their life history traits simultaneously (Wilson and Nussey 2010; *Figure 40*).

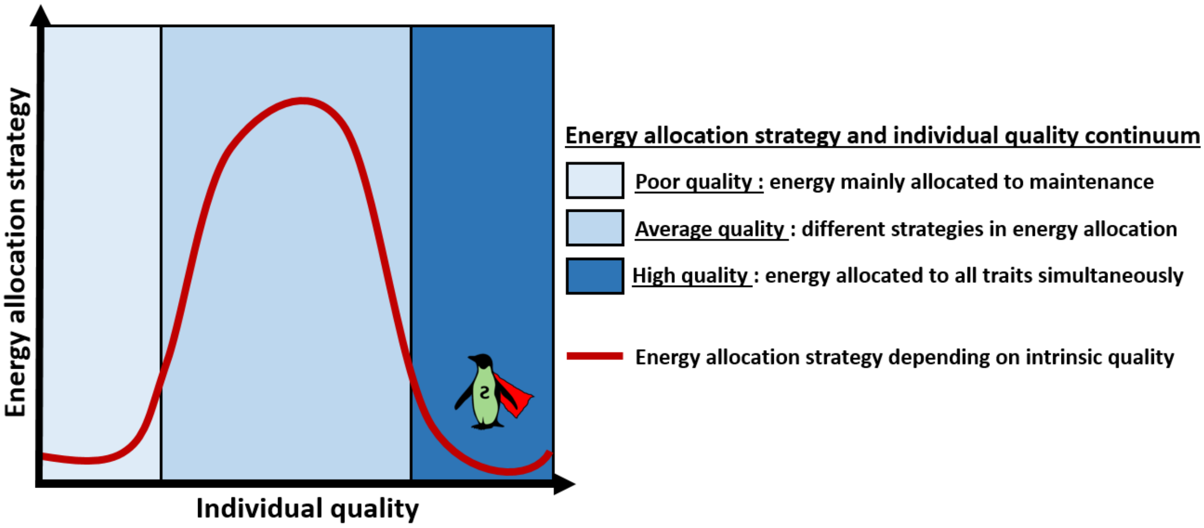


Figure 40: Energy allocation strategies in individuals of different qualities

While looking at the popuation as a whole, we can expect these extreme individuals to account for an important part of the variability in life history. The variability among individuals in the population will therefore be mainly driven by huge differences in individual quality. While looking at the individual continuum, we are therefore able to understand the differences in life history trajectories leading an individual to become a good or poor contributor to its population, which was precisely the point of this work. However, such way of thinking does not really allow to encompass the complexity of life history strategies that can exist in what is actually the biggest part of populations, the "average" individuals, for which energy-allocation strategies are of major importance and probably the most diverse (*Figure 41*), as they can make the difference between quite poor and quite good lifetime performances.

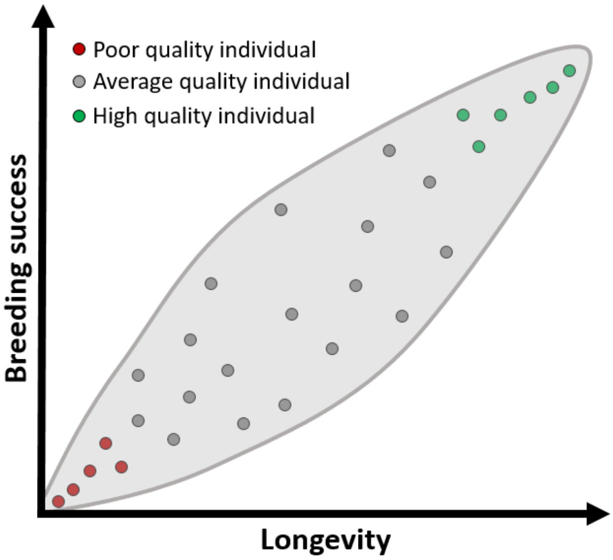


Figure 41: Covariation in two life-history traits with important trade-off depending on individual quality

While the two perspectives (*i.e.* looking at the population as a continuum or looking at each individual life history strategies) can be of great interest, this work sometimes actually struggles in defining which point of view will be adopted. Indeed, in these studies, especially *Chapter 3*, I mainly aimed at viewing the individuals as a population continuum in order to understand the drivers of variability in a global context. However, mainly because of my will to assess numerous life history traits all at once, the individuals I study here are far from being representative of the continuum that exist in the population. First of all, because individuals with the poorest fitness are also often the ones that survived and bred the less, they may lack information on their breeding behavior and thus get excluded from the analysis (*Figure 42*). Second, because I only consider here individuals that at least recruited, while the vast majority of individuals are expected to die as juveniles (Braasch et al. 2009). Therefore, the population I study is actually truncated, mainly displaying individuals that at least managed to maintain themselves in the population that cannot be considered as poor quality individuals. In the meantime, individual displaying the highest fitness in the population are, by definition, overrepresented.

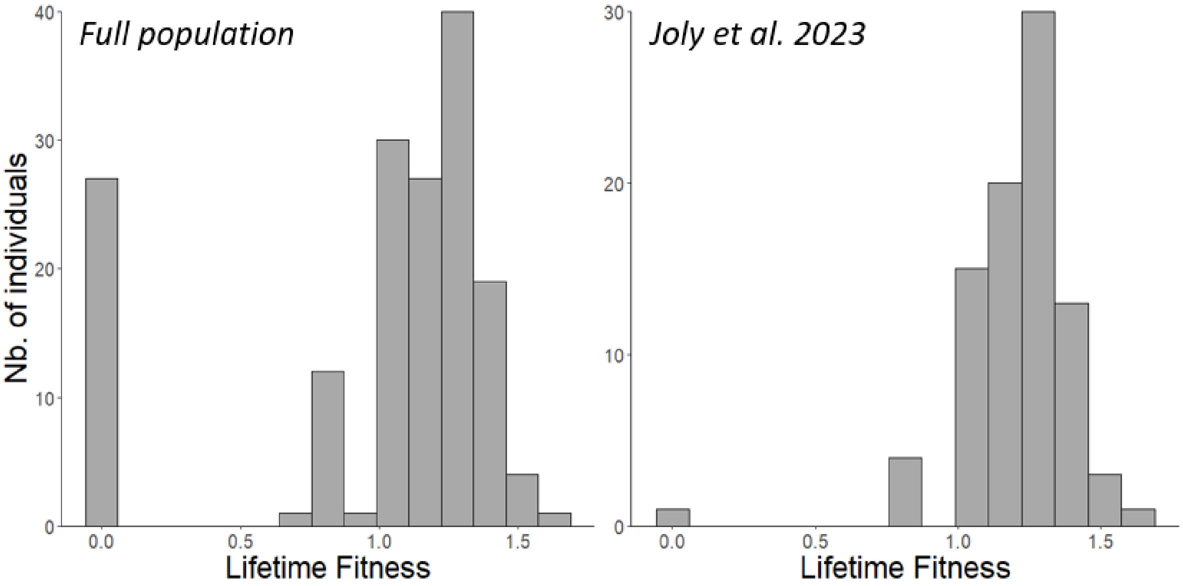


Figure 42: Lifetime fitness of all individuals attempting at least one breeding attempt VS. the individuals included in the final structural equation model (Joly et al. 2023)

While I would not necessarily consider this to be a limit of this work, but rather a completely different question, I think it is of high importance that it can be addressed in the future. Indeed, although average individuals are, by definition individually of limited importance in their contribution to the population, they undoubtedly constitute an important part of any population. Thus, the differences in quality, but also probably mainly in energy allocation strategies, that lead an individual to exhibit slightly different lifetime performances than its conspecifics definitely need to be addressed to get a full picture of the role of inter-individual variability on population dynamics.

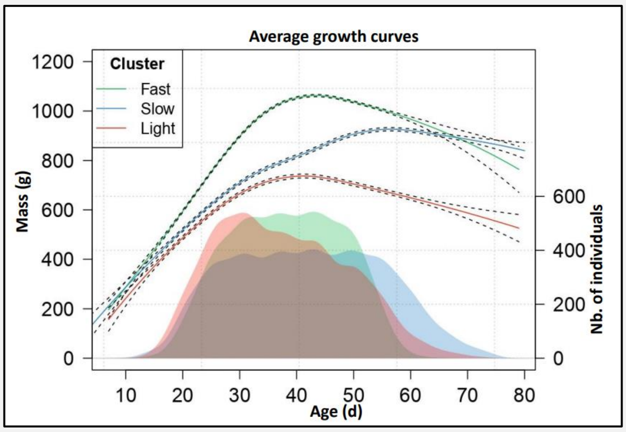
Chapter IX: Perspectives

A long way to go:
Perspectives and future research

1. Dive deeper into early-life

In this work, we confirmed and gave new insights on the major importance of early-life in defining individual life history trajectories, breeding performances and fitness (Visser and Verboven 1999, Inness and Metcalfe 2008). In this context, I participated in the supervision of a master student (Justine Wintz, January-June 2023) with Claire Saraux (CNRS) and Stéphanie Jenouvrier (Woods Hole Oceanographic Institution) in order to dig into the role of early-life on individual life history and population dynamic. This internship gave very interesting insights on the different phenotypes exhibited by the population as offspring (*i.e.* fast, slow, and bad individuals). Using Markov Chain modelling, these phenotypes were associated with different life history trajectories, showing the interplay between early-life and life history. In general, this internship emphasized the crucial role of early development and raised up many questions about its impact on population dynamics (see internship *Abstract* below).

Early-life conditions are known to play an important role in juvenile development, with potential long-term effects on later life-history traits. Yet, because of trade-offs between life-history traits, the ultimate results of early growth on individual fitness and population dynamics are more uncertain. Using a 22-yr dataset, we studied the growth trajectories of 1734 little penguin chicks to understand the effects of early rearing conditions on juvenile survival, and adult reproduction and longevity. We specifically tested for deleterious long-term effects induced by irregular or compensated growth. We identified three types of growth: the fast individuals that reached large masses quickly, the slow ones that exhibited an irregular and slow growth but fairly large masses at the end, and the light ones that exhibited a regular but weak growth. Using Markov chains on each of this group independently, we found a strong impact of early growth on life history traits, including significantly higher survival at fledging in fast and slow chicks (more than 80%) than in light ones (less than 50%). Fast individuals also lived longer and reproduced better, resulting in their rapid spread in the population (reaching 100% after 80 years). Slow-growing individuals matured later and had fewer offspring over life, consistent with pace of life theory. However, they did not survive longer, so that their overall lifetime performances were lower. Finally, light individuals presented a low juvenile survival but the few individuals that managed to recruit into the breeding population did not present any deleterious effects. This emphasizes the crucial role early development plays in shaping individuals' future abilities and highlights the need for further research on the consistency of environmental conditions and food availability during this critical period. Additionally, while no evidence of trade-off between fast growing and longevity was found, slow-growing phenotype was also characterized by a high irregularity in growth. Consequently, further research on what growth irregularity really represents (compensatory growth or stops and starts) and the reasons of the costs induced by irregularity is needed.



Average growth curves per cluster. Curves were smoothed with the loess function (span=0.5) with 95% confidence interval calculation (dotted lines). As the number of individuals measured along the growth curve varies due to chicks dying or fledging, it is indicated below the curves using a Gaussian kernel density (smoothing parameter fixed at 0.2) scaled back to the total number of individuals (right axis).

In order to address these questions left unanswered after the internship, Justine has now started a PhD (in October 2023), which I have the chance to co-supervise. This PhD first aims at using complex analytical methods to precisely characterize the different types of growth exhibited by little penguins' offspring using the entire growth curve rather than discrete parameters (using functional analyses, Králík et al. 2021). Once individual growth can precisely be defined, the project will focus on understanding the causes and consequences of the inter-individual differences in early-life. Regarding the causes, the project aims at investigating the effect of climatic (on-land) and oceanographic parameters (i.e. stochasticity, Fay et al. 2015), parental investment (Rishworth and Pistorius 2015) and quality, chick behaviour and potential heritability in growth. Due to all the previously explained reasons, estimating heritability might prove difficult, and an experimental approach of cross-fostering is foreseen to separate between genetics and maternal effects on chick growth. Regarding the consequences, this project will examine the link between different phenotypes and long-term life history (e.g. longevity, breeding success) but also life history of juveniles (e.g. juvenile survival, age at maturity). This aims at understanding the potential long-term consequences of processes such as compensatory growth (Metcalfe and Monaghan 2001), that are known to increase juvenile survival with important consequences on their life history strategies (although rarely studied in natural conditions; (Metcalfe and Monaghan 2003, Mangel and Munch 2005). Finally, this project aims at understanding how the distribution of such growth phenotypes can affect population dynamics using complex matrix population modelling. In other words, giving important insights on the effect of inter-individual variability on populations.

2. Understanding how individuals drive population dynamics

Earth is currently facing a major biodiversity collapse crisis induced by human activities. To forecast and mitigate our impact on wildlife, we must understand the mechanisms behind the current decline in populations. There have been very limited endeavors to merge forecasts generated by dynamic ocean-atmosphere models with empirically grounded eco-evolutionary population models. The field of ecological forecasting is in its infancy, and the mechanisms governing the predictability of numerous ecological and evolutionary processes remain elusive.

As developed all along this work, what we call a population is a group of very different individuals interacting (Lomnicki 1988). Like humans, they are very diverse; some are bold, others are shy (Réale et al. 2007); some forage well while others do not (Lescroël et al. 2020); some die early, others live to old age; most produce few offspring, a handful produces many. These differences make a few of them more resilient or adaptable to changes in their environment. Part of these abilities may be transmitted to their descendants (Teplitsky et al. 2009). Such diversity among individuals is the cornerstone of our understanding of wildlife ecology, evolution and demography.

In demographic studies of wild populations, substantial attention has been directed towards exploring the diversity of life history traits among individuals over the past several decades. Traditionally, demographic analyses have extensively incorporated variations among individuals based on factors such as age or sex only (Hansen 1989). In more recent times, there has been a growing interest in incorporating additional individual features, including morphological or phenological traits, into these analyses (Jenouvrier and Visser 2011). However, it is important to note that, primarily due to logistical constraints related to monitoring and the complexity of analyzing a large amount of traits at once, the majority of studies tend to focus on a limited set of traits. These commonly studied traits often include aspects such as breeding timing or body condition. Consequently, the subsequent challenge lies in effectively integrating a combination of these selected traits into population models, which remains a complex endeavor.

The significance of understanding individual differences extends beyond the realm of demography and directly pertains to the field of evolution. Within evolutionary biology, individual-level variation is a driving force for adaptation and long-term evolutionary change. Recent advances in the field have prompted heightened interest in constructing demographic models that seamlessly incorporate evolutionary processes (Bjørnstad and Hansen 1994, Doebeli and de Jong 1999). This interest has surged, particularly in response to the pressing challenges posed by on-going climate change. To comprehensively address these challenges and gain a holistic understanding of species extinction in face of climate change, it is imperative to bridge the gap between ecological and evolutionary perspectives, emphasizing the role of individual variation as a cornerstone in this endeavor.

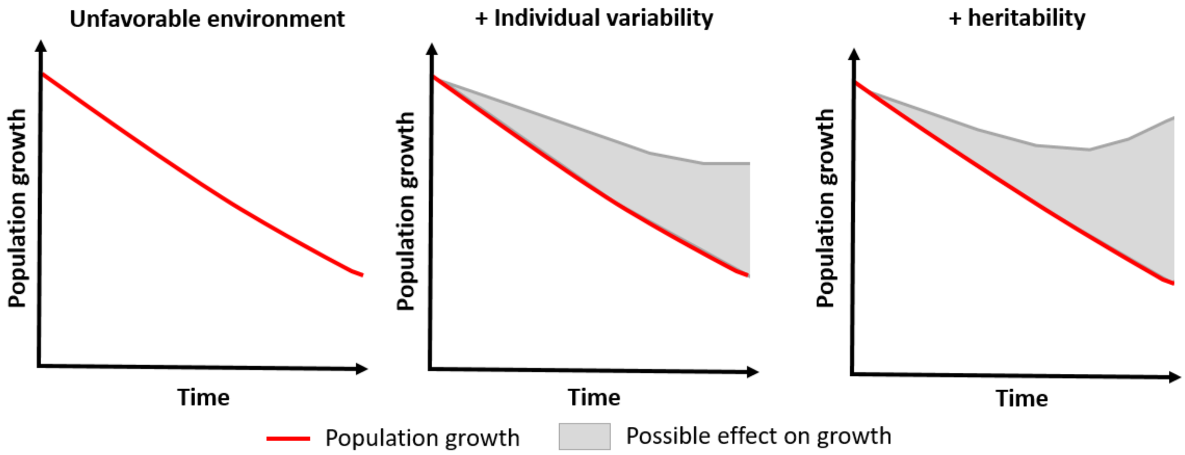


Figure 43: Potential effect of individual variability and evolutionary processes in predicting population dynamics in a context of climate change

In future research projects, my objective will be to explore the implications of the individual diversity I unravelled during the span of this work, seeking to elucidate its influence on addressing pressing ecological and evolutionary questions in the context of climate change. This research will aim at addressing several questions left partially or completely unanswered during my PhD: What factors contribute to certain individuals outperforming the population average? Could a small subset of individuals play a disproportionately significant role in shaping population dynamics? How do variations among individuals influence the eco-evolutionary responses to climate change? How do these individual differences affect the predictability of our population forecasts? Through the exploration of these questions, my objective is to advance our comprehension of the complex interplay between individual diversity and the ecological and evolutionary implications of climate change, ultimately enhancing our capacity to predict the risk of population decline and species extinction (*Figure 43*).

Building on the insights gained during my PhD, my future research will aim at expanding our understanding further by incorporating inter-individual variability into population modelling and population dynamic forecasting. To achieve this, I intend to employ state-of-the-art methods in mathematical ecology and oceanography, encompassing a diverse range of typically understudied traits, including personality, physiology, and at-sea behavior in response to prey availability. Overall, my objective is to incorporate inter-individual variability and environmental fluctuations into increasingly sophisticated eco-evolutionary population models. My approach will involve two key components: Firstly, I will delve into modern mathematical techniques of quantitative ecology, enabling the integration of individual heterogeneity into eco-evolutionary population models using hyper-state matrix models (Roth and Caswell 2016). Additionally, I will work at effectively integrating climate change dynamics into these eco-evolutionary population models (*Figure 44*).

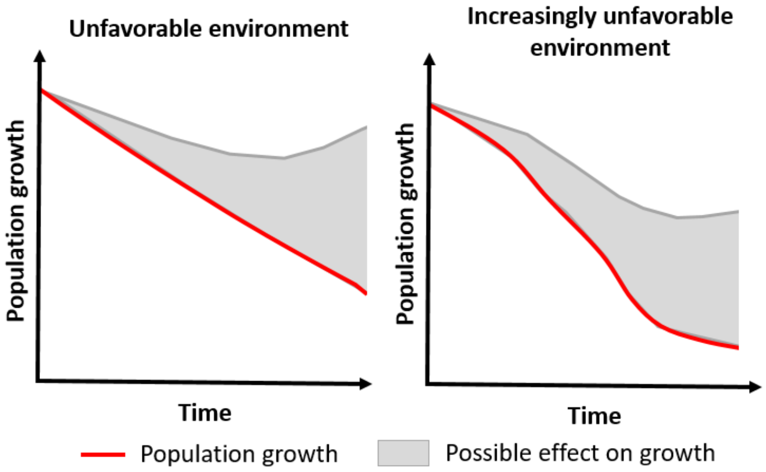


Figure 44: Potential effect of individual variability on population dynamics in a context of climate change

By taking this integrative approach, I will aim at advancing our comprehension of the impacts of climate change on penguin populations within a broader demographic and evolutionary context. As a particularly threatened group (IUCN), seabirds and particularly penguins are among the species for which population dynamic forecasting is the most relevant. In this context, I aim at developing broad modelling tools that could be used by the scientific and management community.

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Variabilité interindividuelle des réponses à l’environnement et conséquences sur la fitness individuelle chez le manchot pygmée. - *Résumé en français*

L’étude de la démographie et de l’évolution des espèces compte parmi les plus anciennes disciplines de la biologie. Dans ce cadre, les espèces et les populations animales ont longtemps été considérées comme des unités évolutives homogènes, dans lesquelles les caractéristiques de l’ensemble des individus pouvaient être résumées aux caractéristiques moyennes de la population. Cette vision est depuis maintenant plusieurs décennies remise en question, notamment concernant la place de l’individu comme moteur principal de l’évolution et de la dynamique de population. En effet, si l’étude de la dynamique des populations animales est un excellent outil d’observation des effets combinés de l’environnement et de processus évolutifs sur le vivant, elle n’est pourtant que le reflet de la vie d’une multitude d’individus à la morphologie, à la physiologie et au comportement très différents. Aussi, l’étude et la prédiction des dynamiques de populations et les questions évolutives fondamentales qui y sont associées tentent de plus en plus de prendre en compte la variabilité interindividuelle. De ce fait, l’étude des différences entre individus a pris une importance grandissante ces dernières décennies, donnant naissance à de nombreux nouveaux concepts.

Si l’on accepte que les individus d’une population sont uniques de par leurs traits, qu’ils soient physiques ou comportementaux, alors il faut admettre que ces spécificités leurs permettent d’expérimenter des vies différentes. Ces traits, que l’on appelle traits d’histoire de vie, impliquent que chaque individu contribue différemment à la population, de par leurs différentes longévités et capacités à se reproduire. Cette contribution différentiée des individus à la population est appelée valeur sélective (ou fitness), et ses causes sont nombreuses.

Par définition, la quantité d'énergie disponible dans le milieu est limitée. Lorsque la quantité d'énergie acquise par un individu n'est pas suffisante pour satisfaire l'ensemble de ses besoins apparaissent des compromis, ou « trade-offs ». La nature de ces compromis peut être extrêmement différentes d'un individu à l'autre (on parle alors de stratégie d'allocation d'énergie) et si deux stratégies très différentes peuvent se valoir, certaines peuvent s'avérer plus efficaces, c'est-à-dire mener à une meilleure fitness. Au-delà de ces compromis, certains individus peuvent aussi être intrinsèquement d'une qualité supérieure à d'autres. On parle de bonne qualité lorsqu'un individu est en capacité de maximiser ses apports énergétiques dans l'ensemble de ces traits d'histoire de vie au-delà de tout compromis. Ces différences de qualité peuvent provenir du patrimoine génétique ou encore des conditions rencontrées pendant le développement. Enfin, la fitness d'un individu dépend également tout simplement de l'environnement dans lequel celui-ci évolue. Deux individus nés à seulement quelques années d'intervalle peuvent parfois rencontrer un environnement plus ou moins favorable au cours de leur vie, impliquant des effets sur leur histoire de vie et donc leur fitness.

Si tous ces concepts sont de nos jours connus et décrits, l'effet intégré de toutes ces sources de variation reste extrêmement difficile à établir. En effet, un individu possède autant de traits d'histoire de vie qu'il ne possède de caractéristiques susceptibles d'affecter plus ou moins directement sa fitness. De plus, l'effet d'un trait sur la fitness ne se mesure précisément qu'à l'échelle d'une vie complète, et en intégrant l'environnement dans lequel les individus ont évolué durant leur vie. Pour toutes ces raisons, la variabilité interindividuelle s'étudiait jusqu'ici à l'échelle d'un trait, et le plus souvent à l'échelle de la reproduction plutôt qu'à celle de la vie.

Lors de ce travail de thèse, j'ai pu bénéficier de données exceptionnelles issues d'un suivi partiellement automatisé de plusieurs centaines de manchots pygmées (*Eudyptula minor*) d'une population australienne, et ce sur une période de plus de 20 ans, incluant non seulement des données de reproduction classiques mais aussi des performances de recherche de nourriture en mer et de croissance des poussins. Grâce à ces données brutes, j'ai pu extraire une grande quantité d'informations sur près d'une vingtaine de traits d'histoire de vie d'environ 500 manchots, dont plus de 150 ont été suivi sur l'ensemble de leur vie et pour lesquels j'ai donc pu calculer précisément la fitness. A partir de toutes ces informations et en utilisant des méthodes de statistiques avancées telles que des équations structurelles (ou analyses en chemin), j'ai tout d'abord pu intégrer ces différents traits d'histoire de vie liés aux performances et habitudes de reproduction ainsi qu'à la recherche de nourriture dans un modèle complexe unique. Ceci avait pour but de comprendre comment et dans quelle proportion les interactions entre ces différents traits et ultimement leur effet sur la fitness dépendait de la qualité individuelle, de compromis dans l'allocation d'énergie ou encore de stochasticité environnementale. Grâce à cela, j'ai pu mettre en avant la coexistence de ces différents processus au sein de la population, bien que la différence de qualité entre les individus, c'est-à-dire la capacité de certains individus à être performants dans l'ensemble des traits d'importance étudiés, semblait prépondérante. De plus, cette étude simultanée d'un grand nombre de traits d'histoire de vie m'a permis de déceler les caractéristiques principales influant la fitness des individus. En l'occurrence, les individus dont la fitness était la plus élevée étaient aussi ceux dont la recherche de nourriture en mer était la plus efficace, la reproduction la plus précoce et qui se reproduisaient régulièrement plus d'une fois par an.

Dans un second temps, j'ai donc cherché à comprendre plus directement le lien entre ces traits prépondérants et la fitness des individus. Pour ce faire, j'ai étudié le lien qui pouvait exister entre phénologie, fourragement et environnement à l'échelle de l'évènement de reproduction pour environ 500 manchots sur plus de 2500 évènements de reproduction, incluant 45000 voyages en mer. J'ai pu mettre en avant le lien fort qui existait entre environnement et fourragement, les individus ayant les meilleures performances en mer étant aussi ceux se reproduisant le plus tôt dans l'année. Ces différences de performance étaient principalement dues à des facteurs environnementaux, les individus se reproduisant le plus tôt étant également ceux rencontrant généralement les meilleures conditions (thermocline, courant…). Ainsi, les manchots se reproduisant plus tardivement tendaient non seulement à rater leur reproduction plus régulièrement, mais également à perdre plus de masse, induisant des effets pluriannuels ou « carry-over effects ». Enfin, les individus se reproduisant le plus tôt tendaient également à produire des poussins plus lourds au terme de leur croissance, et donc probablement de meilleure qualité.

Cette dernière découverte ainsi que la littérature existante sur le sujet m'ont amené à me questionner sur l'importance des conditions de développement en tant que poussin sur les traits d'histoires de vie à l'âge adulte, et donc ultimement la fitness. J'ai alors étudié l'effet de l'année et de la date de naissance, ainsi que de certains paramètres de croissance tels que la vitesse, la masse, l'irrégularité ou la durée des soins parentaux sur la future vie adulte du poussin. J'ai pu mettre en avant l'effet de la croissance et de la période de naissance sur le succès et les traits d'histoire de vie à l'échelle de la reproduction, mais aussi et surtout l'effet des conditions de croissance, et principalement l'irrégularité, sur la fitness et les traits d'histoire de vie à l'échelle de la vie complète des individus.

Ainsi, ce travail de thèse m'a permis de mettre en avant la complexité et l'étendue de la variabilité entre les individus d'une population et son lien avec leur fitness. Cette variabilité dépend à la fois de différences de qualité individuelles, y compris liées aux conditions de développement, mais aussi à des compromis d'allocation d'énergie menant à des stratégies différentes. Au-delà de ces différences inhérentes aux individus d'une population, j'ai pu montrer que la stochasticité environnementale, c'est-à-dire l'imprédictibilité des conditions

d’une année à l’autre, jouait aussi un rôle dans les différences de fitness entre individus. De manière générale, ce travail met en avant la nécessité de considérer l’individu et son histoire de vie dans leur ensemble pour comprendre le rôle de la variabilité interindividuelle dans les processus évolutifs et démographiques.

Nicolas JOLY

Variabilité interindividuelle des réponses à l'environnement et conséquences sur la fitness individuelle chez le manchot pygmée.

Résumé

Les populations animales sont constituées d'individus très différents en interaction. Tout comme les humains, leurs vies peuvent s'avérer très différentes. Certains sont audacieux tandis que d'autres sont timides, certains sont de meilleurs fourrageurs que d'autres, et certains meurent jeunes pendant que d'autres vivent jusqu'à un âge avancé. A la fin de leur vie, ces spécificités peuvent faire une grande différence dans leur capacité à produire une descendance, et donc à propager leurs gènes dans la population (fitness). Au cours de ce travail, j'ai étudié la diversité des trajectoires de vie existant au sein d'une population australienne de manchots pygmées, ainsi que leurs effets sur la fitness des individus. En m'appuyant sur le suivi de plusieurs centaines de manchots tout au long de leur vie, j'ai pu mettre évidence l'importance prépondérante de la qualité individuelle intrinsèque, plutôt que des stratégies individuelles d'histoire de vie, sur leur fitness. Chez cette espèce asynchrone, la qualité individuelle dépendait avant tout de la capacité d'un individu à se reproduire plus tôt que ses congénères, conduisant à de meilleures performances de fourragement via un environnement plus favorable, ainsi qu'à la possibilité de se reproduire deux fois dans une saison. Concernant les causes des variations de la qualité individuelle, j'ai pu souligner l'effet majeur du développement, et notamment de la régularité de la croissance, sur la vie d'adulte. Enfin, la stochasticité environnementale (c'est-à-dire la chance d'un individu de vivre des années plus ou moins favorables) a renforcé l'hétérogénéité interindividuelle de la fitness. De manière générale, ce travail met en avant la diversité existant au sein d'une population et la nécessité de la prendre en compte pour correctement comprendre et prédire sa dynamique.

Mots clés: *Fitness, hétérogénéité individuelle, fourragement, phénologie, stochasticité, développement*

Abstract

Animal populations are made of a variety of individuals interacting. Similarly to humans, they experience very different lives. Some are bold while others are shy, some are good foragers while others are not, and some die early while others live to old age. In the end, these differences can have an important impact on their capacity to produce offspring and thus to propagate their genes in the population (fitness). During this work, I studied the diversity of life history trajectories existing within an Australian population of little penguins, as well as their effects on individuals' fitness. Based on the monitoring of several hundred penguins throughout their entire lives, I highlighted the preponderant importance of individual intrinsic quality, rather than individual life-history strategies, on their fitness. In this asynchronous species, individual quality was first and foremost depending on an individuals' ability to breed earlier than its conspecifics, leading to better foraging performances via a more favorable environment as well as the possibility to breed twice within a season. Regarding the causes of variations in individual quality, I could highlight the major effect of development, and in particular of growth regularity, on life as an adult. Finally, environmental stochasticity (*i.e.* whether an individual was lucky enough to live in favorable years) strengthened the inter-individual heterogeneity in fitness. Overall, this work demonstrates the diversity existing within a population and the need to account for it to accurately understand and predict its dynamics.

Key words: *Fitness, individual heterogeneity, foraging, phenology, stochasticity, early-life*