

PhD project :

Natural selection, causality and demographic feedback in long-lived seabird populations.

### **Location**

Centre d'Études Biologiques de Chizé, UMR 7372, CNRS-La Rochelle Université. 405 route de Prissé la Charrière, 79 360 Villiers en Bois, France

### **Supervision**

100% Timothée Bonnet, CRCN CNRS (permanent research scientist), marine predator team.

### **Announcement**

I have a fully funded PhD to study current natural selection in albatross populations. The student will apply and develop cutting-edge statistical methods to quantify patterns of natural selection acting on series of traits, infer the causal mechanisms of selection, and study the interplay of demography and selection. The work will use data from the long-term monitoring of several albatross populations at French sub-antarctic territories. The student will contribute to fieldwork on Kerguelen island and collect original data on nest properties.

The student will be based at CECB (affiliated La Rochelle Université - CNRS), Chizé, France. The campus is located in the middle of a forest in the countryside, 1h from the coast.

Expected starting date October 2024, for a duration of 3 years. The project description can be found here: <https://timotheenivalis.github.io/Rnotebooks/PhDProjectEnglish.pdf>

Applications are by sending a CV and cover letter to [timothee.bonnet@cebc.cnrs.fr](mailto:timothee.bonnet@cebc.cnrs.fr). Interested candidates can contact me informally for extra details.

### **Project description**

Human activities modify the environment of many species and alter selective pressures (Pelletier & Coltman 2018). The average values or combinations of traits in populations that resulted from long-term evolutionary dynamics are therefore getting further away from optimal phenotypes. This threatens the persistence of populations, but at the same time may allow responses to selection and gradual adaptation to new conditions. Adaptation by genetic responses to selection is classically expected to be rather slow, at least relative to plastic responses. However, theoretical work (Gonzales & al. 2013) and recent empirical research show that this mechanism can be far from negligible (Bonnet & al. 2022), and in particular can make the difference between extinction or survival of a population on the scale of a few generations (Gonzales & al. 2013).

Despite its fundamental and practical importance our understanding of the mechanisms and consequences of adaptation by selection remains deficient due to several technical and

conceptual hurdles. Demographic studies often consider the effect of the selective disappearance of individuals within a generation, but they struggle to take into account the effect between generations, whereas quantitative genetic studies present the opposite defect (van Benthem et al. 2017). Furthermore, quantitative genetic studies generally consider the effect of selection using analyzes carried out on the total reproductive success of individuals over their lifetime, which makes it difficult to understand the causal mechanisms, and therefore to propose long-term predictions. A better understanding of the consequences of selection over several generations could come from models decomposing selection across life-history stages (Huisman & al. 2016). Finally, classical approaches are unsuitable for distinguishing the role of competition in selection, which prevents them from distinguishing between cases where a response to selection is beneficial to population growth, and cases where a response is neutral or even harmful (Wilson & al. 2011).

The thesis will look at these obstacles using the albatross populations of the French southern lands as a system. These populations have been monitored for several decades, with large volumes of data for the traits and life history of individuals, which makes it possible to model selection in great details. As these species are long-lived, they constitute good models for breaking down the selective mechanisms acting at different phases of life. Furthermore, these populations are subject to numerous environmental changes of human origin (e.g. fisheries, climate change, invasive species), are generally threatened, and benefit from conservation measures (Weimerskirch & al 2018). Beyond the opportunity presented by studying this system from a fundamental point of view, a better understanding of selection in these populations could inform conservation measures.

To fully understand and predict the process of adaptation through response to selection, three aspects must be considered: first, the genetic properties (additive genetic variances-covariances, heritability, evolvability) of the selected traits; second, multivariate selection patterns, i.e., taking into account correlations between traits (Lande & Arnold 1983); and finally, an almost always overlooked aspect, the causal mechanisms of selection and the potential for an average trait change to cause an improvement in average survival or reproduction (indeed, this potential may be more or less present, and is notably absent when the selection corresponds to competition in a zero-sum game). The estimation of the genetic properties of the study populations is already underway within the team. The thesis subject will focus on selection and will therefore relate to the two other aspects, approached through 3 main axes of study.

A first axis will focus on the study of selection on the properties of albatross nests in Kerguelen. Traits linked to reproduction have been less studied than those linked to survival in albatrosses, and to my knowledge no study has focused on variation in the properties of albatross nests. However, these elaborate structures appear crucial in the survival of eggs and chicks before fledging, and then throughout life (Perez & al 2020). Furthermore, these traits are conceptually original because they can be seen as extended and shared phenotypes. Variations between individuals or pairs in nest properties could therefore have selective importance. The student will take measurements of dimensions, shape, physical location and relation to other nests. They will then test if there is inter-individual/couple variation and whether the variation is selected.

A second axis will focus on the estimation of multivariate selective pressures on all available traits (morphology, phenology, behavior, life history, and new data on nests) in order to predict intra- and inter-generational phenotypic changes. Different measures can be extracted from these analyses. First, we will be able to measure the total force of selection in each population (Henshaw & Zemel 2017), and break it down into the contributions of different episodes of selection. Then, estimation of selection differentials linked to viability will measure intra-generational phenotypic changes. Finally, multivariate selection gradients will be combined with additive genetic variance-covariance matrices to predict short-term evolutionary responses and test for the presence of evolutionary constraints (Morrissey & al. 2012).

A third axis will focus on the construction of causal models of selection. First, using

demographic models already existing for the species (Fay & al. 2017), the student will break down life histories into episodes of selection: survival at different ages, maturation and access to reproduction, then reproductive success. They will then propose and test causal models of selection in the form of acyclic diagrams and extended selection gradients (Morrissey 2014), while taking into account the effect of environmental variations, missing data and feedback loops. This will be used to formulate predictions on the effect of responses to selection on the average value of demographic parameters (survival, maturation, reproduction), predict which selective pressures are likely or not to increase the growth rate of the population and help the population adapt to different environmental changes. For this axis in particular we will favor Bayesian approaches, which facilitate taking into account missing data, the construction of multi-hierarchical models, and the propagation of uncertainty to derived parameters (Gelman & al 2013).

This thesis will therefore provide valuable knowledge both for the fundamental understanding of selection in nature and for the management of wild populations. The student will be able to develop varied skills, combining field experience, expertise in selection theory, data management, computer programming and advanced statistical modeling.

## **References**

- van Benthem, K. J. et al. *Disentangling evolutionary, plastic and demographic processes underlying trait dynamics: A review of four frameworks. Methods Ecol. Evol.* 8, 75–85 (2017).
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- Morrissey, M. & al. *Genetic analysis of life-history constraint and evolution in a wild ungulate population. The American Naturalist* 179, 4 (2012).
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- Pelletier, F. & Coltman, D. W. *Will human influences on evolutionary dynamics in the wild pervade the Anthropocene? BMC Biol.* 16, 7 (2018).
- Perez, D.M. et al. *Climate as an Evolutionary Driver of Nest Morphology in Birds: A Review. Frontiers in Ecology and Evolution* (2020).
- Weimerskirch et al. *Status and trends of albatrosses in the French Southern Territories, Western Indian Ocean. Polar Biology* 41, 10 (2018).
- Wilson et al. *Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, Cervus elaphus. Journal of Evolutionary Biology* 24, 4 (2011).

## **Partnership**

This thesis will be carried out in collaboration with the French Polar Institute (IPEV) through a project in the French Southern and Antarctic Lands (109 ORNITHOE2, labeled Long-Term Monitoring of Living Things by INEE) and the Antarctic Workshop Zone and Terres Australes (ZATA) which is part of the CNRS Workshop Zones network and the international LTSER (Long-Term Socio-Ecological Research) networks. The results from the thesis can be used to help implement conservation measures for targeted species in close partnership with the National Nature Reserve of the French Southern Territories and with the Agreement for the Conservation of Albatrosses and Petrels ratified by the France.

## **Impact**

The subject is completely part of a fundamental knowledge creation approach and short-term applications are not envisaged. However, the subject responds to societal expectations of understanding the impacts of anthropogenic environmental changes on biodiversity, particularly on flagship and sentinel species such as albatrosses. In the longer term, a more detailed understanding of the demographic and selective processes in albatross populations will inform the conservation measures implemented by our partners in the French southern lands (TAF National Nature Reserve) and more broadly by the managers of the wildlife (Agreement on the Conservation of Albatrosses and Petrels, Convention for the Conservation of Antarctic Marine Living Resources, IUCN).

## **Work expected from the PhD student**

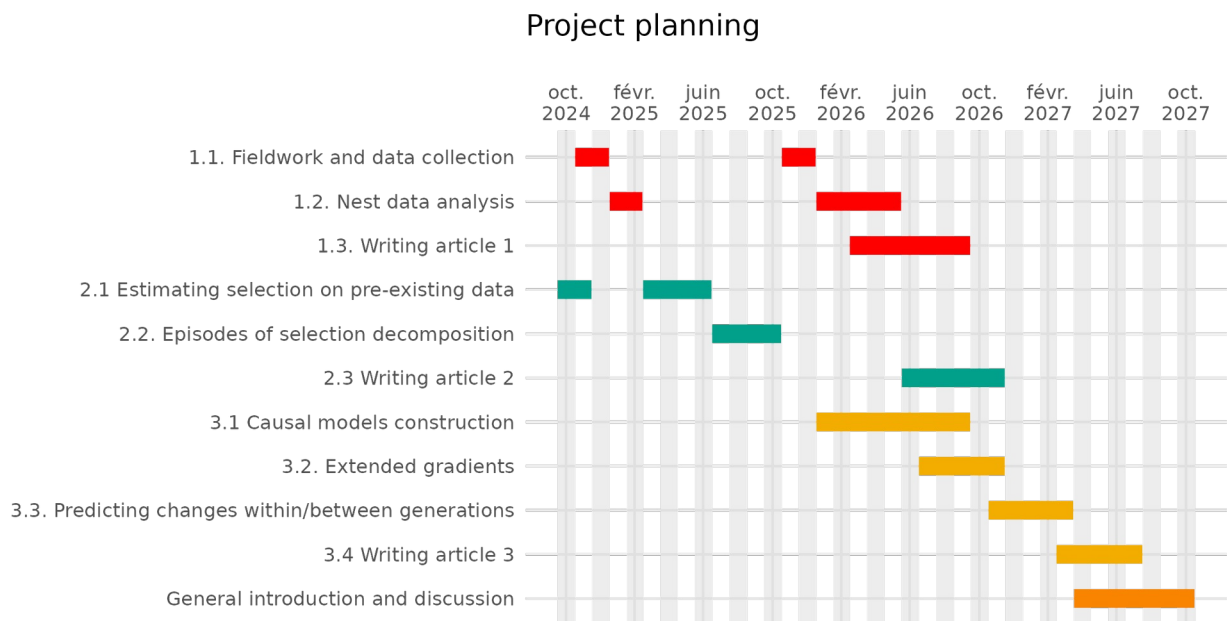
1) Collection of data in the field: The student will carry out measurements on the nests of black-browed albatross on the colony of the Canyon des Sourcils Noirs in Kerguelen which has been monitored and studied for several decades. In addition to this work directly linked to the project, the student will participate in the collection of data for long-term monitoring (e.g.: reproduction monitoring, ring control, morphometric measurements), data which will also be used for axes 2 and 3 of the thesis. The first field campaign taking place early after the start of the thesis, the field protocol will be prepared in advance by the supervisor, in consultation with the rest of the team, but discussed and amended with the student in the first month. thesis. The first data will be analyzed upon return from the field to provide an opportunity to develop or improve the protocol for the second field campaign and for the data collection carried out in the meantime by the wintering volunteers.

2) Statistical analyses: The core of the thesis will be based on statistical analyzes of new and existing data. The student will model selection according to different statistical approaches, some very common and fundamental (e.g.: Lande and Arnold multivariate gradients), others very recent and still in development (e.g.: total selection measure, extended selection gradients, decomposition on life stories). The student will have to familiarize themselves with the mathematical and theoretical foundations of these approaches. These approaches have progressed significantly over the last 5 years, and new avenues of progress, although unpredictable, are entirely possible. The student may therefore propose methodological developments, in the form of an additional axis or as part of one the three proposed axes.

3) Writing of scientific articles and communication: Based on the analyzes carried out, the student will produce scientific articles for international peer-reviewed scientific journals. They will present their work at local conferences (e.g. LUDI days, marine predator days at CEBC/LRU, doctoral students conference) and international conferences. They will also communicate their results to citizens via social networks, potentially general public articles presenting depending on the interest that its work generates, and popular science events.

### **Risks and contingency plan.**

The collection of data in the field will be necessary to carry out axis 1. If the student was not able to carry out the field (e.g.: personal health), the collection of data can be carried out by the supervisor and other workers present on site. In the most extreme case where no data collection would be possible (e.g.: serious international crisis), this first axis would have to be abandoned. It would then be replaced by a chapter making use of already existing data and relating to the synthesis of causal selection models (axis 3) with the demographic models developed by the marine predators team. The other two axes do not present any feasibility risks since they are based on the analysis of large volumes of data already existing and stored at the CEBC.



During the thesis, two missions of 2 to 3 months are planned in the TAAF, in order to participate in the collection of data on the nests and contribute to the long-term monitoring of the populations studied. The analysis of the nest data will be carried out at the end of the first field season to adjust the protocol if necessary, but the final analysis and writing of the article will wait until the end of the second field season. While waiting for the new dataset to be completed, the student will be able to start working on the second axis, which will allow them to acquire all the basic concepts and skills for selection modelling. Depending on progress, the second article may be started in parallel with the first, during the submission stages. The construction of causal models for axis 3 represents an important work of synthesis and development of statistical models and we will devote a significant part of the second year to it. Once completed, this work can be used quickly and lead to a third article and the finalisation of the thesis in the third year. Participation in at least two scientific congresses (if possible one in France and one abroad), as well as in the meeting of the WAMBAM working group on quantitative genetics and selection in wild populations (scheduled for 2025), is expected during the thesis. Throughout the thesis, the student will be involved in the scientific activities of the CEBC, in particular through participation in seminars, journal clubs, results and computer programming.

### **Supervision and support**

This thesis will be 100% supervised by Timothée Bonnet, of whom it will be the only thesis supervised for at least one year. The doctoral student will be able to benefit from the support of collaborators within the marine predators team, in particular Christophe Barbraud and Karine Delord who are experts on the datasets, biological systems and demographic models. Outside of the

CEBC the thesis may benefit from a network of expert collaborators on the methods and theory of quantitative genetics and natural selection.

The project is mainly based on the analysis of already existing data hosted at the CEBC and does not require any particular means. All field logistics for the collection of new data will be supported by the IPEV Polar Institute, via project 109 ORNITHOE2, renewed until 2028. Ordinary costs associated with the doctorate (publication, conference, defense) can be covered partly by recurring grants from the team, partly by specific requests from learned societies and recurring partners of the team (Agreement on the Conservation of Albatrosses and Petrels, Réserve Naturelle Nationale des Terres Australes Françaises).

A desk, a new laptop and associated peripherals are available for the student.

Supervision of the doctoral student will be carried out by a normally weekly meeting with the thesis director. Annual thesis monitoring committees will be organized with external researchers.