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Les capacités d’adaptation des oiseaux marins face aux changements environnementaux : le rôle de l’hétérogénéité au sein des populations.

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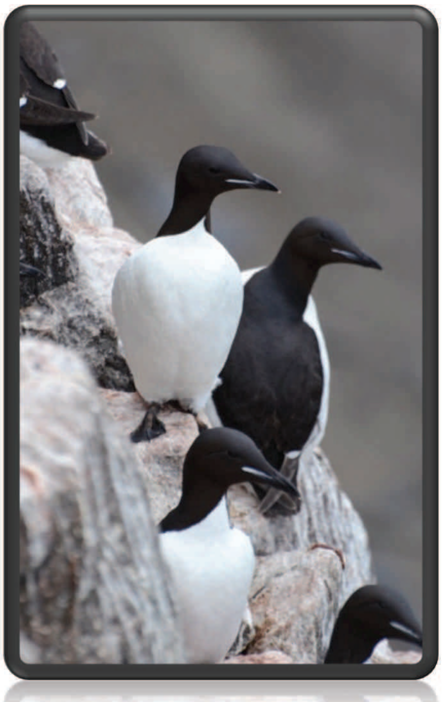
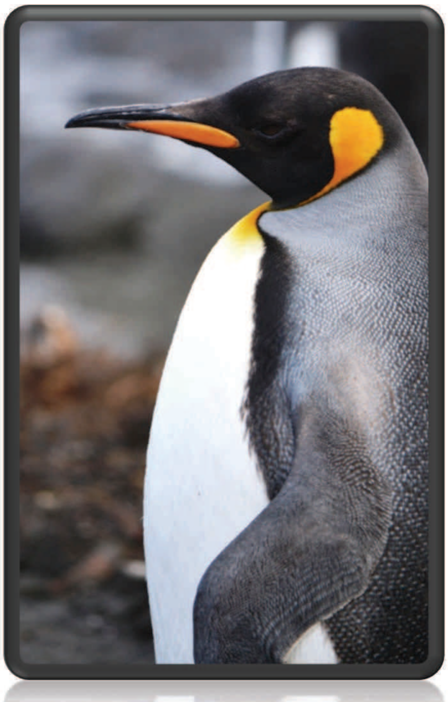
The adaptive capacities of seabirds to face environmental variability: the role of heterogeneity within populations





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Cornet C.C., Descamps S., Gineste B., Hanuise N., Lemonnier G., Orgeret F., Whittington J.D., Le Maho Y. & Le Bohec C. Identifying behavioural syndromes through observations of captive, and non-captive colonial polar seabirds. ***In prep. 2***

Cornet C.C., Descamps S., Amélineau F., Boureau M., Cristofari R., Courtecuisse J., Marpaux S., Morinay J., Tellier P., Le Maho Y. & Le Bohec C. Behavioural consistency on land and at sea in a territorial Antarctic seabird, the Adélie penguin. ***In prep. 3***

Cornet C.C., Courtecuisse J., Marpaux S., Tellier P., Chatelain N., Le Maho Y & Le Bohec C., Impact of sea ice on the breeding phenology and performances of Adélie penguins. ***In prep. 4***

Cornet C.C., Saraux C., Courtecuisse J., Marpaux S., Tellier P., Chatelain N., Le Maho Y. & Le Bohec C. Age-specific return rates and survival in unbanded Adélie penguins. ***In prep. 5***

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Cornet C.C., Descamps S., Bourgeon S., Fluhr J., Jolicoeur L., Labbé-Gigère S., Ludkin R., Vieweg I., Le Maho Y. & Le Bohec C. (2013, April). *Variability in personality traits in a long lived seabird : the Brünnich's guillemot*. Poster presented at the 9th Ecology & Behaviour colloquium, Strasbourg, France.

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Chapter I – General Introduction

Chapitre I – Introduction Générale

1 – Variation in life-history traits and phenotypic traits

Life-history theory aims to explain and understand the evolutionary mechanisms that shape organisms in order to insure their survival and reproduction (Stearns, 1992). That is to say, it seeks to identify and analyse the causes of variability in individual fitness[1] among life-history traits and interactions between these traits. Life-history traits are defined as demographical characteristics (e.g. fecundity, age at sexual maturity, length of reproductive life, number and size of offspring) that allow to describe the life cycle of an individual. Phenotypic traits are then defined as the observable and quantifiable traits, i.e. morphological, physiological, and behavioural characteristics (e.g. dispersion ability, territoriality, foraging strategies, anti-predators behaviours), contributing to the production and survival of descendants, and thus linked to fitness of the individuals. Together they constitute the phenotype of an individual that is likely to be impacted by the environment (Figure I - 1).

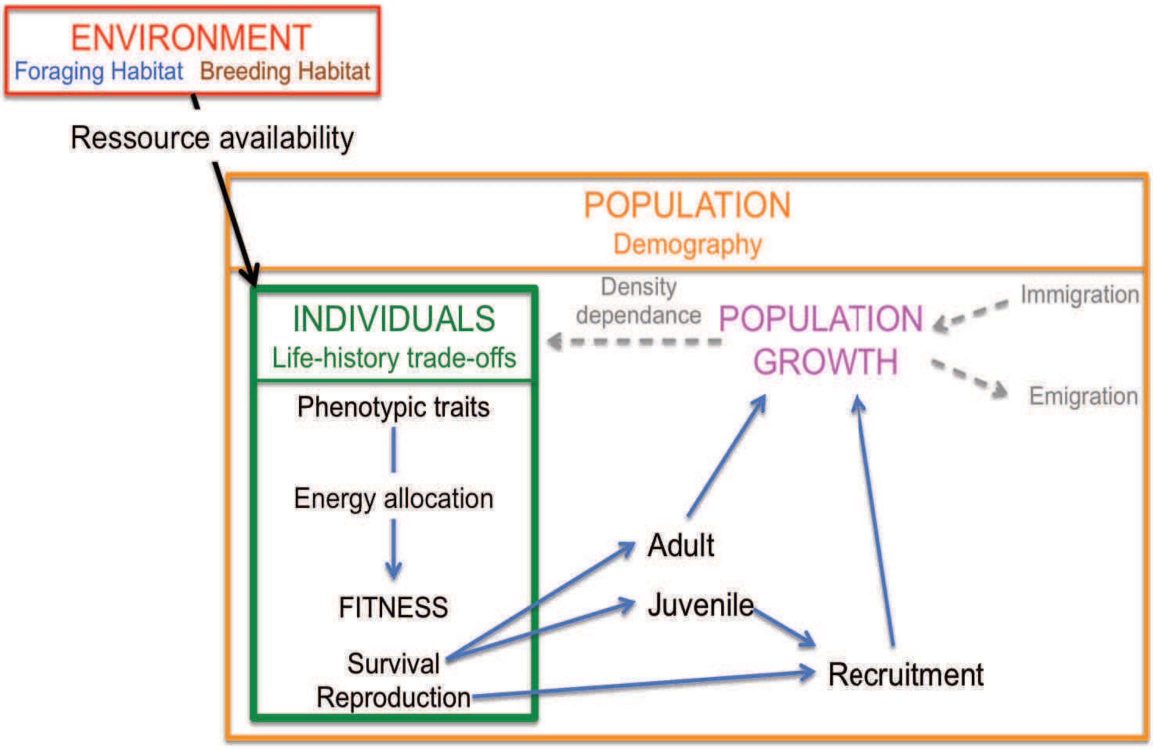

Figure I - 1. Illustration of population dynamics under environmental constraints.

Figure I - 1. *Schématisation de la dynamique de population sous contraintes environnementales.*

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[1] *Fitness*: the ability of an individual to propagate its gene pool to the population through future generations. (Stearns, 1992)

Variability in phenotypic and life-history traits, which can be observed at different biological scales (individual, population, species or biological group), is believed to arise from two different main types of constraints and the interactions between those constraints:

- the environment (and its variability), such as resources (e.g. habitat, food) and their abundance, distribution and temporality, and its abiotic (e.g. climate) and biotic parameters (e.g. competition, predation, parasitism).
- the individual intrinsic constraints, such as size, morphology, growth or development.

These different types of constraints will determine how organisms will allocate their energy between their main functions, such as survival, reproduction and growth throughout their lifespan, and thus shape their life-history (Levins, 1968; Roff, 1992; Stearns, 1992). The co-evolution of life-history traits under these constraints should optimise individual fitness over their lifespan, that is to say their ability to spread their gene pool to future generations (Williams, 1966; Roff, 1992; Stearns, 1992). These constraints also prevent organisms to achieve a 'perfect' fitness and turn into a 'Darwinian demon' (an immortal creature reproducing indefinitely as soon as born without any costs; Law, 1979), resulting in a wide variety of life-history strategies[2] under adaptive trade-offs (Stearns, 1992).

Life-history strategies spread over a continuous gradient, that have been called the 'r-K' gradient (Pianka, 1970), or the 'slow-fast' gradient (Western, 1979; Stearns, 1983; Gaillard et al., 1989), or the 'highly productive – survivor' continuum in birds (Sæther and Bakke, 2000). At the 'r' or 'fast' end of the gradient, species are defined by an early maturity, many small offspring, a short reproductive life and large reproductive effort, while at the 'K' or 'slow' end of the gradient, species are defined by a late maturity, a few and large offspring, a long reproductive life and small reproductive efforts (Stearns, 1976). Population dynamics of fast species, also called short-lived species, should then be more sensitive to variations in fecundity and age at first reproduction, whereas population growth of slow species, also called long-lived species, should be more sensitive to adult survival (Oli and Dobson, 2003; Gaillard et al., 2005; Oli and Dobson, 2005; Stahl and Oli, 2006). As natural selection should shape organisms to optimise their fitness, it should also select for a higher stability in traits contributing the most to the selective value of organisms and populations growth rates such as adult survival in long-lived species or age at maturity in short-lived species (Pfister, 1998;

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[2] *Life-history strategies:* "refers to the coordinated evolution of all the life-history traits together" (Stearns, 1992)

'canalization hypothesis' of Gaillard and Yoccoz, 2003). Accordingly, traits contributing less to population dynamics such as juvenile survival and fecundity in long-lived species or adult survival in short-lived species should be more likely to vary and to be sensitive to variations in environmental conditions.

2 – The role of heterogeneity within populations

Many different mechanisms can allow individuals and populations to cope with changes in their environment and to optimise their fitness components accordingly. Heterogeneity is one of them. Indeed, since Darwin's time it is known that heterogeneity is the substrate on which selection can act, and that allows for adaptation and evolution (Stearns, 1992). Mechanisms underlying this heterogeneity are numerous. First, at the within-individual scale, labile traits[3] can be adjusted to environmental changes in the limits tolerated by the phenotype of an individual. These individual adjustments and their amplitude in response to environmental changes will be responsible for the dynamic component of among-individual heterogeneity. On the other hand, genetic variability that fixes differences at birth, and environmental effects that fixes differences in early-life stages will be responsible for the static component of among-individual heterogeneity. Heterogeneity could, thus, also be seen as the result of selection that acted in the past. Identifying the different types of heterogeneity in wild populations will give us insights for a better understanding of the evolutionary mechanisms shaping the life history of organisms, and how populations could be able to cope with environmental changes in the future.

a) Phenotypic plasticity

An individual with a genotype might display different phenotypes according to the changes in the environment it will encounter during its life. This phenomenon is called phenotypic plasticity (Scheiner, 1993; DeWitt et al., 1998; Gienapp et al., 2008; Visser, 2008). Indeed, even if partially genetically determined a phenotypic trait such as behavioural traits remain labile and is thus likely to be influenced by the environment. Variance in a phenotypic trait thus comes from differences in the genetic structure (G), the environment (E)

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[3] *Labile traits:* "traits that are expressed repeatedly (and typically differently) during an individual's lifetime". (Brommer, 2013)

and the interaction between the two (GxE) (Nussey et al., 2007). The reaction norm, thus, represents the set of phenotypes expressed by a genotype exposed to different environments, which slope and elevation will vary according to the relative importance of variance components (Via et al., 1995; Nussey et al., 2007; Brommer, 2013; Figure I - 2).

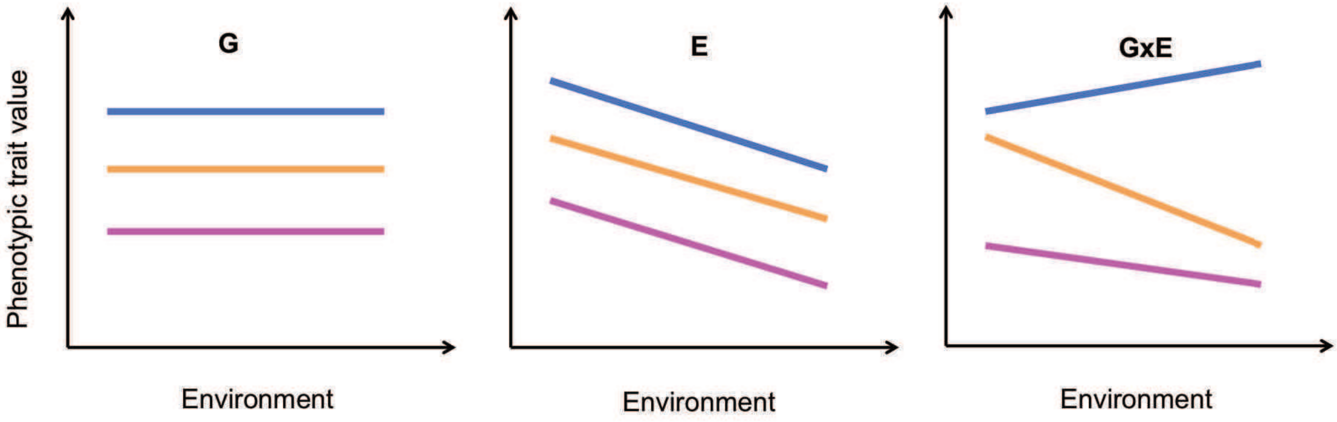

Figure I - 2. Illustration of the reaction norm concept according to the relative importance of the different variance components of a phenotypic trait. Each line represents the reaction norm of a genotype.

Figure I - 2. *Illustration du concept de la norme de réaction en fonction de l'importance relative des différentes composantes de la variance d'un trait phénotypique. Chaque trait représente la norme de réaction d'un génotype.*

Piersma and Drent (2003) described 4 types of phenotypic plasticity (Table I - 1):

- *developmental plasticity*: an irreversible change in the phenotypic traits under the environmental conditions (including parental effects) experienced during the developmental stages (Schlichting and Pigliucci, 1998).
- *polyphenism*: the ability of organisms to produce successive generations with different and discrete phenotypes across a season to adjust to seasonal changes in environmental conditions (Shapiro, 1976; Danks, 1999).
- *phenotypic flexibility*: phenotypic reversible and continuous adjustments in adult organisms in response to environmental changes (Piersma and Lindstrom, 1997).
- *life-cycle staging or cyclic phenotypic variation*: changes in phenotypic traits in relation to external cyclic and predictable environmental changes (Jacobs and Wingfield, 2000; Ricklefs and Wikelski, 2002). It can be considered as a subcategory of phenotypic flexibility.

Such individual adjustments and the extent of these adjustments could enable a whole population to track closely a rapidly changing environment without the immediate necessity of genetic adaptation (Nussey et al., 2007; Charmantier et al., 2008; Grémillet and Charmantier, 2010). For instance, phenotypic plasticity was responsible for part of the adaptive advancement in the phenology in different populations of great tits (*Parus major*) in Great Britain (Charmantier et al., 2008), red deers (*Cervus elaphus*) in Scotland (Moyes et al., 2011), red squirrels (*Sciurus vulgaris*) in Canada (Réale et al., 2003) and common gulls (*Larus canus*) in Estonia (Brommer et al., 2008).

Table I - 1. From Piersma and Drent (2003). Definitions of the 4 different types of phenotypic plasticity historically used.
Tableau I - 1. *D'après Piersma et Drent (2003). Définitions des 4 différentes catégories de plasticité historiquement utilisées.*

Plasticity categories	**Reversible change**	**Intra-individual variability**	**Seasonally cyclic change**
Developmental plasticity	×	×	×
Polyphenism	×	×	✓
Phenotypic flexibility	✓	✓	×
Life-cycle staging	✓	✓	✓

✓ = yes, × = no.

b) Among-individual heterogeneity

A single population of a species can inhabit a heterogeneous natural environment with diverse and varying pressures allowing for more than one way to adaptively reproduce and survive, and differences among individuals could thus be explained as being the product of natural selection[4] (Wilson, 1998). However, among individual heterogeneity could also be considered as the basis on which natural selection works (Stearns, 1992). Individual quality is generally viewed as a property of a phenotype positively correlated to fitness (Wilson and Nussey, 2010). Consequently, heterogeneity observed among individuals could be explained by the heterogeneity in individual quality and in environmental quality.

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[4] *Natural selection:* "process that results in an adaptation of an organism to its environment by means of selectively reproducing changes in its genotype or genetic constitution". (Encyclopedia Britannica)

b-1) Heterogeneity in individual quality

Individuals differ in their intrinsic capacities to survive and reproduce (Partridge and Harvey, 1988; Pettifor et al., 1988; Pettifor et al., 2001). The quantity of energy acquired by an individual for its survival and reproduction will depend on the quantity of resources available in the natural environment, but also on the capacities of this individual to acquire these resources by using the information on its environment (Van Noordwijk and de Jong, 1986). These differences in individual capacities have a static component, meaning that they can be fixed at birth by genetic variations or in early life stages by environmental conditions and maternal effects (Wilson and Nussey, 2010). This will define the average selective value of an individual over its lifespan. However, individual heterogeneity in these capacities can also be dynamically generated by stochastic (probabilistic) variations of fitness components (Ozgul et al., 2009; Tuljapurkar et al., 2009). Indeed, the succession of decisions made by an individual across its lifespan in order to optimise its selective value, and which constitutes its life-history, depends on the 'state' or 'condition' of this individual at the time these decisions are made. This way, the state or condition of an individual can vary according to its age, experience and quality[5], and is, of course, dependant on environmental conditions and their variability. This dynamic component will allow an individual to significantly differ in its selective value from the population mean value at instant *t*, while still significantly differ in the opposite direction from the population mean value across its lifespan. Static and dynamic aspects of individual quality or condition are thus non-exclusive.

b-2) Heterogeneity in habitat quality

The heterogeneity in the quality of the habitat can explain the heterogeneity in the structure of a population in terms of individual quality. Indeed, the characteristics of the habitat that will define its quality will also determine the selective pressures and constraints exerting on individuals such as predation (Martin, 1992; Regehr et al., 1998), competition (Ens et al., 1995), parasitism (Danchin and Wagner, 1997; Gaston et al., 2002), exposure to the elements (Stokes and Boersma, 1998; Danchin et al., 2005), or access to other resource (Crowder and Cooper, 1982). These characteristics vary both spatially and temporally (Danchin et al., 2005) and will thus generate dynamic heterogeneity. In such an

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[5] *Quality:* "an axis of among individual heterogeneity that is positively correlated with fitness". (Wilson and Nussey, 2010)

heterogeneous environment, all individuals will not have access to habitat of equal quality. The quality of an individual might then facilitate its access to, and the monopolisation of, a habitat of good quality, that will in turn enhance the quality of the individual and its performances (Coulson, 1968). Indeed, habitat is also considered as a resource, hence the accession to this resource will depends on the capacities of individuals to access information on this resource, in order to select the habitat that will be the most likely to maximise their fitness (Danchin et al., 2005).

b-3) Another source of inter-individual heterogeneity in populations

Age of individuals can be another important source of heterogeneity in populations, and this is especially true for long-lived species (Nelson, 1988). Indeed, a population can be structured in ‘cohorts’, that is to say groups of individuals born at distinct periods. As we saw previously, biotic and abiotic conditions during early-life stages can have long-term effects on individual quality and thus on life-history traits of individuals (Gaillard et al., 1997; Gaillard and Yoccoz, 2003). This cohort effect can then importantly impact the population dynamic of a population (Lindström and Kokko, 2002), and explain the heterogeneity observed in this population. Populations can also be structured in age classes. Then if a specific phenotypic value is associated with each particular class, this structuration can also explain the differences observed in the population. Moreover, individuals of bad quality should disappear faster of the population (Curio, 1983; Forslund and Pärt, 1995; Nisbet, 2001; Mauck et al., 2004) leading to a higher proportion of good quality individuals in ‘older’ age classes. This ‘intra-cohort’ selection can thus enhance the differences observed in the population (Cam et al., 2002). However, the senescence processes might also affect the performances of individuals, which could decrease from a certain age (Ricklefs, 1998; Reznick et al., 2004; Nussey et al., 2006; McCleery et al., 2008).

3 – Animal personality

a) Definitions and interest in the concept

Contrary to what has been traditionally hypothesised, behaviour is not fully plastic (West-Eberhard, 1989) and animals often exhibit consistent behavioural patterns over time and/or across situations and contexts. This structuration in the behaviour of an individual has been called personality or temperament (Gosling, 2001; Réale et al., 2007), or behavioural syndrome when personality or temperament traits are correlated (Sih et al., 2004a). This concept does not require that individuals are completely consistent in their behaviour, indeed it is highly likely that the behaviour of an individual will vary over time according to endogenous and exogenous parameters such as age, experience, body reserves or environmental variability. However, it requires that differences among individuals are consistent over time and/or across situations (Réale et al., 2007; Dingemanse et al., 2010; Figure I - 3). In order to provide a common framework for animal personality studies, Réale *et al.* (2007) defined 5 personality axes, which define the behavioural type of an individual along a continuous gradient of trait values:

- *shyness/boldness*: describe the reaction of an individual toward a threatening situation such as a predator, and should exclude novelty.
- *exploration/avoidance*: describe the reaction of an individual facing a novel situation in terms of habitat or food for instance, and should exclude dangerousness.
- *activity*: describe the basal level of activity of an individual and can be measured in different situations.
- *aggressiveness*: describe the agonistic reaction of an individual toward a conspecific.
- *sociability*: describe the reaction of an individual to the presence or the absence of conspecifics.

Other behavioural tendencies have been described such as dispersal tendency, impulsivity, docility or responsiveness to an environmental stimulus, even if some of them were potentially related to the ones we have just described above. Furthermore, evidence of the existence of personality and behavioural syndromes have been accumulating in a wide ranges of species from mammals (e.g. Martin and Réale, 2008; Michelena et al., 2010; Twiss and Franklin, 2010), to birds (e.g.Dingemanse et al., 2003; Kontiainen et al., 2009; David et al., 2011; Patrick et al., 2013), reptiles (Stapley, 2006), fish (e.g. Godin and Dugatkin, 1996; Biro and Stamps, 2008; Cote et al., 2010; Wilson et al., 2010), amphibians (Sih et al., 2003), arthropods (e.g. Kortet and Hedrick, 2007; Pinter-Wollman et al., 2012), and cnidarians (Briffa and Greenaway, 2011). This ubiquity of personality in the animal kingdom provides a unique opportunity to unravel the processes that led to its evolution through inter-species comparisons of its functional differences and similitudes.

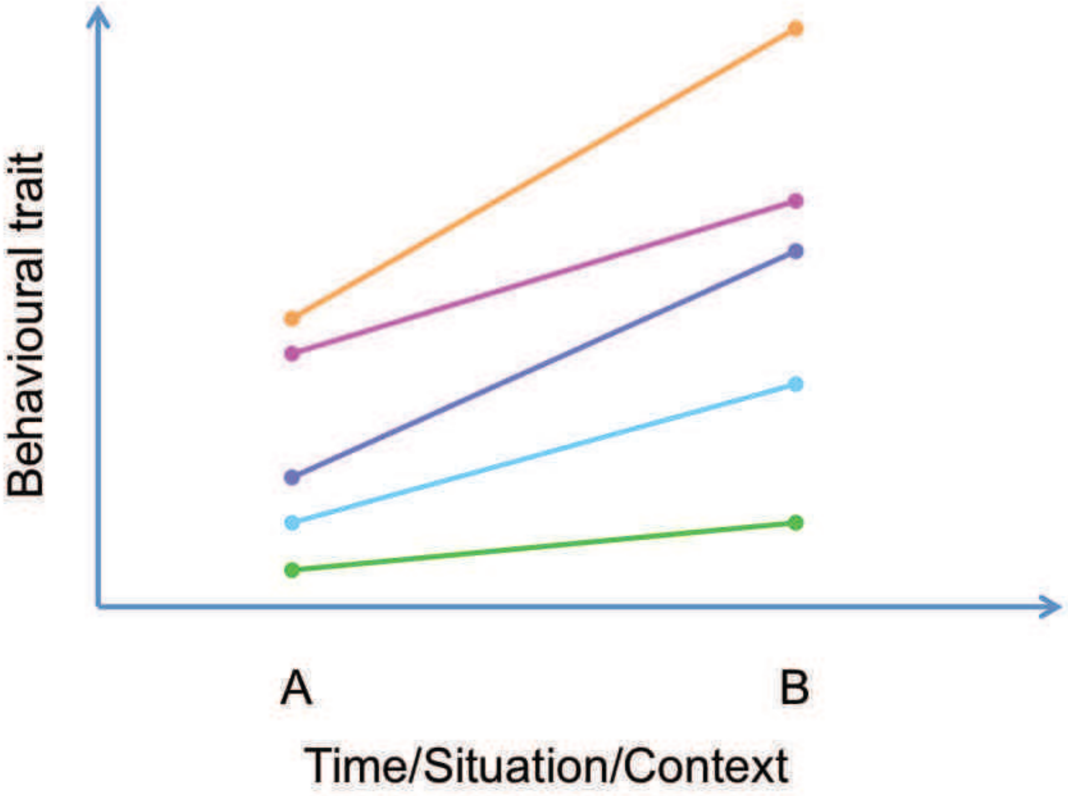

Figure I - 3. Illustration of the concept of personality from the reaction norm point of view (each line represent an individual reaction norm). It shows that if the value of an individual's trait can vary over time or across situations or contexts, the behavioural differences between individuals of the population are maintained.

***Figure I - 3.** Illustration du concept de personnalité du point de vue de la norme de réaction (chaque ligne représente la norme de réaction d'un individu). Cela montre que si la valeur du trait de personnalité d'un individu peut varier au cours du temps ou au travers des contextes ou des situations, les différences comportementales entre les individus de la population sont maintenues.*

Another interest in studying personality lies in its correlation with other traits and biodemographic strategies. Indeed, these correlations could help us explain inter-individual variations observed in other traits and therefore understand inter-individual variation studied in more common behavioural field such as foraging strategies for instance (Kurvers et al., 2010a; Patrick and Weimerskirch, 2014). Furthermore, from these correlations, we would be able to predict individuals' decisions (Dingemanse et al., 2003; Cote et al., 2010; Jones and Godin, 2010). In addition, the correlation between personality traits, and between personality traits and other traits suggest constraints and co-evolution between these traits (Sih et al., 2004a; Sih et al., 2004b; Réale et al., 2010b; Niemelä et al., 2013) and emphasize the need for an integrative approach of animals' behaviour.

The existence of such structuration in the behaviour of animals has multiple evolutionary and ecological implications (reviewed in Wolf and Weissing, 2012). For instance, the existence of personality implies the existence of inter-individual heterogeneity in behavioural phenotypes, and the existence of different behavioural phenotypes in a population could favour its persistence. Indeed, the existence of different behavioural types in a population increases the chances that the behavioural phenotype the most able to cope with the new environmental conditions already exists in the population ('insurance effect', McCann, 2000). Furthermore, the correlation between behavioural phenotypes and fitness components confer to personality an adaptive potential for individuals and populations and could even speed up evolution if heterogeneity in phenotypes is underpinned by heterogeneity in genotypes (Barrett and Schluter, 2008). On the other hand, correlations between behavioural traits, and between behavioural traits and other traits imply constraints between them that could slow down adaptive evolution. Indeed, if the correlation between these traits cannot be broken easily (because it implies common neurophysiological or genetic basis for instance), and if strong opposite directional selection pressures are exerted on the correlated traits, such correlation would prevent individuals to reach an optimal fitness and therefore retard their adaptive evolution (Arnold, 1992; Sih et al., 2004a). The correlation between personality traits, and between personality traits and other traits could also have implications for the evolvability of the population. Indeed, these correlation could also implies that the correlation between this set of traits have been selected for in the past because it helped to solve an ecological problem and it is likely that it could also help to solve the new ecological challenge generated by environmental changes. In such case, adaptive evolution could occur faster, as the right set of traits already exists in the population and co-vary in a systematic way (Wagner and Altenberg, 1996). Finally, the correlation between personality traits and life-history traits in particular, could have implications for the population dynamics, as it would have cumulative effects on fitness (Wolf et al., 2007; Réale et al., 2010b).

b) Evolution of personality

The concept of personality implies constraints on the flexibility of an individual's behaviour as well as the co-existence of different behavioural phenotypes within a population.

As we already saw, the behaviour of an individual has been traditionally seen as fully plastic and therefore the first and easiest way for an individual to optimally adapt to its environment (West-Eberhard, 1989). Furthermore, natural selection should favour the behavioural phenotype with the highest fitness, and other behavioural phenotypes should disappear from the population. In this context, the existence of personality itself is puzzling and questions arise about its emergence and maintenance.

Different hypotheses have been proposed to explain its evolution. First, personality traits files for the three conditions for natural selection to happened, that is to say inter-individual variability (the basis of personality), a link with fitness (e.g. Boon et al., 2008; Kontiainen et al., 2009; Dammhahn, 2012), and a relatively moderate heritability (e.g. Réale et al., 2000; van Oers et al., 2004b). Consequently, varying antagonistic selective pressures associated with spatial and temporal environmental heterogeneity could provide an explanation to the maintenance of different behavioural phenotypes within a population (e.g. Dingemanse et al., 2004). Antagonistic selection could also happen according to the sex of individuals (e.g. Chippindale et al., 2001). Frequency-dependent selection is another mechanism that could explain the maintenance of inter-individual variation in behavioural types when the fitness associated with a behavioural type depends on the frequency of the other behavioural types in the population (Maynard Smith, 1982). Furthermore, if two set of behavioural type (i.e. two combinations of values of two personality traits) have the same fitness value, correlational selection would be another mechanism to explain the existence of personality (Sinervo and Svensson, 2002). Finally, if personality is correlated to life-history strategies has it has been suggested otherwise (Réale et al., 2010b; Niemelä et al., 2013), it could have then co-evolved with it through energy allocation trade offs (Wolf et al., 2007; Biro and Stamps, 2008; Dammhahn, 2012). Many different theories have been proposed so to explain the evolution of personality. Yet only a few of them have been tested until now (see Dingemanse and Réale, 2013) and we still have a lot to discover to understand the existence of personality and how it could help individuals and populations to adapt to their environment.

4 – Environmental context

a) Climate change

The Intergovernmental Panel on Climate Change has defined the climate change as '*a change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forcings such as modulations of the solar cycles, volcanic eruptions and persistent anthropogenic changes in the composition of the atmosphere or in land use.*'. The distinction between 'non-anthropogenic' sources and 'anthropogenic' sources of these changes is important. Indeed, changes (mostly cyclic) in the climate of the Earth have always existed, for instance alternating since the Precambrian between glacial periods where ice covered significant parts of the Earth and temperature were colder and interglacial periods where ice retreated to the poles and temperatures became warmer. However since the beginning of the industrial era at the end of the 19th century, the changes observed in the Earth's climate and the rate of these changes seems far from natural. According to the IPCC (5th Annual Report, 2013; Figure I - 4): '*Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia. The atmosphere and ocean have warmed, the amounts of snow and ice have diminished, sea level has risen, and the concentrations of greenhouse gases have increased*'. They even say that the '*evidence for human influence has grown since [the 4th Annual Report]. It is extremely likely that human influence has been the dominant cause of the observed warming since the mid-20th century.*' Indeed, the concentration of carbon dioxide have increased of about 40% since the beginning of the industrial era which is unprecedented in the last 800 000 years (Figure I - 5). This increase has largely contributed to a change in the energy balance of the Earth leading to an uptake of energy by its climate system.

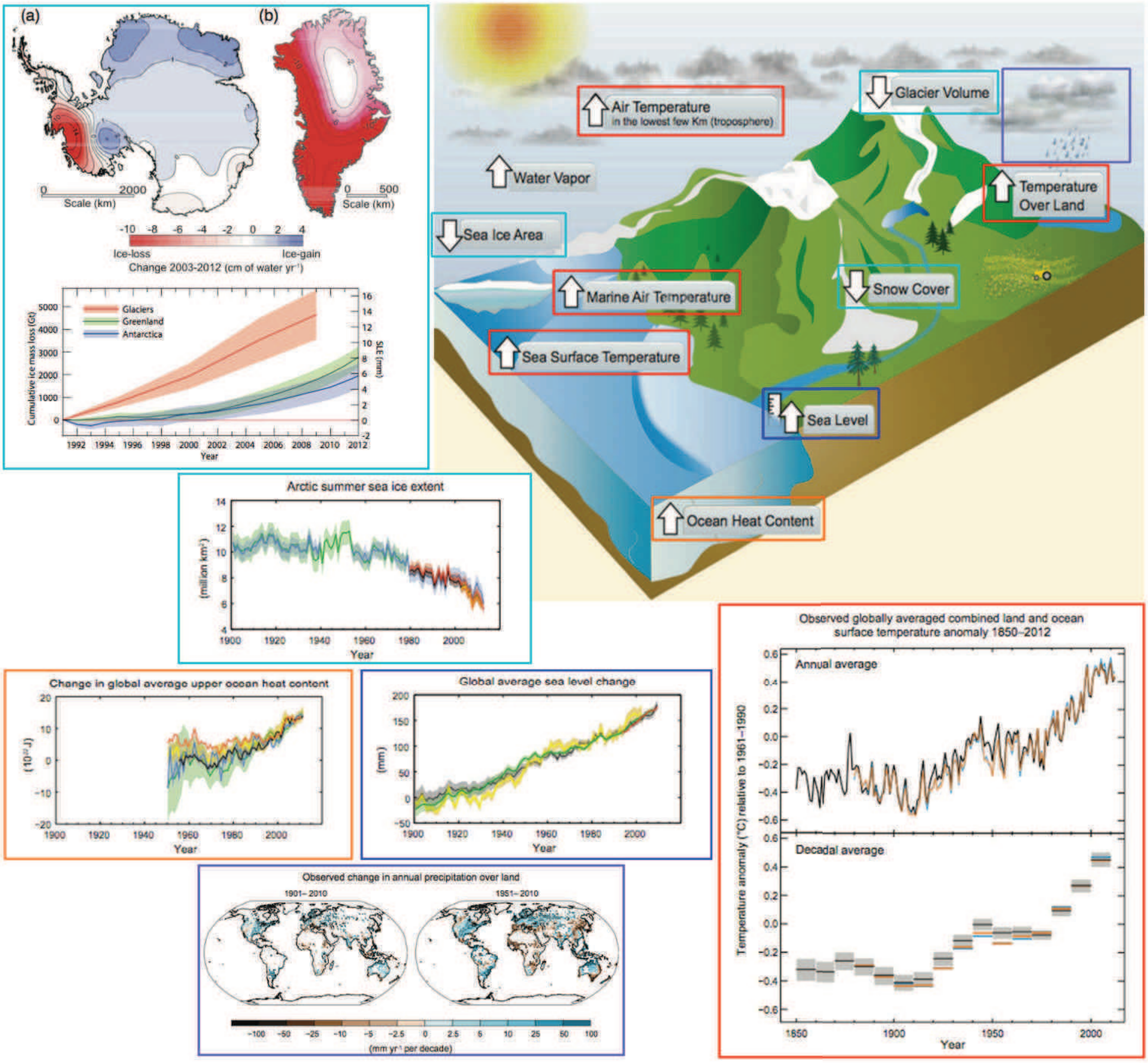

Figure I - 4. Climate changes observed since the beginning of the industrial era. Adapted from the 5th Annual Report of the IPCC (2013).

Figure I - 4. Changements climatiques observés depuis le début de l'ère industrielle. Adapté du 5ème Rapport Annuel de l'IPCC (2013).

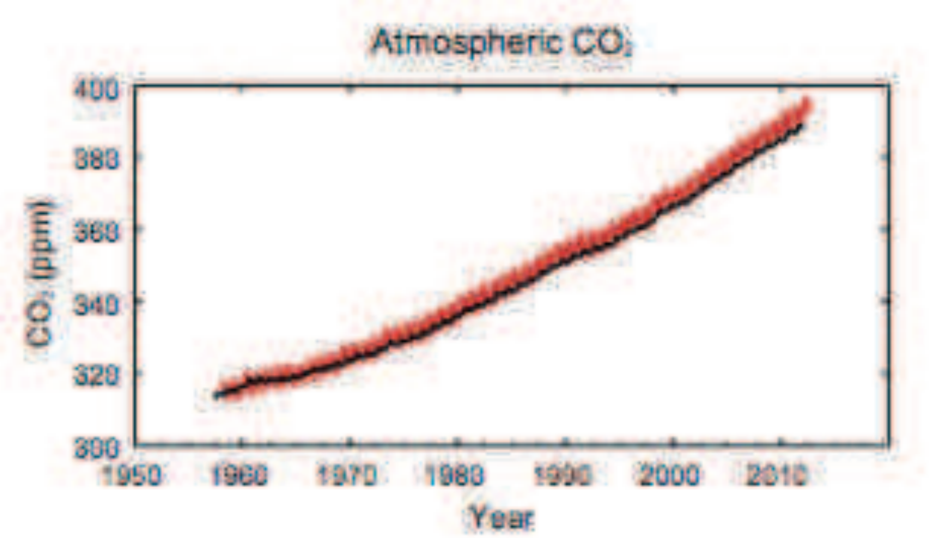

Figure I - 5. Atmospheric concentration of carbon dioxide at Mauna Loa (19°32'N 155°34'W, in red) and at the South Pole (89°59'S 24°48'W, in dark) since 1950. (IPCC, 2013).

***Figure I - 5.** Concentration atmosphérique en dioxyde de carbone à Mauna Loa (19°32'N 155°34'W, en rouge) et au Pôle Sud (89°59'S 24°48'W, en noir) depuis 1950. (IPCC, 2013).*

Despite the proven impact of anthropogenic activities, the geopolitical context of our modern societies makes it unlikely that the emission of greenhouse gas will decrease soon. Actually, it is highly probable that emission of greenhouse gas will continue to increase (IPCC, 2013). Even if difficult to elaborate, predictive models all agreed however that no matter the scenario (according to world population and economic growth, and the introduction of new technologies using or not fossil energy), the 21th century will be characterised by an increase in global mean surface temperature, a shift in wind and precipitations regimes, a strong reduction of arctic sea-ice extent and an increase in the frequency and amplitude of extreme weather and climatic events (Meehl et al., 2007). These previsions are getting even more pessimistic with the 5th Annual Report of the IPCC (Collins et al., 2013, Figure I - 6).

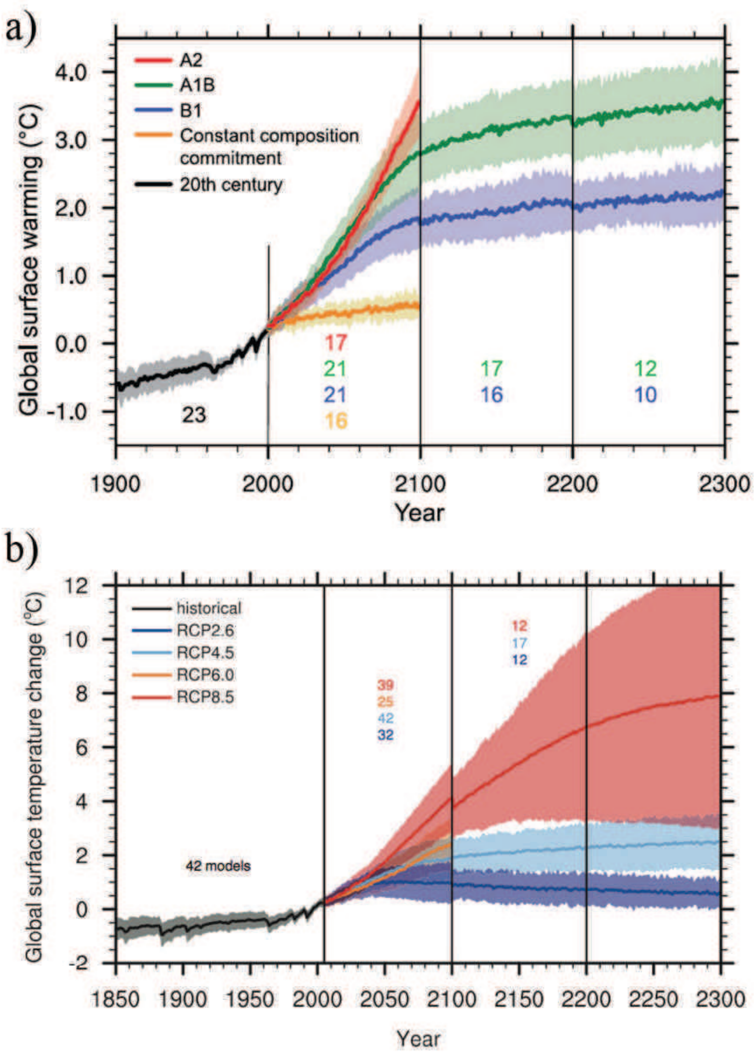

Figure I - 6. After Meehl et al. (2007) and Collins et al. (2013). Global warming projections according to different scenarios proposed by the IPCC in its 4th Annual Report (a) and 5th Annual Report (b). Multi-models means are represented by continuous lines (standard deviation as a shadow) and figures indicate the number of models used for each scenarios and time period.

Figure I - 6. *D'après Meehl et al. (2007) and Collins et al. (2013). Réchauffement global projeté selon différents scénarios proposés par l'IPCC dans son* $4^{\text{ème}}$ *rapport annuel (a) et dans son* $5^{\text{ème}}$ *rapport (b). Les moyennes multi-modèles sont présentées en lignes continues (l'écart-type en ombré) et les chiffres indiquent le nombre de modèles utilisés pour chaque scénarios et chaque période de temps.*

b) The impact of climate on organisms

Human activities and climate changes they induce are numerous; it is therefore difficult to disentangle their impact on ecosystems and populations (Parmesan and Yohe, 2003). Indeed, mechanisms involved in the response of organisms to these changes are complex since they happen at different time scales and biological components. The study of these mechanisms thus requires long-term datasets of numerous biotic and abiotic parameters.

Despite this difficulty numerous studies have already highlighted the widespread influence of climate changes in different biological compartments, from changes in the physiology and the phenology of individuals, to modification in the abundance and distribution of species, as well as in their interactions and the structure and composition of the communities they form (e.g. Hughes, 2000; McCarty, 2001; Stenseth and Mysterud, 2002; Walther et al., 2002; Parmesan, 2006; Brommer et al., 2008; Charmantier et al., 2008). While other studies have shown that local environmental conditions and large-scale climatic oscillations influenced ecological and population processes (Schreiber, 2001; Stenseth et al., 2002; Stenseth et al., 2004) with particularly preoccupying impacts on marine ecosystems (Ottersen et al., 2001; Trathan et al., 2007; Bollens et al., 2011; Descamps et al., 2013).

The ecological effects of environmental changes can be classified in 3 categories:

- *direct effects*: direct ecological response to changes in an environmental parameter such as the temperature, precipitations or atmospheric composition. Mostly impact the physiology of organisms through metabolism and reproductive processes (Pörtner and Farrell, 2008).
- *indirect effects:* ecological response to changes in environmental parameters that involves mechanisms at several levels of physical and biological processes. Impact mostly through habitat and other resources, and repercussions through trophic webs (McCarty, 2001; Stenseth et al., 2002).
- *integrated effects*: ecological response to changes in environmental parameters with a time lag. As for indirect effects, impact either through physical processes (physical inertia), or through ecological mechanisms (adverse conditions during early life-stages might affect accession to reproduction in long-lived species for instance; Gaillard et al., 1997; Lindström, 1999) but with a temporal component.

c) The case of polar marine ecosystems

Marine polar ecosystems are among the most productive ecosystems of the world mainly as a result of short, intensive spring phytoplankton blooms (Tynan, 1998; Smetacek and Nicol, 2005). If the interactions between the topography, the hydrography and ice covers dynamic drive the structure and dynamic of these ecosystems, the main processes leading to their short but highly productive events differ between the two poles. Indeed, the Arctic marine arctic ecosystem is characterised by a land–lock ocean surrounded by extensive shallow shelf seas (~50% of the total area, Sakshaug and Walsh, 2000). The strong stratification of the Arctic water masses prevents the admixture of deep nutrient-rich waters. The melting of the sea-ice over shallow shelves is then the main nutrient input, also enriching the surface layer in iron, the light becoming the only factor limiting the productivity (Smetacek and Nicol, 2005). Where the Arctic Ocean meets with the Atlantic and the Pacific Oceans, processes allowing a high productivity are slightly different. On the Pacific side, nutrient-rich but iron-poor waters coming from the deep Bering Sea flows into the Arctic Ocean through the Bering Strait where they meet its shallow iron-rich waters (Smetacek and Nicol, 2005). The admixture of these two water masses leads to one of the highest productivity in the world ocean (Sakshaug and Walsh, 2000). On the Atlantic side now, the Barents Sea is deeper and most of the primary productivity is maintained in the water column that is enrich in nutrients coming from the Norwegian Sea, sustaining an exceptionally high copepod biomass (Hassel, 1986; Hansen et al., 1996). The Antarctic marine ecosystem on the other hand is characterised by an open and dynamic ocean with by deep continental shelves. Indeed, the weight of the Antarctic ice cap presses over the continent pushing it down below the level of ice-free continents (Smetacek and Nicol, 2005). The Austral Ocean is also the ocean where the Atlantic, the Pacific and the Indian Oceans meet to form an annular water mass surrounding the continent. Under the influence of strong winds, this water mass flows from west to east forming the Antarctic Circumpolar Current. The Antarctic Circumpolar Current is in fact latitudinally segregated by discontinuities or hydrological fronts defining water masses with clear identifying physic-chemical properties (Belkin and Gordon, 1996; Park and Gamberoni, 1997; Figure I - 7). These hydrological structures allow for a mixing of different water masses, and thus enable the uprising of deep nutrient-rich waters to the encounter of iron-rich shallow waters leading to events of intense productivity in open waters. These shallow waters are enriched in iron and nutrients by the melting of sea ice to some extent and the upwelling of deep waters in coastal areas. Around islands, land sediments can also enrich the shallow waters of the coastal shelves, as it is the case in the Crozet Archipelago for instance (iron input from volcanic sediments, Planquette et al., 2009), allowing high productive events to occur in these areas too. This enhanced productivity in island shelves and in frontal zone in open waters of the Austral Ocean (Atkinson and Peck, 1990; Moore and Abbott, 2000; Pakhomov and Froneman, 2000) account for about 20% of the world total marine primary production (Tynan, 1998; Carr et al., 2006).

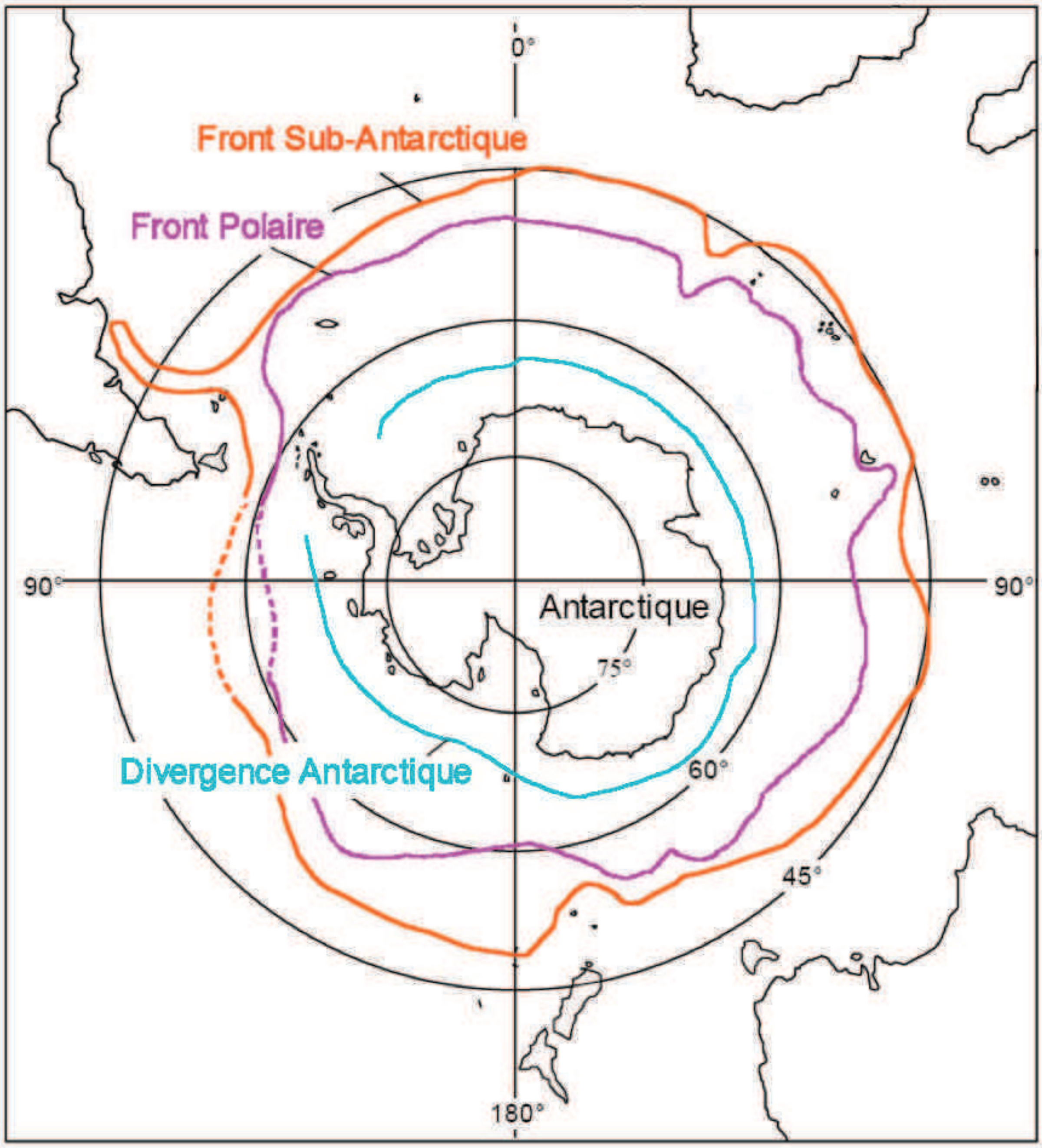

Figure I - 7. Illustration of the different hydrological fronts of the Southern Ocean, from Belkin and Gordon (1996), and Park and Gamberoni (1997).
Figure I - 7. *Illustration des différents fronts hydrologiques de l'Océan Austral d'après Belkin et Gordon (1996), et Park et Gamberoni (1997).*

The pace of changes in polar ecosystems is even greater than for other ecosystems (Clarke and Harris, 2003; Hoegh-Guldberg and Bruno, 2010; IPCC, 2013). In the Arctic, climate models indicate that the trend in surface air temperature and sea ice retreat in the past two decades is different than it would be if following natural cycles and that this difference is probably due to anthropogenic forcing (Johannessen et al., 2004). According to the IPCC 5th

Annual Report: '*the annual mean Arctic sea ice extent decreased over the period 1979 to 2012 with a rate that was very likely in the range 3.5 to 4.1% per decade (range of 0.45 to 0.51 million km2 per decade), and very likely in the range 9.4 to 13.6% per decade (range of 0.73 to 1.07 million km2 per decade) for the summer sea ice minimum (perennial sea ice)*' which is unprecedented. In the Antarctic, the ice sheets have been losing mass and glaciers are shrinking with an average annual ice loss rate for the 2002-2012 period about 5 times higher than it was for the 1992-2001 period (IPCC, 2013), but with regional variability since this loss seems to come mainly from the Antarctic peninsula (Vaughan et al., 2013). Since the productivity of these two ecosystems highly depend on ice in all its forms, they are very likely to be highly sensitive to on-going changes. Indeed, many species of these ecosystems have already been shown to be affected by these changes at all trophic levels, from phytoplankton and zooplankton (e.g. Reid et al., 1998; Hunt et al., 2001; Atkinson et al., 2004; Edwards and Richardson, 2004) to top marine predators (e.g. Croxall et al., 2002; Weimerskirch et al., 2003; Gaston et al., 2005; Jenouvrier et al., 2005; Irons et al., 2008; Gaston et al., 2009).

d) Seabirds as sentinels of their ecosystems

As top marine predators at the apex of the trophic web, seabirds integrate and magnify the variability occurring throughout this web making them good sentinels for their ecosystems (Croxall et al., 2002; Verity et al., 2002; Piatt et al., 2007; Parsons et al., 2008; Grémillet and Charmantier, 2010; Figure I - 8). Indeed, by this position downstream of the energy flow, any change occurring in the abundance and distribution of species at a low trophic level will have repercussion for the top-level species of the trophic web through 'Bottom-Up' and 'Wasp-Waist' control mechanisms involving energy trade-offs and foraging strategies (Bakun, 2006; Frederiksen et al., 2006; Staniland et al., 2006; Figure I - 9). Top-predators species can in turn influence low trophic levels through 'Top-Down' controls involving density-dependent mechanisms (Tamura, 2003; Baum and Worm, 2009; Figure I - 9).

Moreover, most seabird species are 'central-place foragers'. This means that even if they spent most of their time at sea, they still need to come back on land to reproduce and, therefore, that they are bound to forage in a certain perimeter around their breeding ground during the breeding season (Baird, 1991; Costa, 1991). Therefore, they are constrained to cover extended areas for their foraging needs. This is especially true for most polar seabird species, which might be able to forage close the their breeding colony to feed their chicks regularly but also have to forage far away from their breeding colony to replenish their body reserves in richer areas (e.g. Clarke et al., 1998; Baduini and Hyrenbach, 2003; Weimerskirch et al., 2003). In addition, as many of them are also long-lived and philopatric, they are easy to access and to monitor for long time periods.

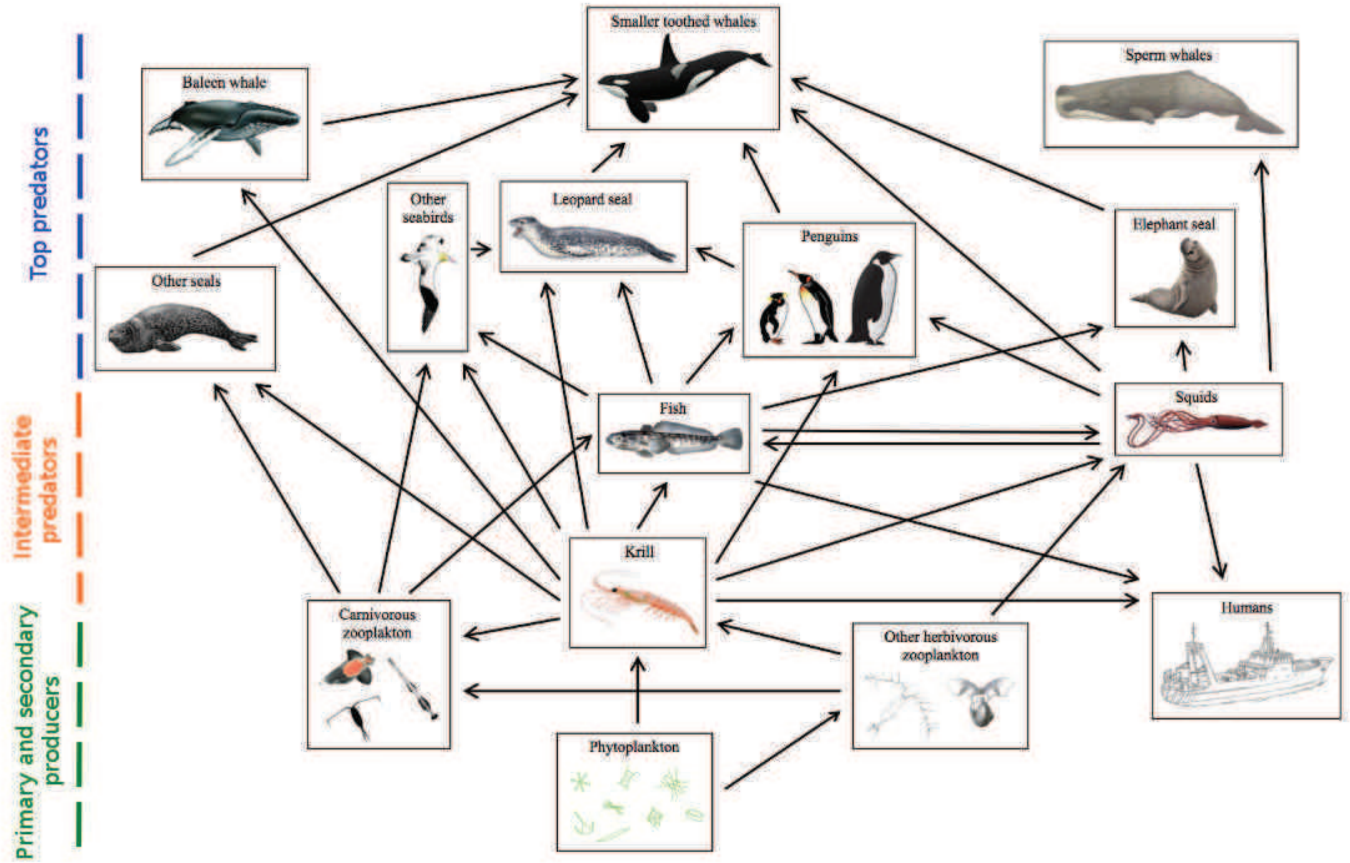

Figure I - 8. Illustration of a Southern Ocean trophic web. Adapted from http://www.discoveringantarctica.org.uk/alevel_3_3.html.

Figure I - 8. *Illustration d'un réseau trophic de l'Océan Austral. Adapté de http://www.discoveringantarctica.org.uk/alevel_3_3.html.*

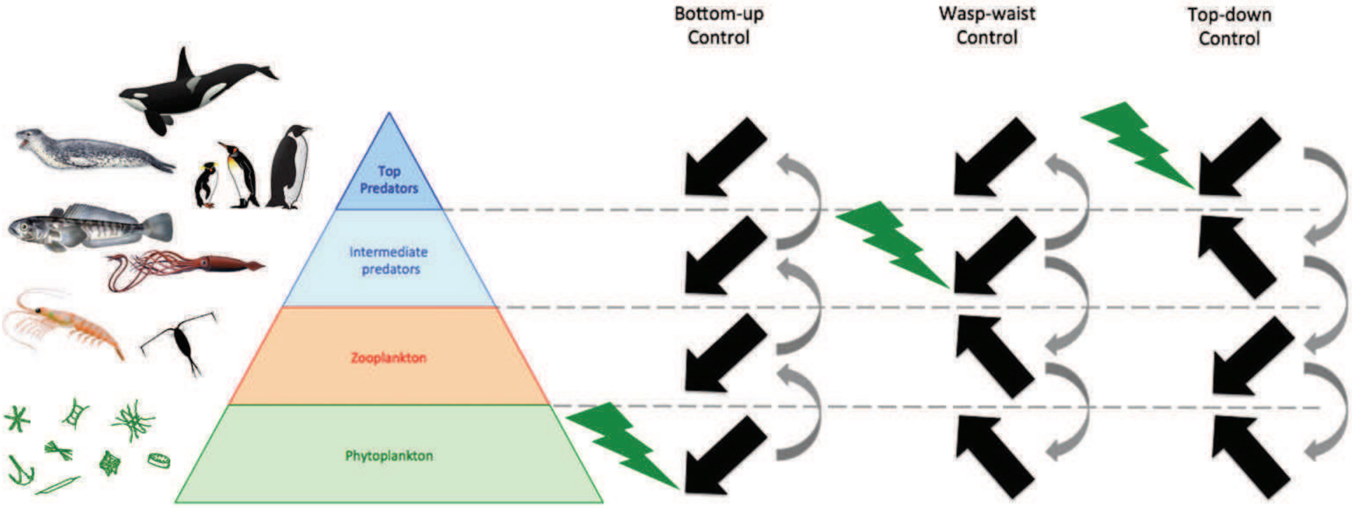

Figure I - 9. Regulating mechanisms of trophic webs. Green lightning bolts indicate a modification of the trophic level (for instance of its abundance) and dark arrows indicate the direction of this modification. Grey arrows indicate repercussions for the other trophic levels and dark arrow the direction of these repercussions.

***Figure I - 9.** Mécanismes régulant les réseaux trophiques. Les éclairs verts indiquent une modification de l'échelon trophique (par exemple de son abondance) et les flèches noires indiquent le sens de cette modification. Les flèches grises indiquent les répercussions pour les autres échelons trophiques et les flèches noires le sens de ces modifications.*

5 – Aims of this work

Identifying and understanding the mecanisms that could allow animal populations to readily adapt to changes in their environment is of crucial interest in the context of current global changes (IPCC, 2013). Because of their position at the apex of the trophic web, polar seabirds present good models to study the impact of these global changes on sensitive polar ecosystems (Piatt et al., 2007; Parsons et al., 2008), and to investigate the adaptive capacity of their populations to cope with these changes.

The adaptive potential of a population is defined as its capacity to respond to selective pressures with consequences for its fitness, i.e. its capacity to modify its phenotype. However, given the rapidity of climate changes we observe (IPCC, 2013), it is unlikely that micro-evolutionary processes, and let alone macro-evolutionary processes, could allow long-lived species to respond fast enough to these changes. During this PhD work we therefore decided to focus on phenotypic flexibility and plasticity as rapid mechanisms to cope with environmental changes. The adaptive potential of a population will then depend on the plastic potential of each of the individuals of this population, i.e. on the ability of each individual to modify its own phenotype in response to environmental pressures and on the amplitude of these responses (Railsback, 2001; Nussey et al., 2007).

In this context, the concept of personality, i.e. a relatively fixed architecture in the behaviour of an individual, implies both reduced flexibility of an individual's behaviour but also the existence of different behavioural types within a population (Sih et al., 2004a; Sih et al., 2004b; Réale et al., 2007; Dingemanse et al., 2010). Moreover, as personality influences the ecology of an individual (e.g. exploration and habitat use, (Duckworth, 2006); or aggressiveness and interaction with conspecifics, (Boyer et al., 2010)), it has potential consequences for individual fitness (Smith and Blumstein, 2008). Therefore the existence of personality within a population has implications for its adaptive potential.

Using three different seabird model species allowing us to explore different issues related to this concept, we therefore investigated:

i) the existence of personality in seabirds populations, i.e. we quantified within- and among-individual variability in relevant behavioural traits and assess their repeatability[6], (Chapter III, IV and V),

ii) the correlation between these personality traits and a fitness component, the breeding success (Chapter III and IV), in order to gauge if selective pressures were acting on personality traits, making them good candidate for adaptation in these seabirds populations.

iii) the origin of potential selective pressures acting on personality by studying its relationship with nesting habitat characteristics (Chapter III, IV and V).

iv) the relationship between personality and individual characteristics (i.e. sex, structural size, body condition and heart rate) to provide evidence for its biological validation (Chapter III, IV and V).

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[6] *Repeatability*: "a concept derived from quantitative genetics theory, it is a statistics that describes the degree to which variation among individuals contributes to total variation in a population". (Boake, 1989)

v) the existence of behavioural syndromes implying constraints between personality traits (Chapter III, IV and V). Furthermore we also explore correlation between traits measured in captivity and in a free natural environment to assess the ecological validity (Chapter IV).

vi) the correlation with other behavioural traits with strong and direct impact for the fitness of individuals through their implication in resource acquisition, i.e. foraging behaviours (Chapter V).

Furthermore the use of three different seabird species both exhibiting common and differing ecological features, and more particularly differing in their life-history strategies (see Table I - 2), provides a unique framework for inter-species comparison of these personality traits and get insights on their evolution (Chapter VI - 4).

Moreover, it has been proposed that personality traits could be incorporated to the pace of life syndrome of a population (Réale et al., 2010b; Niemelä et al., 2013), that is to say the set of physiological and behavioural parameters that have coevolved with the life-history traits of this population. The cumulative effects of personality on life history traits and on individual fitness could then have substantial consequences on the population dynamics. In this work we also consequently started to investigate the variability in life history traits of one of our study species, the Adélie penguin, in relation to environmental variability, in the future prospect of studying their correlation with personality traits and increase the power of our predictive models. In Chapter VII of this manuscript we present the first results of these investigations.

Table I - 2. Summary of the relevant ecological features of the three model species used during this work. Species are ordered from the left to the right according to their relative place on the 'slow-fast' gradient of life-history strategies.

***Tableau I - 2.** Récapitulatif des caractéristiques écologiques pertinentes des trois espèces modèles utilisées dans cette étude. Les espèces sont classées de gauche à droite en fonction de leur place relative sur le gradient 'lent-rapide' des stratégies d'histoire de vie.*

Ecological features	**Brunnich's guillemot**  ***Uria lomvia***	**Adélie penguins**  ***Pygoscelis adeliae***	**King penguins**  ***Aptenodytes patagonicus***
Colony density	High	High	High
Nesting site	Open	Open	Open
Minimal distance between two sites	0 cm	70 cm	50 cm
Nest building	No nest	Nest	No nest
Synchrony	High	High	Moderate
Mobility	Fix in space and time	Fix in space and time	Mobility in space and time
Incubation + Brooding length	*ca.* 56 days	*ca.* 56 days	*ca.* 75 days
Size	~ 40-45 cm	~ 70-75 cm	~ 85-95 cm
Slow/fast gradient	Fast Shorter life Earlier reproduction Higher growth rate	→	Slow Longer life Delayed reproduction Lower growth rate

Chapter II – Material and Methods

Chapitre II – Matériel et Méthodes

1 – Study sites

During this PhD, I studied 3 representative species of both Arctic and Antarctic ecosystems (Figure II - 1).

Figure II - 1. Localisation of the 3 study sites. © GoogleMap

Figure II - 1. *Localisation des 3 sites d'étude. © GoogleMap*

At two occasions, I spent 2 months studying the Brünnich's guillemot (*Uria lomvia*) in Svalbard in collaboration with the Norwegian Polar Insitute. I also went for one summer campaign of 3 months in Adélie Land to study Adélie penguins (*Pygoscelis adeliae*) and emperor penguins (*Aptenodytes forsteri*) as part of the programme 137 of the French Polar Institute Paul-Emile Victor (IPEV).

a) The Svalbard

Brünnich’s guillemots were studied at the Diabbasodden colony (78°21’N, 16°08’E) in the Isfjorden (Figure II - 2), on Spitzebergen, the main island of the Svalbard Archipelago, where about 850 000 pairs are breeding (S. Descamps, personal communication and http://www.npolar.no/no/arter/polarlomvi.html).

The Isfjorden is characterised by inter-annually changing oceanographic features, with significant inter-annual variability in the occupation of warmer Atlantic Water in the cold fjord system (Cottier et al., 2005; Nilsen et al., 2008). This leads to inter-annual changes in the trophic web, with « cold » years during which Atlantic waters do not come too deep in the fjord presenting with large and energy-rich food resources (Arnkværn et al., 2005), and « warm » years presenting with smaller and less energy-rich food. The shelf break also provides a rich feeding ground (Falk-Petersen et al., 2007), though the distance from the colony might be too long for foraging trips during chick rearing.

Figure II - 2. a) Localisation and b) illustration of the Diabassodden colony in the Isfjorden.

Figure II - 2. *a) Localisation et b) illustration de la colonie de Diabassodden dans l’Isfjorden.*

b) Possession Island, Crozet Archipelago

King penguins (*Aptenodytes patagonicus*) were studied at the colony called ‘La Grande Manchotière’ on the Possession Island (46°25’S, 51°45’E), the main of the five islands constituting the Crozet Archipelago, where about 25 000 pairs of king penguins are breeding (Figure II - 3). The study was conducted in a sub-part of ‘La Grand Manchotière’ colony called ‘ANTAVIA’, where about 10 000 pairs are breeding.

The Crozet basin, as well as the Kerguelen basin, is characterised by an enhanced biological production. Indeed, as we saw in the introduction, coastal waters are enriched in dissolved iron coming from these volcanic islands, resulting in particularly intense phytoplankton blooms (Bucciarelli et al., 2001; Smetacek and Nicol, 2005). This high productivity sustains a rich and diverse ecosystem where numerous seabird species are well represented (Jouventin et al., 1984).

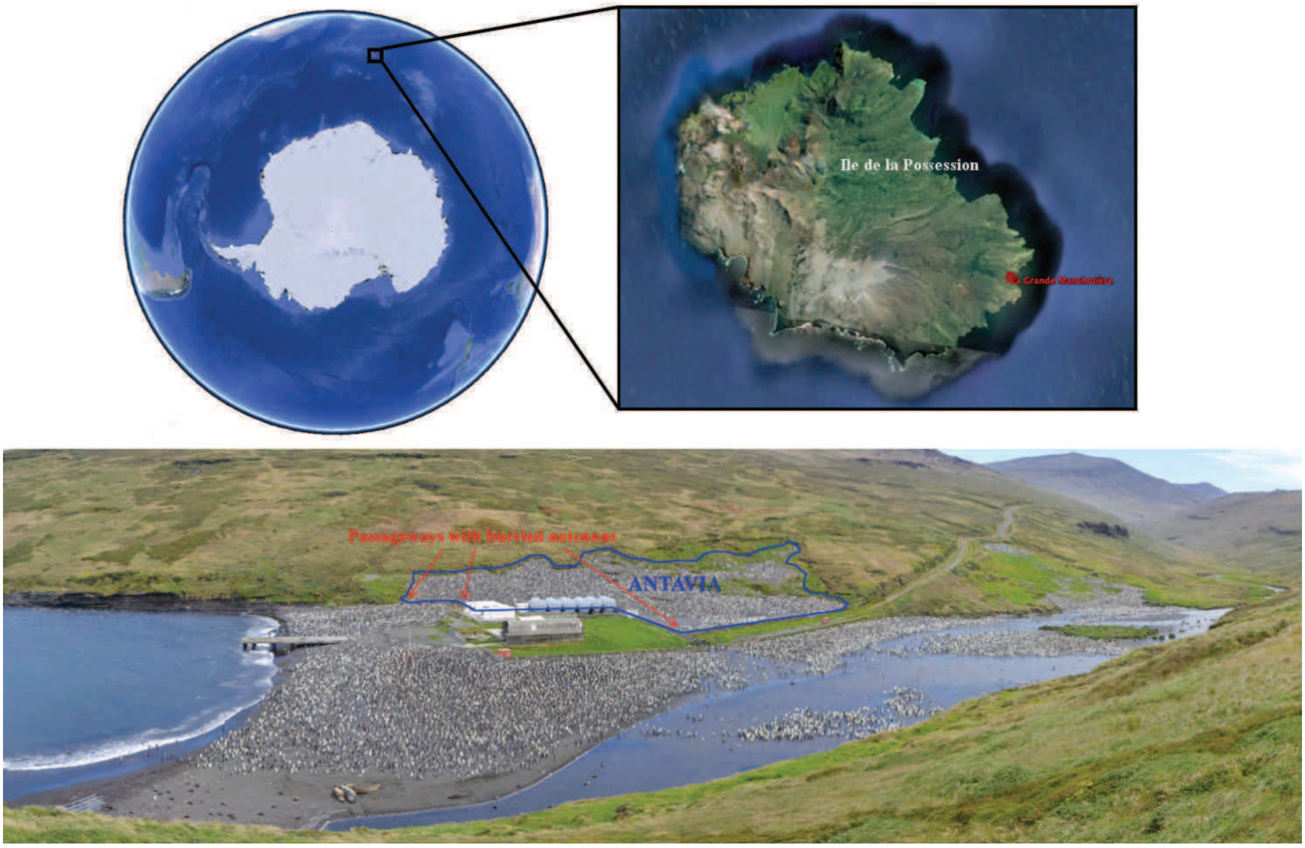


Figure II - 3. 'La Grande Manchotière' colony, Possession Island. The sub-colony 'ANTAVIA' is delimited in blue, and the main access to the sub-colony (where automatic individual detection systems are buried) are indicated by red arrows.

Figure II - 3. *Colonie de 'La Grande Manchotière', Ile de la Possession. La sous-colonie 'ANTAVIA' est délimitée en bleue et l'emplacement des principaux accès à la sous-colonie (au niveau desquels sont enterrés des systèmes de détection automatisés des individus) est indiqué par des flèches rouges.*

c) Adélie Land

Adélie penguins were studied on the Petrel Island (66°40'S, 140°01'E), which is the main island of the Pointe Géologie Archipelago by the Antarctic continent, where about 12 000 pairs of Adélie penguins are breeding (Figure II - 4). This study was conducted at the sub-colony called 'ANTAVIA Canyon', where about 300 pairs are breeding.

The region around Adélie Land is characterised by a seasonal sea-ice cover associated with intense phytoplankton bloom when the sea ice retreat (Riaux-Gobin et al., 2011). As in all regions marked with seasonal sea-ice retreat, the timing of the sea-ice retreat is critical for the structuration of the trophic web as it will define phytoplankton community structure with repercussions for the whole trophic web (Moline et al., 2004; Smetacek and Nicol, 2005).

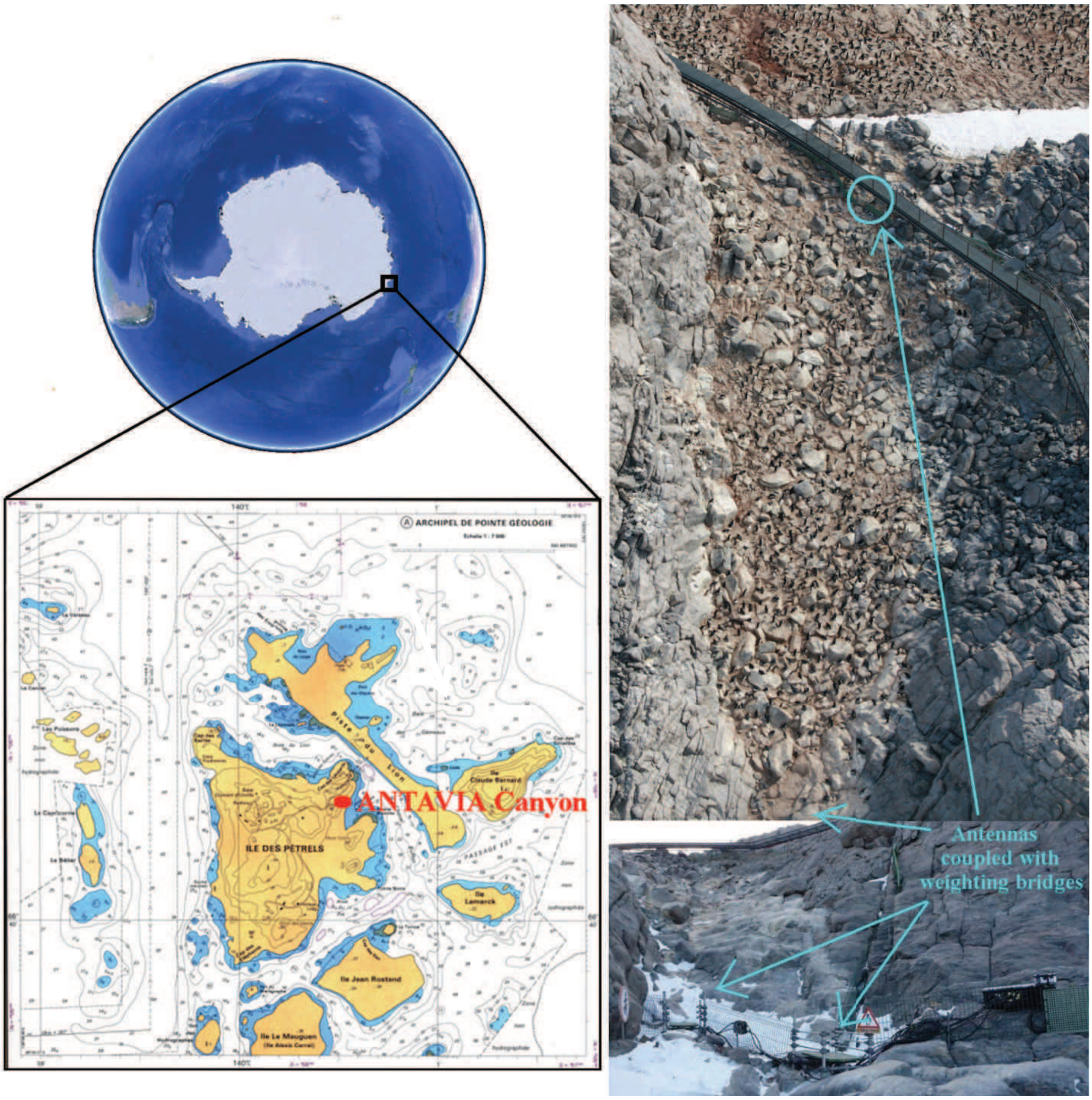


Figure II - 4. Localisation and illustration of the 'ANTAVIA Canyon' colony on Petrel Island, in the Pointe Géologie archipelago, close to Adélie Land, Antarctica. Main access to the colony (and associated automatic individual detection systems) are indicated by blue arrows.

Figure II - 4. *Localisation et illustration de la sous-colonie 'ANTAVIA Canyon' sur l'Ile des Pétrels, au sein de l'Archipel de Pointe Géologie, à proximité de la Terre Adélie, Antarctique. Les principaux points d'accès à la sous-colonie (et les systèmes de détection automatisés des individus qui leurs sont associés) sont indiqués par des flèches bleues.*

2 – Species

a) The Brünnich's guillemot

The Brunnich's guillemot, *Uria lomvia*, has a large circumpolar distribution covering Arctic and sub-Arctic latitudes (Nettleship and Birkhead, 1985). It belongs to the *Alcidae* family. Adults are about 42 cm long and weight on average 1 kg, and present no apparent sexual dimorphism. The Svalbard population mainly feed on polar cod (*Boreogadus saida*), blennies (*Lumpenus lumpretaeformis* and *Leptoclinus maculatus*) and to lesser extent on capelins (*Mallotus villosus*) (http://www.npolar.no/no/arter/polarlomvi.html).

Brünnich's guillemots from Svalbard generally return to the colony to breed in April – May. They breed in dense colony on narrow seacliff ledges at or near the seashore. Females lay a single egg on a bare ledge between the end of May and early June, which will be alternatively incubated by both sexes for about 33-34 days (Figure II - 5). Hatching occurs at the end of June during a highly synchronized time period. The chick will then be fed and guarded alternatively by both parents until it jumps off the cliff, not fully fledged yet, at the age of 15 to 30 days. It is then followed by one of its parents, usually the male, with which it will start a swimming migration toward winter areas (adults usually starts to moult at that time, losing their ability to fly), before it becomes independent 4 to 8 weeks later (Gaston and Hipfner, 2000, http://www.npolar.no/no/arter/polarlomvi.html). Winter areas of the Svalbard population range from southwest Greenland to Newfoundland and Labrador (Bakken&Mehlum 2005).

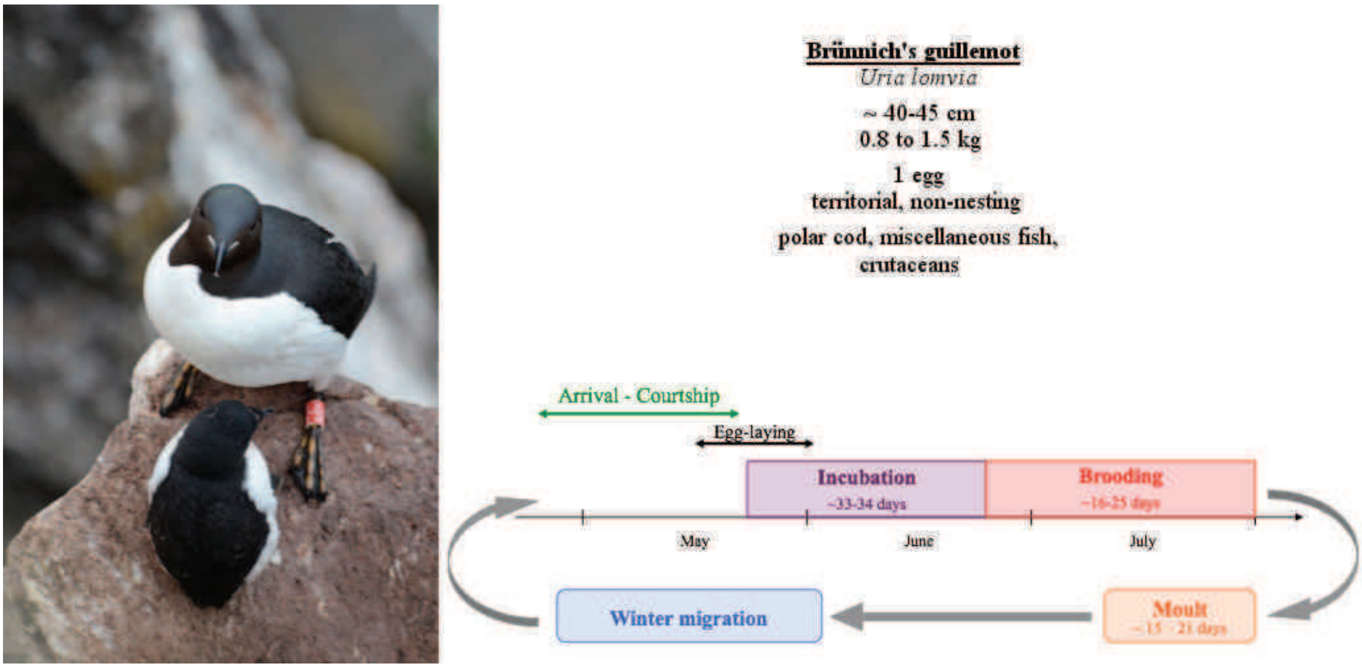


Figure II - 5. Identity card of the Brünnich's guillemot including a diagram of its breeding cycle.
Figure II - 5. *Fiche d'identité du guillemot de Brünnich incluant une schématisation de son cycle de reproduction.*

b) The King penguin

The king penguin, *Aptenodytes patagonicus*, belongs to the *Spheniscidae* family and is the second biggest penguin (after the emperor penguin) of the 19 species composing this family. Adults are about 90 cm and weight between 7 and 20 kg according to the phase of the breeding cycle. The species has a large circumpolar distribution mainly occupying sub-Antarctic islands between 40°S and 60°S. The principal colonies are settled in South Georgia, the Falkland archipelago, Heard Island, the Crozet and Kerguelen archipelagos, and the Macquarie archipelago (Figure II - 6). The Crozet Archipelago is home for about 2/3 of the world population of king penguins with about 1 000 000 breeding pairs (Guinet et al., 2005).

King penguins are offshore seabirds foraging far from their breeding colony, up to 450 km in summer to meet the Polar Front for individuals breeding in the Crozet Archipelago (Charrassin et al., 2001). During this period they feed mainly on *Krefftichthys anderssoni*, *Electrona carlsbergi* and *Protomyctophum spp.* (all *Myctophidae* species) that represent up to 99% of their diet at the time (Cherel and Ridoux, 1992; Cherel et al., 1993). In winter, because of the rarefaction of suitable prey for the species, breeding individuals have to go even farther to forage, down to the Marginal Ice Zone (about 2000 km away from Crozet; Charrassin et al., 2001; Bost et al., 2004). At this time their diet is mainly composed of demersal cephalopods and other species of myctophids (Cherel et al., 1996). However they also keep foraging close to the colony to feed their chick.

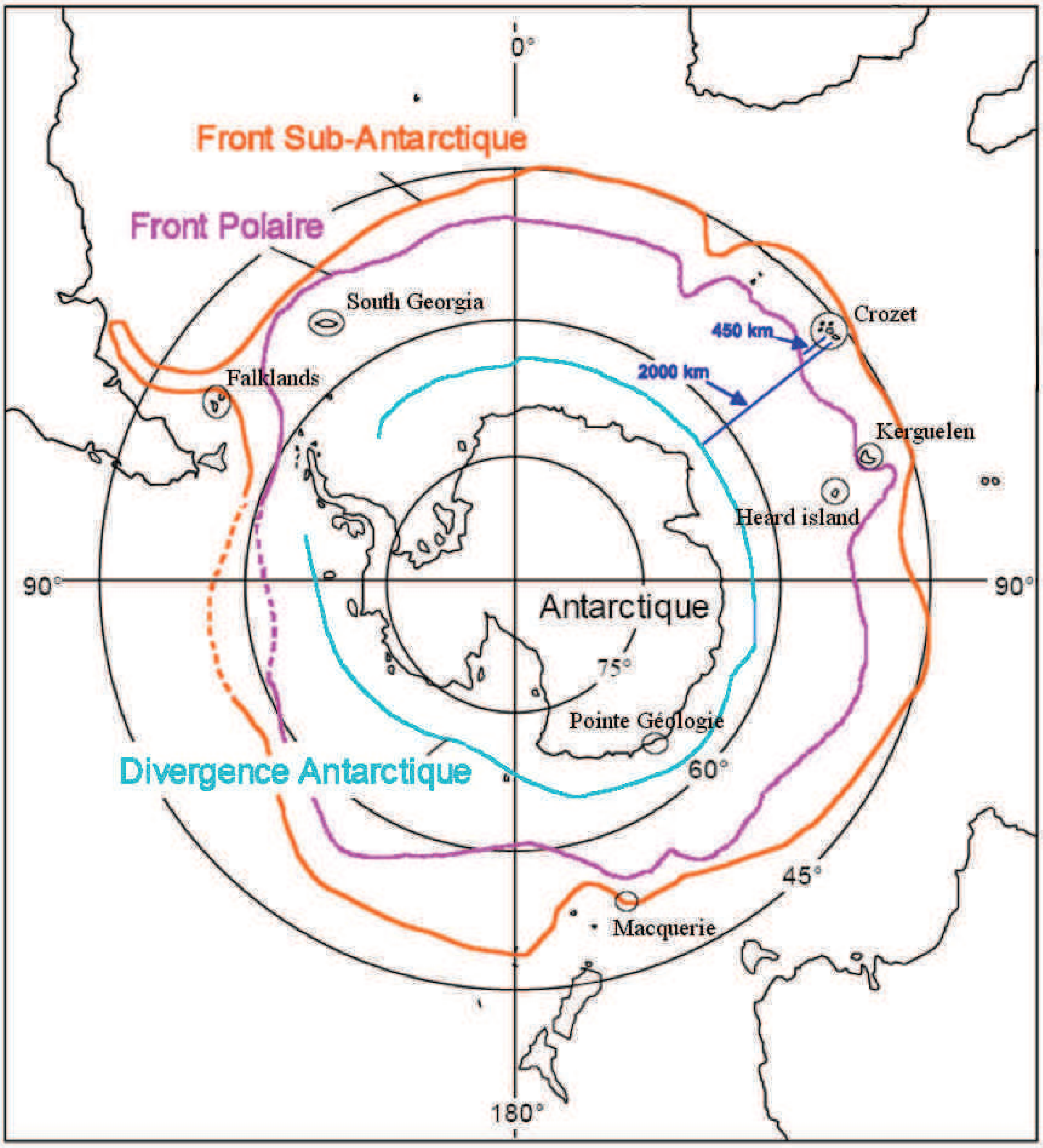


Figure II - 6. Localisation of the principal king penguin colonies and the main front of the Southern Ocean.

Figure II - 6. Localisation des grandes colonies de manchots royaux et des principaux fronts de l'Océan Austral.

The breeding cycle of king penguins has been extensively studied for decades (Stonehouse, 1960; Barrat, 1976; Weimerskirch et al., 1992; Descamps et al., 2002). Both mates share parental care and stay faithful to each other at least for one breeding cycle (Briëd et al., 1999). The breeding cycle of the king penguin last on average of 14 months at Crozet (Barrat, 1976; Descamps et al., 2002). Because of this particularity, laying period is asynchronous as arrival of individuals and subsequent timing of reproduction depends on the breeding output from the previous breeding season (Figure II - 7; Stonehouse, 1960; Barrat, 1976). Two pic of laying can thus be identified, and individuals can be classified as being 'early' breeders if they lay before January 1st or 'late' breeders if they lay after January 1st.

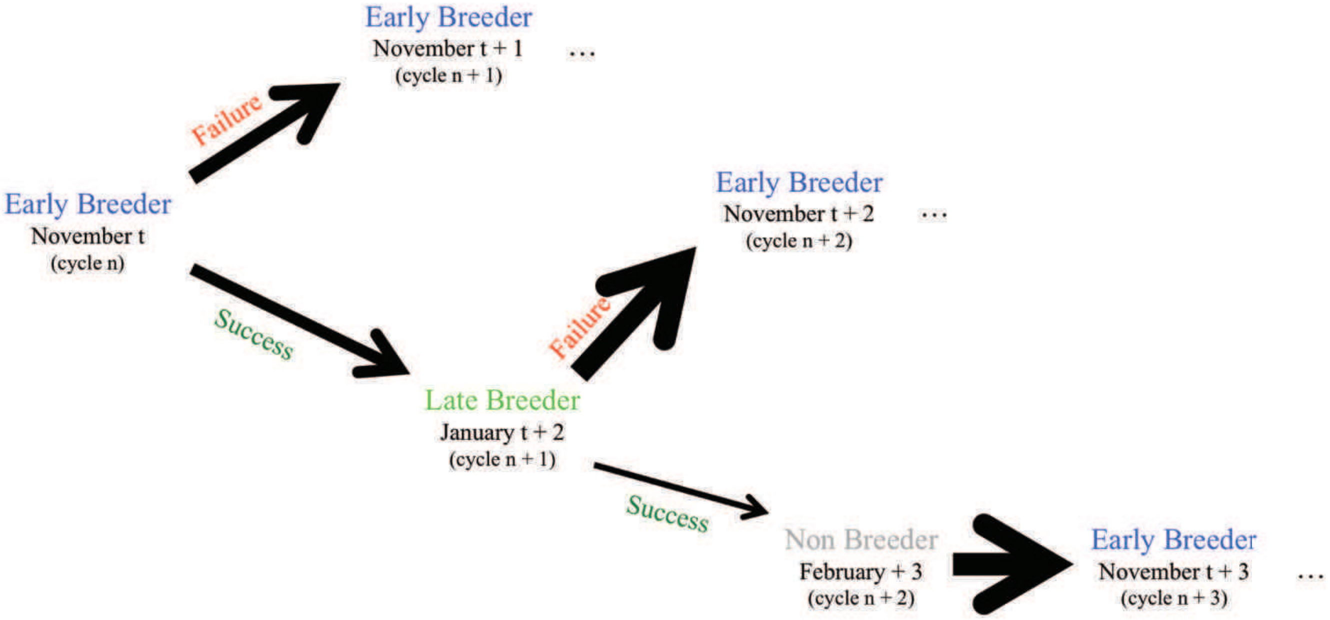


Figure II - 7. Diagram of successive breeding cycles in the King penguin, from Stonehouse (1960) and Barrat (1976).

Figure II - 7. *Schématisation de la succession des cycles reproducteurs chez le manchot royal, d'après Stonehouse (1960) et Barrat (1976).*

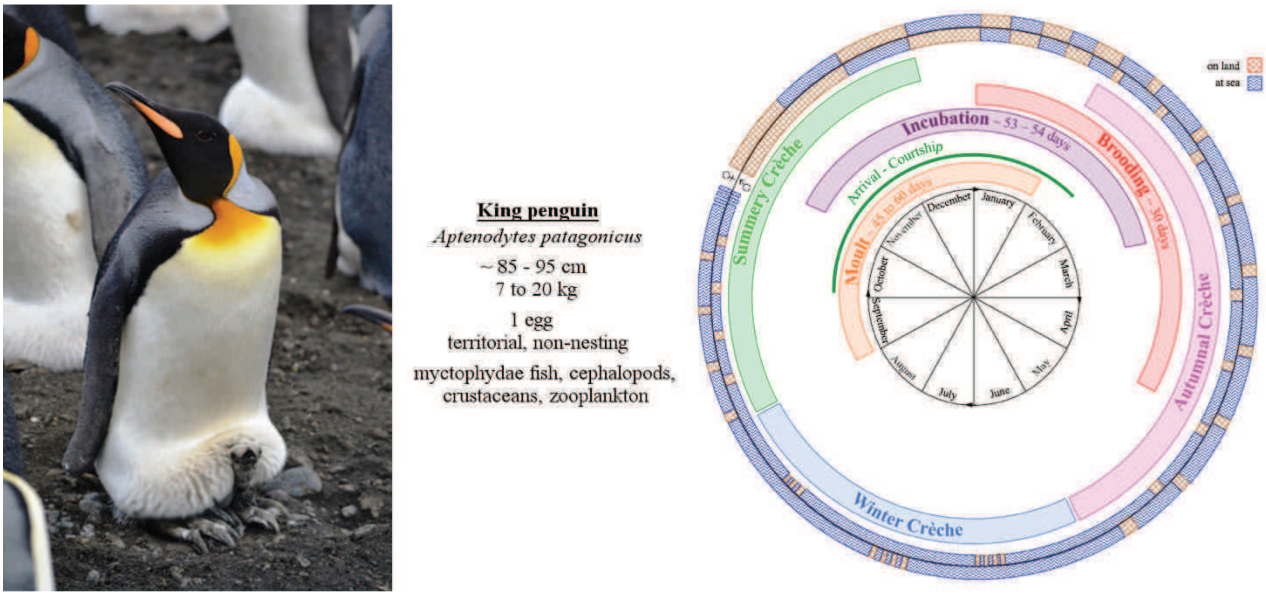


Figure II – 8. Identity card of the King penguin including a diagram of its breeding cycle (for an 'early breeder') and of the on land/at sea sojourn pattern associated.

Figure II - 8. *Fiche d'identité du manchot royal incluant une schématisation de son cycle de reproduction (en 'early breeder') et du motif de séjours à terre et en mer correspondant.*

The breeding cycle of king penguins can be divided into 4 phases (Figure II - 8):

- *the pre-breeding moult*, that include foraging trips before and after the moult for body reserve restoration.
- *the courting*, where individuals are pairing and establishing their territory (as for guillemots this species does not build a nest). It ends when the female lays a single egg and leaves the colony to feed.
- *the incubation,* that lasts about 53 days and during which both mates take turns.
- *the rearing phase,* that can be itself divided into 4 phases (Le Bohec et al., 2005):
  - *the brooding*, that lasts about a month. At hatching, the chick is not capable of thermoregulation and is highly vulnerable to predators, parents thus take turns to guard and feed it.
  - *the autumnal crèche,* that lasts between 1 and 3 months according the 'early' or 'late' status of the bird. During this period, chicks are left alone at the colony where they regroup into crèches (Le Bohec et al., 2005), and parents visit them regularly to fatten them up so they can survive the harsh winter.
  - *the winter crèche,* at which stage parents only come back sporadically to the colony to feed the chick (Descamps et al., 2002). During this period the chick can loose up to a half of its body mass (Stonehouse, 1960; Barrat, 1976; Cherel et al., 1987).

- *the spring crèche,* during which parents come back again regularly to feed the chick for 2 to 4 months until it is ready to moult and fledge.

c) The Adélie penguin

Adélie penguins, *Pygoscelis adeliae*, also belong to the *Spheniscidae* family and are one of the only two penguin species that breed exclusively in Antarctica (Williams, 1995). Adult birds are about 70 cm and weight between 3 and 8 kg according to the phase of the breeding cycle. The species also has a large circumpolar distribution, this time limited to the borders of the Antarctica continent (Figure II - 9). Adélie penguins highly depend on the presence of pack ice and on its seasonality to feed and reproduce, and this dependence constrains their distribution both at sea and on land (Ainley, 2002). Moreover, their distribution on land is also dependant of the presence of ice- and snow-free areas close to glaciers that formed moraines that deposit nest stones on the ground.

As king penguins, Adélie penguins are central place foragers. According to the region of Antarctica, they forage either on the continental shelf up to the shelf break, or on the continental slope. During winter they mainly feed on fish and squids. In summer their diet depends on their foraging habitat. Adélie penguins foraging in the deep waters of the continental slop mainly feed on krill and particularly on *Euphausia superba*, and on mytcophid fish (White and Conroy, 1975; Volkman et al., 1980; Lishman, 1985; Lynnes et al., 2004), while individuals breeding on the continental shelf mainly feed on nototheniid fish such as the Antarctic silverfish *Pleuragramma antarcticum,* and on other species of krill such as *Euphausia crystallorophias* (Emison, 1968; Ainley et al., 1984; Wienecke et al., 2000). In Adélie land, Adélie penguins seem to forage on both continental shelf and slope (Wienecke et al., 2000; Ainley, 2002). Moreover, Clarke et al. (1998) found that males and females differ in their diet and foraging habitat in Béchervaise Island. In this population, females tended to forage farther up to the shelf break and feeding mainly on krill while males foraged closer to the breeding colony feeding on both krill and fish.

As for the King penguin, the breeding cycle of Adélie penguins has been extensively studied and described in details by Ainley (2002) (Figure II - 10). In this species too, both mates equally share parental care of their offspring. At the end of October, Adélie penguins come back to their colony, with males usually arriving a few days earlier than females to

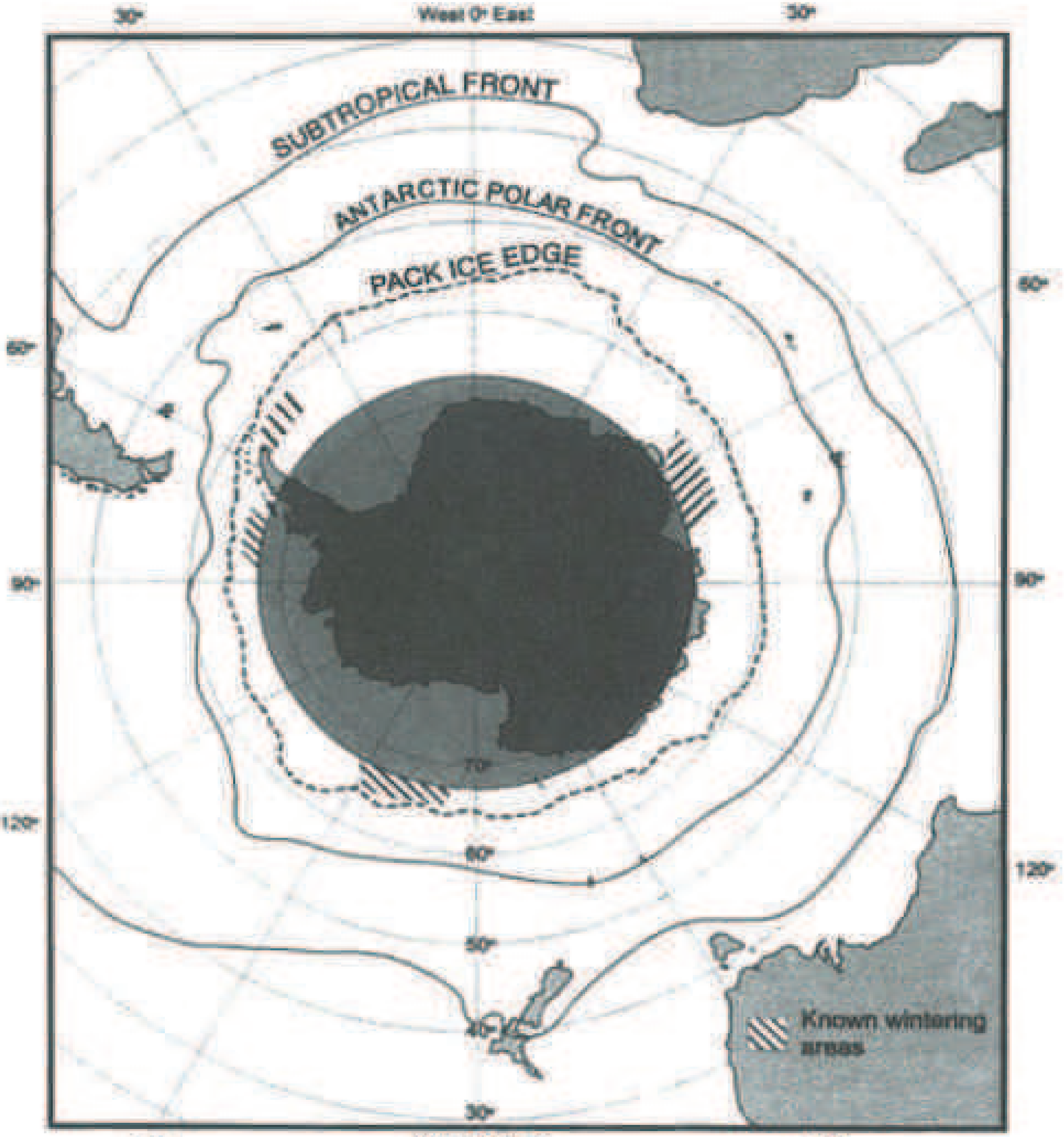


Figure II - 9. From Ainley (2002) (p27). Factors defining wintering grounds of Adélie penguins. Solid line show the Antarctic Polar Front, dash-line show the Antarctic Circumpolar Current and the pack-ice edge, and shading present the Antarctic Circle. Hactched areas show the location of Adélie penguins in winter.

Figure II - 9. *D'Ainley (2002) (p. 27). Facteurs définissant les aires d'hivernage chez des manchots Adélie. La ligne continue représente le Front Polaire Antarctique, la ligne en tirets représente la limite sud du courant circumpolaire antarctique et la limite de la banquise, et la zone ombrée représente le cercle antarctique. Les zones hachurées montrent la localisation des manchots Adélie en hiver.*

establish territories and starting building a nest with small ‘pebble’ rocks. The quality of this ‘pebble’ nest seems to play a role in mate choice along with other criteria such as pairing display calls. After pairing, both mates keep on building the nest and engage in repeated copulation. The female then lays on average 2 eggs (average clutch size 1.9 Ainley (2002), range from 1 to 3) 1 to 3 days apart and leave the nest, leaving the male to ensure the first shift of incubation. Hatching occurs about 33-34 days after the last egg was laid. Mates enter then a guarding or brooding phase, still taking turns with the chicks that are not capable of thermoregulation yet, and typically alternating 1 to 3 days at sea and 1 to 3 days on land. The chicks become thermally emancipated about 3 weeks later. At this point both mates leave the colony while the chicks join crèches mainly to protect themselves from other adults present at the colony and from predation (Ainley, 2002; or see Le Bohec et al., 2005 for king penguins). During this period, both mates come back regularly at the colony (i.e. typically a few hours every 1 to 3 days) to keep feeding the chicks until they are ready to fledge by the end of February. Adélie penguins moult every year at the end of their breeding season before leaving for their annual winter migration.

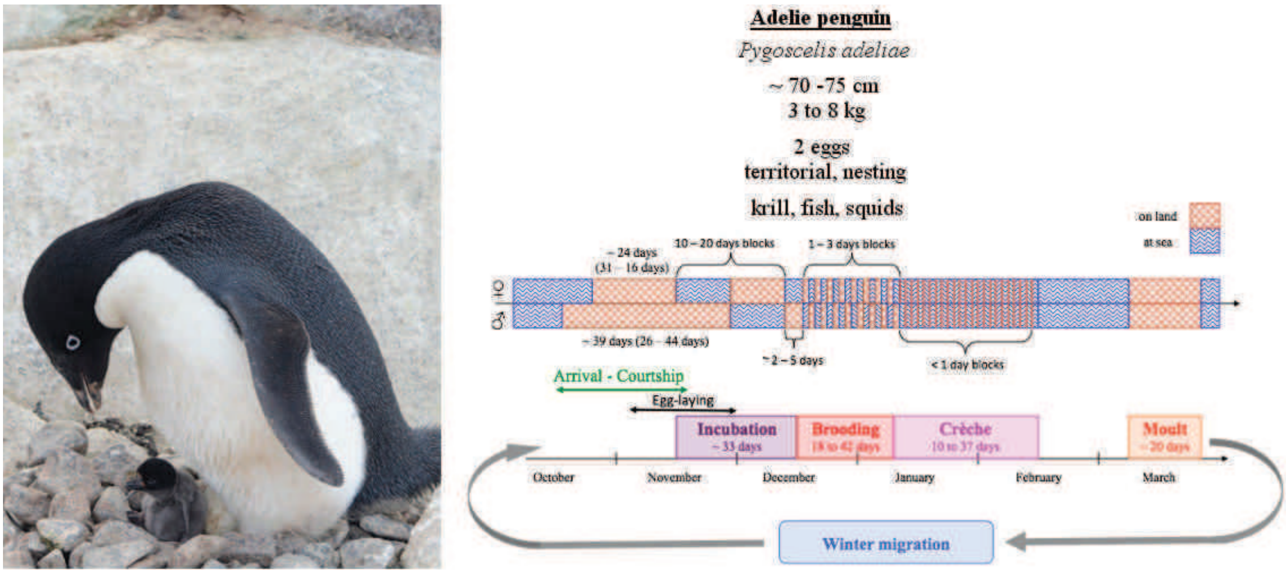


Figure II - 10. Identity card of the Adélie penguin including a diagram of its breeding cycle and of the on land/at sea sojourn pattern associated.

***Figure II - 10.** Fiche d’identité du manchot Adélie, incluant une schématisation de son cycle de reproduction et du motif de séjours à terre et en mer correspondants.*

3 – Methodology

a) Individual monitoring

As we saw previously, longitudinal studies of individuals are essential to study variation in life-history traits and its impact on population dynamics and behavioural strategies (Lebreton et al., 1992). However, the collection of such datasets requires regular identification of individuals over a significant amount of time, which is complicated especially in wild populations. Furthermore, any manipulation by human can be perceived as a threat (Macleod and Gosler, 2006) and can therefore induce physiological and behavioural changes (Wingfield et al., 1982; Le Maho et al., 1992). To limit, potential bias linked to these modifications, long-term monitoring of individuals should then also avoid regular manipulation by humans.

One of the most common individual long-term monitoring methods in birds is the use of bands. Their key advantage is that it can be identified from a distance limiting the stress of manipulation to once in the life of an individual. In flying birds such as the Brünnich's guillemots of this study (in association with the Norwegian Polar Institute), leg bands are used. No detrimental effect of such bands has ever been shown in flying birds, nevertheless they can be lost leading in a bias of survival rates estimated through capture-marking-recapture models for instance. In penguins, because of their morphology, such bands cannot be used and flipper bands are thus preferred. However it has been recently shown that flipper bands can have significant long-term detrimental effects on breeding success and survival of king penguins and that this impact might get even stronger under 'poor' environmental conditions (Gauthier–Clerc et al., 2004; Saraux et al., 2011a; Figure II - 11). The most plausible explanation of these negative effects is that flipper bands create an hydrodynamic impairment for these extremely good swimmers thus affecting their foraging efficiency (Bannasch et al., 1994), and for which they might not be able to compensate especially when environmental conditions are unfavourable.

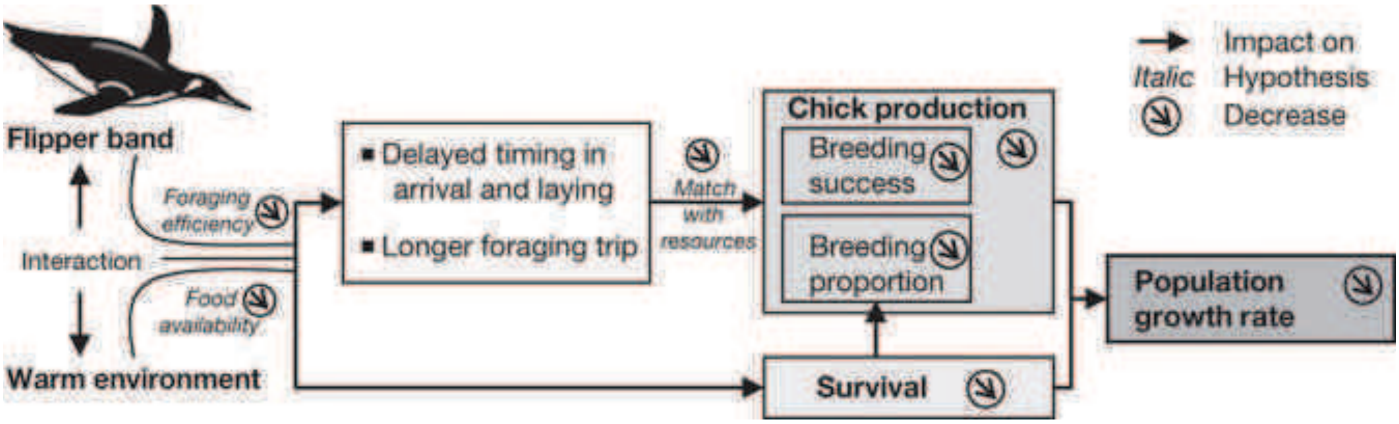


Figure II - 11. From Saraux, Le Bohec et al. (2011). Mecanisms implicated in the negative impact of flipper bands on life-history traits and population dynamics of king penguins.
Figure II -11. *De Saraux, Le Bohec et al. (2011). Mécanismes impliqués dans l'effet négatif des bagues alaires sur les traits d'histoire de vie et la dynamique de population des manchots royaux.*

The demonstration of the negative effects of flipper bands was rendered possible thanks to the development of a new automatic monitoring system based on small subcutaneous electronic tags (or transponder tags) with which 'control' individuals of the studies were equipped, and on Radio-Frequency Identification antennas (RFID). Indeed the studies of Gauthier–Clerc *et al.* (2004) and Saraux et al. (2011a), as this study, are based on data collected in the framework of the ANTAVIA project, an association between the French Polar Institute Paul Emile Victor and the C.N.R.S. with the team based at the D.E.P.E. of Strasbourg, which only use this kind of system to monitor king penguins and Adélie penguins colonies implanted on French austral territories. Transponders have no known adverse effects to date (e.g. in king penguins, Froget et al., 1998; or in great tits, *Parus major*, Nicolaus et al., 2009). Moreover, this new automatic methods only require for the animal to be manipulated once to implant the transponder tag (with a unique number), which means that, as for bands, the stress of the manipulation is limited to once in the lifetime of the animal. The automatic identification of an individual is then achieved thanks to RFID antennas, emitting an electromagnetic signal to detect the transponder, which is passive and has no battery. Doubled antennas are implanted at the usual pathways of birds to the colonies (see Figures II - 3 and II - 4 for implantation of the antennas at Crozet and in Adélie Land respectively, see Figure II - 12 for an illustration of the system in Adélie Land). The way in or out of an individual is determined by the order in which it crosses the double antennas. All detections, that is to say date, time, number of the tag and way in or out, are then stored into datasets, giving us access to the whole breeding history of individuals and to precise features of their breeding cycle such as at-sea/on-land patterns during the different phases of this cycle.

In this study we will focus on demographic and life-history parameters of Adélie penguins since the same parameters have already been extensively studied in king penguins. In Adélie land, the annual pit-tagging of all the chicks of the sub-colony started in austral summer 2006-2007. 50 breeding adults were also pit-tagged at the beginning of the breeding season of 2006-2007 in order to access adult demographic rates while waiting for the first cohort of chicks to access reproduction. In Adélie Land, the system presents the particularity that antennas are also associated to weighting bridges recording penguin body mass every time they cross them (Figure II - 12). The continuous record of body mass of individuals will give us access to precious information on the condition of the birds at different phases of their breeding cycle, and indirectly on resources at sea. However, while the system itself is fully operational, the necessary algorithm to process the data is still being tested and we will not be able to present any results here.

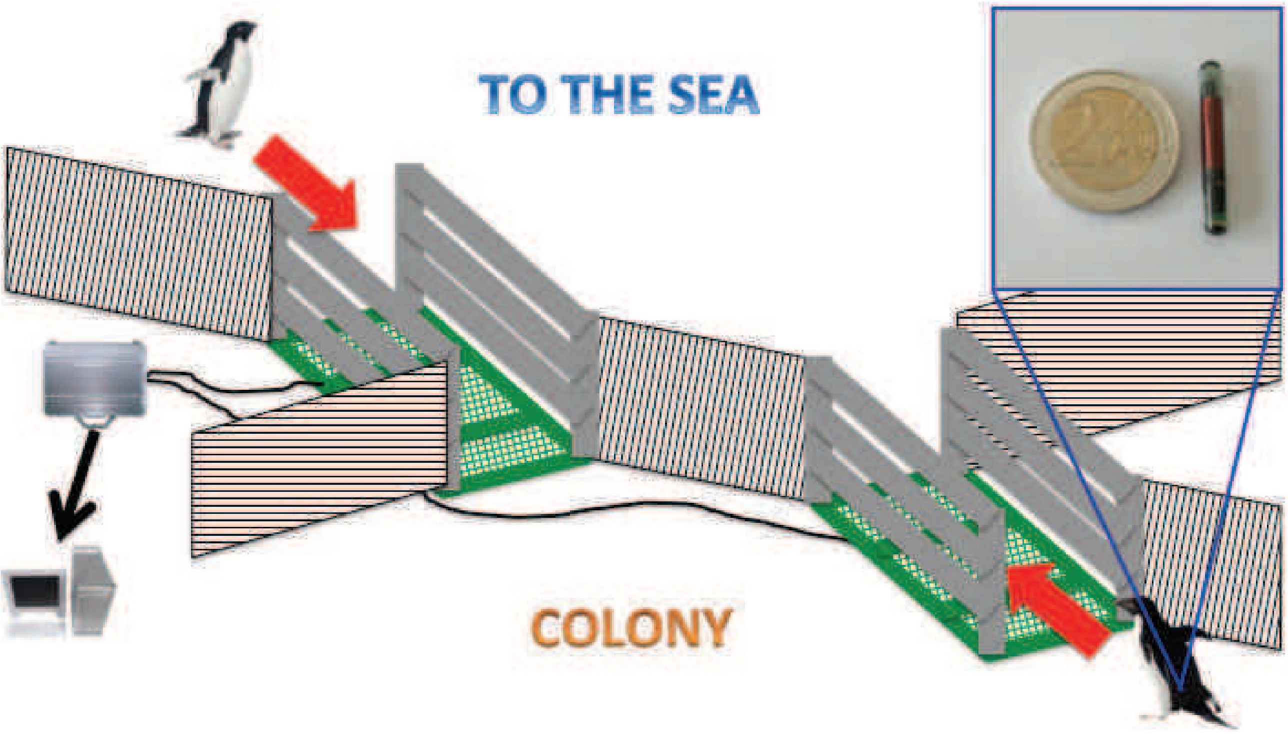


Figure II - 12. Illustration of the automatic individual identification and weighting system implemanted in Adélie Land, and picture of a transponder tag.

Figure II - 12. *Schématisation du système de détection et de pesée automatique installée en Terre Adélie, et illustration d'un transpondeur.*

b) Behavioural tests and observations

When individuals were captured for marking and/or biological sampling, the behaviour of both Brünnich's guillemot and Adélie penguin individuals was recorded directly on the field and through blind video analysis of this 'resistance to handlers' test. These tests were used to assess the boldness of individuals and their activity in a threatening context as defined by Réale *et al.* (2007). Variables recorded during these tests are summarised in Table II – 1).

On king penguins, we also performed 'reaction to novelty' tests through pen experiments of *ca.* 65 minutes. The test was video recorded to avoid any bias linked to the presence of humans. Pens were squarish (w = 3 m, h = 1.7 m) with blind wood walls, a net lid, and a natural soil and grass ground on which a grid of 16 cells (75 x 75 cm) was painted to assess the surface explored. Furthermore, a novel object, a yellow bucket (r = 6 cm, h = 20 cm), was also placed in advance in the pen, as well as a mirror covered by a cloth (w = 1 m, h = 1.5 m). Return to basal heart rate after manipulation by humans take between 15 and 20 minutes in this species (Viblanc et al., 2012). The mirror was therefore unveiled (from outside the pen) after 45 minutes to allow penguins to recuperate and explore the pen before being introduced with this new element. These tests were used to assess exploration (in a new environment and toward a novel object) and aggressiveness (reaction to the mirror) as defined by Réale *et al.* (2007). From blind video analysis we recorded the latency to move and to explore, the surface explored, the time spent grooming and in other comfort and self-maintenance behaviours, number of time defecating, the time spent in pacing the pen, the latency to approach the bucket and the mirror, the number of bites and flipper hits toward the bucket and the mirror, and the time spent in interaction with the bucket and the mirror.

To ecologically validate personality studies in captivity conditions and to better assess the impact of environmental changes on personality traits, behavioural observations of individual in their natural environment are necessary. We therefore repeated individual focal observations of 15 to 20 minutes (depending on the species) on individuals at their breeding site throughout the breeding season for the three studied species. These focal observations were used to assess activity and aggressiveness as defined by Réale *et al.* (2007). Variables recorded during these observations in natural conditions are summarised in Table II – 2).

During all manipulations and experiments animals were always handled carefully to minimize their stress. Animals were black hooded during manipulation, manipulation time was reduced to its minimum, and handlers/experimenters worked in silence. Furthermore, during behavioural focal observation, birds were observed in silence from a distance using binoculars.

Table II - 1. Ethogram of the behavioural variables recorded during 'flights' and 'resistance to handler' tests in the three model species.

***Tableau II - 1**. Ethogramme des variables comportementales mesurées lors des tests de 'fuite' et de 'résistance au manipulateur' chez les 3 espèces modèles.*

Category	Behavioural variable	Description	Species
State (score)	Reaction at capture	1 = calm, 2 = agitated/struggling/try to escape, 3 = aggressive/bite or try to bite the handler	AP
	Activity score	1 = quiet/stay still, 2 = mildly agitated/struggling, 3 = very agitated/almost never stay still	BG, AP
	Boldness score	1 = not aggressive/never bite or try to bite the handler, 2 = mildly aggressive/sometime bite or try to bite the handler, 3 = very aggressive/often bite or try to bite the handler	BG, AP
	Reaction in weighting bag	1 = calm/stay still, 2 = mildly agitated/struggling, 3 = very agitated/almost never stay still	AP
	Vocalisation during manipulation	No (0)/ Yes (1), or 0 = did not vocalise, 1 = vocalised punctually, 2 = vocalised often, depending on the species	BG, AP
	Reaction at release	1 = stay still/freeze, 2 = fly away, 3 = aggressive/turn against the handler and vocalise and/or try to bite	AP
Events (punctual, in occurrences/min)	Bites during capture or manipulation	bite the handler or try to bite the handler (i.e. extend the neck toward the handler and try to reach him with its beak)	BG, AP
Other	Approaching distance	the distance between the handler and the bird when the bird first move in reaction to the handler approach	AP

BG = Brünnich's guillemot, AP = Adélie penguin, KP = king penguin

Table II - 2. Ethogram of the behavioural variables recorded during focal observations in natural environment in the three model species.

***Tableau II - 2**. Ethogramme des variables comportementales mesurées lors des observations focales des individus dans leur milieu naturel chez les 3 espèces modèles.*

Category	Behavioural variable	Description	Species
State (time, in %)	Self-maintenance, comfort	self-grooming, shaking the flippers/wings and/or the head	BG, AP, KP
	Allo-grooming	grooming another adult	BG
	Care to offspring	ventilating/re-positioning its egg(s), grooming its chick(s), feeding the chick(s)	BG, AP, KP
	Nest maintenance	cleaning the nest/breeding site, re-arranging pebble rocks	BG, AP
	Rest/sleep	standing still eyes open or not (standing up or laying depending on the species and breeding phase), might be interrupted by short and slow head movements to look around	BG, AP, KP
	Vocalisation	vocal displays	BG, AP, KP
	Agonistic interactions	time spent biting or flipper/wing hitting another individual (attempted or actually touched) or being bitten/hit by another individual (attempted or actually touched)	BG, AP, KP
	Threat	stretch/bend the neck toward another individual without trying to bite it or to hit it with its flippers/wings, can be accompanied by vocalisations	KP
	Vigilance	fast head movements to look around, can be accompanied by vocalisations	KP
Events (punctual, in occurrences/min)	Vocalisation	vocal displays	AP, KP
	Agonistic interactions	number of agonistic interactions involving at least one bite/flipper-wing hit (attempted or actually touched) and separated from each other by at least 10 to 15 seconds depending on the species of another activity such as resting/sleeping or grooming	BG, AP, KP
	Bites and flipper/wing hits	bite or flipper/wing hits to/from another individual (attempted or actually touched)	BG, AP, KP
Other	Vocalisation	0 = no vocalisations 1 = less than 20 punctual vocalisations 2 = at least one phase of intense vocalisation (i.e. at least 4 vocalisations in one minute)	BG

BG = Brünnich's guillemot, AP = Adélie penguin, KP = king penguin

c) Environmental descriptors

c-1) At sea environmental conditions

As marine predators, seabirds should be affected by environmental conditions at sea where they spend most of their time. Furthermore, both global and local environmental conditions can affect populations (see Stenseth et al., 2002). Large-scale climate indexes, such as the Southern Oscillation Index or the North Atlantic Oscillation Index, integrate variations of several climate factors (also called 'weather packages', see Stenseth and Mysterud, 2005). They have already been used several times with success as proxies of environmental variability that explain seabird population trends in the Southern Ocean (e.g. Jenouvrier et al., 2005; Le Bohec et al., 2008). In this work, to assess the impact of environmental variability on Adélie penguin populations, we consequently used monthly Southern Oscillation Index (SOI) obtained from the Australian Bureau of Meteorology website (www.bom.gov.au) as a large-scale environmental descriptor. The SOI is calculated from the monthly fluctuations in air pressure differences between Tahiti and Darwin (Australia). This differential in air pressure determines the wind regime in the Southwest Pacific with potentially important repercussion in the Southern Ocean. Negative SOI values indicate El Niño events (Deser and Wallace, 1987), that is to say to warmer environmental conditions in the Southern Ocean, while positive values indicate La Niña events (Deser and Wallace, 1987) and colder environmental conditions in the Southern Ocean.

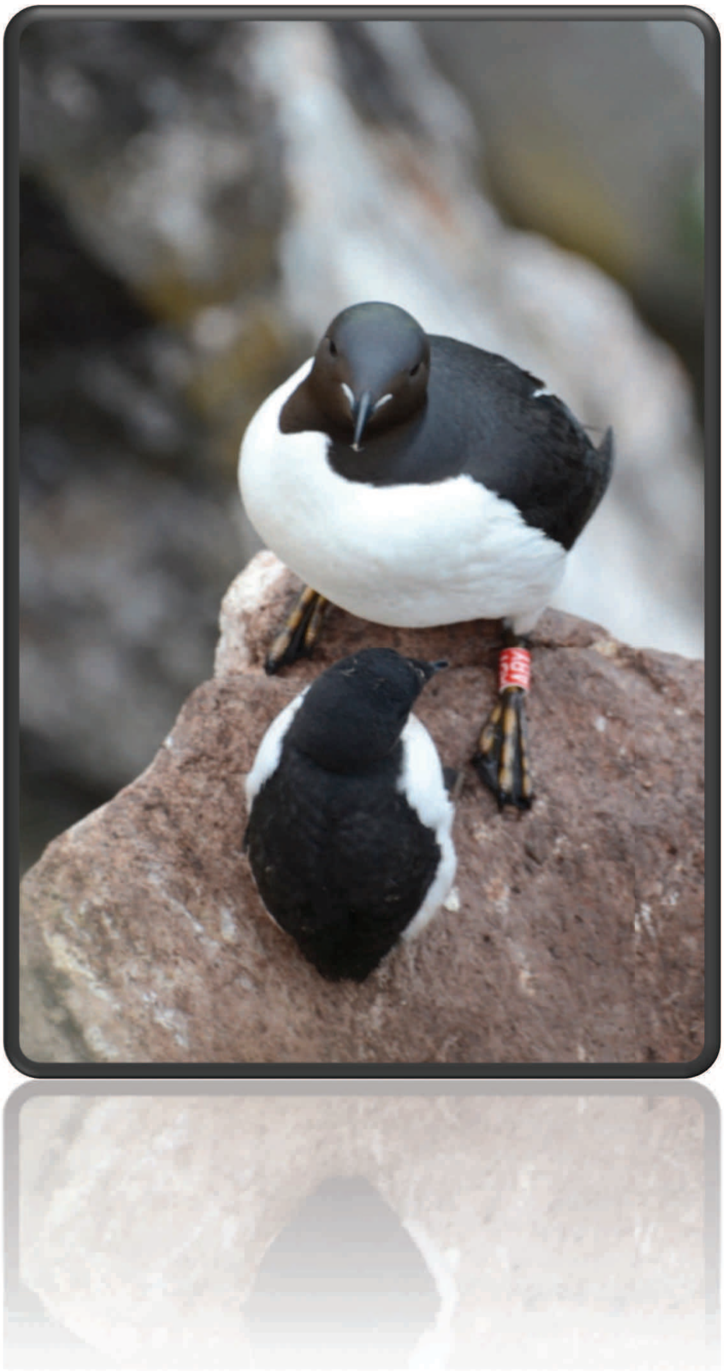
Sea Surface Temperature (SST) and sea-ice extent both have repercussion on the primary production and thus on the trophic web of a region (Gregg et al., 2003; Smetacek and Nicol, 2005). These environmental parameters thus constitute good proxies of at sea resources availability for seabirds (Jenouvrier et al., 2006; Irons et al., 2008; Le Bohec et al., 2008). Moreover, prey availability in one area depends on the location of its spawning ground that might occur at a different location, and on the oceanographic conditions between the two locations (Hofmann et al., 1998). To investigate the effects of environmental variability on Adélie penguins population, we therefore used monthly SST and percentage of sea-ice cover (SIC, extracted from Rayner et al., 2003) on a grid cell of 1°x1° representative of the conditions at the local scale, i.e. direct vicinity of the study breeding colony, and on a grid cell of 2° x 2° representative of the conditions at the broader regional scale.

c-2) On land habitat and weather

Whereas the effects of environmental conditions at sea on fitness are relatively well studied in seabirds, environmental constraints on land still remain poorly investigated. However, these effects can have a significant impact on individual phenotypic traits and fitness, and more particularly on breeding success. For instance, heavy rains that flood a colony or strong snow storms could have severe effects on the breeding success of a colony independently of environmental conditions at sea. Furthermore, the local breeding habitat can be associated with different predation (Martin, 1992; Descamps et al., 2005) or parasitic pressures for instance (Gauthier-Clerc et al., 1999; Gaston et al., 2002). In this work, we therefore also studied the impact that the environmental conditions on land and the quality of breeding habitat may have on phenotypic traits of the individuals and their fitness. We consequently assess habitat characteristics associated with different pressures, i.e. breeding site as being central or peripheral, exposed or protected to different pressures such as predation, weather or parasitism, and the density of the breeding site inferred from the number of breeders and non-breeders directly around. We also collected weather variables from data-loggers placed close to the colonies (i.e. temperature (°C), humidity (%) and luminosity (Lux) from Hobo® U23 Pro v2 Temperature/Relative Humidity data logger and Hobo® Pendant Temperature/Light data logger, www.onsetcomp.com). In addition, we used weather variables for the Pointe Géologie archipelago provided by the Météo France meteorological station settled in Dumont D'Urville station on Petrel Island (i.e. daily average temperature (°C), humidity (%), atmospheric pressure (hPa), wind speed (m/s), and wind direction (in ° from the North)). Finally, we also used wind speed (m/s) measured with an anemometer when no data were available from meteorological stations, and cloud cover and rain intensity from observer assessment.

Chapter III – Personality and Heterogeneity

Chapitre III –Personnalité et Hétérogénéité



Are personality traits indicators of individual and/or habitat quality in wild seabirds? *– in prep Article 1* *(Animal Behaviour)*

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To understand the causes and consequences of individual differences in behavioural traits and their plasticity, we need to determine their potential relationships and the selection pressures that affect them in natural environments. The personality of an individual, through its association with its intrinsic quality, is believed to have consequences on the acquisition of resources such as habitat. The quality of these resources should then enhance the individual's performances and quality. Nevertheless, only a few studies have sought to identify a potential relationship between personality and habitat quality in wild populations. Here, we tested for the first time whether individuals of a wild population of Brünnich's guillemots, *Uria lomvia*, breeding in the Arctic, were consistent in their personality traits (i.e. activity, aggressiveness and boldness), and if these traits were correlated into behavioural syndromes suggesting physiological and/or genetic constraints between them. We then investigated whether behavioural differences among individuals were associated with differences in individual characteristics (i.e. morphological and physiological traits) and/or breeding habitat. During behavioural tests conducted in the field, we quantified behaviours related to boldness and activity of captured individuals ($N = 305$). Through focal observations of some of these birds in their natural environment ($N = 107$), we quantified behaviours related to activity and aggressiveness. We found that individuals were consistent over time in their activity, aggressiveness and boldness, and that some of these traits were correlated into a behavioural syndrome. Activity in natural environment was mainly explained by breeding habitat features and structural size, while aggressiveness was only explained by breeding habitat characteristics. We also found that successful breeders vocalised more intensely than failed breeders. These results bring new insights on the relationships existing between avian personalities, breeding habitat quality, and fitness, emphasizing the importance of considering them when aiming to gauge adaptive capacities of populations to face environmental changes.

Keywords: activity; aggressiveness; behavioural syndromes; Brünnich's guillemot; fitness; habitat characteristics; plasticity; seabirds; shyness-boldness; *Uria lomvia*

1 – Introduction

Contrary to what has been traditionally hypothesized, behaviour is not fully plastic and animals often exhibit consistent behavioural patterns across time and/or situations, within and between behavioural contexts, defined as personality (Gosling, 2001), temperament (Réale et al., 2007) or behavioural syndrome when these personality traits are correlated (Sih et al., 2004a). Thanks to a growing interest in the concept, personality has been shown to be common in a wide range of species (see Bell et al., 2009) and to have potential implications on the adaptive capacities of individuals and populations to respond to ecological and environmental challenges (e.g. Dall et al., 2004; Sih et al., 2004a; Bell, 2007; Réale et al., 2007; Biro et al., 2010; Wolf and Weissing, 2010). Indeed, personality is reflected in the behaviour of an animal but also in its ecology (interactions with conspecifics and predators, habitat use, mating, and dispersal, for instance) and may consequently have an impact on the individual fitness (Boon et al., 2008; Smith and Blumstein, 2008; Kontiainen et al., 2009; Dammhahn, 2012).

Habitat quality, through variation in resource availability and environmental pressures such as parasitism or predation, is known to be an important factor impacting the performances of individuals in territorial species (Fretwell and Lucas, 1969; Southwood, 1977; Pulliam, 2000; Johnson, 2007). Several studies have shown that the quality of an individual facilitated its access to good quality habitats and that the intense competition for good quality habitat resulted in a strong selection for high quality individuals with lower quality individuals being relegated to lower quality sites (Coulson, 1968; Fretwell and Lucas, 1969; Rodenhouse et al., 1997). While individual quality and habitat quality have been seen as distinctly impacting breeding performances (Carrete et al., 2006), it has been proposed that the combination of the two factors influences individual breeding performances (Espie et al., 2004). However, to date, only a few studies have sought to identify links between personality, as reflecting individual quality, and habitat quality to explain the spatial distribution of individuals and better gauge their influence on individual fitness (e.g. Cote et al., 2008; Boyer et al., 2010; van Overveld and Matthysen, 2010).

Despite their importance in evolutionary ecology and their implications in the adaptive capacity of individuals, most studies have focused on personality traits in captivity, and relatively few studies have tried to identify these traits in the wild (e.g. Boon et al., 2008; Garamszegi et al., 2009; Kontiainen et al., 2009; Dammhahn, 2012; Dammhahn and

Almeling, 2012). Captivity experiments, allowing for instance to control for potentially confounding factors or to manipulate the environment to test the response to two extremes conditions, are good tools to study underlying mechanisms shaping personality (e.g. identify genes and behaviours under selection; Falconer, 1992; Fuller et al., 2005). However, they rarely match the reality of the natural environment of the studied species where selective pressures might act differently (Réale et al., 2007; Archard and Braithwaite, 2010). To fill this gap, the current study focused on a wild population of a sub-Arctic/Arctic philopatric seabird species, the Brünnich's guillemot, *Uria lomvia*.

Through behavioural observations and tests in natural environment, we first measured personality traits (such as activity, aggressiveness and boldness, as defined by Réale et al., 2007) and behavioural syndromes in the Brünnich's guillemots, a wild Arctic seabird species breeding in the Svalbard Archipelago. We predicted that behavioural differences may be linked with the breeding habitat quality and expected personality to be related to individual quality (i.e. physical and physiological characteristics) with individuals of higher quality breeding in higher quality habitat. More specifically, we predicted that individuals breeding in high quality habitats (i.e. protected from predation, sheltered from wind and rain, and with moderate density) would be i) more aggressive to better defend their breeding territory against conspecifics, ii) less bold because less exposed and less used to threatening situations, and iii) more active since a good quality habitat may allow to allocate more time to activities important for their maintenance, such as grooming or breeding site cleaning. Finally, we predicted that individual fitness, e.g. breeding success here, is mediated by personality.

2 – Material and Methods

a) Study area

We conducted fieldwork in 2 breeding seasons, from June to July 2011 and 2012, at the Brünnich's guillemot, *Uria lomvia*, colony of Diabasodden (78°21' N 16°08' E), Svalbard Archipelago. Brunnich's guillemots are seabirds spending most of their time at sea except during summer, when they breed very synchronously in dense colonies on narrow sea cliff ledges at or near the seashore. Females lay a single egg on bare ledge end of May-early June that will be incubated for about four weeks. The chick will then be fed during *ca.* three weeks until it jumps off the cliff not yet fully fledged, and stay at sea with one of its parents for another four to eight weeks until it become independent (Birkhead and Nettleship, 1981). During the breeding season, its main predators are glaucous gulls, *Larus hyperboreus*, and polar foxes, *Vulpes lagopus*, which feed on their eggs and chicks (Frafjord, 1993; Gilchrist et al., 1998).

b) Capture and handling

A total of 305 birds were captured at the nest with a collar pole and handled at a short distance from the colony. Upon capture, each individual was ringed (if not already) with a unique identifier. Some individuals were captured multiple times during the study period, up to three times in total. Restraint was used as a test to record the behavioural responses of the target birds to a threatening situation. Bird behaviour was assessed using both the handler's judgment and blind video analyses (only one observer). Namely, we recorded Activity and Boldness scores (ACTs and BOLs scaled from 1 to 3), an Attack score (ATTs quantified as the frequency of successful bites), and the intensity of vocalisation (VOCs scaled from 0 to 3). We are using the terms 'activity' and 'boldness' here as defined by Réale et al. (2007), i.e. the general level of activity of the individual during manipulation, and its reaction toward a threatening situation, respectively. Consequently, an individual was considered active when very agitated during the manipulation, and bold when reacting aggressively toward the handler.

Potential confounding covariates were recorded, that is, the handling start and end times as well as the handler's identity. Individual covariates were measured: sex, weight, and morphological measurements (tarsus, wing chord, and culmen lengths). Using the morphometric measurements and following Peig and Green (2010) recommendations, we performed a principal component analysis (PCA) to establish structural size index (SSI) as follows: SSI = PC1 = 0.62 * (log(wingcord), scaled-centred) + 0.63 * (log(culmen), scaled-centred) + 0.47 * (log(tarsus), scaled-centred). Following Jacobs et al. (2012) recommendations then, a body condition index (BCI) was defined as the residuals of the regression of the SSI on body mass. Blood samples were also collected for DNA sexing. Furthermore, heart rate at the beginning of the manipulation (HRi, number of beats per minute, ca. 1 minute after capture) was measured with a stethoscope as a physiological indicator of reaction to stress (Koolhaas et al., 1997; Ferrari et al., 2013).

c) Focal observations

Focal observations of 20 minutes were randomly performed through the season ca. every 5 days, on 107 individuals (among which 49 were followed both years) from 56 nests, From 1 to 8 focal observations were achieved for each individual depending on the year and the timing of the breeding failure. From these focal observations of the individuals in the colony, we assessed birds' behaviour by recording the intensity of vocalisation (not vocalising/vocalising punctually/vocalising intensely; VOC) and the proportion of time spent grooming (themselves or other individuals), cleaning the nest, resting/sleeping, vocalising intensely, and in agonistic interaction with other individuals. We also recorded the number of agonistic interactions during the focal observation and the number of bites exchanged during these agonistic interactions. Start time of the focal observation was recorded as potential confounding covariate. All focal observations were conducted by the same observer (C.C.).

Breeding status of the birds (i.e. with an egg or a chick) was recorded before each focal observation. Two density scores were also recorded at the beginning of each focal observation, that is to say the number of breeders (breeder density), or breeders and non-breeders (global density) in 0.5 m around the observed individual. Pictures were taken for density score validation and to assess nest site characteristics. Nest site was defined as peripheral (first row of breeding sites) or central, and as exposed or protected (empirical assessment of exposure to predation and to weather conditions according to the topography of the nest site, e.g. an exposed nest was a nest on a really narrow ledge with almost no physical protection conferred by rocks or the cliff wall).

Cloud cover (0-20%, 20-80%, or 80-100%), intensity of the rain (light, medium, or heavy), and maximum and mean speed of the wind (m/s) were recorded twice a day, while temperature (°C) and humidity (%) data were continuously recorded every 30 s thanks to data-loggers placed close to the colony (Hobo® U23 Pro v2 Temperature/Relative Humidity data logger, www.onsetcomp.com). To assess individual breeding success, all breeding sites were checked ca. every other day and their content (egg, chick, empty) recorded.

d) Ethical Note

This study has been approved by the Governor of Svalbard (program number 361). Capturing and ringing seabirds was not considered as an "animal experiment" and did not require any permit from the Norwegian Animal Care Authority (Forsøkdyrutvalget). Captured birds were handled at short distance from the colony to avoid disturbance. Manipulations lasted about 10-15 minutes, and were processed in silence with the head of the birds black-hooded to minimise the stress of the birds. All birds came back to their nest shortly after their release. Behavioural observations were made in silence, under a camouflage blanket, from an average distance of 20 m using binoculars.

e) Statistical analyses

A PCA was performed on quantitative variables measured during focal observation in order to reduce the number of dependent variables prior to statistical analysis. PC1 and PC2, the two first principal components, were retained based on visual examination of the scree plot and on the Kaiser-Guttman 'Eigenvalues greater than one' criterion (Legendre and Legendre, 2012).

e-1) Assessing behavioural consistency and behavioural syndromes

Repeatability estimates were computed in order to assess temporal consistency of behavioural variables within a population (across the two breading seasons). As suggested by Nakagawa and Schielzeth (2010), we first controlled for confounding factors and we found that the identity of the handler and the time of the day were confounding factors for the attack score (ATTs, continuous variable). We therefore used the variances extracted from a Generalized Additive Mixed Models (GAMM) with an inverse-link Gamma distribution to compute a repeatability score for this variable as defined by Lessells and Boag (1987), i.e. an intra-class correlation coefficient (r), and we performed a parametric bootstrap to assess confidence intervals (C.I. 95%) of the estimate as suggested by Nakagawa and Schielzeth (2010). The gamma inverse-link distribution was selected based on inspection of the residuals that reveals skewness. On the other hand, we found no confounding factors for neither the continuous variables extracted from focal observations (i.e. PC1, PC2) nor the qualitative variables extracted from focal (VOC) and handling observations (ACTs, BOLs and VOCs). We therefore calculated repeatability as defined by Lessells and Boag (1987), based on variance components derived from a parametric ANOVA on the rank (Hedrick and Kortet, 2012) with individual as a factor and each composite behavioural variable as the dependent variable. A non-parametric analysis of variance (Kruskal-Wallis test) was performed to assess the significance of repeatability of individual behaviours (Hedrick and Kortet, 2012).

Using this last method, we also assess the temporal consistency of individuals behaviours expressed in natural environment according to their individual (i.e. sex, SSI and BCI) and nesting habitat characteristics (i.e. centrality, exposure and density), and to the breeding seasons. Finally, still using the same method, we assess the consistency of behavioural differences between individuals of different individual and nesting habitat characteristics, and between individuals breeding during two subsequent seasons (therefore only for individuals we had observations for both seasons in this case).

The existence of behavioural syndromes was then assessed using Spearman rank correlations between behavioural variables extracted from two different contexts (i.e. natural environment and manipulation by human).

We decided to not exclude individuals observed only once because they contribute to the population-level variation in behavioural traits (Dammhahn and Almeling, 2012).

e-2) Assessing the link between behaviour and individual and nesting habitat characteristics

There was not confounding effect of the start time of the focal observations, and we did not expect non-linear relationship with any other variable. We therefore used Generalised Linear Mixed Models (GLMMs), fitted with Penalized Quasi-Likelihood (PQL) and an inverse-link Gamma distribution, to evaluate the relationship between focal behavioural variables and individual (SSI, BCI, breeding status, sex) and environmental (nest site exposure, centrality, density; and local weather conditions: cloud cover, rain, wind, temperature and humidity) descriptors. Bird identity was included as a random term enabling us to account for repeated measures on the same individual. The most appropriate model was selected using the Quasi Akaike's Information Criterion (QAIC) computed with PQL (see Sharples et al., 2012). Because the residuals from the models, especially explaining PC2, revealed patterns that imply a failure of one or more assumptions of the models, we thus decided to average observations over individuals and use Generalised Linear Models (GLMs, with inverse link-Gamma distribution) to improve model fits. Same selected variables and trends were obtained for both PC1 and PC2, we thus decided to conserve these models with better residuals.

To assess intrinsic temporal consistency of the behaviours expressed at the nest site excluding variance linked to nesting habitat characteristics selected, we then performed

GLMs on the global datasets (i.e. with all observations) including these parameters. We subsequently computed repeatability estimates on the residuals of these models. As previously, we used the variance components derived from a parametric ANOVA on the rank with individual as a factor and residuals of each model as the dependent variable to do so, and a non-parametric analysis of variance (Kruskal-Wallis test) to assess the significance of repeatability scores.

We did not have enough individuals with repeated measures to run GLMMs on manipulation behavioural variables. Consequently, we used non-parametric Wilcoxon rank-sum tests to compare different groups (e.g. centre vs. periphery, exposed vs. protected, males vs. females, and 1st breeding season vs. 2nd breeding season), and Spearman rank correlations to assess relationships with continuous variables (e.g. heart rate). Differences were considered significant for $p < 0.05$, and Bonferroni's correction was applied whenever multiple comparisons were tested (differences were thus considered significant for $p < \frac{0.05}{n}$ with n the number of comparisons performed).

e-3) Breeding success

To investigate the relationship between breeding success and personality expressed at the nest site, we run a GLM with binomial distribution on the breeding success of the nest with the averaged behaviours of both mates and the interaction between both mates' behaviours as explaining variables. We also evaluated differences in behaviour between successful and failed breeders using non-parametric Wilcoxon rank-sum tests with Bonferroni's correction. We then assessed the temporal consistency of individuals behaviours expressed in natural environment according to their breeding output, and the consistency of behavioural differences between individuals of different breeding output, by computing repeatability score using the same method as for variables with no confounding factors. Finally, to assess the differences in breeding success according to the habitat and individual characteristics, we used Fisher's exact tests. All the analyses are performed for 2012 season only, as dataset was not sufficient for 2011.

All statistics were computed using the R 2.10.0 statistical environment (R Development Core Team, 2012). Except when Bonferroni's corrections were applied, the significance level is set at 0.05.

3 – Results

We retained the two first components of the PCA on focal observation variables with eigenvalues greater than 1 and almost twice higher than the other components (Table III - 1). The first component of the PCA (PC1 = Activity, later called ACT) explained 25% of the total variance and was mainly characterized by grooming, vocalising intensly and resting/sleeping behaviours. The second component of the PCA (PC2 = Aggressiveness, later called AGG) explained 22% of the total variance and was mainly characterized by the number of agonisitic interactions and the number of bites exchanged. We are using the terms 'activity' and 'aggressiveness' here as defined by Réale et al. (2007), i.e. the general level of activity of the individual while at its nest site, and its agonistic reaction toward a conspecific, respectively.

Table III - 1. PCA loadings of behaviours expressed by Brünnich's guillemots (N = 107 individuals) in their natural environment during focal observations (PC1: activity = ACT; PC2: aggressiveness = AGG). Bold type indicates behaviours that contributed importantly to a component.

***Tableau III - 1**. Poids de la PCA sur les comportements exprimés par les guillemots de Brünnich (N = 107 individus) dans leur environnement naturel durant les observations focales (PC1 : activité = ACT ; PC2 : agressivité = AGG). Les caractères gras indiquent les comportements qui contribuent de façon importante à une composante.*

Behaviour	PC1	PC2
# aggressive interactions[a]	0.11	**- 0.68**
# bites[b]	0.09	**- 0.68**
Aggression[c]	0.14	- 0.17
Grooming[d]	**0.34**	- 0.06
Grooming other[e]	0.03	0.05
Nest maintenance[f]	0.07	0.03
Vocalising[g]	**0.60**	0.17
Resting/Sleeping[h]	**- 0.69**	- 0.11
Eigenvalue	2.02	1.78
Variance explained (%)	25.30	22.30

[a] Number of aggressive interactions, [b] Number of bites (given/received/exchanged), [c] Proportion of time spent in aggressive interactions, [d] Proportion of time spent self-grooming, [e] Proportion of time spent allo-grooming (adult and /or chick), [f] Proportion of time spent in nest maintenance, [g] Proportion of time spent vocalising intensely, [h] Proportion of time spent standing still (resting/sleeping)

a) Behavioural consistency

Activity and boldness during handling were repeatable over all observations (ACT*s*: r = 0.11, χ^2_{118} = 147.47, p = 0.034; BOL*s*: r = 0.09, χ^2_{117} = 147.11, p = 0.031) but not attack (ATT*s*: r = 0.07, *C.I.* = [-0.09, 0.13]). Repeatability in the intensity of vocalisation during handling was similar than for the previous variables but was only marginally significant (VOC*s*: r = 0.13, χ^2_{118} = 141.8, p = 0.067). Among behaviours expressed at the breeding site then, activity, aggressiveness and vocalisation intensity were repeatable over all observations (ACT: r = 0.11, χ^2_{105}= 157.86, $p < 0.001$; AGG: r = 0.09, χ^2_{105} = 146.79, p = 0.004; VOC: r = 0.13, χ^2_{105} =164.99, $p < 0.001$; Table III - S1).

Moreover, individuals were more consistent in their aggressiveness in 2011 than in 2012 (AGG: r = 0.14, χ^2_{81} = 104.98, p = 0.039; AGG: r = 0.03, χ^2_{72} = 80.38, p = 0.2, respectively; Table III - S1), while they were equivalently consistent in 2011 and 2012 for activity (ACT: r = 0.13, χ^2_{81} = 102.41, p = 0.054; ACT: r = 0.13, χ^2_{72} = 104.07, p = 0.008) and vocalisation (VOC: r = 0.14, χ^2_{81} = 104.96, p = 0.038; VOC: r = 0.12, χ^2_{72} = 102.38, p = 0.011). In addition, we did not find any evidence of variance in averaged individual behaviour between the two breeding seasons in any behavioural parameters (all $p > 0.05$) (i.e. all variance observed was between individuals within a breeding season).

Temporal individual consistency varied according to individual and nesting habitat characteristics (Table III - S1). Interestingly, activity was more consistent for medium structural size index (SSI) individuals (ACT: r = 0.15, χ^2_{62} = 108.54, $p < 0.001$) than for low and high SSI individuals (ACT: r = 0.04, χ^2_{16} = 19.69, p = 0.2; r = 0.12, χ^2_{10} = 14.49, p = 0.2, respectively). Moreover, individual behaviour was significantly consistent for activity in protected habitat (ACT: r = 0.17, χ^2_{37} = 64.16, p = 0.004) but not in exposed habitat (ACT: r = 0.05, χ^2_{61} = 75.64, p = 0.1). Aggressiveness was also repeatable in both central (AGG: r = 0.11, χ^2_{40} = 59.90, p = 0.022) and peripheral habitats (AGG: r = 0.09, χ^2_{64} = 87.95, p = 0.025) with equivalent consistency. Furthermore, activity was consistent in high global density habitat (ACT: r = 0.14, χ^2_{41} = 63.15, p = 0.013) but not in low and medium global density habitat (ACT: r = 0.19, χ^2_{21} = 30.91, p = 0.075; r = 0.07, χ^2_{61} = 77.74, p = 0.073, respectively), and aggressiveness was significantly consistent in medium breeder density habitat (AGG: r = 0.11, χ^2_{62} = 82.95, p = 0.039) but not in low and high breeder density habitat (AGG: r = 0.05, χ^2_{38} = 44.57, p = 0.2; r = 0.08, χ^2_{33} = 41.84, p = 0.1, respectively).

Between individual differences were also consistent according to habitat characteristics but not to individual characteristics (Table III - S1). It is worth noticing that individuals breeding in exposed habitat differ consistently from protected breeders in their activity level (ACT: $r = 0.10$, $\chi^2_1 = 5.71$, $p = 0.017$).

b) Behavioural syndromes

Activity observed in the natural environment (ACT) was correlated to activity and boldness during the handling (ACT*s*: Spearman rank correlations: $r_s = -0.29$, $N = 89$, $p = 0.006$ and BOL*s*: $r_s = -0.22$, $N = 87$, $p = 0.043$, respectively). No correlation was found with intensity of the attacks (ATT*s*: $r_s = -0.16$, $N = 88$, $p = 0.1$), neither with intensity of vocalisation during the capture and handling (VOC*s*: $r_s = -0.12$, $N = 88$, $p = 0.3$). No correlation was found between aggressiveness (AGG) measured in the natural environment and the capture/handling-related behaviours (all $p > 0.05$). Vocalisation in the colony (VOC) was only correlated with the activity during the capture/handling (ACT*s*: $r_s = -0.22$, $N = 89$, $p = 0.032$).

c) Link between behaviour and individual and nesting habitat characteristics

Activity was explained by the global density and the exposure of the habitat, but also by the interaction between density and SSI (AIC = 191.24, ΔAIC = 1.87 with the closest model that also included the SSI and the interaction between exposure of the habitat and SSI; $n = 85$ observations; Table III - 2). Individuals breeding in low density habitat were less active than individuals breeding in medium and high density habitat (GLM: $t = -3.10$, $p = 0.003$ and $t = 2.01$, $p = 0.048$, respectively), but interestingly individuals breeding in medium density habitat were more active than individuals breeding in high density habitat ($t = 2.85$, $p = 0.006$; Fig. III - 1a and III - 2a). It is also interesting to note that individuals breeding in high density habitat were more active as their SSI increase ($t = -3.11$, $p = 0.003$), while we did not find any effect of SSI for individuals breeding in low or medium density habitat ($t = 0.36$, $p = 0.7$ and $t = -0.90$, $p = 0.4$, respectively). Individuals breeding in exposed habitat were less active than individuals breeding in protected habitat ($t = -3.81$, $p < 0.001$; Fig. III - 1b and III - 2b). After controlling for these nesting habitat parameters, individuals activity remained significantly temporally consistent ($r = 0.09$, $\chi^2_{99} = 138.28$, $p = 0.006$).

Table III - 2. Estimates of the fixed effects of generalised linear models of averaged a) activity (PC1: activity = ATC) and b) aggressiveness (PC2: aggressiveness = AGG) expressed by Brünnich's guillemots in their natural environment (N = 85 individuals).

***Tableau III - 2**. Estimations des effets fixes des modèles linéaire généralisés sur a) l'activité (PC1 : activité = ACT) et b) l'agressivité (PC2 : agressivité = AGG) moyennes exprimées par les guillemots de Brünnich dans leur environnement naturel (N = 85 individus).*

	Estimate	Std. Error	*t* value	*p*
a) PC1: ACT				
Intercept	2.841	0.617	4.604	**< 0.001**
Exposure (Exposed-Protected)	- 0.530	0.139	- 3.809	**< 0.001**
GDS – Low/Medium	-1.912	0.617	- 3.102	**0.003**
GDS – Low/High	-1.301	0.647	- 2.012	**0.048**
GDS – Medium/High	0.612	0.215	2.849	**0.006**
GDS - Low x SSI	0.182	0.502	0.362	0.719
GDS - Medium x SSI	-0.049	0.054	- 0.902	0.370
GDS - High x SSI	-0.417	0.134	- 3.112	**0.003**
b) PC2: AGG				
Intercept	0.301	0.017	17.879	**< 0.001**
Centrality (Central-Peripheral)	- 0.046	0.013	- 3.494	**< 0.001**
BDS – Low/Medium	-0.022	0.014	- 1.491	0.100
BDS – Low/High	-0.046	0.018	- 2.514	**0.010**
BDS – Medium/High	-0.024	0.015	- 1.669	0.100

Exposure referred to the exposure of the breeding site in terms elements and predation; bimodal.
Global Density Score (GDS) referred to the number of breeders and non-breeders within ca. 0.5 m around the breeding site; 3 categories defined as follow: Low for GDS < 4, Medium for 4 ≤ GDS < 8, and High for GDS ≥ 8 (classes of equal size according to the distribution of the score).
SSI referred to the structural size index; continuous.
Centrality referred to the centrality of the breeding site in the colony according to its position within or above the first row of breeding sites; bimodal.
Breeder Density Score (BDS) referred to the number of breeders within ca. 0.5 m around the breeding site; 3 categories defined as follow: Low for BDS < 2.5, Medium for 2.5 ≤ BDS < 5, and High for BDS ≥ 5 (classes of equal size according to the distribution of the score).

Aggressiveness was explained by the breeder density and the centrality of the nest (AIC = 245.2, ΔAIC = 1.06 with the closest model that also included the SSI; n = 85 observations; Table 2). Individuals breeding in high breeder density habitat were less aggressive than the ones breeding in low breeder density habitat (GLM: $t = -2.51$, $p = 0.010$; Fig. III - 1a and III - 1c). In contrast, no differences were observed between individuals breeding in low and medium breeder density habitat ($t = -1.49$, $p = 0.1$) and between individuals breeding in medium and high breeder density habitat ($t = -1.67$, $p = 0.1$). Individuals breeding in peripheral habitat were less aggressive than the ones breeding in central habitat ($t = -3.49$, $p < 0.001$; Fig. III - 1c and III - 2d). After controlling for these nesting habitat parameters, individuals aggressiveness became more temporally consistent ($r = 0.29$, $\chi^2_{105} = 241.14$, $p < 0.001$).

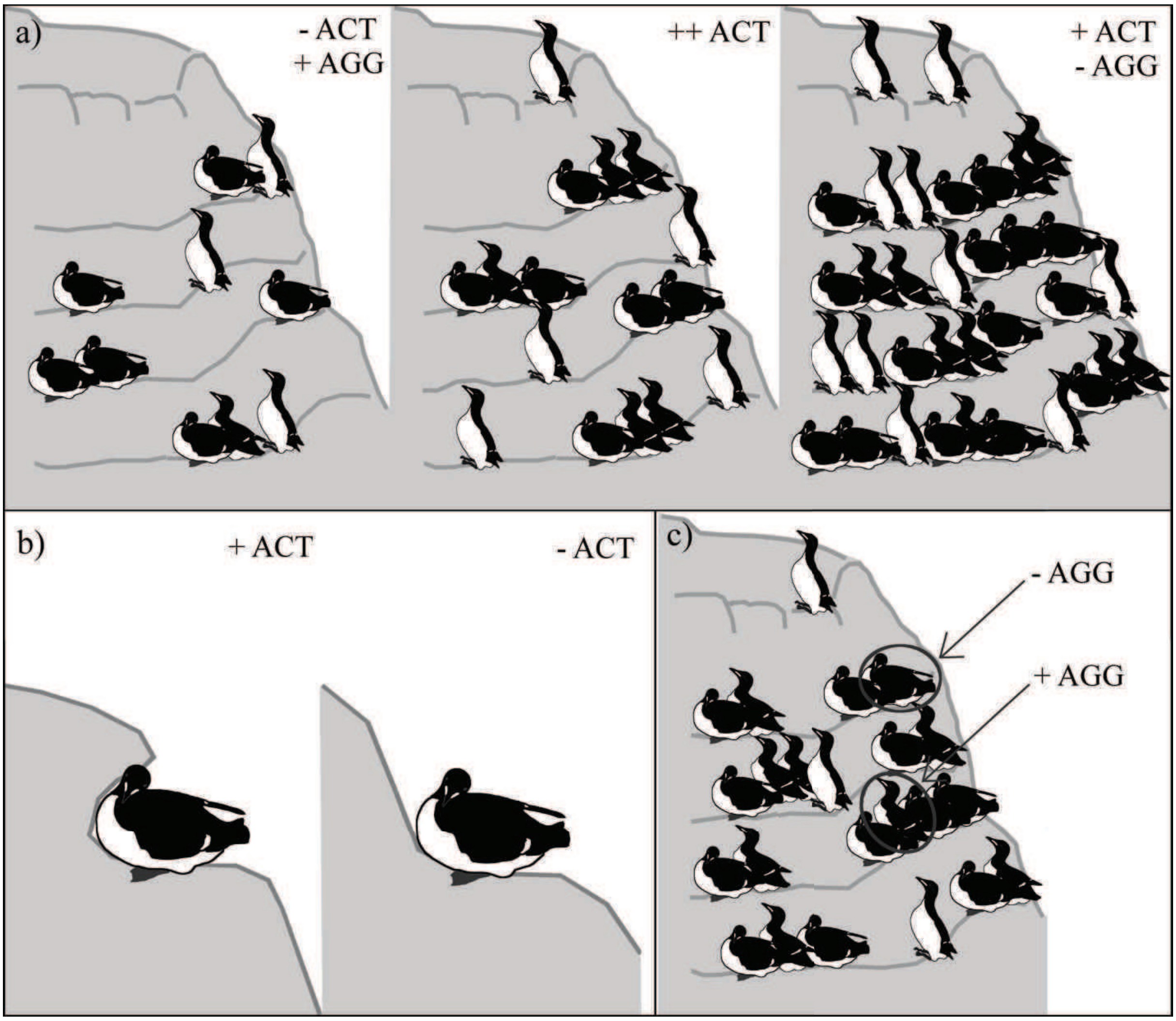

Figure III - 1. Summary of observed behaviours in natural environment according to a) the breeder and global density around the nest, b) the exposure of the nest, and c) the centrality of the nest. ACT = Activity; AGG = Aggressiveness; signs indicate the relative level of behaviour of individuals compared to other habitat types. Standing birds represent 'non-incubating'/'non-guarding' individuals, sitting birds represent incubating/guarding individuals.

***Figure III - 1**. Résumé des comportements observés en milieu naturel en fonction de a) la densité de reproducteurs et la densité globale autour du nid, b) l'exposition du nid, et c) la centralité du nid. ACT = activité ; AGG = agressivité ; les signes indiquent le niveau comportemental relatif des individus dans un type d'habitat par rapport aux individus des autres types d'habitat. Les oiseaux debout représentent les individus qui n'incubent pas/ne sont pas en phase de garde, les oiseaux assis représentent les individus qui incubent/sont en phase de garde.*

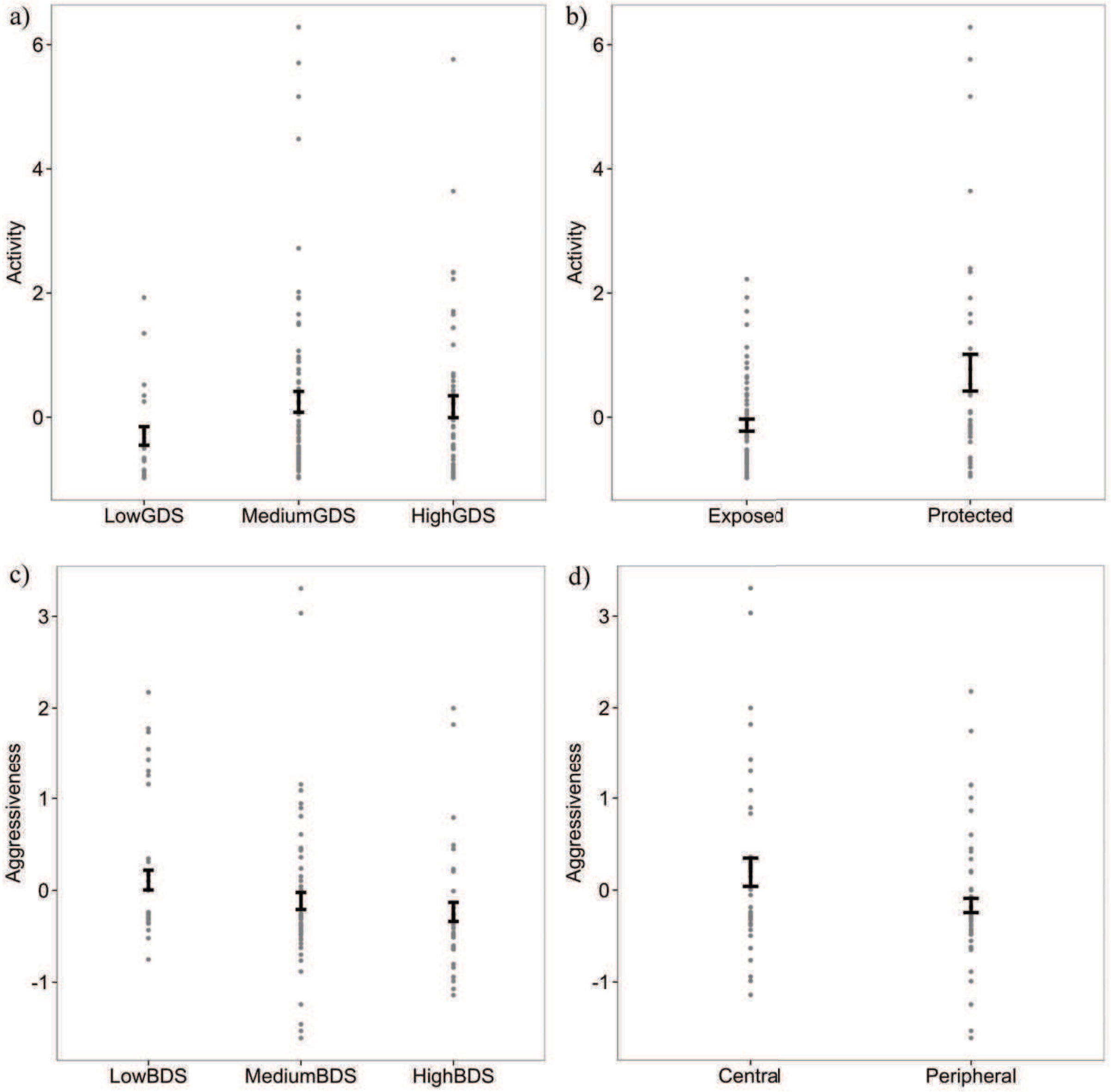

Figure III - 2. Behaviours expressed by Brünnich's guillemots (N = 107 individuals) in their natural environment: Activity (ACT) according to a) the global density (GDS) around the breeding site (Low: less than 4 individuals on average around the breeding site; Medium: between 4 and 8 individuals; High: more than 8 individuals) and b) the exposure of the breeding site; and Aggressiveness (AGG) according to c) the breeder density (BDS) around the breeding site (Low: less than 2.5 breeders on average around the breeding site; Medium: between 2.5 and 5 breeders; High: more than 5 breeders) and d) the centrality of the breeding site. Error bars represent means ± standard error.

Figure III - 2*. Comportements exprimés par les guillemots de Brünnich (N = 107 individus) dans leur environnement naturel : Activité (ACT) en fonction de a) de la densité globale (GDS) autour du site de reproduction (« Low » : moins de 4 individus en moyenne autour du site de reproduction ; « Medium » : entre 4 et 8 individus ; « High » : plus de 8 individus) et b) l'exposition du site de reproduction ; et Agressivité (AGG) en fonction de c) la densité de reproducteurs (BDS) autour du site de reproduction (« Low » : moins de 2,5 reproducteurs en moyenne autour du site de reproduction ; « Medium » : entre 2,5 et 5 reproducteurs ; « High » : plus de 5 reproducteurs) et d) la centralité du site de reproduction. Les barres d'erreur représentent les moyennes ± erreur standard.*

Activity and aggressiveness were explained neither by sex, nor year, nor climate variables.

Our results also showed that some of these capture/handling-related personality traits differed between sexes and were correlated with heart rate at the beginning of the manipulation (HR*i*). Females were significantly more active than males (ACT*s*: $W = 580$, $N_{♂} = 38$, $N_{♀} = 43$, $p = 0.011$) and were biting more (ATT*s*: $W = 573$, $N_{♂} = 37$, $N_{♀} = 43$, $p = 0.015$), but they were not bolder than males (BOL*s*: $W = 701$, $N_{♂} = 36$, $N_{♀} = 43$, $p = 0.5$). HR*i* was positively correlated to the activity and boldness scores of the individuals (ACT*s*: Spearman rank correlations: $r_s = 0.31$, $N = 49$, $p = 0.028$, and BOL*s*: $r_s = 0.36$, $N = 49$, $p = 0.010$). Individuals caught in 2011 were significantly more active and bolder, and they were biting less than individuals caught in 2012 (ACT*s*: $W = 2832$, $N_{2011} = 79$, $N_{2012} = 60$, $p = 0.018$; BOL*s*: $W = 2778$, $N_{2011} = 78$, $N_{2012} = 59$, $p = 0.013$; ATTs: $W = 1057$, $N_{2011} = 78$, $N_{2012} = 60$, $p < 0.001$). We did not find any other behavioural difference during the 'Resistance to handler' tests, neither according to the nesting habitat or weather descriptors, nor the individual characteristics or their breeding output (all $p > 0.05$).

d) Breeding success

Personality at the nest expressed by both mates did not explain their breeding success. However, successful breeders vocalised, on average, more intensely than failed breeders (VOC: $W = 874$, $N_{\text{success}} = 35$, $N_{\text{failure}} = 34$, $p < 0.001$). Moreover, vocalisation intensity in the colony was significantly repeatable between individuals with the same breeding output (VOC: $r = 0.25$, $\chi^2_1 = 10.60$, $p = 0.001$). Individual behaviour of the successful birds was repeatable for activity and vocalisation intensity observed in the natural environment (ACT: $r = 0.19$, $\chi^2_{35} = 65.60$, $p < 0.001$; VOC: $r = 0.09$, $\chi^2_{35} = 48.84$, $p = 0.048$), but not for aggressiveness (AGG: $r = 0.05$, $\chi^2_{35} = 41.99$, $p = 0.2$), while for failed birds, neither activity, nor aggressiveness, nor vocalisation intensity were repeatable (all $p > 0.05$).

There were no significant differences in terms of breeding success between habitats or between individual characteristics. However, individuals seemed to breed more successfully in central habitat than in peripheral habitat (62% *vs.* 44%; $p = 0.2$, $N = 45$), and in high global density habitat than in low and medium global density habitats (67% *vs.* 47% and 36%, respectively; $p = 0.2$, $N = 45$).

4 – Discussion

a) Behavioural consistency and behavioural syndromes

We found consistent individual variations in three behavioural axes in wild Brünnich's guillemots: activity and aggressiveness at the breeding site as well as activity and boldness in a threatening situation (i.e. handling). Individual behavioural differences were consistent over time and repeatability indices increased for activity and aggressiveness at the breeding site after removing the variation explained by habitat and individual characteristics. These results suggest that activity and aggressiveness in this species are intrinsic personality traits and that habitat and individuals' characteristics are sources of inter-individual heterogeneity in these traits. Although significant, repeatability of personality traits in Brünnich's guillemots was relatively moderate (see Bell et al., 2009 for a review of range of repeatability observed in personality traits), suggesting a probable moderate heritability and genetic influence over these traits (Boake, 1989) that are likely to be influenced by the environment (Nussey et al., 2007).

Contrary to numerous previous studies, no correlation was found between aggressiveness at the breeding site and boldness in a threatening situation in the Brünnich's guillemot. Personality is reflected in the ecology of an individual, that is to say in its habitat use and its interactions with conspecifics and predators, for instance. It should therefore affect the fitness of an individual through its impact on survival and breeding performance (Both et al., 2005; Boon et al., 2008; Cote et al., 2008; Kontiainen et al., 2009; Boyer et al., 2010). Wilson (1998) proposed that context specificity in personality should be favoured by natural selection, theory that could explain our absence of aggressiveness-boldness behavioural syndrome. For instance, aggressiveness may be advantageous in a social context where it may lead to a better access to and defence of resources (Oakeshott, 1974; Fornasieri et al., 1990; Henderson and Hart, 1995; Sih et al., 2014), but disadvantageous in an anti-predator context (referred to as boldness in this context) because it might increase mortality (Wilson et al., 2010). However, many studies have already shown the existence of an aggressiveness-boldness syndrome in different species (e.g. three-spined sticklebacks, *Gasterosteus aculeatus*, Tulley and Huntingford, 1988; web spiders, *Agelenopsis aperta*, Riechert and

Hedrick, 1993), but also between other personality traits such as aggressiveness and exploration (e.g. field cricket, *Gryllus integer*, Kortet and Hedrick, 2007) or sociability, boldness and activity (e.g. comb-footed spiders, *Anelosimus studiosus*, Pruitt and Riechert, 2009). Here, we also found that activity at the breeding site was negatively correlated to activity and boldness in a threatening situation, revealing the existence of a behavioural syndrome in Brünnich's guillemots. Activity at the breeding site reveals self-maintenance behaviours, such as grooming and resting/sleeping behaviours, but also vocalisation implying communication that can be linked to resource acquisition and conservation (Danchin et al., 2005). Activity can therefore be considered as enhancing individual survival and breeding success. In contrast, boldness is often assumed to be costly, since it can increase mortality (Wilson et al., 2010). However, the optimal behaviour can also differ across situations within the same context. For instance, Quinn and Cresswell (2005) found that, in low predation risk situation, 'freezing' behaviour toward a predator, which was negatively correlated with low level of activity measured in a novel environment, was the optimal response in common chaffinches, *Fringilla coelebs*, since it allows individuals to be less detectable by the predator. On the other hand, on a high predation risk situation, 'freezing' behaviour was considered as maladaptive, since it increases the risks of predation. In wild animals, handling by human represents a threatening situation (Macleod and Gosler, 2006). A high degree of boldness and activity measured during this context might therefore be considered as adaptive, since they suggest a greater chance for escape. The hypothesis that boldness can be adaptive in Brünnich's guillemots is reinforced by their propensity to chase, and even attack, their offspring's predator, the Glaucous gull, *Larus hyperboreus* (personal observation), decreasing risks of breeding failure. Phenotypic correlations between personality traits are known to arise from common behavioural structure with common underlying physiological, neurobiological and/or cognitive system, and/or genetic backgrounds between traits (Fairbanks et al., 1999; Koolhaas et al., 1999; Drent et al., 2003; Koolhaas et al., 2010; Ferrari et al., 2013) implying constraint in their co-evolution. These correlations might be advantageous in an evolutionary context, since it might facilitate the adaptation and evolution of the traits (see Wolf and Weissing, 2012). However, if strong opposite directional selection pressures are exerted on two correlated traits of a behavioural syndrome, it might become disadvantageous and explain the coexistence of different behavioural types associated with different fitness values (see Stearns, 1992; Sih et al., 2004a). Our results support both hypotheses of context specificity and phenotypic correlations in personality, which suggests that the latter hypotheses are not mutually exclusive to explain the maintenance of different behavioural types, associated with different fitness values in a population.

b) Personality as indicator of individual and/or habitat characteristics?

We found a relationship between activity at the breeding site and individual structural size. Moreover, activity and boldness in a threatening situation were related to sex and initial heart rate (at the beginning of the manipulation). The state of an individual refers to all the features that can affect its performances and behaviour, and therefore have an influence on its fitness (McNamara and Houston, 1996; Clark and Mangel, 2000). It includes age, experience, and quality (Wilson and Nussey, 2010) that is characterised by intrinsic individual parameters, such as size and/or morphology, physical and/or physiological conditions (body reserves, hormonal levels, etc.). In a state-dependent behavioural model, individual differences in any component of the state should be reflected in the individual differences in behaviour (see Wolf and Weissing, 2010). Consequently, consistent individual behavioural differences (or personality) might reflect individual differences in inherently stable state components, such as the size, basal metabolic rates or neurological structure (e.g. Careau et al., 2008; Gardini et al., 2009). Our results support this hypothesis of the personality reflecting the quality of an individual. However, no relationships were found between heart rate or sex and activity at the breeding site, and between structural size and activity and boldness in a threatening situation, suggesting that we did not succeed in capturing the common stable structure underlying behavioural syndromes formed by these personality traits in the population.

Activity and aggressiveness at the breeding site of Brünnich’s guillemots varied according to microhabitat characteristics. As expected, individuals were consistent in their behaviour within a habitat, although we observed different degrees of plasticity according to the habitat, and behavioural differences between individuals breeding in different habitats were also consistent. For instance, we found differences in activity and aggressiveness at the breeding site according to conspecific density. Individuals breeding in low global density habitat were less active than individuals breeding in medium and high global density, and individuals breeding in medium density habitat were more active than individual breeding at high density. According to the ‘many eyes’ hypothesis (Dimond and Lazarus, 1974), in a group of individuals such as a seabird colony, individuals may benefit from the vigilance of the other group members and, consequently, they may decrease their own vigilance in favour of other behaviours, such as self-maintenance (Le Bohec et al., 2005). This theory might explain the lower level of activity observed in low global density habitat compared to medium and high global density habitat. Moreover, we found that individuals breeding in high breeder density habitat were less aggressive. Territoriality often implies agonistic interactions to defend the territory (Burt, 1943), which might be costly in a colonial environment where high densities might be reached. For instance, Viera et al. (2011) found that, in the colonial and territorial King penguin, *Aptenodytes patagonicus*, agonistic interactions were energetically costly, with physical agonistic interactions being more costly than non-physical ones. In Brünnich's guillemots, almost all agonistic interactions imply physical contact (personal observation). This might explain why individuals breeding in high breeder density habitat were less aggressive. In our study species, being consistently more aggressive would therefore be too costly, and considered as maladaptive in habitats where the probability of agonistic interactions is high. In contrast, the moderate levels of aggressiveness and high levels of activity observed in medium density habitat appeared to reflect the higher quality of this habitat, in terms of equilibrium between the benefits and costs of breeding density in a colonial system. We also found that breeders more exposed to predation and weather conditions according to the topography of the nest were less active and more plastic in this behaviour than individuals breeding in protected habitats. Therefore, protected habitats appeared more suitable to allocate time to self-maintenance activities, in addition to offer individuals a more clement micro-environment allowing them to decrease their energy expenditure. On the other hand, individuals breeding in exposed habitats where external pressures are certainly more variable, displayed a higher degree of plasticity in their activity, suggesting that they were more 'reactive' to their environment ('reactive-proactive' axis, Koolhaas et al., 1997; Sih et al., 2004a), This result is in accordance with those obtained by Quinn and Cresswell (2005) showing that individuals with low activity levels were more plastic in their response to risky situations, which was associated with reactivity. Moreover, we found that central Brünnich's guillemots were more aggressive than peripheral ones. The 'central-periphery model' (Coulson, 1968) predicts that central territories are of higher quality compared to peripheral territories. Thus, higher level of aggressiveness we observed in central breeding sites revealed better territory defence from those individuals, supposed to enhance their breeding performances. Brünnich's guillemot is a highly philopatric territorial species (Gaston et al., 1994; Steiner and Gaston, 2005). Consequently, breeding habitat in this species may be considered as an inherently stable state to some extent at the individual level. Heterogeneity of breeding site quality within a colony is known to affect individual quality components and performances (Southwood, 1977). However, individual quality may also facilitate the access to (and the preservation of) a good quality habitat, enhancing, in turn, the performances of the individual and therefore subsequent selection of this habitat (Coulson, 1968) through information acquisition and learning processes (Danchin et al., 2005). Such positive feedback might even further stabilise the relationship between individual and habitat quality, giving rise to behavioural consistency (Wolf et al., 2008; Dingemanse and Wolf, 2010), and explaining the strong relationships we found between personality and individual/habitat characteristics in this species.

c) Fitness consequences and conclusions

We found that successful breeders vocalised consistently more than unsuccessful ones. They were also more consistent in their activity level than failed breeders. Though, personality did not directly explain breeding success, these results support our previous hypothesis that higher self-maintenance and communication, yielded by higher quality habitats, might indirectly enhance breeding performances. Furthermore the higher repeatability displayed by successful breeders could suggest selection against flexibility (Dingemanse and Réale, 2013). Breeding success tended to be better in central habitats compared to the periphery of the colony (62% *vs.* 44%), and in high density habitat compared to low/medium density ones (67% *vs.* 47%/36%). The high aggressiveness level of central breeders and the low aggressiveness and moderate activity levels of the individuals breeding in high density parts of the colony consequently appeared to confer them better breeding performances. In one of the rare studies linking personality, habitat and breeding success, Cote et al. (2008) have shown that social female common lizards, *Lacerta vivipara*, reproduced better in low-density populations.

Our study reveals for the first time strong relationships between personality, individual and habitat qualities in a wild Arctic species, and highlights the role of personality in the structuration of animal colony. The monitoring of personality traits in longitudinal studies, combined with measures of heritability through pedigree construction or cross-fostering experiments, should help disentangling the multiple levels of selection (e.g. ecological conditions, social context) that favour the evolution and co-evolution of personality traits. Personality is now recognized to be part of the pace of life syndrome of a population (Réale et al., 2010b; Niemelä et al., 2013), that is to say the set of physiological and behavioural parameters that co-evolved with the life-history traits of this population. Therefore, it is very likely that the cumulative effects of personality traits on individual fitness and life-history traits play a key role on population dynamics (see Wolf and Weissing, 2012). Our results bring new insight on the relationship between environmental conditions on land (i.e. breeding habitat) and avian personalities, which ultimately can affect the individual fitness and population persistence. This further emphasises the need for more long-term integrative studies on these two parameters in order to explain a greater amount of observed variance and better gauge the adaptive potential of these polar populations to face future ecosystem changes.

Acknowledgments

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Supplementary Material

Table III - S 1. Estimation of repeatability indices (r) of behaviours expressed by Brünnich's guillemots (N = 107 individuals) in their natural environment (a) PC1: Activity = ACT; b) PC2: Aggressiveness = AGG; c) Vocalisation intensity = VOC). Results of the Kruskal-Wallis tests. Bold type indicates repeatability indices that were significantly different from zero.

***Tableau III - S1**. Estimation des indices de répétabilité (r) des comportements exprimés par les guillemots de Brünnich (N = 107 individus) dans leur environnement naturel (a) PC1 : Activité = ACT ; b) PC2 : Agressivité = AGG ; c) Intensité de vocalisation = VOC). Résultats des tests de Kruskal-Wallis. Les caractères en gras indiquent les indices de répétabilité qui diffèrent significativement de zéro.*

Table footnotes :

r: repeatability index
χ^2, *df*: chi-squared statistic and degree of freedom
p: p-value
V_a: variance among groups
V_w: variance within groups
N: number of groups
k: number of observations per group adjusted for unbalanced design
Exposed/Protected: exposure of the breeding site in terms of elements and predation
Central/Peripheral: centrality of the breeding site
GDS: Global Density Score of the breeding site (Low: less than 4 individuals on average around the breeding site; Medium: between 4 and 8 individuals; High: more than 8 individuals, classes of equal size)
BDS: Breeder Density Score of the breeding site (Low: less than 2.5 breeders on average around the breeding site; Medium: between 2.5 and 5 breeders; High: more than 5 breeders, classes of equal size)
Males/Females: sex of the individuals
SSI: Structural Size Index of the individuals (Low: SSI < mean(SSI) – sd(SSI); Medium: mean(SSI) – sd(SSI) ≤ SSI < mean(SSI) + sd(SSI); High: mean (SSI) + sd(SSI) ≤ SSI)
BCI: Body Condition Index of the individuals (Low: BCI < mean(BCI) – sd(BCI); Medium: mean(BCI) – sd(BCI) ≤ BCI < mean(BCI) + sd(BCI); High: mean (BCI) + sd(BCI) ≤ BCI)
Success/Failure: breeding output at jumping for the 2012 breeding season as inferred from breeding site monitoring
2011/2012: year of the two breeding seasons

a) ACT	r	χ^2, df	p	V_a	V_w	N	k
Individual	**0.11**	157.86, 105	< 0.001	3078.84	23970.43	106	5.41
Exposed	0.05	75.64, 61	0.098	499.90	8696.11	62	5.39
Protected	**0.17**	64.16, 37	0.004	569.38	2695.98	38	5.16
Between-individual	**0.10**	5.71, 1	0.017	84.99	801.20	2	47.12
Central	**0.13**	63.53, 40	0.010	549.69	3623.84	41	5.42
Peripheral	**0.09**	88.35, 64	0.024	864.64	9121.33	65	5.37
Between-individual	**0.06**	3.93, 1	0.048	55.56	918.55	2	50.28
Low GDS	0.19	30.91, 21	0.075	91.21	397.92	22	3.47
Medium GDS	0.07	77.74, 61	0.073	524.32	6763.81	62	4.79
High GDS	**0.14**	63.15, 41	0.015	476.44	2812.84	42	4.68
Between-individual	0.01	3.18, 2	0.204	25.72	1999.13	3	46.95
Low BDS	0.08	48.65, 38	0.116	197.60	2150.71	39	4.29
Medium BDS	**0.14**	89.56, 62	0.013	782.46	4777.70	63	4.13
High BDS	0.08	41.61, 33	0.144	140.58	1592.97	34	4.17
Between-individual	**0.10**	10.83, 2	0.004	210.44	1957.49	3	50.66
Males	**0.10**	61.98, 43	0.030	472.70	4367.27	44	5.48
Females	**0.18**	87.33, 47	< 0.001	1147.19	5347.96	48	5.81
Between-individual	-0.01	0.46, 1	0.499	-8.52	717.30	2	45.91
Low SSI	0.04	19.69, 16	0.235	42.09	926.47	17	6.22
Medium SSI	**0.15**	108.54, 62	< 0.001	1729.26	9507.21	63	5.85
High SSI	0.12	14.49, 10	0.152	26.66	188.94	11	4.48
Between-individual	-0.02	1.28, 2	0.528	-12.04	703.40	3	21.44
Low BCI	0.02	17.06, 16	0.381	8.14	322.73	17	3.63
Medium BCI	**0.15**	105.44, 73	0.008	1027.44	5646.26	74	3.87
High BCI	**0.16**	35.28, 22	0.036	160.37	838.86	23	4.69
Between-individual	-0.02	0.74, 2	0.693	-26.10	1125.16	3	29.49
Success	**0.19**	65.60, 34	< 0.001	659.79	2791.67	35	5.81
Failure	-0.06	28.22, 32	0.658	-48.16	858.22	33	2.96
Between-individual	0.04	2.45, 1	0.118	16.92	382.27	2	33.97
2011	0.13	102.41, 81	0.054	655.28	4530.05	82	3.08
2012	**0.13**	104.07, 72	0.008	1116.71	7443.60	73	4.39
Between-individual	-0.02	0.38, 1	0.540	-9.78	717.89	2	46.00

b) AGG	r	χ^2, df	p	V_a	V_w	N	k
Individual	**0.09**	146.79, 105	0.004	2434.09	24608.09	106	5.41
Exposed	0.07	78.68, 61	0.063	603.75	8594.15	62	5.39
Protected	**0.14**	59.14, 37	0.012	464.15	2797.87	38	5.16
Between-individual	-0.02	0.11, 1	0.741	-16.08	849.31	2	47.12
Central	**0.11**	59.90, 40	0.022	464.85	3706.36	41	5.42
Peripheral	**0.09**	87.95, 64	0.025	850.57	9135.15	65	5.37
Between-individual	0.03	2.70, 1	0.100	32.34	929.67	2	50.28
Low GDS	-0.02	19.72, 21	0.539	-11.82	496.65	22	3.47
Medium GDS	**0.08**	80.12, 61	0.050	599.00	6690.60	62	4.79
High GDS	0.07	51.60, 41	0.124	227.98	3053.84	42	4.68
Between-individual	0.01	3.08, 2	0.215	23.39	2000.55	3	46.95
Low BDS	0.05	44.57, 38	0.215	121.91	2224.21	39	4.29
Medium BDS	**0.11**	82.95, 62	0.039	594.71	4961.99	63	4.13
High BDS	0.08	41.84, 33	0.139	144.28	1589.40	34	4.17
Between-individual	**0.08**	9.27, 2	0.009	171.21	1982.81	3	50.66
Males	0.08	58.77, 43	0.055	392.82	4445.08	44	5.48
Females	**0.09**	67.10, 47	0.028	571.85	5909.37	48	5.81
Between-individual	-0.02	0.01, 1	0.922	-15.55	720.84	2	45.91
Low SSI	-0.04	12.23, 16	0.728	-43.02	1005.66	17	6.22
Medium SSI	**0.07**	83.38, 62	0.036	794.45	10425.56	63	5.85
High SSI	**0.24**	18.81, 10	0.043	52.32	165.94	11	4.48
Between-individual	0.03	3.39, 2	0.184	23.10	686.66	3	21.44
Low BCI	-0.03	14.73, 16	0.544	-9.71	339.46	17	3.63
Medium BCI	0.06	85.85, 73	0.144	406.77	6259.17	74	3.87
High BCI	**0.16**	35.45, 22	0.035	162.42	836.91	23	4.69
Between-individual	0	1.75, 2	0.416	-0.45	1111.90	3	29.49
Success	0.05	41.99, 34	0.163	166.90	3271.28	35	5.81
Failure	0.02	33.44, 32	0.397	18.41	793.96	33	2.96
Between-individual	-0.03	0.01, 1	0.946	-11.63	369.75	2	33.97
2011	**0.14**	104.98, 81	0.038	733.76	4452.39	82	3.08
2012	0.03	80.38, 72	0.233	291.92	8256.28	73	4.39
Between-individual	0.01	1.57, 1	0.210	8.95	708.42	2	46.00

Chapter IV – Behavioural Syndromes

Chapitre IV – Syndromes Comportementaux

Identifying behavioural syndromes through observations of captive, and non-captive colonial polar seabirds *– in prep Article 2*

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Keywords: personality; behavioural syndrome; natural environment; novelty test; habitat; individual quality.

1 – Introduction

Behaviour has been considered to be one of the most plastic phenotypic traits (West-Eberhard, 1989). However, animals often exhibit consistent behavioural patterns across time and/or situations, within and between behavioural contexts, which is called personality, temperament or behavioural syndrome (Gosling, 2001; Sih et al., 2004a; Réale et al., 2007). Understanding the emergence and the maintenance of personality traits, as well as their ecological and evolutionary consequences, have been of central interest for behavioural ecologists in the past decade, as attested by the growing literature on the topic (e.g. Dall et al., 2004; Sih et al., 2004a; Sih et al., 2004b; Dingemanse and Réale, 2005; Bell, 2007; Réale et al., 2007; Dingemanse and Wolf, 2010; Réale et al., 2010a; Wolf and Weissing, 2010; Wolf and Weissing, 2012).

To date, most studies in the new field of personality have been conducted under laboratory conditions with hand-reared models, artificially selected or not (Verbeek et al., 1996; Koolhaas et al., 1999; Marchetti and Drent, 2000; Drent et al., 2003; van Oers et al., 2004a; Hedrick and Kortet, 2012). This approach presents some advantages, such as to highlight contrasts between two extreme phenotypes and to limit the noise from uncontrolled parameters (Falconer, 1992; Koolhaas et al., 1999; Fuller et al., 2005; Koolhaas et al., 2010; Ferrari et al., 2013). However, in the wild, animals often exhibit a wide range of behaviours between the two extremes phenotypes of a studied trait, and their behaviour might not match the one expressed in captivity. For instance, Dingemanse and de Goede (2004) found that exploratory behaviour expressed in laboratory conditions, which predicted dominance in these conditions, did not correlate with the dominance in the wild in non-territorial great tits juveniles (*Parus major*). Moreover, environmental conditions that can influence personality traits and their impacts on fitness are more diverse and complex in the wild than in laboratory conditions (Archard and Braithwaite, 2010). Therefore, to understand how natural selection shapes or maintains individual differences in behaviour, personality research in wild populations is needed (Sih et al., 2004a; Réale et al., 2007; Archard and Braithwaite, 2010). Yet, for logistical and methodological reasons, personality studies on wild populations are difficult to implement. Indeed, they require long-term datasets on large numbers of individuals, and the design of experimental tests easy and quick to perform on the field (Réale et al., 2007; Archard and Braithwaite, 2010). Some studies conducted on wild populations have already succeeded identifying personality traits in natural conditions and to relate them to fitness components (e.g. Réale et al., 2003; Boon et al., 2008; Kontiainen et al., 2009; Dammhahn, 2012; Patrick et al., 2013) and environmental conditions (e.g. Biro et al., 2010; Carvalho et al., 2013). Despite that progress, experimental tests conducted on wild populations still need ecological and biological validations (Réale et al., 2007) that only rare studies have attempted. Indeed, biological validation of personality traits is necessary to identify the neurophysiological processes underlying them. For instance, Ferrari et al. (2013) found that, in wild alpine marmot (*Marmota marmota*), activity measured during experimental tests was positively correlated to breathing and heart rates (both indicators of metabolism) at the between-individual level, and to basal cortisol level at the within-individual level. Moreover, ecological validation is also needed to put personality in perspective into the evolutionary ecology framework. For instance, Dingemanse et al. (2003) found that in great tits (*Parus major*) exploration was positively correlated with natal dispersion.

In this study, we investigated if the behaviours expressed during tests performed in temporary captivity predicted the behaviour expressed in natural conditions in a wild population of king penguins (*Aptenodytes patagonicus*) breeding in a sub-Antarctic island. We first assessed the variation between individuals in behaviours expressed during novelty tests in captivity conditions. We then assessed the between-individual variation and within-individual consistency of behaviours expressed by individuals at their breeding site in natural conditions. We investigated the correlations between behaviours expressed in captivity and the personality traits measured in natural conditions into behavioural syndromes. Finally, to better understand forces that shape personality traits in natural environment, we examined the sources of inter-individual behavioural variation together with heterogeneity in individual and habitat quality.

2 – Material and Methods

a) Study area and capture protocol

The study was carried out in the king penguin *Aptenodytes patagonicus* colony of 'La Grande Manchotière' (ca. 20,000 breeding pairs, 46°25'S 51°45'E) on Possession Island, Crozet

Archipelago. During the austral summer 2011/2012, a total of 118 breeding individuals have been captured while they were leaving the colony. They were handled in a shelter several meters away from the colony. Birds were measured (flippers and beak), weighted, implanted under the skin with a passive transponder tag of 0.8 g (if not already marked), and blood-sampled for DNA sexing and haematocrit measurements. Individuals were marked with a unique code on their chest using non-permanent dye for visual identification in the colony.

b) Individual and habitat descriptors

Breeding status of the bird (i.e. on egg or chick) was recorded before each manipulation or observation. A structural size index (SSI) was defined as the first component of the principal component analysis (PCA) on morphometric measurements. PC1 = SSI = - 0.71 * (flipper, averaged, scaled-centred) - 0.71 * (beak, averaged, scaled-centred) explained 75% of the variation. SSI was better correlated with body mass than single measures. We therefore established a body condition index (BCI) as the residuals of the OLS regression of the SSI on body mass (Schulte-Hostedde et al., 2005; Peig and Green, 2010).

King penguins breed in dense colonies (Stonehouse, 1960; Barrat, 1976). They do not build a nest, but fiercely defend a *ca.* 0.5-0.8 m^2 territory (Côté, 2000). Thus, at the beginning of each observation, we assessed the density of the individual breeding territory by recording the number of settled breeders and wandering individuals present in a radius of *ca.* 0.5 m. We established two density scores for the breeding territory as follow: a breeder density score (BDS, composed of only settled breeders) and a global density score (GDS, composed of settled breeders and wandering individuals). Breeding sites were also defined as peripheral (*ca.* within the first 4 rows of breeding individuals) or central, and tick-infestation level was measured as the proportion of infested adults in a randomly-selected sample ($N = 50$ individuals) within a *ca.* 100 m^2 area.

c) Behavioural data collection

After manipulation, we performed a ‘novelty’ test by introducing each individual (N = 118) in an enclosed wooden pen ($l = 3$ m x $w = 3$ m x $h = 2$ m) situated *ca.* 10 m away from the colony, to avoid external stimuli, and monitored with video records. Pen was covered with a net, and made of a natural soil and grass ground on which a grid of 16 cells (75 cm x 75 cm) was painted to assess the surface explored. The experiment started when the hood was taken off the bird's head and lasted *ca.* 65 minutes. A novel object, a yellow bucket ($r = 6$ cm x $h = 20$ cm), was placed in advance in the pen, as well as a draped mirror ($l = 1.5$ m x $w = 1$ m). Return to basal heart rate after manipulation by humans take between 15 and 20 minutes in this species (Viblanc et al., 2012). The mirror was therefore unveiled (from outside the pen) 45 minutes after the beginning of the experiment to allow penguins to recover from the handling stress and explore the pen before being introduced with this new element. For ethical reasons, birds were only tested once.

Behavioural focal observations of 15 minutes of previously captured individuals at their breeding site were also performed ca. every 5 days during the incubation and brooding phases of the breeding cycle. To avoid bias linked to the daily pattern of activity previously identified in this species (Nesterova et al., 2010), focal observations were randomly conducted between 6 a.m. and 10 a.m. We collected data from 1 to 9 focal observations on 106 individuals (i.e. both members of a pair whenever it was possible, and depending on the timing of their breeding failure).

d) Measuring personality

From 'novelty' tests, we recorded the latency before the first movement of the bird (in min), the surface of the pen explored (in %), the time spent walking around inside the pen (in %), the time spent in self-maintenance behaviours (i.e. grooming, shaking itself) (in %), the time spent resting/sleeping (in %), the number of random vocalisations (excluding vocalisations towards novel objects) (number/hour), and the number of times the birds defecated (total number). We also extracted behaviours linked to the reaction of the bird towards a novel object: the latency before approaching the bucket and the mirror (in min), the number of bites and flipper hits towards the bucket and the mirror (total number), the number of vocalisations towards the bucket and the mirror (total number), and the time spent in interactions with the bucket and the mirror.

From focal observations of the individual on its breeding territory, we recorded the time spent resting/sleeping, in self-maintenance (i.e. grooming, shaking itself), in offspring care (i.e. ventilating, grooming, or feeding the chick), in vigilance (i.e. continuously moving the head around, watching out), and in agonistic interactions (both threatening and physical interactions). We also extracted the number of agonistic interactions, the number of bites and flipper hits given by the focal individual during agonistic interactions, and the number of vocalisations during threatening and vigilant phases.

e) Statistics

PCAs were performed independently on quantitative variables collected during ‘novelty’ tests and focal observations in order to reduce the number of dependent variables prior to further analyses. The number of components retained was based on visual examinations of the scree plot and on the Kaiser-Guttman ‘Eigenvalues greater than one’ criterion.

Then, the consistency of behaviours displayed in natural environment was established by computing repeatability scores within the population. Following Dammhahn and Almeling (2012) suggestion, we did not exclude individuals for which we had only one observation, as they contributed to behavioural trait variation at the population level. After examining residual normality and between-group homoscedasticity, we used a non-parametric Kruskal-Wallis ANOVA to assess the statistical significance of repeatability scores (Hedrick and Kortet, 2012). We calculated repeatability indices as an intra-class correlation coefficient (*r*) (Lessells and Boag, 1987) based on variance components derived from a parametric ANOVA on the rank (Hedrick and Kortet, 2012), with individual identity and each composite behavioural variable as the dependent variable. We then first examined the behavioural temporal consistency within individuals, and the consistency of the differences between individuals within each group, i.e. birds with the same individual features: sex, SSI, BCI; birds breeding in the same type of habitat: centrality, density, tick-infestation; same breeding output, and same breeding season. These ‘within-individual consistency’ scores gave us insights on potential influences of biotic and abiotic parameters on individual flexibility. In a second step, we explored the behavioural consistency between individuals within each group, and the consistency of the between-individual differences between those groups. These ‘between-individual consistency’ scores informed us on the behavioural homogeneity between individuals with the same characteristics.

Moreover, we used Generalised Linear Models (GLMs), fitted with an inverse-link Gamma distribution, to evaluate the relationship between composite behavioural variables extracted from focal observations averaged on individuals, and individual (sex, SSI, BCI, haematocrit level) and breeding habitat (density, centrality, tick infestation) characteristics. The most appropriate model was selected using the Akaike’s Information Criterion (AIC)

(Symonds and Moussalli, 2011). Model validation was based on the analysis of the residuals that did not reveal any violation of model assumptions.

Finally, the existence of behavioural syndromes was assessed using Spearman rank correlations between behavioural variables extracted from ‘novelty’ tests and focal observations.

f) Ethical statement

All procedures were in compliance with the French laws on animal experiments and welfare and all protocols were approved by the ethical committee of the French Polar Institute (Institut Polaire Paul-Emile Victor, IPEV). Authorizations to enter the breeding site (permits n° 2011-107 issued on the 14th of October 2011) and handle birds (permits n° 2011-98 issued on the 14th of October 2011) were delivered by the Terres Australes et Antarctiques Françaises (TAAF). Birds head was blackhooded during manipulation, which lasted about 10 minutes and was conducted in silence outside the colony in order to minimise the stress of the handled bird and the disturbance to the colony. Birds were then placed in blinded experimental pens. The time the birds spent in the pens was defined to optimise behavioural measurements while minimising the stress of the experiment. During focal observations, birds were observed in silence at a distance ranging from 10 to 40 m using binoculars.

3 – Results

a) Captive experiments

Overall, birds did their first movement on average 5.67 minutes after the beginning of the experiment (Table IV - 1). The surface of the pen explored by the birds was highly variable (between 6% and 100% of the pen). They spent up to 24% of their time walking around inside the pen. They also approached the mirror faster than the bucket (average latency 22.02 minutes vs. 49.87 minutes, respectively) but did not spent much time in interactions with neither of them.

Table IV - 1. Summary of behavioural parameters expressed by king penguins (N = 118 individuals) during novelty tests.

Tableau IV - 1*. Résumé des paramètres comportementaux exprimés par les manchots royaux (N = 118 individus) lors des tests de nouveauté.*

	Mean	**Std. Dev.**	**Minimum**	**Maximum**
Latency before the 1^{st} movement (min)	5.67	14.85	0	65.00
Surface of the pen explored (%)	50.00	31.95	6.25	100.00
Time spent walking around inside the pen (%)	2.64	3.76	0	23.76
Time spent grooming/shaking (%)	4.44	7.16	0	59.30
Time spent resting/sleeping (%)	92.86	8.43	0	100.00
# of random vocalisations (number/hour)	0.03	0.17	0	0.90
# of time a bird defecated (total number)	0.85	0.95	0	3.82
Latency before approaching the bucket (min)	49.87	25.94	0.07	65.00
# of bites/flipper hits towards the bucket (total number)	0.20	0.53	0	3.00
# of vocalisations towards the bucket (total number)	0.04	0.46	0	5.00
Latency before approaching the mirror (min)	14.23	4.32	0.45	20.00
# of bites/flipper hits towards the mirror (total number)	0.03	0.21	0	2.00
# of vocalisations towards the mirror (total number)	0.01	0.09	0	1.00
Time spent in interactions with novel objects (min)	0.04	0.21	0	2.20

The three first components of the PCA on the behavioural variables obtained during the captive experiment explained 22%, 17% and 12% of the total variance, respectively. The first component was mainly characterised by the surface of the pen explored by the birds, and the time spent walking around inside the pen and resting/sleeping. It therefore described an axis of exploration in a novel environment, later called EXPe (Table IV - 2). The second component was mainly characterised by the number of beak and flipper hits towards the bucket, and the number of vocalisations towards the bucket and the mirror. It was defined a first axis of interactions with a novel object, later called EXPo1. The third component was mainly characterised by the time spent in self-maintenance, the latency before approaching the mirror, the number of beak and flipper hits towards the mirror, and the time spent in interactions with the novel objects. We therefore defined a second axis of interactions with a novel object, later called EXPo2.

Table IV - 2. PCA of the behaviours expressed during novelty test in 118 king penguins. Bold type indicates behaviours mainly contributing to a component.

***Tableau IV - 2**. Analyse en composante principale des comportements exprimés durant des tests de nouveauté par 118 manchots royaux. Les caractères en gras indiquent les comportements contribuant principalement à une composante.*

Behaviour	Exploration in novel environment (EXPe)	Interaction with novel objects 1 (EXPo1)	Interaction with novel objects 2 (EXPo2)
Latency before the 1st movement	- 0.24	0.01	0.11
% of surface of the pen explored	**0.46**	- 0.05	0.02
% in walking around inside the pen	**0.41**	- 0.06	0.00
% in grooming/shaking	0.29	- 0.16	**- 0.43**
% in resting/sleeping	**- 0.43**	0.16	0.35
# of random vocalisations	0.01	0.00	- 0.07
# of time a bird defecated	0.01	0.00	- 0.30
Latency before approaching the bucket	- 0.30	0.03	- 0.05
# of bites/flipper hits towards the bucket	0.22	**0.42**	0.02
# of vocalisations towards the bucket	0.08	**0.62**	- 0.07
Latency before approaching the mirror	- 0.26	0.04	**- 0.45**
# of bites/flipper hits towards the mirror	0.16	- 0.05	**0.40**
# of vocalisations towards the mirror	0.08	**0.62**	- 0.07
% in interactions with novel objects	0.22	0.01	**0.46**
Eigenvalue	3.08	2.36	1.73
Variance explained (%)	21.99	16.85	12.33

b) Behavioural observations of the birds in their natural environment

The two first components of the PCA on the behavioural variables obtained during the focal observations of the birds at their breeding site explained 42% and 16% of the total variance. The first component, describing an axis of aggressiveness (later called AGG), was mainly characterised by the time spent in threatening and aggressive behaviours, the number of aggressive interactions, the number of beak and flipper hits given by the focal individual during agonistic interactions, and the number of threatening and vigilant vocalisations (Table IV - 3). The second component was mainly characterized by self-maintenance, offspring care and resting/sleeping behaviours, and therefore defined as activity (later called ACT).

Individual repeatability of the behaviours observed in natural habitat ranged from -0.16 to 0.41 (Table IV – S1). Overall, both aggressiveness and activity were significantly repeatable (AGG: $r = 0.15$, $\chi^2_{105} = 138.85$, $p = 0.015$; ACT: $r = 0.18$, $\chi^2_{105} = 146.21$, $p = 0.005$).

Table IV - 3. PCA of the behaviours expressed in natural environment in 106 king penguins. Bold type indicates behaviours mainly contributing to a component.

***Tableau IV - 3**. Analyse en composante principale des comportements exprimés en environnement naturel par 106 manchots royaux. Les caractères en gras indiquent les comportements contribuant principalement à une composante.*

Behaviour	**Aggressiveness (AGG)**	**Activity (ACT)**
# of bites/attempts to bite	**0.37**	0.10
# of flipper hits/attempts to hit	**0.34**	0.19
# of agonistic interactions	**0.35**	- 0.16
# of threatening or vigilant vocalisations	**0.39**	0.06
% in threatening	**0.39**	- 0.01
% in agonistic interactions	**0.39**	0.19
% in vigilance	0.29	- 0.09
% in resting/sleeping	- 0.26	**0.59**
% in self-maintenance (grooming, shaking)	- 0.11	**- 0.60**
% in offspring care (grooming, feeding)	0.05	**- 0.42**
Eigenvalue	4.21	1.60
Variance explained (%)	42.08	16.00

When considering individual features, within-individual consistency in aggressiveness was significant in individuals of medium structural size index (AGG_{SSI}: $r = 0.22$, $\chi^2_{57} = 81.30$, $p = 0.019$) and with a high body condition index (AGG_{BCI}: $r = 0.29$, $\chi^2_{15} = 24.09$, $p = 0.045$). Activity was repeatable for medium BCI individuals ($ACT_{mediumBCI}$: $r = 0.24$, $\chi^2_{62} = 90.71$, $p = 0.010$) and tended to be repeatable in low SSI ones (ACT_{lowSSI}: $r = 0.19$, $\chi^2_{57} = 27.52$, $p = 0.051$). Individuals with medium haematocrit level were repeatable in both their aggressiveness and activity ($AGG_{mediumH}$: $r = 0.17$, $\chi^2_{64} = 90.32$, $p = 0.021$; $ACT_{mediumH}$: $r = 0.22$, $\chi^2_{64} = 97.83$, $p = 0.005$). Finally, males were consistent in their aggressiveness and activity ($AGG_{♂}$: $r = 0.16$, $\chi^2_{44} = 63.98$, $p = 0.026$; $ACT_{♂}$: $r = 0.22$, $\chi^2_{44} = 71.49$, $p = 0.005$), while females were not (both $p > 0.05$). We only found between-individual consistency in activity for individuals with the same SSI (ACT_{SSI}: $r = 0.08$, $\chi^2_{2} = 6.36$, $p = 0.042$).

When considering habitat characteristics, we found that peripheral breeders were repeatable in both their aggressiveness and activity (within-individual consistency: AGG_{periph}:

r = 0.15, χ^2_{69} = 94.87, p = 0.021; ACT$_{\text{periph}}$: r = 0.17, χ^2_{69} = 98.36, p = 0.011), while central breeders were not repeatable for either trait (both $p > 0.05$). Activity was repeatable for individuals breeding in medium global/breeder density habitats (ACT$_{\text{mediumGD}}$: r = 0.21, χ^2_{43} = 82.94, p = 0.005; ACT$_{\text{mediumBD}}$: r = 0.21, χ^2_{56} = 88.46, p = 0.003), while aggressiveness only tended to be repeatable in birds breeding in low density habitats (AGG$_{\text{lowBD}}$: r = 0.35, χ^2_{17} = 27.06, p = 0.057). Individuals breeding in medium tick-infested habitats were repeatable in their aggressiveness (AGG$_{\text{medimTick}}$: r = 0.31, χ^2_{12} = 21.81, p = 0.040), while individuals breeding in high tick-infested habitats were repeatable in their activity (ACT$_{\text{highTick}}$: r = 0.19, χ^2_{27} = 41.83, p = 0.034). When considering between-individual variance, we found that aggressiveness was repeatable between individuals breeding in the same habitat in terms of centrality of the breeding territory (AGG$_{\text{centrality}}$: r = 0.16, χ^2_{1} = 9.09, p = 0.003), and tended to be repeatable between individuals breeding in the same habitat in terms of breeder density (AGG$_{\text{density}}$: r = 0.06, χ^2_{2} = 5.83, p = 0.054). In contrast, no evidence of between-individual variance was found for activity (all $p > 0.05$).

Aggressiveness (averaged on individuals) was explained by the global density score of the breeding site (AIC = 267.5, ΔAIC = 1.1 with the closest model including the sex of the individuals; N = 85 individuals, Table IV - 4). Aggressiveness of the individuals increased with the global density of their breeding site (GLM: t = -4.63, $p < 0.001$). Activity (averaged on individuals) was explained by the SSI of the individuals, their sex, and the interaction between sex and centrality of the breeding territory (AIC = 245.2, ΔAIC = 0.9 with the closest model including the BCI of the individuals; N = 85 individuals, Table IV - 4). Activity of the individuals increased with their SSI increasing (GLM: t = 2.99, p = 0.004). Males were more active than females (t = 2.35, p = 0.021). However, central males were more active than peripheral ones (t = -2.86, p = 0.005), while there was no difference between central and peripheral females (t = 1.18, p = 0.241).

Table IV - 4. Results from generalised linear models of the behavioural variables (a) PC1: aggressiveness (individually averaged) = AGG and b) PC2: activity (individually averaged) = ACT) expressed by king penguins at their breeding site (N = 85 individuals). Significant parameters are indicated in bold type.

***Tableau IV - 4**. Résultats des modèles linéaires généralisés sur les variables comportementales (a) PC1 : agressivité (moyennée sur l'individu) = AGG et b) PC2 : activité (moyennée sur l'individu) = ACT) exprimés par les manchots royaux sur leur site de reproduction (N = 85 individus). Les paramètres significatifs sont indiqués en caractères gras.*

	Estimate	Std. Error	*t* value	*p*
a) PC1: AGG				
Intercept	0.573	0.057	10.049	**< 0.001**
GDS	- 0.057	0.012	- 4.631	**< 0.001**
b) PC2: ACT				
Intercept	0.194	0.009	21.899	**< 0.001**
Sex	0.031	0.013	2.347	**0.021**
SSI	0.011	0.004	2.987	**0.004**
Female x Centrality	0.014	0.012	1.180	0.241
Male x Centrality	-0.033	0.012	- 2.856	**0.005**

Global Density Score (GDS) referred to the number of breeders and non-breeders within ca. 0.5 m around the breeding site; continuous.
Sex referred to males and females; categorical.
SSI referred to the structural size index; continuous.
Centrality referred to the location of the breeding site in the colony: within (periphery) or above the first four rows (centre) of breeding birds; categorical.
Full models also included the body condition index (BCI) and the tick-infestation level of the breeding site.

c) Behavioural syndrome

Aggressiveness at the breeding site (AGG) was negatively correlated with the second axe of interactions with a novel object (EXPo2: Spearman rank correlations: $r_s = -0.25$, $N = 90$, $p = 0.017$; Fig. IV – 1-a). When considering the sex of the individuals independently, we found that only AGG of the females remained correlated with EXPo2 ($r_s = -0.39$, $N = 36$, $p = 0.020$; Fig. IV – 1-c). Moreover, activity of females at their breeding site (ACT) was also negatively correlated with the exploration in a novel environment (EXPe: $r_s = -0.44$, $N = 36$, $p = 0.007$; Fig. IV – 1-d). Considering the location of the breeding site, we found that AGG displayed by peripheral breeders was negatively correlated with EXPo2 ($r_s = -0.35$, $N = 56$, $p = 0.009$; Fig. IV – 1-b).

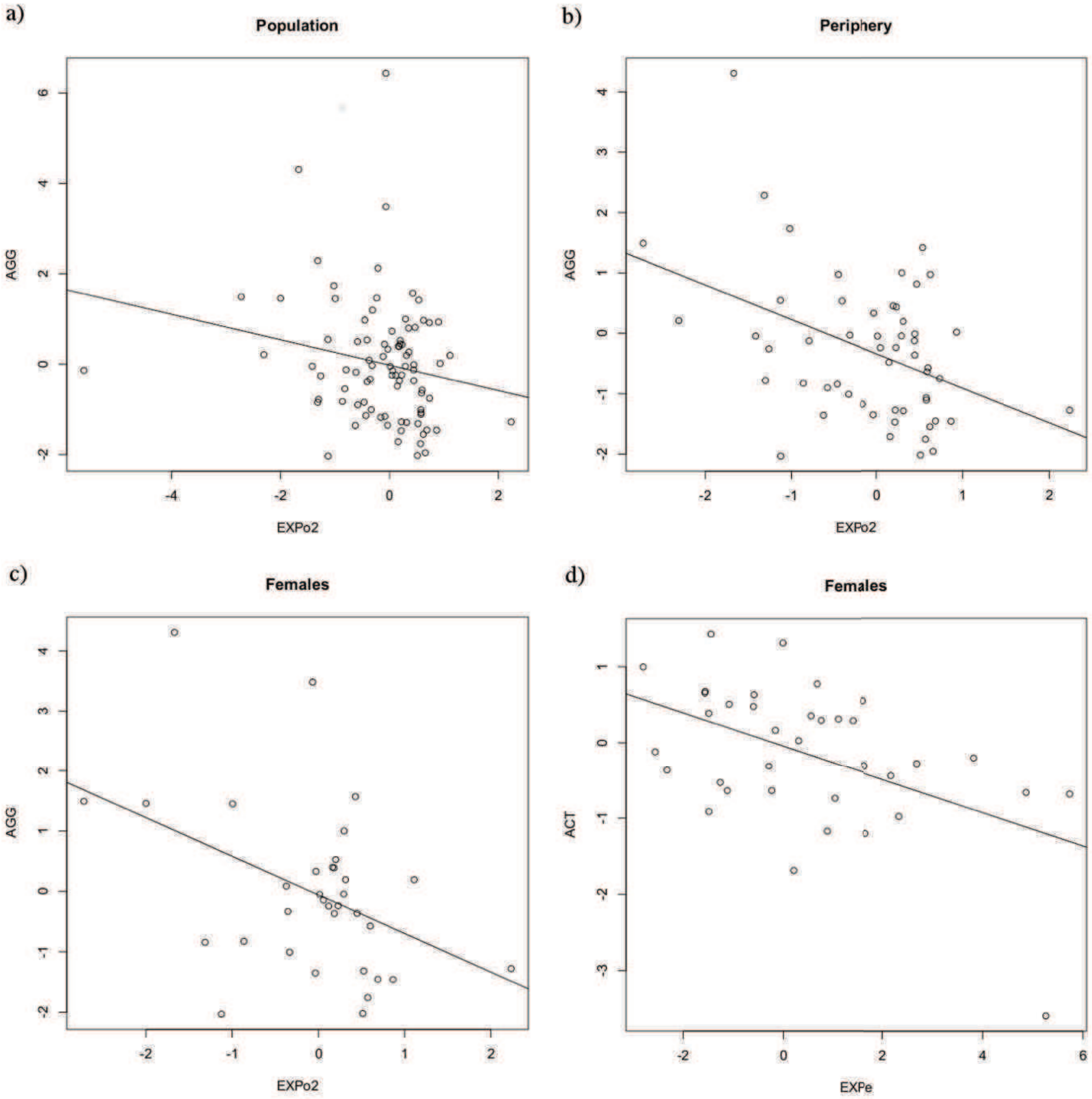

Figure IV - 1. Correlations between aggressiveness (AGG) expressed in natural environment and the second axis of interaction with novel object (EXPo2) a) in the population, b) in peripheral habitat, c) in females; d) and correlation between activity (ACT) expressed in natural environment and exploration (EXPe) during novelty test in females.

***Figure IV - 1**. Corrélations entre agressivité (AGG) exprimée en environnement naturel et le deuxième axe d'interaction avec un nouvel objet (EXPo2) a) dans la population, b) en habitat périphérique et c) chez les femelles ; et d) corrélation entre activité exprimée en environnement naturel et exploration (EXPe) durant les tests de nouveauté chez les femelles.*

4 – Discussion

a) Behavioural syndrome

We identified two axes of personality expressed in natural environment in king penguins: aggressiveness and activity, which are defined as agonistic reactions toward conspecifics and the general level of activity of an individual, respectively (Réale et al., 2007). Repeatability scores for these behaviours were moderate compared to the range of repeatability scores found in other species (Bell et al., 2009), suggesting potentially moderate heritability (Boake, 1989) and thus greater sensitivity to environmental variation (Nussey et al., 2007). Moreover, we identified three axes of behavioural variations expressed during novelty experiments: exploration of a novel environment and two axes of interactions with novel objects. Exploration has been defined as the reaction of individuals toward a new element that can be a new environment, a new object, or new food (Réale et al., 2007).

We found that exploration expressed in captivity was correlated with aggressiveness and activity expressed in natural environment. Indeed, in females, exploration of the novel environment was positively correlated with activity at the breeding site. The 'coping style[7]' theory predicts that individuals should evolve along a 'proactive-reactive' gradient, where proactive individuals should be more aggressive, more active and fast explorers than reactive ones (Koolhaas et al., 1999; Sih et al., 2004a; Koolhaas et al., 2010). According to this theory, our results suggest that we identified coping styles, at least in females, linking activity and exploration. On the other hand, the second axe of interaction with a novel object was also negatively correlated with aggressiveness at the population scale and even more strongly in peripheral habitats and for females. It has been demonstrated in birds that exploration was correlated with dispersal (Dingemanse et al., 2003; van Overveld and Matthysen, 2010). Moreover, younger inexperienced individuals are more likely to disperse (within or outside of the colony) than older experienced individuals(reviewed in Greenwood and Harvey, 1982), and they should therefore display higher levels of exploration. If aggressiveness is associated with better nest defence (Renton, 2004; Margalida and Bertran, 2005), then experienced individuals should be more aggressive and more attach to their breeding territory than young

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[7] *Coping style*: "a coherent set of behavioural and physiological stress responses which is consistent over time and which is characteristic to a certain group of individuals. It seems that coping styles have been shaped by evolution and form general adaptive response patterns in reaction to everyday challenges in the natural habitat." (Koolhaas et al., 1999).

individuals which still lack reproductive skills (Barrat, 1976; Lavery and Laveryl, 1995). This could thus explain the co-existence of two behavioural types ‘slow exploration-high aggressiveness’ and ‘fast exploration-low aggressiveness’ within the colony and the correlation observed between those traits at the colony scale. Furthermore, experienced breeders should breed preferentially in the centre of the colony (i.e. high quality habitat according to Coulson (1968). While the peripheral areas of the colony, where the studied birds have been selected, were mainly composed of inexperienced individuals and late breeders (i.e. considered as experienced birds but in a lower body condition than early breeders because of the cost of the previous successful breeding season). This would explain why the correlation between aggressiveness and exploration was also found in peripheral areas, but not in central ones where there should be lower heterogeneity in terms of experience and quality. Moreover, females are also more likely to disperse than males in philopatric birds, and to change breeding site especially after a breeding failure (reviewed in Greenwood and Harvey, 1982). Lower quality females (i.e. lower successful breeding attempts) should therefore be fast explorers and less aggressive, while experienced/higher quality females (i.e. higher successful breeding attempts) should be more attached to their breeding territory and therefore slow explorers and more aggressive. On the contrary, lower quality males should display the same level of aggressiveness and exploration as experienced/higher quality ones as their territoriality is stronger and more independent of their reproductive experience than in females. This would explain why we observed negative correlation between aggressiveness and exploration in females but not in males.

b) Personality variation in natural environment

Activity and aggressiveness observed in natural environment were related to individual and breeding habitat characteristics. Indeed, we found that activity was explained by the structural size of the individuals, with smaller individuals being more active than taller ones. Small individuals are assumed to have a higher metabolic rate (Schmidt-Nielsen, 1984). When individuals have a fixed energy budget, such as during a fasting period, the ‘allocation model’ predicts that the ones with a higher metabolic rate will have less energy to allocate to activity or other behaviours (see Speakman, 1997). However, according to the ‘performance model’, individuals with a higher metabolic rate should be able to accumulate more energy and therefore to re-allocate more energy to behaviours, such as activity or aggressiveness (see Speakman, 1997). This would explain why we observed that smaller individuals displayed higher levels of activity in this study. In addition, we found that males were more active than females. Differences in hormonal status between males and females can result in differences in morphology and biological processes (e.g. Wood and Shors, 1998; Peterson et al., 2013). It is now recognized that personality traits have a neuro-physiological basis (e.g. Fairbanks et al., 1999; Koolhaas et al., 2010; Ferrari et al., 2013). Therefore, the difference in hormonal status between males and females could also explain the differences we observed in their personality. Furthermore, we found that central king penguin males were more active than peripheral ones, and activity was mainly characterised by self-maintenance and offspring care behaviours. Central parts of a colony are considered to be of good quality and to host individuals of good quality (Coulson, 1968). Moreover, grooming is considered to be an important defence against ecto-parasites (Clayton et al., 2010). In this context, activity may be a good indicator of habitat and/or individual quality. Furthermore the quality of an individual could also facilitate its access to a good quality habitat (Coulson, 1968). As we already saw, males are more attached to their breeding territory than females. In this context, the quality of the breeding territory a pair would have access to would then be more dependent on the quality of the male than on the quality of the female. This could explain why we observed a relationship between individual quality (as reflected by personality) and habitat quality in males but not in females.

We also found that aggressiveness increased with global density of the breeding site. Though aggressiveness is potentially detrimental for survival and breeding success (Hatchwell, 1991; Clair and Clair, 1996; Descamps et al., 2009), its adaptive significance could be context dependent. Indeed, Viera et al. (2011) found that, in king penguins, physical agonistic interactions were more costly than non-physical ones. They also showed that individuals were more often engaged in non-physical interactions, which are potentially as efficient as physical ones in the defence of their territory. Consequently, the higher levels of aggressiveness (reflected by a mix of physical and non physical interactions) displayed by high density breeders in this colony could be considered adaptive, as it would allow them to better defend their breeding territory at moderate energy costs.

Thus, our results linking activity to the structural size and the sex of individuals, support the hypothesis that personality can reflect individual quality, which can be defined as the physical and physiological state of an individual (McNamara and Houston, 1996; Wilson and Nussey, 2010). Moreover, the quality of the breeding habitat is known to influence individual fitness through different pressures, such as parasitism or predation (Southwood, 1977; Martin, 1992; Gaston et al., 2002). On the other hand, as we already saw, the quality of an individual may allow it to access a territory of higher quality that will, in turn, enhance its performance (Coulson, 1968). Both possibilities could explain the strong relationship we observed between personality (that would reflect individual quality), and habitat characteristics reflecting the quality of the habitat. Both individual and breeding habitat characteristics could then be considered as 'inherently stable state components'[8] in this highly philopatric species (Stonehouse, 1960; Barrat, 1976) explaining both the consistency of the behaviours associated with these characteristics, and the consistency of the differences observed between individuals (Wolf and Weissing, 2010).

c) Conclusion and perspectives

As observed in Brünnich's guillemots, *Uria lomvi* (see Cornet et al. *in prep 1*), our results highlight the strong relationship between personality and individual and habitat quality. Moreover, some but not all behaviours expressed by birds in captivity were correlated with behaviours expressed by birds in their natural environment, highlighting the importance of using both captive and undisturbed methodologies to measure personality to better understand the forces shaping it. Furthermore, we identified a behavioural syndrome with implications for the dispersive potential of this population, and therefore with consequences for its dynamics (Wolf and Weissing, 2012).

Using cardio frequency meter data collected during captive experiments, we will now be able to biologically validate the observed behavioural syndromes. Moreover, using our long-term datasets on individuals' survival and breeding success, we will be able to assess the fitness consequences of these behavioural syndromes. Furthermore, using new modelling approaches, such as Bayesian modelling, we will be able to disentangle reversible from irreversible environmental effects on personality (Ferrari et al., 2013). That is to say we should be able to discriminate sources of behavioural variation in the population among phenotypic flexibility[9] (reversible environmental effects) on one hand, and developmental

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[8] *Inherently stable state component:* "features of an organisms that are very costly, time-consuming or even impossible to change" (Wolf & Weissing, 2010). It includes morphological, physiological and neurobiological structures of an individual, but also potentially its environment in some cases (e.g. reduced mobility or social context)

[9] *Phenotypic flexibility:* phenotypic reversible adjustments in adult organisms (Piersma and Drent, 2003)

phenotypic plasticity[10] and genetic variability (irreversible environmental effects) on the other hand.

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[10] *Developmental phenotypic plasticity:* an irreversible variation of the phenotypic traits under the environmental conditions (including parental effects) experienced during the developmental stages (Piersma and Drent, 2003)

Supplementary Material

Table IV - S 1. Repeatability scores (r) of behaviours expressed by king penguins at their breeding site (a) AGG = Aggressiveness = PC1 and b) ACT = Activity = PC2; N = 106 individuals). Bold type indicates within- and between- individual scores statistically significant.

***Tableau IV – S1**. Scores de répétabilité (r) des comportements exprimés par les manchots royaux sur leur site de reproduction (a) AGG = Agressivité = PC1 et b) ACT = Activité = PC2 ; N = 106 individus). Les caractères gras indiquent les scores intra- et interindividuels statistiquement significatifs.*

Table footnotes :

r: repeatability index
χ^2, *df*: chi-squared statistic and degree of freedom
p: p-value
V_a: variance among groups
V_w: variance within groups
N: number of groups
k: number of observations per group
SSI: Structural Size Index of the individuals (Low: SSI < mean(SSI) – sd(SSI); Medium: mean(SSI) – sd(SSI) ≤ SSI < mean(SSI) + sd(SSI); High: mean (SSI) + sd(SSI) ≤ SSI)
BCI: Body Condition Index of the individuals (Low: BCI < mean(BCI) – sd(BCI); Medium: mean(BCI) – sd(BCI) ≤ BCI < mean(BCI) + sd(BCI); High: mean (BCI) + sd(BCI) ≤ BCI)
Haematocrit: volume of circulating cells in the blood as percentage of total blood volume of a sample (Low: less than 49%; Medium: between 49% and 57%; High: more than 57%, classes of equal size)
Males/Females: sex of the individuals
Central/Peripheral: centrality of the breeding site
GDS: Global Density Score of the breeding site (Low: less than 3 individuals on average around the breeding site; Medium: between 3 and 5 individuals; High: more than 5 individuals, classes of equal size)
BDS: Breeder Density Score of the breeding site (Low: less than 2 breeders on average around the breeding site; Medium: between 2 and 4 breeders; High: more than 4 breeders, classes of equal size)
Ticks: the proportion of tick-infested adults in a randomly-selected sample (N = 50 individuals) within a *ca.* 100 m^2 area (Low: less than 2%; Medium: between 2% and 4%; High: more than 4%, classes of equal size)

a) AGG	r	χ^2, df	p	V_a	V_w	N	k
Individual	**0.15**	138.85, 147	0.015	1407.33	8155.14	106	3.18
Low SSI	0.02	18.08, 17	0.384	9.61	491.35	18	4.26
Medium SSI	**0.22**	81.30, 57	0.019	536.93	1923.97	58	2.93
High SSI	0.07	21.90, 19	0.289	23.67	292.87	20	2.97
Between-individuals	-0.02	1.06, 2	0.587	-13.88	783.80	3	26.71
Low BCI	0.10	22.35, 17	0.172	46.52	406.38	18	3.99
Medium BCI	0.11	74.59, 62	0.131	299.99	2541.43	63	2.90
High BCI	**0.29**	24.09, 14	0.045	67.28	167.05	15	3.39
Between-individuals	0	1.83, 2	0.400	-2.76	777.42	3	24.47
Low Haematocrit	0.24	18.89, 11	0.063	46.53	145.61	12	3.81
Medium Haematocrit	**0.17**	90.32, 65	0.021	671.28	3281.23	66	3.27
High Haematocrit	-0.16	11.98, 16	0.745	-26.11	189.56	17	2.53
Between-individuals	-0.02	1.16, 2	0.561	-14.67	766.96	3	22.29
Males	**0.16**	63.98, 44	0.026	400.57	2117.01	45	3.82
Females	0.12	46.75, 39	0.184	113.43	816.90	40	2.60
Between-individuals	0	0.82, 1	0.365	-2.59	610.47	2	42.35
Central	0.06	38.35, 35	0.320	43.56	655.17	36	2.51
Peripheral	**0.15**	94.87, 69	0.021	757.61	4358.66	70	3.51
Between-individuals	**0.16**	9.09, 1	0.003	162.41	871.62	2	47.55
Low GDS	0.16	33.58, 25	0117	89.43	454.19	26	3.03
Medium GDS	0.11	68.82, 53	0.071	371.16	3019.32	54	3.70
High GDS	**0.29**	33.68, 25	0.115	80.12	198.34	26	2.16
Between-individuals	0.05	5.22, 2	0.074	47.12	915.66	3	32.87
Low BDS	0.35	27.06, 17	0.057	70.32	130.30	18	2.58
Medium BDS	0.07	66.34, 56	0.162	258.43	3651.93	57	3.77
High BDS	0.24	40.01, 30	0.105	111.84	354.81	31	2.34
Between-individuals	0.06	5.83, 2	0.054	58.43	909.98	3	31.61
Low Ticks	0.15	29.74, 21	0.097	86.07	471.47	22	3.63
Medium Ticks	**0.31**	21.80, 12	0.040	57.43	126.68	13	3.49
High Ticks	0.05	30.98, 27	0.272	51.42	968.12	28	3.88
Between-individuals	-0.05	0.09, 2	0.958	-16.53	346.71	3	20.10

b) ACT	r	χ^2, df	p	V_a	V_w	N	k
Individual	**0.18**	146.21, 105	0.005	1713.26	7852.24	106	3.18
Low SSI	0.19	27.52, 17	0.051	93.68	411.27	18	4.26
Medium SSI	0.13	71.02, 57	0.100	309.91	2146.80	58	2.93
High SSI	0.11	23.41, 19	0.220	35.95	281.30	20	2.97
Between-individuals	**0.08**	6.36, 2	0.042	64.68	739.63	3	26.71
Low BCI	0.14	24.29, 17	0.111	63.35	390.53	18	3.99
Medium BCI	**0.24**	90.71, 62	0.010	684.01	2163.50	63	2.90
High BCI	0.13	18.52, 14	0.184	30.14	201.62	15	3.39
Between-individuals	-0.02	1.16, 2	0.560	-13.62	783.02	3	24.47
Low Haematocrit	**0.29**	20.54, 11	0.039	56.22	136.78	12	3.81
Medium Haematocrit	**0.22**	97.83, 65	0.005	870.41	3085.17	66	3.27
High Haematocrit	-0.10	13.42, 16	0.642	-16.77	180.78	17	2.53
Between-individuals	0.03	3.14, 2	0.209	19.77	750.62	3	22.29
Males	**0.22**	71.49, 44	0.005	551.29	1969.70	45	3.82
Females	0.10	45.45, 39	0.221	94.39	835.46	40	2.60
Between-individuals	0	1.14, 1	0.287	1.96	608.18	2	42.35
Central	0.15	42.87, 35	0.169	102.30	597.86	36	2.51
Peripheral	**0.17**	98.36, 69	0.011	859.76	4258.06	70	3.51
Between-individuals	0.03	2.46, 1	0.117	29.26	931.92	2	47.55
Low GDS	0.06	28.05, 25	0.305	31.83	509.46	26	3.03
Medium GDS	**0.21**	82.94, 53	0.005	702.39	2694.32	54	3.70
High GDS	0.25	32.49, 25	0.144	69.11	208.94	26	2.16
Between-individuals	-0.01	1.42, 2	0.492	-8.53	950.50	3	32.87
Low BDS	0.25	24.10, 25	0.117	49.66	149.60	18	2.58
Medium BDS	**0.21**	88.46, 56	0.003	810.96	3108.69	57	3.77
High BDS	0.10	34.14, 25	0.275	46.24	417.97	31	2.34
Between-individuals	-0.03	0.10, 2	0.952	-28.99	962.62	3	31.61
Low Ticks	0.03	22.44, 21	0.374	14.17	539.99	22	3.63
Medium Ticks	0.16	17.06, 12	0.147	29.66	152.55	13	3.49
High Ticks	**0.19**	41.83, 27	0.034	191.68	833.43	28	3.88
Between-individuals	-0.02	1.39, 2	0.500	-5.30	339.43	3	20.10

Chapter V – Personality and Foraging Strategies

Chapitre V – Personnalité et Stratégies de Prospection Alimentaire

Behavioural consistency on land and at sea in a territorial Antarctic seabird, the Adélie penguin *– in prep Article 3*

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Individuals exhibit consistent behavioural differences in their foraging activities. Despite this common background with personality concepts, rare are the studies considering them within the same framework. Here, we investigated for the first time in a wild penguin population (the Adélie penguin *Pygoscelis adeliae*) the consistency of both on land and at sea behaviours, as well as their associations into behavioural syndromes. We then sought after potential sources of heterogeneity observed in these behaviours among individual and breeding habitat features. Finally, we explored their consequences on individuals breeding success. To do so, we used an extensive dataset of behavioural variables collected through behavioural tests conducted on penguins in the field, focal observations of those same individuals at their nest, and the analyse of their patterns of at sea/on land sojourns during the guarding phase of their breeding cycle. We found that Adélie penguins were individually consistent in both their personality traits measured at the nest (i.e. aggressiveness, activity and vocalisation) and at sea (i.e. foraging trip duration), but also that these traits were correlated, suggesting the existence of behavioural syndromes. We also found that the consistency of these behaviours, as well as the observed behavioural syndromes, varied both according to individual (i.e. sex, structural size, and body condition) and nesting habitat characteristics (i.e. centrality of the nest, disturbance by conspecifics, exposure to snow, and density). Finally, we found that successful breeders were more aggressive at their nest than failed ones, but also more consistent in this aggressiveness, as well as in their activity at the nest and at sea during crèching. Together, our results bring new insights on the implications of personality in the inter-individual differences observed in foraging strategies along with potential impacts on individual fitness, highlighting the importance of integrative studies to better gauge the adaptive potential of populations.

Keywords: behavioural syndrome; fitness; foraging; personality; plasticity.

1 – Introduction

Interest in personality or temperament traits in animals is very recent, but evidence of their existence is already accumulating in a wide variety of taxa (e.g. Réale et al., 2000; Martin and Réale, 2008; Michelena et al., 2010; Twiss and Franklin, 2010; Briffa and Greenaway, 2011; Pinter-Wollman et al., 2012), and reveals possible implications in animal adaptive potential to cope with stochastic environments (e.g. Sih et al., 2004a; Réale et al., 2007; Biro et al., 2010). Personality has been defined as consistent individual differences in behaviour (Gosling, 2001; Réale et al., 2007), and a behavioural syndrome as a suite of correlated personality traits across multiple situations and/or contexts (Sih et al., 2004a). As in human personality, five major axes of personality have been defined (reviewed in Réale et al., 2007) that reflect in the ecology of an animal, such as habitat exploration, aggressiveness, or sociability, and therefore have a potential impact on individual fitness (Boon et al., 2008; Kontiainen et al., 2009; Dammhahn, 2012). However, consistent inter-individual differences can be found in multiple behaviours. Individual variations in foraging strategies have been first regarded as noise around an optimal strategy (reviewed in Stephens, 1986), but in the new light of the evolutionary and personality frameworks, consistent individual behavioural differences in foraging parameters might now be considered as personality-shaped, with potential for natural selection and evolution. To date, a few studies have focused on the influence of personality on foraging strategies (e.g. Kurvers et al., 2010a; van Overveld and Matthysen, 2010; Bergvall et al., 2011; Dammhahn and Almeling, 2012), however, almost none of them attempted to estimate the consistency in foraging activities in itself as a component of personality (to our knowledge only one study: Patrick and Weimerskirch, 2014). Considering the importance of foraging efficiency on fitness components, such as survival and breeding success (e.g. Godin and Smith, 1988; Morse and Stephens, 1996; Watson et al., 2007; Visser et al., 2009), investigating personality influence on foraging strategies might bring important new insights on the adaptive capacities of individuals and populations to cope with environmental changes.

The difficulty of monitoring, under field conditions, numerous individuals multiple times along their lifespan, is one of the main obstacles to study personality in the wild. It explains why such studies remain so rare (e.g. Boon et al., 2008; Kontiainen et al., 2009; Dammhahn, 2012; Patrick et al., 2013) despite the importance of personality in evolutionary ecology. Nevertheless, since environmental conditions and animal behaviours in captivity might not match those of wild populations in their natural environment (Réale et al., 2007;

Archard and Braithwaite, 2010), such studies are still needed to gauge how personality is affected and responds to environmental fluctuations. In this study, we focused on a wild population of a highly philopatric Antarctic seabird species, the Adélie penguin (*Pygoscelis adeliae*). As other seabirds, while spending most of their time at sea, penguins still need to come back on land to reproduce (Baird, 1991; Costa, 1991). Direct behavioural observations can therefore be carried out during their presence on land. Moreover, the recent technological developments allow easy access to breeding and foraging parameters with relatively minimal disturbance (Wilson et al., 2002; Gendner et al., 2005; Le Bohec et al., 2007). Thus, penguins should represent good models to study personality both during the breeding duties on land and their foraging activities at sea. Yet, personality studies on (wild) penguins are inexistent and, to our knowledge, only four studies to date have been conducted on seabirds (see Kazama and Watanuki, 2010; Kazama et al., 2012; Patrick et al., 2013; Patrick and Weimerskirch, 2014). Moreover, as upper-level predators, they magnify variations occurring throughout their trophic web, making them good indicators of ecosystem changes (Piatt et al., 2007; Parsons et al., 2008; Grémillet and Charmantier, 2010). However, Adélie penguin populations have been shown to have strong and contrasted responses to recent climate changes (IPCC, 2013). Indeed, the impact of environmental variations, such as the observed changes in sea-ice extent on which Adélie penguins are highly dependant, is not the same around Antarctica (Smith et al., 1999; Vaughan et al., 2001; Wilson et al., 2001; Ainley, 2002; Ainley et al., 2005), highlighting the urgent need to study the adaptive capacities of this species in the context of global warming.

In this study, we first assessed between-individual consistency in personality traits, such as activity, aggressiveness, and boldness (as defined by Réale et al., 2007), obtained in Adélie penguins breeding at Pointe Géologie archipelago thanks to 'flight'/'resistance to handler' tests and focal observations in natural environment. We then evaluated the correlations between these traits at the population level to determine the existence of behavioural syndromes. During brooding and crèching phases of the breeding cycle, chicks require important and regular food supplies, and meeting with these needs while insuring its self-maintenance is critical for a successful reproduction. We therefore expected high regularity in foraging trips during these two phases and consistent individual differences reflecting foraging efficiency and personality. Consequently, we also assessed individual repeatability in behaviours at sea extracted from pattern analyses of at sea/on land sojourns of previous individuals during the guarding phases of their breeding cycle. We then examined whether and how these latter parameters were related to the personality traits previously defined. We tested the hypothesis that behavioural differences might reflect individual and habitat quality, and we predicted:

- i) consistency in the behavioural differences observed between individuals with different individual or habitat characteristics,
- ii) consistency of the behaviours in individuals with the same individual or habitat characteristics,
- iii) individuals with higher individual and/or habitat quality to be more aggressive, bolder, more active, to spend less time at sea because foraging more efficiently, and to be more consistent in these behaviours, since they might confer adaptive advantages in the defence of their breeding territory, their offspring, and themselves, as well as in the maintenance of their offspring and themselves.

Finally, we expected personality at the nest and at sea to have an impact on individual fitness, thus assessed their relationships with individual breeding success.

2 – Material and Methods

a) Study site and birds

Our study was conducted on Adélie penguins (*Pygoscelis adeliae*) breeding on Petrel Island (66°40'S 140°01'E, in '*ANTAVIA Canyon*' colony), Pointe Géologie Archipelago, Adélie Land, Antarctica. During 2011/2012 and 2012/2013 austral summers, a total of 128 breeding adults has been captured while they were leaving the colony and handled outside the colony. Handling time and duration, and identity of the persons measuring and handling the birds were recorded. Each individual was weighted and measured (flippers and beak). These morphometric measurements were used to establish a structural size index (SSI ù; based on a principal component analysis (PCA): SSI = PC1 = 0.71 * (flipper, averaged, scaled-centred) + 0.71 * (beak, averaged, scaled-centred)), as well as a body condition index (BCI ; defined as the residuals of the regression of the SSI on body mass) (see details in Cornet et al. *in prep1*). Birds were also implanted with a passive electronic tag (if not already), blood sampled for DNA sexing, and marked with a unique code on the chest using temporary hair dye for visual identification in the colony. Transponder tags weigh 0.8g and have no known adverse effects (Froget et al., 1998; Nicolaus et al., 2009).

b) Measuring parental guarding and provisioning consistency

Micro-tagged individuals are detected automatically by double antennas settled at the usual pathways of the birds to enter and exit the colony (see Gendner et al., 2005 for a similar system on king penguins). By interpreting the movements of the birds between the sea and the colony, we are thus able to identify the different phases of their breeding cycle (method adapted from our long-term monitoring system, see Descamps et al., 2002; Le Bohec et al., 2007).

Adélie penguins have been shown to equally share parental care of 2 eggs/chicks on average between sexes (Ainley, 2002). After pairing, the female generally lay 2 eggs, 1 to 3 days apart, and leave the nest, while the male ensures the first shift of incubation. She will come back to exchange with the male about 15 days later. Hatching occurs about 33-34 days after the last egg was laid. At hatching, chicks are not yet thermally emancipated. Therefore, both mates take turns to guard and feed the chicks, alternating 1 to 3 days on land and 1 to 3 days at sea. After *ca.* 3 weeks of brooding phase, chicks are finally ready to be left alone at the colony and join crèches, mainly to protect themselves from other adults present at the colony and from predation (Ainley, 2002). At this point and until chicks are ready to fledge, both mates leave the colony to forage and come back regularly (i.e. a few hours, every 1 to 3 days) to feed the chicks.

For each of the 128 pit-tagged individuals, we first estimated the incubation length (in days), and we defined birds incubating between i) 28-32 days as Short INC, ii) 33-37 days as Medium INC, and iii) 38-43 days as Long INC. We then extracted the duration (in hours) of each foraging trip at sea and sojourn on land during the brooding phase (SeaB and LandB) and during the crèching phase (SeaC and LandC), to assess the consistency of these behaviours under different constraints of the breeding cycle.

c) Measuring behavioural consistency in a threatening situation and at the nest

'Flight' tests followed by 'resistance to handler' tests were performed and behavioural responses of the target penguins (N = 128 individuals, among which 27 were captured both years) were recorded through posterior blind video analyses.

From ‘flight’ tests, we recorded, when possible, the minimum distance before the bird reacted (in meters), the reaction of the bird at capture (calm, agitated, attempting to escape), the vocalisation intensity at the capture (VOC*c* scaled from 0 to 3), and an attack score (quantified as the frequency of bites).

From ‘resistance to handler’ tests, we extracted activity and boldness scores (ACT*h* and BOL*h* scaled from 1 to 3), an attack score (ATT*h* quantified as the frequency of bites), the vocalisation intensity during handling (VOC*h* scaled from 0 to 3), the number and the time attempting to escape (ES*n* and ES*t*), and the reaction of the bird in the weighting bag (calm, mildly agitated, very agitated). Finally, we extracted the reaction of the bird when released (freeze, escape, bold).

Additional behavioural focal observations of 15 minutes were randomly carried out every 2 to 3 days on average, on both mates of a nest whenever it was doable (*N* = 148 individuals, among which 35 were observed both years. Note that we were not able to capture and pit-tag 19 of them). Birds were observed between 7 a.m. and 11 a.m. to avoid bias from a potential daily activity (e.g. king penguins Aptenodytes patagonicus, Nesterova et al., 2010). Breeding status of the birds (i.e. with egg(s) or chick(s)) was recorded before each focal observation. Depending on the year and the timing of the breeding failure, from 1 to 12 focal observations were conducted for each individual during incubation and chick-rearing phases of their breeding cycle. We decided to not exclude individuals tested only once because they still contribute to the population-level variation in behavioural traits (Dammhahn and Almeling, 2012).

From focal observations of the individual on its nest, we recorded the time budget allocated to daily activities: grooming, cleaning the nest, taking care of their offspring (i.e. ventilating the eggs, grooming the chicks, feeding them), resting/sleeping, vocalising, and in agonistic interaction with other individuals. We also recorded the number of vocalisation and agonistic interactions, as well as the number of bites exchanged during these agonistic interactions. A PCA was performed on these quantitative variables in order to reduce the number of dependent variables prior to statistical analysis. We retained the three first components, PC1, PC2 and PC3, based on visual examination of the scree plot and on the Kaiser-Guttman 'Eigenvalues greater than one' criterion (Legendre and Legendre, 2012).

d) Habitat data collection

Adélie penguins are nesting seabirds breeding synchronously in relatively dense colonies in rocky area at or near the seashore (Ainley, 2002). Therefore, at the beginning of each focal observation, we recorded the number of nesting breeders (breeder density, BD), or nesting and wandering birds (global density, GD), in ~ 0.75 m around the observed individual, which is the maximal distance for physical interactions between nesting Adélie penguins (Ainley, 2002). Pictures were taken for density estimate validation and to assess habitat characteristics, i.e. nest at the periphery (first row of nests) or centre of the colony (above first row of nests), disturbed by or sheltered from regular passages of conspecifics (empirical assessment according to the usual paths used by the birds to reach their breeding site), and exposed to or protected from snowfall accumulation (empirical assessment according to the position of the nests within the colony and its topography, and measurements of snow height performed at the end of the season). Temperature (°C), humidity (%) and luminosity (Lux) data of the colony were continuously recorded every minute using data-loggers (Hobo® U23 Pro v2 Temperature/Relative Humidity data logger, and Hobo® Pendant Temperature/Light data logger, www.onsetcomp.com). We also used daily average temperature (°C), humidity (%), atmospheric pressure (hPa), wind speed (m/s), and wind direction (in ° from the North) of the archipelago provided by the Météo France meteorological station settled in Dumont D'Urville station on Petrel Island.

e) Data analyses

In order to assess the consistency of behavioural variables from capture, handling, focal, and breeding cycle observations, repeatability indices within a population and according to year, habitat and individual characteristics were computed. Prior to the computation of these indices, we controlled for confounding factors, as suggested by Nakagawa and Schielzeth (2010). No continuous variables followed a Gaussian distribution. Consequently, we calculated repeatability scores as defined by Lessells and Boag (1987). An intra-class correlation coefficient (r) was therefore obtained based on variance components derived from a parametric ANOVA on the rank (Hedrick and Kortet, 2012) with individual identity, year, individual or habitat characteristics as a factor, and each behavioural variable as the dependent variable. A non-parametric Kruskal-Wallis ANOVA was then performed to assess the significance of repeatability of behaviours (Hedrick and Kortet, 2012).

We first examined the within-individual behavioural consistency within each group of individuals presenting the same characteristic (i.e. sex, SSI, BCI, breeding status, incubation length), breeding in the same habitat (i.e. disturbance by passages of conspecifics, exposure to snow, centrality, and density), having the same breeding output, and breeding the same season. These repeatability scores, later on referred to as 'Within-individual consistency', gave us insights on the potential influence of biotic/abiotic parameters on individual flexibility. In a second step, we explored the between-individuals behavioural consistency within each of the previously-defined group, and the consistency of the differences between those groups. These repeatability scores, later on referred to as 'Between-individual consistency', gave us insights on the behavioural homogeneity between individuals with the same characteristics.

The existence of behavioural syndromes between behaviours (monitored during the tests and inside the colony, and extracted from automatic detections) was assessed using Spearman rank correlations.

We then investigated the relationship between behavioural variables extracted from focal observations and individual, nesting habitat, and weather characteristics. We first used Generalised Linear Mixed Models (GLMMs), fitted with Penalized Quasi-Likelihood (PQL) and an inverse-link Gamma distribution. Bird identity was set as a random term, enabling us to account for repeated measures on the same individual. Because the residuals from these models revealed problems that imply a failure of one or more assumptions, we thus decided to average observations over individuals and use Generalised Linear Models (GLMs, with inverse link-Gamma distribution) to improve model fits. The most appropriate model was then selected based on the Akaike's Information Criterion (AIC), using both ΔAIC and AIC weights (Symonds and Moussalli, 2011). The analysis of the residuals did not reveal any problem in the models explaining PC1, PC2 and PC3 this time, and we thus decided to conserve these models. We also performed GLMs (fitted with inverse link-Gamma distribution) on the global datasets including variables previously selected as fixed effects, in order to compute repeatability estimates on residuals. This allowed us to assess intrinsic consistency excluding variance linked to the environment and individual characteristics.

To compare different groups (e.g. centre vs. periphery, exposed vs. protected, low density vs. medium density vs. high density, males vs. females, low SSI vs. medium SSI vs. high SSI, successful vs. failed breeders), we first checked for normality and homoscedasticity between groups, and non-parametric Wilcoxon rank-sum tests were used consequently. Bonferroni correction was applied whenever multiple comparisons were tested, and differences were thus considered significant for $p < \frac{0.05}{n}$, with n the number of comparisons performed. Finally, we used Fisher's exact tests to assess the differences in breeding success according to the individual and habitat characteristics, and according to the years.

All statistics were computed using the R 2.10.0 statistical environment (R Development Core Team, 2012). Data are presented as mean ± s.e., unless stated otherwise.

3 – Results

a) 'Flight and 'Resistance to handler' tests

None of the behaviours related to 'flight' and 'resistance to handler' tests were significantly repeatable (all $p > 0.05$).

Males vocalised significantly more than females during capture and handling (VOC*c*: $W = 42$, $N_♂ = 11$, $N_♀ = 14$, $p = 0.016$, and VOC*h*: $W = 357$, $N_♂ = 30$, $N_♀ = 35$, $p = 0.009$, respectively). Individuals with high structural size index (SSI) also vocalised significantly more during handling than low and medium SSI individuals (VOC*h*: $W = 15$, $N_{\text{lowSSI}} = 11$, $N_{\text{highSSI}} = 7$, $p = 0.013$; $W = 79$, $N_{\text{mediumSSI}} = 46$, $N_{\text{highSSI}} = 7$, $p = 0.011$, respectively), but there was no difference between the last two categories of individuals (VOC*h*: $W = 217$, $N_{\text{lowSSI}} = 11$, $N_{\text{mediumSSI}} = 46$, $p = 0.4$). Individuals with high body condition index (BCI) vocalised more during handling than individuals with medium BCI (VOC*h*: $W = 155$, $N_{\text{mediumBCI}} = 51$, $N_{\text{highBCI}} = 13$, $p < 0.001$). They also attempted to escape from the handler significantly more and longer than individuals with medium BCI (ES*n*: $W = 194$, $N_{\text{mediumBCI}} = 52$, $N_{\text{highBCI}} = 13$, $p = 0.008$; ES*t*: $W = 152$, $N_{\text{mediumBCI}} = 52$, $N_{\text{highBCI}} = 13$, $p = 0.001$) and low BCI (ES*n*: $W = 17$, $N_{\text{lowBCI}} = 6$, $N_{\text{highBCI}} = 13$, $p = 0.028$; ES*t*: $W = 11$, $N_{\text{lowBCI}} = 6$, $N_{\text{highBCI}} = 13$, $p = 0.021$). Individuals with low BCI attacked significantly more during handling than medium BCI individuals (ATT*h*: $W = 217$, $N_{\text{lowBCI}} = 6$, $N_{\text{mediumBCI}} = 52$, $p = 0.010$).

Individuals breeding in habitats sheltered from regular passages of conspecifics attempted to escape from the handler significantly more than individuals breeding in disturbed habitat (ESn: $W = 441$, $N_{\text{disturbed}} = 35$, $N_{\text{sheltered}} = 33$, $p = 0.044$). Individuals breeding in medium breeder density habitat bit significantly more during handling than the ones breeding in low breeder density habitat (ATTh: $W = 456$, $N_{\text{lowBD}} = 30$, $N_{\text{mediumBD}} = 38$, $p = 0.011$).

b) Behavioural observations at nest

The three first components of the PCA, with eigenvalues greater than 1, were retained (Table V - 1). The first component of the PCA, PC1 (Aggressiveness, later called AGG) explained 29% of the total variance and was mainly characterized by the number of agonistic interactions, the number of bites exchanged, and the time spent in agonistic interactions. PC2 (Activity, later called ACT) explained 21% of the total variance and was mainly characterized by grooming and resting/sleeping behaviours. PC3 (Vocalisation, later called VOC) explained 18% of the total variance and was mainly characterized by the number of vocalisations and the time spent vocalising. Aggressiveness was repeatable over all individuals' observations (AGG: $r = 0.03$, $\chi^2_{147} = 182.43$, $p = 0.025$), while activity only tended to be repeatable, and vocalisation was not repeatable (see Table V – S1).

Table V - 1. Results of the PCA of behavioural variables collected during focal observations on 148 Adélie penguins at their nests (PC1: aggressiveness; PC2: activity; PC3: vocalisation). Bold type indicates behaviours with major contribution to a component.

Tableau V - 1*. Résultats de l'analyse en composante principale des variables comportementales collectées durant les focales d'observation sur 148 manchots Adélies sur leur nid (PC1 : agressivité ; PC2 : activité ; PC3 : vocalisation). Les caractères gras indiquent les comportements ayant une contribution majeure pour une composante.*

Behaviour	PC1	PC2	PC3
# agonistic interactions [a]	**0.40**	- 0.29	0.09
# bites [b]	**0.52**	- 0.37	0.07
Aggression [c]	**0.46**	- 0.33	0.04
Grooming [d]	0.25	**0.44**	- 0.32
Offspring care [e]	0.16	0.20	- 0.24
Nest maintenance [f]	0.14	0.16	- 0.22
Resting/Sleeping [g]	**- 0.45**	**- 0.43**	0.28
Vocalising [h]	0.16	0.35	**0.58**
# vocalisations [i]	0.16	0.33	**0.60**
Eigenvalue	2.60	1.92	1.63
Variance explained (%)	28.84	21.46	18.14

[a] number of agonistic interactions, [b] number of bites (given/received/exchanged), [c] proportion of time spent in agonistic interactions, [d] proportion of time spent grooming itself, [e] proportion of time spent taking care of egg(s)/chick(s) (i.e. ventilating, grooming, feeding), [f] proportion of time spent in nest maintenance, [g] proportion of time spent vocalising intensely, [h] proportion of time spent resting or sleeping, [i] number of vocalisations

b.1) Individual characteristics

'Within-individual consistency' - Medium SSI, and medium and high BCI individuals expressed consistent aggressiveness ($AGG_{mediumSSI}$: $r = 0.07$, $\chi^2_{66} = 107.66$, $p < 0.001$; $AGG_{mediumBCI}$: $r = 0.04$, $\chi^2_{72} = 93.42$, $p = 0.046$; $AGG_{highBCI}$: $r = 0.07$, $\chi^2_{23} = 35.28$, $p = 0.049$). Birds with medium incubating phase expressed also consistency in their aggressiveness, as well as in their activity ($AGG_{mediumINC}$: $r = 0.06$, $\chi^2_{44} = 82.58$, $p = 0.007$; $ACT_{mediumINC}$: $r = 0.06$, $\chi^2_{44} = 82.21$, $p = 0.008$).

'Between-individual consistency' – Interestingly, activity at the nest was the only variable significantly repeatable between individuals of the same sex (ACT_{sex}: $r = 0.08$, $\chi^2_{1} = 6.91$, $p = 0.009$), while vocalisation at the nest was the only variable significantly repeatable between individuals of the same SSI (VOC_{SSI}: $r = 0.14$, $\chi^2_{2} = 9.44$, $p = 0.009$).

b.2) Environmental conditions

'Within-individual consistency' - Aggressiveness was the only variable significantly repeatable in medium global density habitat ($AGG_{mediumGD}$: $r = 0.06$, $\chi^2_{43} = 65.67$, $p = 0.015$), whereas activity was the only one in high global density habitat (ACT_{highGD}: $r = 0.08$, $\chi^2_{20} = 32.01$, $p = 0.043$). When considering breeder density alone, aggressiveness and activity were both significantly consistent in habitat of medium breeder density ($AGG_{mediumBD}$: $r = 0.04$, $\chi^2_{95} = 119.83$, $p = 0.043$; $ACT_{mediumBD}$: $r = 0.05$, $\chi^2_{95} = 122.40$, $p = 0.031$). In both study years, aggressiveness was significantly consistent within individuals ($AGG_{2011/2012}$: $r = 0.05$, $\chi^2_{77} = 98.95$, $p = 0.047$; $AGG_{2012/2013}$: $r = 0.06$, $\chi^2_{102} = 137.57$, $p = 0.011$).

'Between-individual consistency' - Vocalisation was significantly consistent between individuals breeding in the same type of habitat in terms of disturbance from passages of conspecifics ($VOC_{disturbance}$: $r = 0.05$, $\chi^2_{1} = 4.41$, $p = 0.035$).

b.3) Behavioural variables explained by individual and environmental factors

Aggressiveness was explained by the location of the nest in the colony (in terms of disturbance from regular passages of conspecifics and exposure to snowfall), the density of breeders (BD) around the nest, the interaction between BD and exposure to snowfall, and the interaction between BD and the sex of the individuals (see model selection in Table V – S2a). Individuals breeding in disturbed habitats were more aggressive than individuals breeding in sheltered habitat (GLM: $t = 2.13$, $p = 0.036$; Table V - 2 and Figure V - 1). Overall, aggressiveness decreased with increasing BD ($t = 4.56$, $p < 0.001$), but interestingly, the relationship was even deeper for individuals breeding in habitat exposed to snow compared to individuals breeding in habitat very exposed and protected from snow ($t = -2.16$, $p = 0.033$; $t = -2.83$, $p = 0.006$, respectively). The relationship between aggressiveness and BD was also deeper for females than for males ($t = -2.52$, $p = 0.014$), resulting in equivalent levels of aggressiveness in both sex at low BD and males being more aggressive than females at high BD. After controlling for these parameters, aggressiveness became more consistent over all individuals' observations (AGG: $r = 0.13$, $\chi^2_{145} = 297.30$, $p < 0.001$).

Table V - 2. Generalised linear models explaining the behavioural variables collected during focal observations on 95 Adélie penguins at their nests: a) PC1 = Aggressiveness = AGG, b) PC2 = Activity = ACT, c) PC3 = Vocalisation = VOC. Bold type indicates significant parameters.

Tableau V - 2*. Modèles linéaires généralisés expliquant les variables comportementales collectées durant les focales d'observation sur 95 manchots Adélie sur leur nid : a) PC1 = Agressivité = AGG, b) PC2 = Activité = ACT, c) PC3 = Vocalisation = VOC. Les caractères gras indiquent les paramètres significatifs.*

	Estimate	Std. Error	*t* value	*p*
a) PC1: AGG				
Intercept	0.496	0.102	4.878	< **0.001**
Disturbance (Disturbed – Sheltered)	0.224	0.105	2.127	**0.036**
Exposure – Exposed/HighlyExposed	0.569	0.252	2.257	**0.027**
Exposure – Exposed/Protected	0.609	0.165	3.698	< **0.001**
Exposure – HighlyExposed/Protected	- 0.041	0.276	- 0.147	0.884
BD	0.545	0.120	4.557	< **0.001**
BD x Exposure (Exposed/HighlyExposed)	- 0.432	0.200	- 2.160	**0.033**
BD x Exposure (Exposed/Protected)	- 0.465	0.164	- 2.832	**0.006**
BD x Exposure (HighlyExposed/Protected)	0.033	0.209	0.162	0.872
BD x Sex	- 0.259	0.103	- 2.521	**0.014**
b) PC2: ACT				
Intercept	0.516	0.025	20.819	< **0.001**
Sex	- 0.129	0.024	- 5.352	< **0.001**
SSI – Low/Medium	0.063	0.029	2.187	**0.031**
SSI – Low/High	0.108	0.039	2.708	**0.008**
SSI – Medium /High	- 0.044	0.030	- 1.458	0.148
c) PC3: VOC				
Intercept	0.613	0.036	16.865	< **0.001**
Centrality (Central – Peripheral)	- 0.079	0.036	- 2.205	**0.030**
Sex (Female – Male)	- 0.309	0.032	- 9.630	< **0.001**
SSI – Low/Medium	- 0.065	0.039	- 1.664	0.099
SSI – Low/High	- 0.108	0.077	- 1.394	0.167
SSI – Medium/High	- 0.026	0.082	- 0.317	0.752
Centrality (Peripheral) x SSI (Low/Medium)	0.100	0.042	2.397	**0.019**
Centrality (Peripheral) x SSI (Low/High)	0.116	0.055	2.097	**0.039**
Centrality (Peripheral) x SSI (Medium/High)	- 0.017	0.048	-0.343	0.733
Sex (Male) x SSI (Low/Medium)	0.318	0.038	8.473	< **0.001**
Sex (Male) x SSI (Low/High)	0.286	0.085	3.366	**0.001**
Sex (Male) x SSI (Medium/High)	0.032	0.081	0.399	0.691
GD x Disturbance (Sheltered)	-0.061	0.013	- 4.662	< **0.001**

Disturbance referred to the disturbance of the nest by regular passage of conspecifics (categorical: Disturbed/Sheltered)

Exposure referred to the exposition of the nest to snowfall accumulation (categorical: Highly Exposed/Exposed/Protected)

BD referred to the Breeder Density of the nest (categorical: Low: less than 1 breeders on average around the breeding site; Medium: between 1 and 3 breeders; High: more than 3 breeders, classes of equal size)

Sex referred to males and females; (categorical: Females/Males)

SSI referred to the structural size index; continuous for ACT and categorised as follow for VOC: Low: SSI < mean(SSI) – sd(SSI); Medium: mean(SSI) – sd(SSI) ≤ SSI < mean(SSI) + sd(SSI); High: mean (SSI) + sd(SSI) ≤ SSI

Centrality referred to the centrality of the nest in the colony according to its position within (periphery) or above the first row (centre) of nests (categorical: Central/Peripheral)

GD referred to the Global Density of the nest (categorical: Low: less than 1.5 individuals on average around the breeding site; Medium: between 1.5 and 3 individuals; High: more than 3 individuals, classes of equal size)

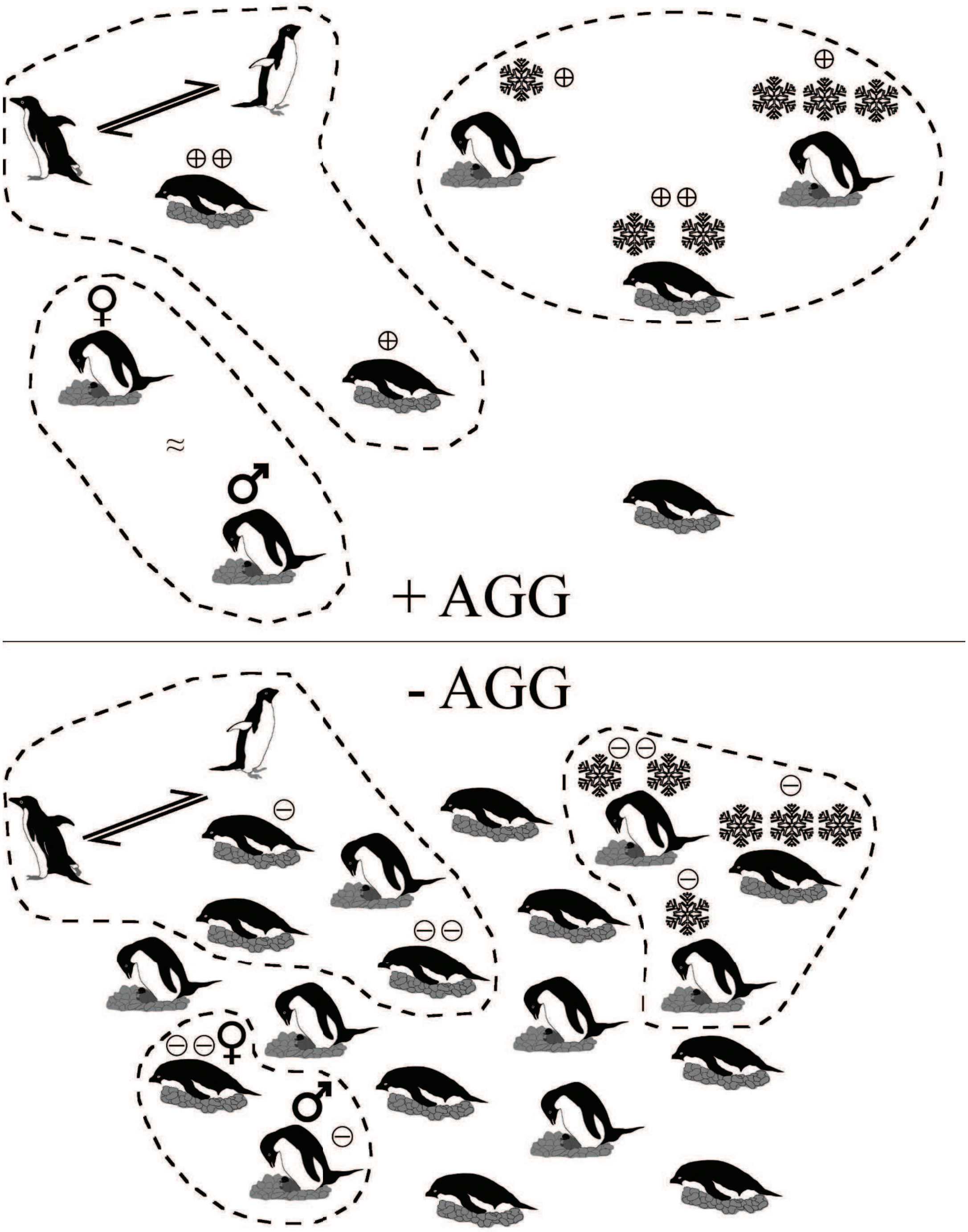


Figure V - 1. Summary of levels of aggressiveness (AGG) observed in Adélie penguins in natural environment according to the breeder density of the nest (upper panel = low density and lower panel = high density), to its exposure to snow (indicated by the number of snowflakes), the disturbance by passage by conspecifics (indicated by walking penguins and double arrows), and the sex of the individuals; signs indicate the relative level of behaviour of individuals compared to other habitat/individual types. Standing birds represent 'non-incubating'/'non-guarding' individuals, sitting/laying birds represent incubating/guarding individuals.

***Figure V - 1**. Résumé des niveaux d'agressivité (AGG) observés chez les manchots Adélie en environnement naturel en fonction de la densité de reproducteurs autour du nid (panneau supérieur = fable densité et panneau inférieur = forte densité), de l'exposition à la neige (figurée par le nombre de flocons de neige), du degré de perturbation par le passage de congénères (figuré par les manchots marchant et les doubles flèches), et du sexe des individus ; les signes indiquent le niveau relatif du comportement des individus en comparaison des autres types d'habitat et de caractéristiques individuelles. Les oiseaux debout représentent des individus qui n'incubent pas/qui ne sont pas en phase de garde, les oiseaux assis/allongés représentent les individus qui incubent/sont en phase de garde.*

Activity was explained by the sex of the individuals and their SSI (see model selection in Table V – S2a). Males were more active than females (GLM: $t = -5.35$, $p < 0.001$; Table V - 2b and Figure V - 2). Low SSI individuals were more active than medium and high SSI individuals ($t = 2.19$, $p = 0.031$ and $t = 2.71$, $p = 0.008$, respectively) but there was no difference between the last two categories of individuals ($t = -1.46$, $p = 0.1$). After controlling for these parameters, activity became significantly consistent over all individuals' observations (ACT: $r = 0.22$, $\chi^2_{99} = 303.13$, $p < 0.001$).

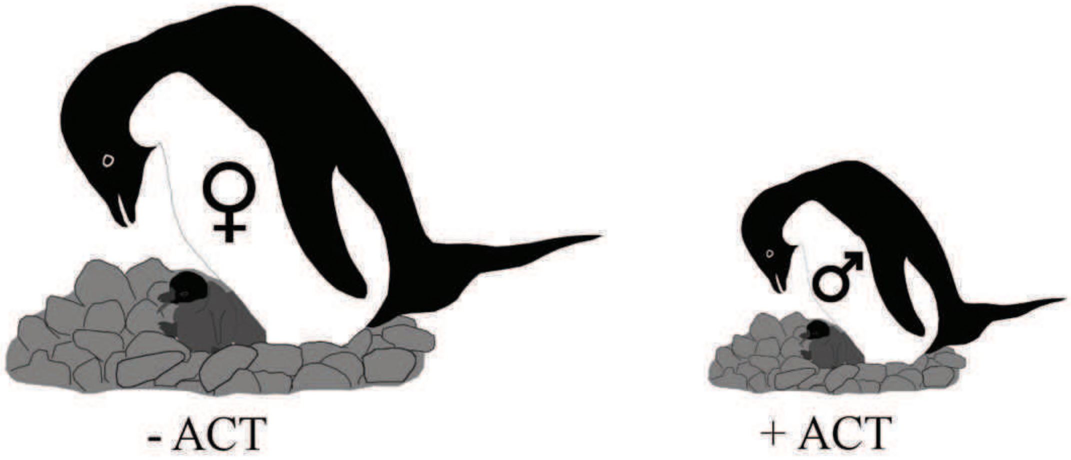


Figure V - 2. Summary of levels of activity (ACT) observed in Adélie penguins in natural environment according to sex and structural size; signs indicate the relative level of behaviour of individuals compared to other individual types. Sitting birds represent incubating/guarding individuals.

***Figure V - 2**. Résumé des niveaux d'activité (ACT) observés chez les manchots Adélies en environnement naturel en fonction du sexe et de la taille structurelle des individus ; les signes indiquent le niveau relatif du comportement des individus par rapport aux autres types d'individus. Les oiseaux assis représentent les individus qui incubent/sont en phase de garde.*

Vocalisation was explained by the centrality of the nest, the sex of the individuals, the SSI, the interaction between the centrality and the SSI, the interaction between the sex and the SSI, and the interaction between the global density (GD) of the nest and the disturbance by regular passages of conspecifics (see model selection in Table V – S2c). Central individuals vocalised less than peripheral ones (GLM: $t = -2.21$, $p = 0.030$; Table V - 2c and Figure V - 3). Males vocalised more than females ($t = -9.63$, $p < 0.001$), and males with low SSI vocalised more than males with medium and high SSIs ($t = 2.40$, $p = 0.019$ and $t = 2.10$, $p = 0.039$, respectively). At low GD, there was no difference between individuals breeding in habitats disturbed by and sheltered from passages of conspecifics, while at high GD, sheltered breeders were vocalising significantly more than regularly disturbed breeders ($t = -4.66$, $p < 0.001$). After controlling for these parameters, vocalisation became significantly consistent over all individuals' observations ($r = 0.30$, $\chi^2_{95} = 381.41$, $p < 0.001$).

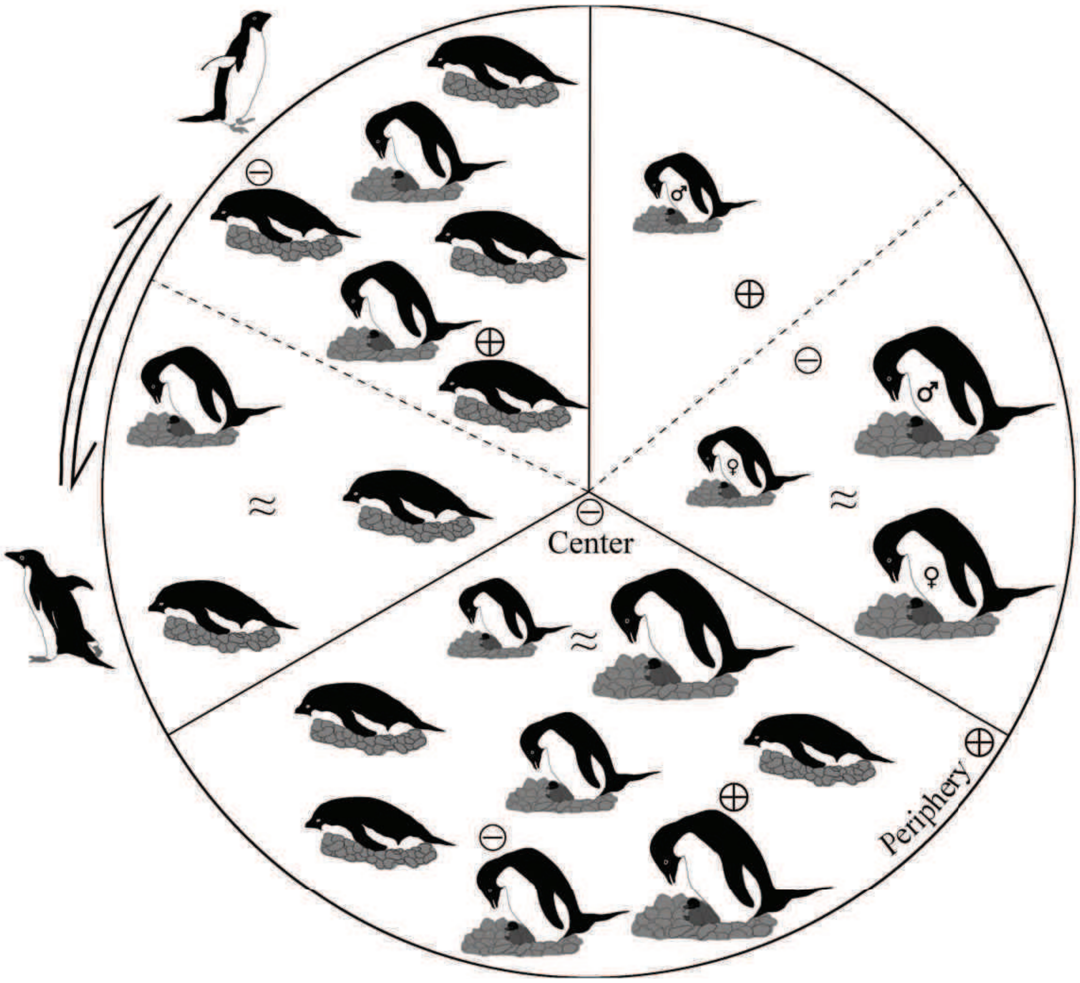


Figure V - 3. Summary of levels of vocalisation (VOC) observed in Adélie penguins in natural environment. In the upper left third are represented the effects of the interaction between global density and level of disturbance by passage by conspecifics. In the upper right third are presented the effects of the interaction between sex and structural size. In the lower third are presented the effects of the interaction between structural size and centrality of the nest; signs indicate the relative level of behaviour of individuals compared to other habitat/individual types. Standing birds represent 'non-incubating'/'non-guarding' individuals, sitting/laying birds represent incubating/guarding individuals.

Figure V - 3*. Résumé des niveaux de vocalisation (VOC) observés chez les manchots Adélies en environnement naturel. Dans le tiers supérieur gauche sont représentés les effets de l'interaction entre densité globale et degré de perturbation par le passage des congénères. Dans le tiers supérieur droit sont représentés les effets de l'interaction entre le sexe et la taille structurelle. Dans le tiers inférieur sont représentés les effets de l'interaction entre taille structurelle et centralité du nid ; les signes indiquent le niveau relatif du comportement des individus par rapport aux autres types d'habitats et d'individus Les oiseaux debout représentent des individus qui n'incubent pas/qui ne sont pas en phase de garde, les oiseaux assis/allongés représentent les individus qui incubent/sont en phase de garde.*

c) Parental guarding and provisionning

The durations of trips at sea and sojourns on land during the brooding and crèching phases were temporally consistent (SeaB: $r = 0.45$, $\chi^2_{72} = 284.90$, $p < 0.001$; LandB: $r = 0.38$, $\chi^2_{72} = 260.41$, $p < 0.001$; SeaC: $r = 0.17$, $\chi^2_{72} = 204.81$, $p < 0.001$; LandC: $r = 0.31$, $\chi^2_{72} = 341.76$, $p < 0.001$) (see Tables V – S3a and V – S3b).

c.1) Individual characteristics

'Within-individual consistency' (see Table V – S3a and S3b) - Except for the duration patterns on land during brooding phase of high SSI, low BCI and long INC individuals, all other durations were significantly repeatable within each individual characteristic. However, individuals presented different degrees of consistency. For instance, females were more repeatable, thus more consistent, than males in the duration of their trips at sea during the crèching phase (SeaC$_{♀}$: $r = 0.21$, $\chi^2_{21} = 93.39$, $p < 0.001$; SeaC$_{♂}$: $r = 0.12$, $\chi^2_{25} = 83.23$, $p < 0.001$; Table V – S5). Moreover, brooding females spent on average more time at sea than males (SeaB$_{\text{sex}}$: 44.69 ± 1.44 hours vs. 28.42 ± 0.92 hours, Table 7; $W = 288$, $N_{♂} = 43$, $N_{♀} = 41$, $p < 0.001$), and less time on land (LandB$_{\text{sex}}$: 32.45 ± 0.98 hours vs. 46.18 ± 1.23 hours; $W = 1434$, $N_{♂} = 43$, $N_{♀} = 41$, $p < 0.001$). Still during brooding, low SSI individuals spent on average more time at sea than individuals with medium and high SSI (SeaB$_{\text{SSI}}$: 47.72 ± 3.31 hours vs. 34.91 ± 1.03 hours and 31.00 ± 1.60 hours; $W = 481$, $p = 0.014$; $W = 172$, $p = 0.005$), and less time on land (LandB$_{\text{SSI}}$: 30.81 ± 1.48 hours vs. 38.98 ± 1.09 hours and 48.53 ± 1.78 hours; $W = 217$, $p = 0.020$; $W = 28$, $p < 0.001$). Medium SSI individuals also spent also less time on land than high SSI individuals (LandB$_{\text{SSI}}$: 38.98 ± 1.09 hours vs. 48.53 ± 1.78 hours; $W = 304$, $p = 0.022$). During brooding, high BCI individuals spent on average less time at sea than medium BCI individuals (SeaB$_{\text{BCI}}$: 27.31 ± 1.12 hours vs. 38.56 ± 1.30 hours; $W = 693$, $p = 0.003$), and spent more time on land than medium BCI individuals (LandB$_{\text{BCI}}$: 44.01 ± 2.02 hours vs. 37.07 ± 1.01 hours; $W = 346$, $p = 0.034$).

'Between-individual consistency' (see Table V – S4a and S4b) - During the brooding phase, duration patterns at sea and on land were repeatable among individuals of the same sex (SeaB$_{\text{sex}}$: $r = 0.48$, $\chi^2_1 = 21.57$, $p < 0.001$; LandB$_{\text{sex}}$: $r = 0.55$, $\chi^2_1 = 25.49$, $p < 0.001$). Duration patterns on land among individuals of the same SSI and at sea among individuals of the same BCI were also repeatable (LandB$_{\text{SSI}}$: $r = 0.25$, $\chi^2_2 = 11.04$, $p = 0.004$; SeaB$_{\text{BCI}}$: $r = 0.24$, $\chi^2_2 = 11.03$, $p = 0.004$).

c.2) Environmental conditions

'Within-individual consistency' (see Table V – S3a and S3b) - Except for the duration patterns at sea of the birds breeding in high density habitat during brooding phase, all other durations were significantly repeatable within each environment. However, different degrees of plasticity emerged. For instance, individuals sheltered from passages of conspecifics were more repeatable, thus less plastic, than disturbed individuals in the duration of their sojourns on land during brooding phase ($\text{Land}_{\text{Sheltered}}$: $r = 0.51$, $\chi^2_{26} = 121.03$, $p < 0.001$; $\text{Land}_{\text{Disturbance}}$: $r = 0.26$, $\chi^2_{38} = 99.02$, $p < 0.001$). These sheltered brooders seemed to spend on average less time on land than disturbed ones though the difference was non-significant ($\text{SeaL}_{\text{Disturbance}}$: 37.15 ± 1.25 days vs. 41.33 ± 1.15 days; $W = 704$, $p = 0.6$),

'Between-individual consistency' (see Table V – S4a and S4b) - During the crèching phase, duration patterns at sea were repeatable among individuals of the same global density habitat (SeaC_{GD}: $r = 0.13$, $\chi^2_{2} = 6.70$, $p = 0.0035$). During the brooding phase, duration patterns at sea and on land among individuals monitored during the same year were also repeatable ($\text{SeaB}_{\text{years}}$: $r = 0.18$, $\chi^2_{1} = 9.17$, $p = 0.002$; $\text{LandB}_{\text{year}}$: $r = 0.11$, $\chi^2_{1} = 5.90$, $p = 0.015$).

d) Behavioural syndromes

Overall, vocalisation intensity in the colony was positively correlated with the distance at which the birds first reacted during the 'trappability' tests ($r_s = 0.67$, $N = 18$, $p = 0.001$).

When considering sexes separately, vocalisation and activity of females at their nests were positively correlated with the reaction distance during capture ($r_s = 0.74$, $N = 14$, $p = 0.002$; $r_s = -0.57$, $N = 14$, $p = 0.035$, respectively). Aggressiveness in their natural environment was positively correlated with vocalisation during capture ($r_s = 0.63$, $N = 14$, $p = 0.016$), as well as with the reaction in the weighting bag ($r_s = 0.39$, $N = 32$, $p = 0.029$). In contrast, in males, only activity in their natural environment was negatively correlated with vocalisation during handling ($r_s = -0.39$, $N = 31$, $p = 0.030$). Vocalisation intensity in the colony of medium SSI individuals was positively correlated with their reaction distance during the 'trappability' tests ($r_s = 0.67$, $N = 14$, $p = 0.008$, respectively). In low SSI birds, vocalisation and activity in the colony were correlated with vocalisation during handling ($r_s = -0.91$, $N = 11$, $p < 0.001$; $r_s = 0.63$, $N = 11$, $p = 0.037$, respectively. Still in low SSI birds, aggressiveness in their natural environment was positively correlated with vocalisation at capture and to birds' reaction in the weighting bag ($r_s = 0.85$, $N = 7$, $p = 0.016$; $r_s = 0.67$,

$N = 9$, $p = 0.025$, respectively). No correlation between capture/handling and natural environment behavioural variables was found for high SSI individuals (all $p > 0.05$).

Moreover, we found that vocalisation of individuals breeding in habitats disturbed by passages of conspecifics and in periphery of the colony were positively correlated with the reaction distance at capture ($r_s = 0.77$, $N = 12$, $p = 0.003$; $r_s = 0.57$, $N = 15$, $p = 0.027$, respectively). Activity of individuals nesting in periphery of the colony was correlated with their vocalisation during handling ($r_s = 0.30$, $N = 45$, $p = 0.047$). Vocalisation of birds exposed to snowfall was positively correlated with their reaction distance at capture ($r_s = 0.90$, $N = 7$, $p = 0.006$), while activity of birds breeding in snow-protected habitats was negatively correlated with their reaction distance at capture ($r_s = -0.74$, $N = 9$, $p = 0.022$). Vocalisation of individuals breeding in low breeder/global density habitats were positively correlated with their reaction distance at capture ($r_s = 0.80$, $N = 12$, $p = 0.002$, $r_s = 0.83$, $N = 12$, $p < 0.001$), while only activity was correlated with this variable for individuals breeding in low global density habitats ($r_s = -0.89$, $N = 12$, $p < 0.001$). No correlation was observed for individuals breeding in medium and high breeder/global density habitats (all $p > 0.05$).

Finally, aggressiveness and activity at the nest were negatively correlated with the duration of trips at sea during the brooding phase ($r_s = -0.24$, $N = 73$, $p = 0.038$; $r_s = -0.26$, $N = 73$, $p = 0.027$, respectively). Moreover, vocalisation at the nest was negatively correlated with the duration of sojourns on land during the crèching phase ($r_s = -0.31$, $N = 50$, $p = 0.028$). We also found that, in males, the variance in aggressiveness, activity and vocalisation at the nest were positively correlated with the variance in the duration of trips at sea during the crèching phase (AGG: $r_s = 0.67$, $N = 27$, $p < 0.001$; ACT: $r_s = 0.62$, $N = 27$, $p < 0.007$; VOC: $r_s = 0.65$, $N = 27$, $p < 0.003$; Figure V - 4). No other correlation was found (all $p > 0.05$).

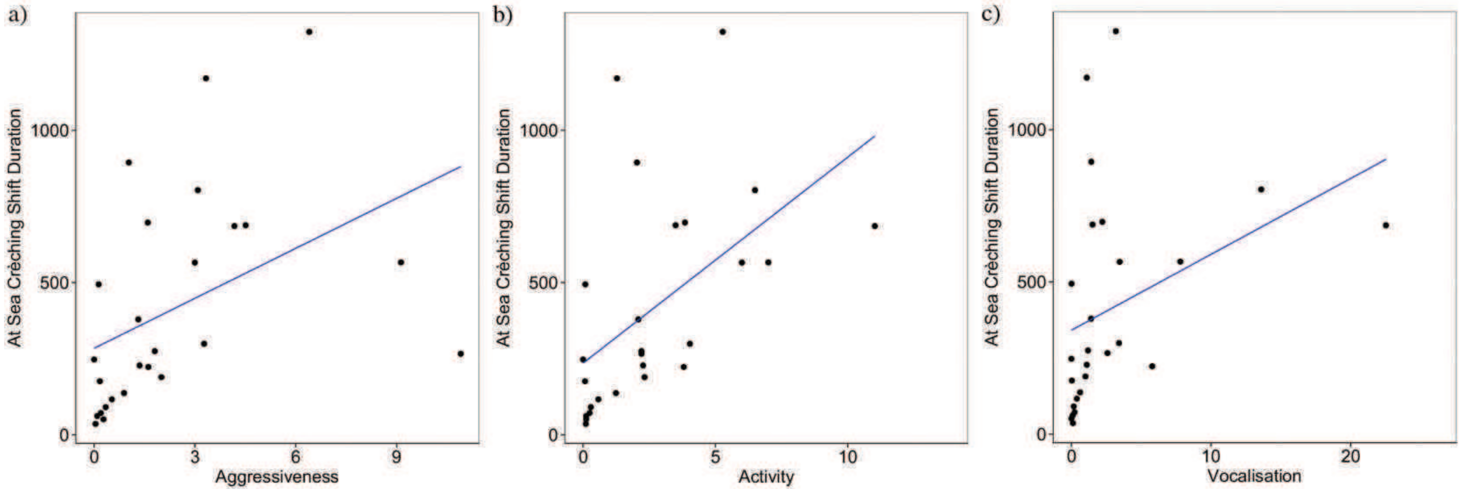


Figure V - 4. Phenotypic correlations between averaged foraging trips duration during crèching and average a) aggressiveness, b) activity and c) vocalisation at the nest in 28 males Adélie penguins.

***Figure V - 4**. Corrélation phénotypiques entre durée moyenne des voyages alimentaires en phase de crèche et a) agressivité, b) activité et c) vocalisation moyennes au nid chez 28 manchots Adélie mâles.*

e) Breeding success

Successful breeders were more aggressive than failed ones at their nests ($W = 4601$, $N_{\text{success}} = 66$, $N_{\text{failure}} = 111$, $p = 0.002$), while no difference was found in terms of activity and vocalisation (all $p > 0.05$). Aggressiveness was significantly repeatable between individuals with the same breeding output (AGG: $r = 0.08$, $\chi^2_1 = 8.11$, $p = 0.004$; Table V – S1). Within-individual aggressiveness and activity of successful birds were consistent (AGG: $r = 0.04$, $\chi^2_{56} = 78.57$, $p = 0.025$; ACT: $r = 0.04$, $\chi^2_{56} = 76.33$, $p = 0.037$), whereas for failed breeders only aggressiveness tended to be repeatable (AGG: $r = 0.04$, $\chi^2_{101} = 123.07$, $p = 0.067$).

Considering within-individual consistency, both successful and failed breeders were repeatable in the durations of their trips at sea and their sojourns on land during the brooding phase, only successful breeders were repeatable in the durations of their trips at sea and sojourns on land during the crèching phase (SeaC: $r = 0.17$, $\chi^2_{40} = 176.51$, $p < 0.001$; LandC: $r = 0.34$, $\chi^2_{40} = 313.86$, $p < 0.001$; Table V – S3a and S3b). The durations of trips at sea and sojourns on land during the crèching phase were significantly repeatable between individuals of the same breeding output (SeaC: $r = 0.34$, $\chi^2_1 = 4.47$, $p = 0.035$; LandC: $r = 0.54$, $\chi^2_1 = 5.00$, $p = 0.025$; Table V – S4a and S4b).

Breeding success varied according to habitat and individual characteristics, even though differences were no significant. The breeding success of the birds monitored in 2011/2012 was however lower than in 2012/2013 (29% vs. 40%, $p = 0.3$, $N = 94$). Breeders nesting in central habitat tended to be more successful than peripheral breeders (45% vs. 30%, $p = 0.2$, $N = 94$). Birds breeding in habitat very exposed to snow were also more successful than in habitat less exposed and protected from the snow (53% vs. 36% and 26% respectively, $p = 0.2$, $N = 94$), and birds breeding in low global density habitat tended to fail more often than birds breeding in medium and high global density habitats (29% vs. 50% and 50% respectively, $p = 0.1$, $N = 88$). Interestingly, in both breeding seasons, individuals incubating their egg longer had a lower breeding success (2011/2012: $p = 0.3$, $N = 23$, 29% vs. 63% for longINC and mediumINC, respectively, and no observation for shortINC; 2012/2013: $p = 0.2$, $N = 36$ 40% vs. 67% for mediumINC and shortINC, respectively, and no observation for longINC).

4 – Discussion

a) Context specificity of personality on land

Using behavioural observations of individuals in their colony, we identified three personality dimensions in Adélie penguins: aggressiveness, activity, and vocalisation. Moreover, we found a positive correlation between one of these personality dimensions, vocalisation at the nest, and approaching distance at capture. This behavioural syndrome was also observed in specific habitats (exposed to snow and low global/breeder density habitats) and in individuals with specific characteristics (females and medium sized individuals). In addition, we found other behavioural syndromes according to specific habitat characteristics (e.g. approaching distance at capture and activity at the nest in protected to snow and low global density habitats) and to individual characteristics (e.g. vocalisation during handling and activity at the nest in males). These results suggest context specificity of the behavioural syndromes we observed in Adélie penguins (Wilson et al., 1994; Wilson, 1998). The moderate repeatability scores found for personality traits in the colony suggested potential moderate heritability (Boake, 1989). Furthermore repeatability estimates increased when variance explained by habitat and individual characteristics was removed. These results point out differences in habitat and individual characteristics as potential sources of inter-individual heterogeneity observed in these personality traits (Nussey et al., 2007; Wilson and Nussey, 2010).

As expected, we found strong relationships between personality and individual/habitat characteristics in Adélie penguins. Activity and vocalisation at nest were explained by sex and structural size. This result supports the hypothesis of a relatively stable neurophysiological structure of behaviour, which might explain, at least to some extent, the consistence of between individual differences in these behaviours ('inherently stable state component hypothesis', Wolf and Weissing, 2010). Indeed, small individuals were more active than tall individuals, and males were consistently more active than females. Moreover, small males vocalised more than tall males and small and tall females. Small individuals are assumed to have a higher specific metabolic rate (Schmidt-Nielsen, 1984) that can explain the level of activity observed in these individuals. In the same way, differences between males and females can be explained by differential hormonal status that has already been shown to explain differences in morphology and different biological processes in a wide range of species (e.g. Groscolas et al., 1986; Handa et al., 1994; Wood and Shors, 1998; Peterson et al., 2013). Individual quality is partially defined by the physical and physiological state of an individual (McNamara and Houston, 1996; Wilson and Nussey, 2010). Our results linking personality to physical and physiological characteristics of individuals therefore support the hypothesis that personality can reflect previously defined individual quality.

We also found that high density breeders were less aggressive than low density breeders. Furthermore, high density breeders vocalised consistently less when regularly disturbed by passage by conspecifics. Aggressiveness might become too energetically costly (Viera et al., 2011) and risky for offspring (increased risk of loosing the egg for instance, Hatchwell, 1991; Clair and Clair, 1996) in an environment where aggressive interactions are more likely to happen. Moreover, vocalisation in this species can be used to mark territory or signal condition (Spurr, 1975), and therefore might be involved in resources acquisition through information transmission (Danchin et al., 1998; Patten et al., 2004; Danchin et al., 2005). We thus considered these two behaviours adaptive of their contexts and signalling of the quality of the nest and their occupants. These results were supported by the tendency to a higher breeding success observed for high and medium density breeders. Moreover, independently of other habitat characteristics, individuals breeding in habitat regularly disturbed by passage by conspecifics were consistently more aggressive, which might reflect a better defence against 'pebble thefts' (pebble being an important feature of Adélie penguins nest quality, Ainley, 2002). The adaptive advantage conferred by this behaviour in this situations was supported by the consistently higher level of aggressiveness observed in successful breeders. However, individuals breeding in habitat regularly disturbed by passage by conspecifics were also less prone to attempt escaping during ‘resistance to handler’ tests. These results are in opposition to what would be expected from the well-studied ‘aggressiveness-boldness’ syndrome (e.g. Huntingford, 1976; Tulley and Huntingford, 1988; Riechert and Hedrick, 1993), suggesting that there was no common structure between these two behaviours under opposite selective pressures. We also found that central individuals vocalised less than peripheral individuals. Central habitats are considered to be of good quality and to host experienced birds (Ainley, 2002). As previously mentioned, vocalisation can be used to signal quality and mark territory, therefore we did not expected central individuals to vocalise less than peripheral ones. However, in our colony, given the topography, some peripheral nests might have been better protected from exposure to some pressures such as passage by other individuals, predation and flooding (personal observations) than more central nest, which might explain this result. Nevertheless we observed that breeding success tended to be higher in central nests of this colony, contradicting this last theory and suggesting a more complex relationship between vocalisation and habitat quality. The small sample of central-small and peripheral-small individuals did not give enough power to conclude on the potential modulation of the relationship between vocalisation and centrality of the nest by structural size. In an heterogeneous environment where all individuals will not have access to habitat of equal quality, the quality of an individual might facilitate its access to a good quality habitat that will in turn enhance its performances and quality (Coulson, 1968). The Adélie penguin is a highly philopatric species (Ainley, 2002; Dugger et al., 2006) where individuals often come back to breed in the same area with nests of equivalent characteristics (personal observation). The positive feedback between habitat and individual quality might therefore be even stronger in this species, stabilising their relationship. This theory (lable state component-positive feedback theory, Wolf and Weissing, 2010) would explain the strong relationship we found between personality and habitat characteristics as well as the behavioural consistency we observed in individuals. However, selection pressures on habitats can also vary according to time and space within the sub-colony, promoting the maintenance of different behavioural types observed in this population (Southwood, 1977; Wolf and Weissing, 2010).

b) Can personality in land reflect personality at sea?

The consistency of on-land sojourn was homogeneous with the consistency of foraging trip during guarding. Moreover, the consistency of sojourn on land during guarding depends on the quality of both mates that we were not able to distinguish here. In addition, sojourn on land during crèching were homogeneously more consistent than foraging trips, but they did not differ much according to habitat and individual variables measured.

As expected, we observed individual consistency in foraging trip duration in both phases of the breeding cycle of Adélie penguins. We also observed that individuals were less plastic during guarding than during crèching which might be explained by the stronger constraints during this first stage of chick rearing when chicks are still vulnerable (Davis, 1982; Clarke et al., 1998; Ainley, 2002). In addition, we found consistent differences in at sea trip duration during guarding between individuals of different body condition. Foraging efficiency is considered as an indicator of individuals' quality (Lescroël et al., 2010) since it is tightly link to resources acquisition, and such relationship between foraging strategies and individual characteristics was therefore to be expected. Moreover, we found that successful breeders were consistent in their foraging trip during crèching while failed breeders were not, supporting our hypothesis that regularity in foraging trips was an indicator of individual quality and an important characteristic for a successful reproduction. Furthermore, since both personality and foraging efficiency reflect individual quality, we predicted a strong relationship between personality at the nest, foraging behaviour, and individual characteristics. As expected, we found that average aggressiveness and activity in the colony were negatively correlated to the duration of the trips at sea during guarding. The Adélie penguin is a territorial species (Ainley, 2002), where more aggressive and active birds are assumed to better defend and care for their nest. We would therefore expect these individuals to spend more time on land and indirectly less time at sea (Clarke et al., 1998, personal observations), which would explain the negative correlations we observed. However we did not find correlations between aggressiveness and activity at the nest and the duration of sojourn on land. Another potential explanation is that aggressiveness and activity might influence foraging at sea of individuals through habitat use as it has been demonstrated in other species (e.g. Boon et al., 2008; Boyer et al., 2010; van Overveld and Matthysen, 2010). Furthermore, almost nothing is known about interactions between individuals at sea in free ranging penguins species. However, thanks to cameras mounted on the back of individuals, Takahashi et al. (2004) found the first evidence of individuals interactions at sea in this penguin species. It would therefore not be surprising to find that personality also influence the interactions between individuals during foraging (e.g. Dyer et al., 2009; Harcourt et al., 2009; Kurvers et al., 2010a; Kurvers et al., 2010b; Michelena et al., 2010). We also found consistent behavioural differences between sexes during guarding, which is congruent with previous studies that demonstrated a difference of energy allocation in brooding between males and females in this species (Chappell et al., 1993; Clarke et al., 1998). The differences in plasticity observed between sexes during crèching are also congruent with the results of Clarke et al. (1998) that found a shift toward mixed foraging grounds in males in crèching when constraints linked to guarding were reduced. Furthermore, our results support the hypothesis that sex differences in foraging strategies can be mediated by personality, as we found that, in males, variance in personality at nest predicted variance in foraging trip duration during crèching period. It is interesting to note that Patrick and Weimerskirch (2014) found that correlation between boldness and foraging personalities varied according to both sex of individuals and year quality in black browed albatross (*Thalassarche melanophrys*).

Individuals breeding in central habitat and in habitats disturbed by regular passing by conspecifics were less consistent in their foraging trips during guarding than peripheral and sheltered individuals. In contrats, individuals breeding in habitat protected from snow were more consistent in their foraging trip during crèching than exposed individuals. Since foraging efficiency can reflect individual quality (Lescroël et al., 2010) and individual quality might favour the access to habitat of good quality (Coulson, 1968), we expected higher foraging consistency from individual in good quality habitat but we observed contradictory results to that regard for central birds. The same explanation as for the differences in vocalisation can apply here, that is to say central nests might not be the nests of better quality in our colony. Another explanation is that quality components involved in the acquisition of a good quality habitat (both at sea and on land) and their interactions are complex (Danchin et al., 2005) and we might not have captured them all here.

c) Conclusion and perspectives

Our results showed for the first time in a penguin species the existence of personality traits tightly linked to individual and habitat quality with an influence on individual fitness. Furthermore, as we previously saw with another seabird species, the Brunnich's guillemot, *Uria lomvi*, (Cornet et al. *in prep. 1*), personality traits are now included in the 'pace of life syndrome' of a population (Réale et al., 2010b; Niemelä et al., 2013) and can therefore facilitate the evolution and the adaptive conservation of the other traits of a population they are correlated to (Dall et al., 2004). Our new results implicating personality in foraging behaviour agree with this theory, and bring new insight on the emergence and the maintenance of individual differences in seabird foraging strategies. In the future, with the help of consistently developing technology, we will be able to access even more foraging and personality parameter with minimal disturbance to animals. This will allow us to sharpen our knowledge on the implication of these two parameters in habitat use and social interactions between individuals as well as on the selective pressures shaping them, and this in the full range of seabird habitat. Because seabirds depend on both at sea and on land environmental conditions to survive and reproduce (Baird, 1991; Costa, 1991), such studies integrating adaptive potential of seabirds in both environments are crucial to gauge the future of their populations.

Supplementary material

Table V - S 1. Within- and between-individual repeatability indices (r) of behaviours expressed by 148 Adélie penguins in their breeding colony: a) PC1 = Aggressiveness = AGG, b) PC2 = Activity = ACT, and c) PC3 = Vocalisation = VOC. Bold type indicates repeatability indices that were significantly different from zero.

***Tableau V – S1**. Indices de répétabilité (r) intra- et interindividuels des comportements exprimés par 148 manchots Adélie dans leur colonie de reproduction : a) PC1 = Agressivité = AGG, b) PC2 = Activité = ACT, et c) PC3 = Vocalisation = VOC. Les caractères gras indiquent les indices de répétabilité significativement différents de zéro.*

Table footnotes :

r: repeatability index
χ^2, *df*: chi-squared statistic and degree of freedom
p: p-value
V_a: variance among groups
V_w: variance within groups
N: number of groups
k: number of observations per group adjusted for unbalanced design
Central/Peripheral: centrality of the nest
Disturbed by/Sheltered from regular passages: disturbance of the nest by regular passages of conspecifics
Highly Exposed/Exposed/Protected: exposure of the nest to snowfall accumulation
GDS: Global Density Score of the nest (Low: less than 1.5 individuals on average around the breeding site; Medium: between 1.5 and 3 individuals; High: more than 3 individuals, classes of equal size)
BDS: Breeder Density Score of the nest (Low: less than 1 breeders on average around the breeding site; Medium: between 1 and 3 breeders; High: more than 3 breeders, classes of equal size)
Males/Females: sex of the individuals
SSI: Structural Size Index of the individuals (Low: SSI < mean(SSI) – sd(SSI); Medium: mean(SSI) – sd(SSI) ≤ SSI < mean(SSI) + sd(SSI); High: mean (SSI) + sd(SSI) ≤ SSI)
BCI: Body Condition Index of the individuals (Low: BCI < mean(BCI) – sd(BCI); Medium: mean(BCI) – sd(BCI) ≤ BCI < mean(BCI) + sd(BCI); High: mean (BCI) + sd(BCI) ≤ BCI)
INC: incubation length (in days). We defined birds incubating between i) 28-32 days as Short INC, ii) 33-37 days as Medium INC, and iii) 38-43 days as Long INC
Success/Failure: breeding output at as inferred from nest monitoring and cycle analysis
2011/2012 and 2012/2013: the two breeding seasons

a) AGG	r	χ^2, df	P	V_a	V_w	N	k
Individual	**0.03**	182.43, 147	0.025	3650.67	114516.90	148	8.79
Central	0.05	64.07, 48	0.060	547.80	11455.43	49	8.30
Peripheral	0.02	111.80, 97	0.145	1018.37	52192.52	98	8.96
Between-individual	0.02	2.17, 1	0.141	32.54	1797.46	2	65.33
Disturbed by regular passages	0.03	104.65, 86	0.084	1148.68	39494.43	87	8.66
Sheltered from regular passages	0.02	71.08, 60	0.155	468.31	19713.15	61	8.93
Between-individual	0.03	3.51, 1	0.061	64.80	1805.08	2	71.72
Highgly Exposed to snow	0.02	26.41, 23	0.282	66.25	4298.19	24	10.71
Exposed to snow	0.04	84.87, 68	0.081	751.38	20351.01	69	7.95
Protected from snow	0.03	65.61, 54	0.134	474.27	17000.50	55	8.90
Between-individual	-0.01	1.05, 2	0.592	-19.38	1848.76	3	45.75
Low GDS	0.01	82.69, 75	0.254	383.62	26743.22	76	8.23
Medium GDS	**0.06**	65.67, 43	0.015	783.50	11844.90	44	9.46
High GDS	-0.01	17.79, 20	0.601	-34.76	2405.52	21	8.47
Between-individual	0.01	2.49, 2	0.288	11.58	2166.35	3	46.80
Low BDS	0.01	59.61, 54	0.279	258.59	22575.41	55	10.16
Medium BDS	**0.04**	119.83, 95	0.043	1380.25	32005.25	96	7.31
High BDS	-0.12	2.68, 6	0.848	-11.18	101.02	7	5.39
Between-individual	0.04	5.40, 2	0.067	101.81	2689.58	3	46.34
Males	0.03	95.82, 77	0.072	1076.72	34121.50	78	8.97
Females	0.02	80.12, 69	0.170	518.49	23837.47	70	8.55
Between-individual	0.02	2.17, 1	0.141	29.34	1821.97	2	73.78
Low SSI	-0.06	8.97, 16	0.915	-91.34	1702.33	17	8.71
Medium SSI	**0.07**	107.66, 66	< 0.001	2290.77	32278.33	67	10.50
High SSI	-0.04	8.68, 15	0.894	-100.69	2605.74	16	11.44
Between-individual	-0.04	0.23, 2	0.891	-30.60	856.91	3	24.83
Low BCI	0.06	13.73, 10	0.186	26.24	399.53	11	6.90
Medium BCI	**0.04**	93.42, 72	0.046	1105.45	28078.56	73	8.83
High BCI	**0.07**	35.28, 23	0.049	218.67	2829.13	24	8.38
Between-individual	0.05	4.75, 2	0.093	59.51	1141.53	3	27.46
Short INC	0.02	52.90, 45	0.196	253.34	10400.05	46	8.35
Medium INC	**0.06**	82.58, 54	0.007	1239.96	19495.97	55	9.84
Long INC	0	15.02, 15	0.450	0.24	1244.87	16	7.82
Between-individual	0	1.97, 2	0.373	-0.49	1291.92	3	36.94
Success	**0.04**	78.57, 56	0.025	1118.24	26119.80	57	10.79
Failure	0.04	123.07, 101	0.067	1167.84	27563.33	102	6.36
Between-individual	**0.08**	8.11, 1	0.004	226.40	2515.77	2	82.78
2011/2012	**0.05**	98.95, 77	0.047	982.77	19892.23	78	7.04
2012/2013	**0.06**	137.57, 102	0.011	2194.47	37583.42	103	7.31
Between-individual	-0.01	0.39, 1	0.530	-18.82	2751.18	2	88.77

b) ACT	r	χ^2, df	p	V_a	V_w	N	k
Individual	0.02	172.50, 147	0.074	2627.41	115531.70	148	8.79
Central	0.03	58.25, 48	0.148	349.27	11648.88	49	8.30
Peripheral	0.01	106.22, 97	0.245	633.97	52572.14	98	8.96
Between-individual	-0.01	0.45, 1	0.503	-15.39	1818.91	2	65.33
Disturbed by regular passages	0.01	93.75, 86	0.266	477.47	40156.23	87	8.66
Sheltered from regular passages	0.02	69.81, 60	0.181	414.90	19765.49	61	8.93
Between-individual	0	0.69, 1	0.407	-8.02	1840.61	2	71.72
Highly Exposed to snow	-0.01	20.56, 23	0.608	-47.41	4405.87	24	10.71
Exposed to snow	0.03	80.22, 68	0.232	543.95	20554.83	69	7.95
Protected from snow	0.03	68.62, 54	0.094	597.11	16880.32	55	8.90
Between-individual	0	1.81, 2	0.405	-3.92	1839.14	3	45.75
Low GDS	0.01	82.59, 75	0.257	378.65	26748.12	76	8.23
Medium GDS	0.02	51.76, 43	0.169	302.93	12313.65	44	9.46
High GDS	**0.08**	32.01, 20	0.043	189.34	2194.65	21	8.47
Between-individual	-0.02	0.36, 2	0.837	-38.66	2195.74	3	46.80
Low BDS	0.01	59.67, 54	0.277	261.07	22572.99	55	10.16
Medium BDS	**0.05**	122.40, 95	0.031	1522.84	31864.44	96	7.31
High BDS	0.13	9.48, 6	0.148	11.71	81.56	7	5.38
Between-individual	0	2.11, 2	0.349	3.22	2740.34	3	46.34
Males	0.03	97.67, 77	0.056	1182.84	34017.09	69	0.17
Females	0	69.82, 69	0.450	38.32	24309.50	70	8.55
Between-individual	**0.08**	6.91, 1	0.009	148.24	1762.29	2	73.78
Low SSI	-0.08	6.01, 16	0.988	-129.73	1737.99	17	8.71
Medium SSI	0.03	85.39, 66	0.055	1066.03	33481.86	67	10.50
High SSI	0.04	21.24, 15	0.129	99.36	2420.14	16	11.44
Between-individual	-0.04	0.08, 2	0.963	-33.29	858.27	3	24.83
Low BCI	-0.03	8.18, 10	0.612	-12.82	434.06	11	6.90
Medium BCI	0.03	90.49, 72	0.069	954.67	28226.98	73	8.83
High BCI	0	23.66, 23	0.423	11.74	3027.56	24	8.38
Between-individual	**0.17**	12.41, 2	0.002	225.51	1063.62	3	27.46
Short INC	0.03	55.06, 45	0.145	322.57	10332.26	46	8.35
Medium INC	**0.06**	82.21, 54	0.008	1220.97	19511.65	55	9.84
Long INC	0.01	16.39, 15	0.357	16.74	1229.39	16	7.82
Between-individual	0.05	5.61, 2	0.061	64.08	1253.14	3	36.94
Success	**0.04**	76.33, 56	0.037	1007.44	26228.49	57	10.79
Failure	0.01	104.77, 101	0.379	199.52	28520.58	102	6.36
Between-individual	-0.01	0.54, 1	0.461	-14.53	2629.09	2	82.78
2011/2012	0.03	89.87, 77	0.150	576.45	20293.25	78	7.04
2012/2013	**0.02**	117.80, 102	0.136	974.86	38790.80	103	7.31
Between-individual	0	1.01, 1	0.316	0.20	2741.90	2	88.77

c) VOC	r	χ^2, df	p	V_a	V_w	N	k
Individual	0	150.24, 147	0.410	334.21	117805.90	148	8.79
Central	0	49.30, 48	0.421	44.14	11946.20	49	8.30
Peripheral	0.01	101.03, 97	0.370	277.11	52924.57	98	8.96
Between-individual	0.02	2.52, 1	0.113	42.37	1793.06	2	65.33
Disturbed by regular passages	-0.01	80.31, 86	0.653	-350.56	40972.64	87	8.66
Sheltered from regular passages	0.02	70.27, 60	0.171	434.19	19746.58	61	8.93
Between-individual	**0.05**	4.41, 1	0.036	87.96	1793.78	2	71.72
Highgly Exposed to snow	-0.03	16.52, 23	0.832	-125.77	4480.11	24	10.71
Exposed to snow	0.01	73.11, 68	0.314	227.53	20865.73	69	7.95
Protected from snow	0.01	57.57, 54	0.345	145.82	17321.85	55	8.90
Between-individual	0	2.08, 2	0.354	1.60	1835.70	3	45.75
Low GDS	0	72.70, 75	0.554	-114.54	27233.84	76	8.23
Medium GDS	0.03	53.86, 43	0.124	375.29	12243.07	44	9.46
High GDS	0.03	23.77, 20	0.252	59.48	2316.85	21	8.47
Between-individual	-0.01	1.44, 2	0.486	-13.07	2180.77	3	46.80
Low BDS	0.01	56.78, 54	0.349	156.40	22676.00	55	10.16
Medium BDS	0.03	114.41, 95	0.085	1088.75	33103.00	96	7.31
High BDS	-0.03	5.08, 6	0.534	-3.10	94.14	7	5.38
Between-individual	0	2.05, 2	0.359	1.50	2741.23	3	46.34
Males	0.02	88.92, 77	0.167	681.74	34510.11	78	8.97
Females	-0.02	57.01, 69	0.848	-559.41	24897.09	70	8.55
Between-individual	0.02	2.13, 1	0.145	28.21	1822.54	2	73.78
Low SSI	0.01	17.03, 16	0.384	13.41	1605.01	17	8.71
Medium SSI	0	64.06, 66	0.545	-106.74	34634.32	64	10.50
High SSI	-0.04	8.11, 15	0.919	-109.78	2614.18	16	11.44
Between-individual	**0.14**	9.44, 2	0.009	128.77	776.97	3	24.83
Low BCI ssi	-0.08	5.37, 10	0.865	-32.55	451.51	11	6.90
Medium BCI	0.01	77.08, 72	0.320	262.33	28908.52	73	8.83
High BCI	0.02	26.00, 23	0.301	53.39	2987.62	24	8.38
Between-individual	-0.02	0.92, 2	0.632	-23.45	1180.47	3	27.46
Short INC	0	45.97, 45	0.432	31.02	10617.72	46	8.35
Medium INC	0	53.02, 54	0.512	-42.40	20750.44	55	9.84
Long INC	0.09	24.09, 15	0.064	109.61	1142.21	16	7.82
Between-individual	-0.02	0.34, 2	0.843	-29.48	1309.33	3	36.94
Success	0.01	63.79, 56	0.222	386.14	26837.98	57	10.79
Failure	-0.01	96.15, 101	0.618	-256.40	28971.29	102	6.36
Between-individual	-0.01	0.03, 1	0.867	-30.97	2636.83	2	82.78
2011/2012	0.02	85.90, 77	0.228	398.57	20468.82	78	7.04
2012/2013	0.01	109.06, 102	0.298	435.60	39324.65	103	7.31
Between-individual	-0.01	0.24, 1	0.626	-23.68	2753.68	2	88.77

Table V - S 2. Model selection of the generalised linear models explaining the behavioural variables collected during focal observations on 95 Adélie penguins at their nests: a) PC1 = Aggressiveness = AGG, b) PC2 = Activity = ACT, c) PC3 = Vocalisation = VOC. Bold type indicates the selected model for each behavioural variable.

***Tableau V – S2**. Sélection des modèles linéaires généralisés expliquant les variables comportementales collectées durant les focales d'observation sur 95 manchots Adélie sur leur nid: a) PC1 = Agressivité = AGG, b) PC2 = Activité = ACT, c) PC3 = Vocalisation = VOC. Les caractères gras indiquent le modèle sélectionné pour chaque variable comportementale.*

Table footnotes :

AIC: Aikaike's Information Criterion
ΔAIC: absolute difference with lowest AIC
wj: model weight
k: number of parameters in the model
ED: percentage of deviance explained by the model
Disturbance referred to disturbance of the nest by regular passages of conspecifics (categorical: Disturbed/Sheltered)
Exposure referred to the exposure of the nest to snowfall accumulation (categorical: Highly Exposed/Exposed/Protected)
BD referred to the Breeder Density of the nest (categorical: Low: less than 1 breeders on average around the breeding site; Medium: between 1 and 3 breeders; High: more than 3 breeders, classes of equal size)
Sex referred to the sex of the individuals (categorical: Females/Males)
SSI referred to the Structural Size Index of the individuals (categorical: Low: $SSI < mean(SSI) - sd(SSI)$; Medium: $mean(SSI) - sd(SSI) \leq SSI < mean(SSI) + sd(SSI)$; High: $mean(SSI) + sd(SSI) \leq SSI$)
GD referred to the Global Density of the nest (categorical: Low: less than 1.5 individuals on average around the breeding site; Medium: between 1.5 and 3 individuals; High: more than 3 individuals, classes of equal size)
Centrality referred to the centrality of the nest in the colony according to its position within (periphery) or above the first row (centre) of nests (categorical: Central/Peripheral)

	Explaining variables	AIC	ΔAIC	w_j	k	ED
a) PC1: AGG	Disturbance, Exposure, BD, Sex	117.66	15.73	< 0.01	4	16
	Disturbance, Exposure, BD, Sex, Disturbance x Exposure, Disturbance x BD, Disturbance x Sex, Exposure x BD, Exposure x Sex, BD x Sex	107.32	5.39	0.04	10	37
	Disturbance, Exposure, BD, Sex, Disturbance x Exposure, Disturbance x Sex, Exposure x BD, BD x Sex	101.95	0.02	0.59	8	36
	Disturbance, Exposure, BD, Exposure x BD, BD x Sex	**101.93**	**0**	**0.36**	**5**	**31**
b) PC2: ACT	Sex, SSI, GD, Sex x SSI, Sex x GD, SSI x GD	132.02	8.74	0.01	6	22
	Sex, SSI, GD, Sex x SSI, Sex x GD	129.41	6.13	0.03	5	21
	Sex, SSI, GD, Sex x SSI	127.47	4.19	0.08	4	21
	Sex, SSI, Sex x SSI	125.59	2.31	0.21	3	21
	Sex, SSI	**123.28**	**0**	**0.67**	**2**	**19**
c) PC3: VOC	Centrality, Sex, SSI, Disturbance, GD	90.99	54.48	< 0.01	5	16
	Centrality, Sex, SSI, Disturbance, GD, Centrality x Sex, Centrality x SSI, Centrality x Disturbance, Centrality x GD, Sex x SSI, Sex x Disturbance, Sex x GD, SSI x Disturbance, SSI x GD, Disturbance x GD	44.83	8.32	< 0.01	15	62
	Centrality, Sex, SSI , Distrubance, GD, Centrality x Sex, Centrality x SSI, Centrality x Disturbance, Centrality x GD, Sex x SSI, Sex x Disturbance, Sex x GD, SSI x GD, Disturbance x GD	41.49	4.98	0.02	14	61
	Centrality, Sex, SSI, Disturbance, GD, Centrality x Sex, Centrality x SSI, Centrality x Disturbance, Centrality x GD, Sex x SSI, Sex x GD, SSI x GD, Disturbance x GD	39.65	3.14	0.04	13	61
	Centrality, Sex, SSI, Disturbance, GD, Centrality x Sex, Centrality x SSI, Centrality x GD, Sex x SSI, Sex x GDS, SSI x GD, Disturbance x GD	38.70	2.19	0.07	12	61
	Centrality, Sex, SSI, Disturbance, GD, Centrality x Sex, Centrality x SSI, Centrality x GD, Sex x SSI, SSI x GD, Disturbance x GD	38.41	1.90	0.08	11	60
	Centrality, Sex, SSI, Disturbance, GD, Centrality x Sex, Centrality x SSI, Centrality x GD, Sex x SSI, Disturbance x GD	38.50	1.99	0.08	10	58
	Centrality, Sex, SSI, GD, Centrality x Sex, Centrality x SSI, Centrality x GD, Sex x SSI, Disturbance x GD	36.51	0	0.21	9	58
	Centrality, Sex, SSI, GD, Centrality x Sex, Centrality x SSI, Sex x SSI, Disturbance x GD	36.64	0.13	0.20	8	57
	Centrality, Sex, SSI, GD, Centrality x SSI, Sex x SSI, Disturbance x GD	37.14	0.63	0.15	7	57
	Centrality, Sex, SSI, Centrality x SSI, Sex x SSI, Disturbance x GD	**37.14**	**0.63**	**0.15**	**6**	**56**

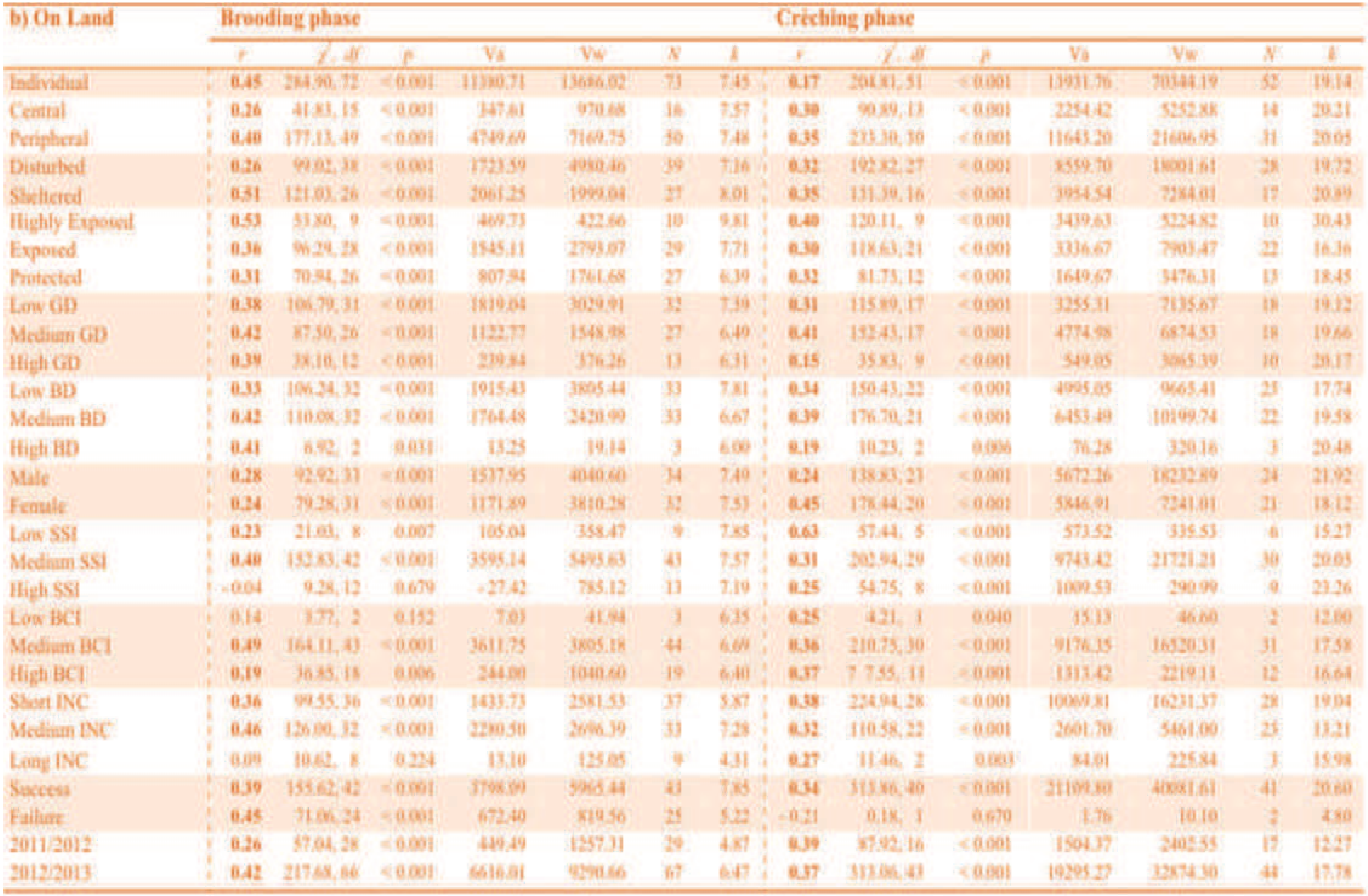
Table V - S 3. Within-individuals repeatability estimates (r) of the duration of a) trips at sea and b) sojourns on land of breeding Adélie penguins (N = 128 individuals), and Kruskal-Wallis tests statistics. Repeatability scores significantly different from zero are indicated by bold type.

***Tableau V – S3**. Estimation de la répétabilité intra-individuelle (r) de la durée a) des voyages en mer et b) des séjours à terre de manchots Adélie reproducteurs (N = 128 individus), et statistiques des tests de Kruskal-Wallis. Les scores de répétabilité qui diffèrent significativement de zéro sont indiqués en gras.*

Table footnotes :

r: repeatability index
χ^2, df: chi-squared statistic and degree of freedom
p: p-value
V_a: variance among groups
V_w: variance within groups
N: number of groups
k: number of observations per group adjusted for unbalanced design
Central/Peripheral: centrality of the nest
Disturbed/Sheltered: disturbance of the nest by regular passages of conspecifics
Highly Exposed/Exposed/Protected: exposure of the nest to snowfall accumulation
GD: Global Density of the nest (Low: less than 1.5 individuals on average around the breeding site; Medium: between 1.5 and 3 individuals; High: more than 3 individuals, classes of equal size)
BD: Breeder Density of the nest (Low: less than 1 breeders on average around the breeding site; Medium: between 1 and 3 breeders; High: more than 3 breeders, classes of equal size)
Males/Females: sex of the individuals
SSI: Structural Size Index of the individuals (Low: SSI < mean(SSI) – sd(SSI); Medium: mean(SSI) – sd(SSI) ≤ SSI < mean(SSI) + sd(SSI); High: mean (SSI) + sd(SSI) ≤ SSI)
BCI: Body Condition Index of the individuals (Low: BCI < mean(BCI) – sd(BCI); Medium: mean(BCI) – sd(BCI) ≤ BCI < mean(BCI) + sd(BCI); High: mean (BCI) + sd(BCI) ≤ BCI)
INC: incubation length. We defined birds incubating between i) 28-32 days as Short INC, ii) 33-37 days as Medium INC, and iii) 38-43 days as Long INC
Success/Failure: breeding output inferred from nest monitoring and cycle analysis
2011/2012 and 2012/2013: the two breeding seasons

a) At Sea	Brooding phase							Crèching phase						
	r	χ^2, df	p	Va	Vw	N	k	r	χ^2, df	p	Va	Vw	N	k
Individual	**0.45**	284.90, 72	< 0.001	11380.71	13686.02	73	7.45	**0.17**	204.81, 51	< 0.001	13931.76	70344.19	52	19.14
Central	**0.36**	49.35, 15	< 0.001	423.84	759.16	16	7.14	**0.11**	40.89, 13	< 0.001	806.06	6507.28	14	20.13
Peripheral	**0.48**	191.20, 49	< 0.001	5002.38	5526.12	50	7.02	**0.19**	139.73, 32	< 0.001	6220.70	27148.91	33	18.89
Disturbed	**0.37**	119.70, 38	< 0.001	2193.22	3750.55	39	6.73	**0.16**	112.34, 29	< 0.001	4328.60	22149.75	30	18.39
Sheltered	**0.53**	118.99, 26	< 0.001	1915.35	1680.63	27	7.53	**0.14**	60.80, 16	< 0.001	1540.21	9584.88	17	20.94
Highly Exposed	**0.41**	41.06, 9	< 0.001	315.61	447.10	10	9.11	**0.12**	40.89, 9	< 0.001	988.50	7377.56	10	30.42
Exposed	**0.43**	104.36, 28	< 0.001	1625.96	2134.60	29	7.15	**0.11**	56.42, 21	< 0.001	1211.57	9924.80	22	16.36
Protected	**0.48**	92.12, 26	< 0.001	1133.89	1250.53	27	6.12	**0.29**	76.77, 14	< 0.001	1507.42	3687.55	15	15.97
Low GD	**0.46**	118.69, 31	< 0.001	2023.60	2402.25	32	7.04	**0.12**	55.67, 17	< 0.001	1273.32	8989.76	18	19.12
Medium GD	**0.54**	97.86, 26	< 0.001	1222.91	1029.08	27	5.93	**0.22**	90.18, 18	< 0.001	2568.55	9030.83	19	18.68
High GD	**0.28**	29.70, 12	0.003	156.76	397.31	13	5.99	**0.11**	30.05, 10	< 0.001	412.48	3187.90	11	18.16
Low BD	**0.43**	120.30, 32	< 0.001	2167.64	2930.58	33	7.36	**0.07**	47.17, 22	0.001	979.65	13462.62	23	17.74
Medium BD	**0.47**	113.71, 32	< 0.001	1757.87	1959.46	33	6.28	**0.29**	138.59, 23	< 0.001	4845.52	11933.20	24	18.01
High BD	0.11	3.09, 2	0.214	2.68	20.77	3	5.31	**0.17**	8.90, 2	0.012	63.72	317.66	3	19.97
Male	**0.34**	103.92, 33	< 0.001	1772.98	3476.12	34	7.25	**0.12**	83.23, 24	< 0.001	2912.00	20952.82	25	21.05
Female	**0.30**	86.32, 31	< 0.001	1241.41	2891.74	32	6.84	**0.21**	93.39, 21	< 0.001	2688.35	10266.75	22	17.31
Low SSI	**0.21**	19.06, 8	0.015	83.85	307.23	9	7.12	**0.15**	16.08, 5	0.007	121.18	695.73	6	15.27
Medium SSI	**0.52**	178.15, 42	< 0.001	4177.76	3815.87	43	7.09	**0.19**	139.93, 31	< 0.001	6146.61	25391.23	32	18.83
High SSI	**0.25**	30.42, 12	0.002	183.32	560.69	13	7.01	**0.07**	21.47, 8	0.006	290.99	3616.79	9	23.26
Low BCI	0.31	5.64, 2	0.060	13.62	30.69	3	5.71	**0.31**	6.47, 2	0.039	21.12	47.11	3	6.73
Medium BCI	**0.44**	143.07, 43	< 0.001	2830.19	3660.96	44	6.25	**0.17**	113.21, 30	< 0.001	4221.78	21204.69	31	17.55
High BCI	**0.39**	54.51, 18	< 0.001	450.42	705.30	19	6.04	**0.19**	45.63, 12	< 0.001	669.92	2840.94	13	15.35
Short INC	**0.45**	107.56, 36	< 0.001	1504.41	1851.64	37	5.36	**0.18**	121.58, 28	< 0.001	4787.32	21309.81	28	19.04
Medium INC	**0.48**	124.62, 32	< 0.001	2161.58	2376.84	33	6.95	**0.14**	62.27, 24	< 0.001	1138.90	6955.13	25	12.20
Long INC	**0.50**	22.42, 8	0.004	71.96	73.09	9	4.31	0.02	2.64, 2	0.267	5.72	272.14	3	15.98
Success	**0.42**	154.48, 42	< 0.001	3527.45	4864.57	43	7.27	**0.17**	176.51, 40	< 0.001	10531.03	50367.90	41	20.59
Failure	**0.60**	86.00, 24	< 0.001	882.97	598.12	25	5.17	0.30	4.78, 3	0.189	4.25	10.10	4	2.50
2011/2012	**0.34**	63.56, 28	< 0.001	530.67	1016.66	29	4.63	**0.09**	32.31, 16	0.009	341.49	3482.27	17	12.27
2012/2013	**0.47**	226.15, 66	< 0.001	6672.99	7541.29	67	6.12	**0.19**	181.42, 45	< 0.001	9812.51	42525.28	46	17.06



b) On Land	Brooding phase							Crèching phase						
	r	χ^2, *df*	*p*	Va	Vw	*N*	*k*	*r*	χ^2, *df*	*p*	Va	Vw	*N*	*k*
Individual	**0.45**	284.90, 72	< 0.001	11380.71	13686.02	73	7.45	**0.17**	204.81, 51	< 0.001	13931.76	70344.19	52	19.14
Central	**0.26**	41.83, 15	< 0.001	347.61	970.68	16	7.57	**0.30**	90.89, 13	< 0.001	2254.42	5252.88	14	20.21
Peripheral	**0.40**	177.13, 49	< 0.001	4749.69	7169.75	50	7.48	**0.35**	233.30, 30	< 0.001	11643.20	21606.95	31	20.05
Disturbed	**0.26**	99.02, 38	< 0.001	1723.59	4980.46	39	7.16	**0.32**	192.82, 27	< 0.001	8559.70	18001.61	28	19.72
Sheltered	**0.51**	121.03, 26	< 0.001	2061.25	1999.04	27	8.01	**0.35**	131.39, 16	< 0.001	3954.54	7284.01	17	20.89
Highly Exposed	**0.53**	53.80, 9	< 0.001	469.73	422.66	10	9.81	**0.40**	120.11, 9	< 0.001	3439.63	5224.82	10	30.43
Exposed	**0.36**	96.29, 28	< 0.001	1545.11	2793.07	29	7.71	**0.30**	118.63, 21	< 0.001	3336.67	7903.47	22	16.36
Protected	**0.31**	70.94, 26	< 0.001	807.94	1761.68	27	6.39	**0.32**	81.73, 12	< 0.001	1649.67	3476.31	13	18.45
Low GD	**0.38**	106.79, 31	< 0.001	1819.04	3029.91	32	7.39	**0.31**	115.89, 17	< 0.001	3255.31	7135.67	18	19.12
Medium GD	**0.42**	87.50, 26	< 0.001	1122.77	1548.98	27	6.49	**0.41**	152.43, 17	< 0.001	4774.98	6874.53	18	19.66
High GD	**0.39**	38.10, 12	< 0.001	239.84	376.26	13	6.31	**0.15**	35.83, 9	< 0.001	549.05	3065.39	10	20.17
Low BD	**0.33**	106.24, 32	< 0.001	1915.43	3805.44	33	7.81	**0.34**	150.43, 22	< 0.001	4995.05	9665.41	23	17.74
Medium BD	**0.42**	110.08, 32	< 0.001	1764.48	2420.99	33	6.67	**0.39**	176.70, 21	< 0.001	6453.49	10199.74	22	19.58
High BD	**0.41**	6.92, 2	0.031	13.25	19.14	3	6.00	**0.19**	10.23, 2	0.006	76.28	320.16	3	20.48
Male	**0.28**	92.92, 33	< 0.001	1537.95	4040.60	34	7.49	**0.24**	138.83, 23	< 0.001	5672.26	18232.89	24	21.92
Female	**0.24**	79.28, 31	< 0.001	1171.89	3810.28	32	7.53	**0.45**	178.44, 20	< 0.001	5846.91	7241.01	21	18.12
Low SSI	**0.23**	21.03, 8	0.007	105.04	358.47	9	7.85	**0.63**	57.44, 5	< 0.001	573.52	335.53	6	15.27
Medium SSI	**0.40**	152.83, 42	< 0.001	3595.14	5493.63	43	7.57	**0.31**	202.94, 29	< 0.001	9743.42	21721.21	30	20.03
High SSI	-0.04	9.28, 12	0.679	-27.42	785.12	13	7.19	**0.25**	54.75, 8	< 0.001	1009.53	290.99	9	23.26
Low BCI	0.14	3.77, 2	0.152	7.03	41.94	3	6.35	**0.25**	4.21, 1	0.040	35.13	46.60	2	12.00
Medium BCI	**0.49**	164.11, 43	< 0.001	3611.75	3805.18	44	6.69	**0.36**	210.75, 30	< 0.001	9176.35	16520.31	31	17.58
High BCI	**0.19**	36.85, 18	0.006	244.00	1040.60	19	6.40	**0.37**	7 7.55, 11	< 0.001	1313.42	2219.11	12	16.64
Short INC	**0.36**	99.55, 36	< 0.001	1433.73	2581.53	37	5.87	**0.38**	224.94, 28	< 0.001	10069.81	16231.37	28	19.04
Medium INC	**0.46**	126.00, 32	< 0.001	2280.50	2696.39	33	7.28	**0.32**	110.58, 22	< 0.001	2601.70	5461.00	23	13.21
Long INC	0.09	10.62, 8	0.224	13.10	125.05	9	4.31	**0.27**	11.46, 2	0.003	84.01	225.84	3	15.98
Success	**0.39**	155.62, 42	< 0.001	3798.09	5965.44	43	7.85	**0.34**	313.86, 40	< 0.001	21109.80	40081.61	41	20.60
Failure	**0.45**	71.06, 24	< 0.001	672.40	819.56	25	5.22	-0.21	0.18, 1	0.670	1.76	10.10	2	4.80
2011/2012	**0.26**	57.04, 28	< 0.001	449.49	1257.31	29	4.87	**0.39**	87.92, 16	< 0.001	1504.37	2402.55	17	12.27
2012/2013	**0.42**	217.68, 66	< 0.001	6616.01	9290.66	67	6.47	**0.37**	313.06, 43	< 0.001	19295.27	32874.30	44	17.78

Table V - S 4. Between-individuals repeatability estimates (r) of the duration of a) trips at sea and b) sojourns on land of breeding Adélie penguins (N = 128 individuals), and Kruskal-Wallis tests statistics. Repeatability scores significantly different from zero are indicated by bold type.

***Tableau V – S4**. Estimation de la répétabilité interindividuelle (r) de la durée a) des voyages en mer et b) des séjours à terre de manchots Adélie reproducteurs (N = 128 individus), et statistiques des tests de Kruskal-Wallis. Les scores de répétabilité qui diffèrent significativement de zéro sont indiqués en gras.*

Table footnotes :

r: repeatability index
χ^2, *df*: chi-squared statistic and degree of freedom
p: p-value
V_a: variance among groups
V_w: variance within groups
N: number of groups
k: number of observations per group adjusted for unbalanced design
Centrality: the centrality of the nest in the colony according to its position within (periphery) or above the first row (centre) of nests
Disturbance: the disturbance of the nest by regular passage by conspecifics (disturbed/sheltered)
Exposure: exposure of the nest to snowfall accumulation (highly exposed/exposed/protected)
Global Density: gobal density of the nest (Low: less than 1.5 individuals on average around the breeding site; Medium: between 1.5 and 3 individuals; High: more than 3 individuals, classes of equal size)
Breeder Density: breeder density of the nest (Low: less than 1 breeders on average around the breeding site; Medium: between 1 and 3 breeders; High: more than 3 breeders, classes of equal size)
Sex: sex of the individuals (Females/Males)
Structural Size Index: structural size index of the individuals (Low: SSI < mean(SSI) – sd(SSI); Medium: mean(SSI) – sd(SSI) ≤ SSI < mean(SSI) + sd(SSI); High: mean (SSI) + sd(SSI) ≤ SSI)
Body Condition Index: body condition index of the individuals (Low: BCI < mean(BCI) – sd(BCI); Medium: mean(BCI) – sd(BCI) ≤ BCI < mean(BCI) + sd(BCI); High: mean (BCI) + sd(BCI) ≤ BCI)
Incubation: incubation length. We defined birds incubating between i) 28-32 days as Short INC, ii) 33-37 days as Medium INC, and iii) 38-43 days as Long INC
Breeding Output: breeding output inferred from nest monitoring and cycle analysis (Successful/Failed)
Year: year of the two breeding seasons (2011/2012 and 2012/2013)

a) At Sea	Brooding phase							Crèching phase						
	r	χ^2, *df*	*p*	Va	Vw	*N*	*k*	*r*	χ^2, *df*	*p*	Va	Vw	*N*	*k*
Individual	**0.45**	284.90, 72	< 0.001	11380.71	13686.02	73	7.45	**0.17**	204.81, 51	< 0.001	13931.76	70344.19	52	19.14
Centrality	- 0.03	0.26, 1	0.611	- 11.44	372.77	2	24.24	0.00	1.05, 1	0.306	0.47	187.80	2	19.66
Disturbance	- 0.01	0.60, 1	0.438	- 4.67	370.79	2	31.91	0.03	1.71, 1	0.192	6.26	185.05	2	21.70
Exposure	- 0.03	0.88, 2	0.644	- 10.46	375.05	3	20.35	- 0.07	0.14, 2	0.931	- 12.24	195.93	3	14.89
Global Density	- 0.03	0.25, 2	0.882	- 20.32	607.85	3	26.25	**0.13**	6.70, 2	0.035	36.22	251.54	3	18.53
Breeder Density	- 0.02	1.19, 2	0.553	- 11.14	600.98	3	22.27	- 0.05	0.60, 2	0.741	- 12.80	282.64	3	15.61
Sex	**0.48**	21.57, 1	< 0.001	233.53	250.05	2	32.97	0.04	2.04, 1	0.153	8.54	183.65	2	23.40
Structural Size Index	0.06	4.07, 2	0.130	23.40	345.54	3	16.35	0.00	2.05, 2	0.358	0.42	187.80	3	11.36
Body Condition Index	**0.24**	11.03, 2	0.004	127.16	403.70	3	16.88	0.05	3.04, 2	0.219	9.88	207.80	3	11.66
Incubation	0.02	2.94, 2	0.230	11.57	588.09	3	24.77	0.07	4.12, 2	0.128	19.44	264.70	3	15.56
Breeding Output	0.02	1.63, 1	0.202	9.29	535.65	2	36.98	**0.34**	4.78, 1	0.035	118.12	230.99	2	7.41
Year	**0.18**	9.17, 1	0.002	158.28	708.56	2	40.48	0.06	2.40, 1	0.122	19.23	328.30	2	24.83

b) On Land	Brooding phase							Crèching phase						
	r	χ^2, *df*	*p*	Va	Vw	*N*	*k*	*r*	χ^2, *df*	*p*	Va	Vw	*N*	*k*
Individual	**0.38**	269.41, 72	< 0.001	10552.56	17 402.57	73	7.88	**0.31**	341.76, 49	< 0.001	26372.30	57671.19	50	19.86
Centrality	- 0.04	0.16, 1	0.686	- 12.92	373.30	2	24.24	- 0.01	0.82, 1	0.364	- 1.62	173.21	2	19.29
Disturbance	- 0.02	0.25, 1	0.616	- 8.77	372.79	2	31.91	- 0.04	0.27, 1	0.607	- 6.13	175.45	2	21.16
Exposure	- 0.04	0.53, 2	0.765	- 13.69	377.05	3	20.35	- 0.04	0.84, 2	0.658	7.43	177.27	3	14.13
Global Density	- 0.02	0.90, 2	0.638	- 12.77	603.06	3	26.25	- 0.04	0.75, 2	0.687	- 9.36	262.82	3	17.78
Breeder Density	0.03	3.14, 2	0.208	15.58	596.62	3	22.27	0.02	2.44, 2	0.295	3.90	254.47	3	15.13
Sex	**0.55**	25.49, 1	< 0.001	278.00	227.48	2	32.97	- 0.04	0.05, 1	0.820	- 7.47	176.30	2	22.40
Structural Size Index	**0.25**	11.04, 2	0.004	101.98	305.37	3	16.35	- 0.07	0.48, 2	0.785	- 12.23	178.72	3	11.20
Body Condition Index	0.04	3.39, 2	0.184	19.56	453.44	3	16.88	- 0.10	0.05, 2	0.976	- 19.18	204.49	3	10.42
Incubation	0.01	2.43, 2	0.297	5.25	591.85	3	24.77	0.05	3.41, 2	0.182	12.56	249.70	3	14.96
Breeding Output	- 0.01	0.78, 1	0.376	- 3.19	541.47	2	36.98	**0.54**	5.00, 1	0.025	243.72	211.28	2	3.83
Year	**0.11**	5.90, 1	0.015	95.00	735.50	2	40.48	0.01	1.21, 1	0.271	2.80	314.01	2	24.52

Table V - S 5. Summary of the durations of the foraging trips at sea and the sojourns on land (mean ± SE, in hours) during the brooding and the crèching phases of 128 monitored Adélie penguins.

***Tableau V – S5**. Estimation de la répétabilité interindividuelle (r) de la durée a) des voyages en mer et b) des séjours à terre de manchots Adélie reproducteurs (N = 128 individus), et statistiques des tests de Kruskal-Wallis. Les scores de répétabilité qui diffèrent significativement de zéro sont indiqués en gras.*

Table footnotes :

Mean/SE (Standard Error): in hours
N_{obs}: total number of sojourns
N_{ind}: number of individuals
Central/Peripheral: centrality of the nest
Disturbed/Sheltered: disturbance of the nest by regular passages of conspecifics
Highly Exposed/Exposed/Protected: exposure of the nest to snowfall accumulation
GD: Global Density of the nest (Low: less than 1.5 individuals on average around the breeding site; Medium: between 1.5 and 3 individuals; High: more than 3 individuals, classes of equal size)
BD: Breeder Density of the nest (Low: less than 1 breeders on average around the breeding site; Medium: between 1 and 3 breeders; High: more than 3 breeders, classes of equal size)
Males/Females: sex of the individuals
SSI: Structural Size Index of the individuals (Low: SSI < mean(SSI) – sd(SSI); Medium: mean(SSI) – sd(SSI) ≤ SSI < mean(SSI) + sd(SSI); High: mean (SSI) + sd(SSI) ≤ SSI)
BCI: Body Condition Index of the individuals (Low: BCI < mean(BCI) – sd(BCI); Medium: mean(BCI) – sd(BCI) ≤ BCI < mean(BCI) + sd(BCI); High: mean (BCI) + sd(BCI) ≤ BCI)
INC: incubation length. We defined birds incubating between i) 28-32 days as Short INC, ii) 33-37 days as Medium INC, and iii) 38-43 days as Long INC
Success/Failure: breeding output inferred from nest monitoring and cycle analysis
2011/2012 and 2012/2013: the two breeding seasons

	Brooding phase								Crèching phase							
	At Sea				On Land				At Sea				On Land			
	Mean	SE	N_{obs}	N_{ind}	Mean	SE	N_{obs}	N_{ind}	Mean	SE	N_{obs}	N_{ind}	Mean	SE	N_{obs}	N_{ind}
Individual	36.07	0.91	472	73	39.51	0.85	300	73	25.75	0.60	909	52	7.68	0.29	921	52
Central	35.28	1.56	117	16	43.31	1.64	124	16	28.01	1.18	291	14	6.67	0.53	295	14
Peripheral	36.33	1.10	355	50	38.25	0.99	376	50	24.68	0.68	618	33	8.15	0.34	626	31
Disturbed	36.59	1.17	265	39	41.33	1.15	282	39	27.22	0.81	553	30	7.31	0.39	559	28
Sheltered	35.41	1.45	207	27	37.15	1.25	218	27	23.47	0.86	356	17	8.24	0.42	362	17
Highly Exposed	37.14	1.89	93	10	40.19	1.88	100	10	24.22	1.05	310	10	8.49	0.56	314	10
Exposed	32.88	1.27	211	29	37.56	1.23	226	29	27.39	0.90	357	22	7.38	0.47	364	22
Protected	39.48	1.68	168	27	41.64	1.49	174	27	25.28	1.19	242	15	7.08	0.43	243	13
Low GD	35.94	1.46	230	32	37.97	1.25	239	32	24.20	0.89	346	18	8.53	0.42	348	18
Medium GD	37.23	1.47	162	27	39.65	1.37	177	27	25.74	0.94	363	19	7.18	0.48	367	18
High GD	34.08	1.62	80	13	43.58	2.14	84	13	28.44	1.44	200	11	7.11	0.67	206	10
Low BD	37.18	1.43	247	33	39.23	1.25	260	33	25.66	0.84	409	23	7.61	0.41	415	23
Medium BD	34.36	1.15	209	33	40.63	1.21	222	33	25.36	0.87	436	24	8.22	0.46	440	22
High BD	41.17	2.69	16	3	29.53	2.25	18	3	28.95	2.87	64	3	4.47	0.57	66	3
Male	28.42	0.92	250	34	46.18	1.23	257	34	24.44	0.70	525	25	7.69	0.38	532	24
Female	44.69	1.44	222	32	32.45	0.98	243	32	27.54	1.03	384	22	7.66	0.44	389	21
Low SSI	47.72	3.31	68	9	30.81	1.48	73	9	29.94	2.07	94	6	9.28	0.93	97	6
Medium SSI	34.91	1.03	307	43	38.98	1.09	328	43	25.07	0.75	603	32	7.22	0.34	609	30
High SSI	31.00	1.60	94	13	48.53	1.78	95	13	25.83	1.05	212	9	8.25	0.67	215	9
Low BCI	45.96	3.37	21	3	41.31	4.22	23	3	34.56	4.71	25	3	7.72	1.34	25	2
Medium BCI	38.56	1.30	278	44	37.07	1.01	296	44	25.46	0.75	539	31	7.52	0.35	550	31
High BCI	27.31	1.12	117	19	44.01	2.02	123	19	26.06	1.36	201	13	8.11	0.63	202	12
Short INC	34.52	1.25	200	37	38.01	1.20	218	37	24.01	0.77	549	28	7.31	0.32	556	28
Medium INC	36.63	1.41	232	33	40.13	1.34	242	33	28.14	1.02	303	25	9.09	0.61	308	23
Long INC	40.57	3.11	40	9	43.86	2.04	40	9	29.73	2.27	57	3	3.64	0.83	57	3
Success	34.47	0.98	315	43	39.27	0.99	340	43	25.74	0.62	839	41	7.71	0.30	851	41
Failure	41.13	2.09	133	25	42.07	1.82	132	25	31.52	5.77	10	4	23.57	5.70	10	2
2011/2012	45.14	1.97	125	29	46.31	1.58	131	29	30.79	1.35	212	17	8.66	0.75	213	17
2012/2013	32.80	0.96	347	67	37.09	0.98	369	67	24.21	0.65	697	46	7.38	0.30	708	44

Chapter VI – Discussion and Perspectives

Chapitre VI –Discussion et Perspectives

Table VI - 1. Summary of results on personality obtained during this PhD work.

Tableau VI - 1. *Résumé des résultats concernant la personnalité obtenus lors de ce travail de thèse.*

	Brunnich's guillemots  *Uria lomvia*	**Adélie penguins**  *Pygoscelis adeliae*	**King penguins**  *Aptenodytes patagonicus*
Personality traits	• Aggressiveness • Activity • Vocalisation • Boldness	• Aggressiveness • Activity • Vocalisation • Foraging personality	• Aggressiveness • Activity • Exploration
Breeding success	• Successful breeders → vocalise more	• Successful breeders → more aggressive & consistent in their foraging trip duration at sea during crèching	• To come soon
Individual characteristics	• Small breeders → more active • Breeding females → more active and attack more during handling • Breeders with higher heart rates → more active and bold	• Small breeders → more active • Breeding males → more active	• Small breeders → more active • Breeding males → more active
Habitat	• High density → lower aggressiveness and moderate activity • Central → more aggressive • Protected from elements and predation → more active	• High density → lower aggressiveness • Central → vocalise less • Disturbed by regular passages by conspecifics → more aggressive	• High density → higher aggressiveness • Central males → more active
Behavioural syndromes and correlations to other behaviours	• Activity in the colony/Activity during handling • Activity in the colony/Boldness • Vocalisation in the colony/Activity during handling	• Vocalisation/Approaching distance • Aggressiveness/ Brooding foraging • Activity/ Brooding foraging • Vocalisation/ Brooding guarding • Variance (Aggressiveness, Activity, Vocalisation)/ Variance (Crèching foraging) • Sex differences in foraging strategies mediated by personality	• Aggressiveness/Interaction with novel object • Activity/Exploration in breeding females

There has been a growing interest in the concept of personality in the past decades since its evolutionary and ecological implications have been widely recognized (e.g. Dall et al., 2004; Sih et al., 2004a; Réale et al., 2007; Wolf and Weissing, 2012). Indeed, personality reflects in many aspects of the ecology of an individual, meaning that it can affect the fitness of the individuals, and, therefore, be involved in many mechanisms playing an important role in individual and population adaptations.

1 - Personality, environmental variability, and fitness

The adaptive potential of personality traits lies in the existence of inter-individual heterogeneity in behavioural phenotypes linked with the individual fitness (see Wolf and Weissing, 2012). Indeed, the co-existence of different phenotypes within a population increases the chances that the phenotype adapted to the new environmental conditions already exists in the population ('insurance effect', McCann, 2000). Furthermore, even though the concept of personality implies that behavioural flexibility is limited, the moderate heritability of personality traits usually found (e.g. Réale et al., 2000; Drent et al., 2003; Fairbanks et al., 2004; van Oers et al., 2004b) also indicates a moderate genetic influence over these traits that are thus likely to be influenced to some extent by the environment. Repeatability has been traditionally used to set an upper limit on heritability (Boake, 1989). Therefore, the moderate repeatability indices found in this work also suggest a moderate heritability and consequently support this hypothesis. The interest of studying personality also lies in its ubiquity in the animal kingdom as it allows for inter-species comparisons (see Réale et al., 2007). In this PhD work, we identified personality (i.e. intra-individual consistency and inter-individual heterogeneity) in three different species (Cornet *et al. Articles 1*, *2* and *3*). Two of these personality traits were common to the three species (aggressiveness and activity, Table VI - 1). Furthermore, we found that the aggressiveness explained the breeding success in Adélie penguins (Article 3, Table VI - 1), attesting to the adaptive potential of this personality trait in this species. On the other hand, we only found a weak relationship between personality and fitness in Brünnich's guillemots (Article 1, Table VI - 1). However, the weakness of the relationship does not necessarily mean that personality traits measured in this species do not have an adaptive potential. Indeed, we only used a single proxy of fitness in this study (i.e. the breeding success), and we would need to study more fitness-related traits, such as survival or chick body mass at fledging, to unravel the relationship between personality and fitness in this species (see Réale et al., 2007). In addition, we investigated the relationship between personality and fitness only during one breeding season, and it has been demonstrated that the adaptive advantage of a personality trait can be context dependent (e.g. Duckworth, 2006). For instance, in birds, aggressiveness is associated with the ability to establish a breeding territory (see van Oers and Naguib, 2013). In seabirds, colony size is positively correlated with competition for food resources at sea (Forero et al., 2002) and is linked to the availability of nesting sites of good quality (Kokko et al., 2004). In our case, during years of good environmental conditions at sea (i.e. lower competition for food resources), there should be stronger competition for on-land resources, such as breeding site where aggressiveness would confer an adaptive advantage. On the other hand, during years of harsher environmental conditions at sea, we should observe stronger competition for resources at sea and weaker competition for resources on land where aggressiveness may not confer an adaptive advantage anymore. Temporal variation in selective pressures could therefore be another explanation to the absence of relationships observed between personality and fitness at the scale of one breeding season in the Brünnich's guillemot. Relationships between personality and fitness remain to be tested for the King penguin.

Furthermore, behavioural differences between individuals were also strongly related to habitat characteristics in our three model species, and more particularly aggressiveness differences (Cornet *et al. Article 1, 2* and *3*, Table VI - 1). As already mentioned above, birds' aggressiveness is associated with the ability to establish a breeding territory (see van Oers and Naguib, 2013). It is therefore likely that the spatial distribution of behavioural types within the colonies observed in our three species is non-random. Personality may affect habitat use and thus the spatial structuration within a colony. Consequently, personality may also influence the selective pressures exerted on individuals at the local scale (e.g. Martin and Réale, 2008; Boyer et al., 2010; van Oers and Naguib, 2013). This is in accordance with the hypothesis of Coulson (1968), which predicts that the quality of an individual facilitates its access to good quality habitats that will in turn enhance its performances and quality. By its influence on the selective pressures exerted at the local scale, personality also influences the selective pressures that may exert back on it. This could first enhance the personality trait under selection, and, in the long run, it may stabilise personality by positive feedback loop ('labile state component with positive feedback loop' theory of Wolf and Weissing, 2010). Personality would therefore also be able to respond to environmental pressures, as suggested by its moderate heritability and repeatability.

The consistency of personality should arise from an underpinning neurophysiological structure (Fairbanks et al., 1999; Koolhaas et al., 1999; Drent et al., 2003; Koolhaas et al., 2010; Ferrari et al., 2013). In this PhD work, we found that the activity was explained by the sex (i.e. reflecting stable differences in hormonal status) and the structural size (i.e. reflecting stable differences in basal metabolic rate) of individuals in all three species. These results therefore support the hypothesis of an underpinning neurophysiological structure to consistent behavioural differences, and they provide evidence for the biological validation of this personality trait (Réale et al., 2007).

Finally, we also observed that, by removing the variation explained by habitat and individual characteristics, repeatability indices of the activity and the aggressiveness at the breeding site increased in both Brünnich's guillemots and Adélie penguins (this remains to be tested for king penguins). These results provide further evidence that these personality traits are intrinsic individual characteristics, i.e. part of the very nature of an individual, and that habitat and individual characteristics are additional sources of inter-individual heterogeneity. A next step to fully unravel the influence of both genetic and non-genetic factors on personality would be to estimate its heritability.

2 - Behavioural syndrome, constraints, and evolvability[11]

As already mentioned, personality is reflected in the ecology of an individual (e.g. habitat use or territoriality, Duckworth, 2006; Boon et al., 2008; Boyer et al., 2010) and affects its fitness (Both et al., 2005; Boon et al., 2008; Cote et al., 2008; Kontiainen et al., 2009; Boyer et al., 2010). The optimal behaviour of an individual is therefore supposed to differ across situations and/or contexts. For instance, 'freezing' behaviour has been shown to be adaptive in a low risk predation context, since individuals would be less detectable by predators (Quinn and Cresswell, 2005).In contrast, in high risk predation context, 'freezing' behaviour has been considered maladaptive, since it may increase the risk of being predated. Furthermore, aggressiveness towards conspecifics is considered adaptive if it allows individuals to secure their resources, for instance (Duckworth, 2006). In contrast, aggressiveness towards predators (then called boldness) is considered maladaptive, since it

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[11] *Evolvability*: "an organism's capacity to generate heritable phenotypic variation." (Kirschner and Gerhart 1998)

can increase mortality (see Smith and Blumstein, 2008). It is also plausible that optimal behaviour differs according to the sex of the individual because of its neurophysiological or ecological particularities (e.g. hormonal status, mating stratgeies, or foraging strategies; Dingemanse and de Goede, 2004; Hedrick and Kortet, 2012; Patrick and Weimerskirch, 2014). Consequently, it has been proposed that context specificity in personality should be favoured by natural selection (Wilson, 1998). This hypothesis is supported by the absence of aggressiveness-boldness syndrome in Brünnich's guillemots and Adélie penguins (Cornet *et al. Articles 1* and *3*, Table VI - 1), and by the existence of correlations between traits only according to some habitat characteristics or the sex of the individuals in king penguins and Adélie penguins (Cornet *et al. Articles 2* and *3*, Table VI - 1). However, we also found that, at the population scale, the activity at the breeding site was negatively correlated with the activity and boldness in a threatening situation in the Brünnich's guillemot (Cornet *et al. Article 1*, Table VI - 1), the aggressiveness was negatively correlated with the interactions with a novel object (a measure of exploration) in the King penguin (Cornet *et al. Articles 2*, Table VI - 1), and the vocalisation at the breeding site was positively correlated with the approaching distance in the Adélie penguin (Cornet *et al. Articles 3*, Table VI - 1). First, these correlations provide some evidence for the ecological validation of the personality traits assessed in this PhD work (Réale et al., 2007). In king penguins, aggressive individuals in the colony also interacted less with the novel objects (mirror and bucket). Birds did not show strong reactions towards their mirror image. Thus, the 'reaction to a mirror image' that has been proposed as an experimental test to measure aggressiveness, might not be a good indicator for this trait in this species. Furthermore, the correlations between personality traits observed at the population scale in the two other species revealed potential behavioural syndromes (e.g. Tulley and Huntingford, 1988; Riechert and Hedrick, 1993; Kortet and Hedrick, 2007; Pruitt and Riechert, 2009). Phenotypic correlations between personality traits are known to arise from common behavioural structure with common underlying physiological, neurobiological, cognitive system and/or genetic background (Fairbanks et al., 1999; Koolhaas et al., 1999; Drent et al., 2003; Koolhaas et al., 2010; Ferrari et al., 2013). Correlations between personality traits therefore imply constraints in their co-evolution. If these constraints are difficult to break and if strong opposite directional selection pressures are exerted on two correlated traits, such behavioural syndrome may prevent individuals to reach an optimal fitness (see Stearns, 1992; Sih et al., 2004a; Wolf and Weissing, 2012). It would thus explain the maintenance of maladaptive behaviours. For instance, Duckworth (2006) found that in Western bluebirds, *Siala mexicana*, males' aggressiveness levels were consistent over male competition and nest defence contexts. However, the most aggressive males also had a lower breeding success as they had to compromise provisioning to the incubating female while investigating in resource defence. On the other hand, correlations between personality traits might also be advantageous in an evolutionary context. Indeed, the co-evolution of a set of traits could also impliy that in the evolutionary history of a species, the association between these personality traits was selected to help individuals and populations to solve an ecological challenge. This set of correlated behaviours may also solve new ecological challenges yielded by future environmental changes and speed up adaptation (see Wolf and Weissing, 2012). Correlations were evaluated only at the phenotypic level in this PhD work. However, we also identified that some personality traits may have neurophysiological bases, suggesting a genetic background of these traits. Next step is to test for genetic correlations to fully validate the existence of the observed behavioural syndromes.

3 - Personality and foraging strategies

Until now we focused on environmental conditions and acquisition of resources on land, since their impacts on fitness are less well established in seabirds. However, although better studied, the acquisition of resources at sea is also critical for the fitness of the individuals, since it has direct consequences on both breeding success (e.g. Monaghan et al., 1989; Suryan et al., 2000; Lescroël et al., 2010) and survival (e.g. Daunt et al., 2007; Le Bohec et al., 2008). Therefore, the role of personality in foraging strategies may also have major consequences for the adaptive abilities of individuals to face environmental change at sea. During this PhD work, we observed relationships between the personality at the nest and foraging behaviours in Adélie penguins (Cornet *et al. Article 3*). Indeed, the aggressiveness and the activity at the breeding site were negatively correlated with the duration of the foraging trips at sea during the brooding period. There are several hypotheses that may explain the link between personality and foraging activity:

i) it has been demonstrated in several species that personality had an influence on the habitat use of an animal (e.g. Boon et al., 2008; Boyer et al., 2010; van Overveld and Matthysen, 2010). For instance, Boyer et al. (2010) found that activity-exploration was correlated with the space use in the Siberian chipmunk, *Tamias sibiricus*, impacting therefore its parasitic load. Boon et al. (2008) found that active female red squirrels, *Tamiasciurus hudsonicus*, had a higher home range. They also showed that the interaction between the aggressiveness and the activity was related to the maximal capture distance from their nests (reflecting the home range). In our case, the aggressiveness and the activity observed in the Adélie penguin colony may reflect the individuals' habitat use at sea (e.g. foraging range/distance reflected by foraging duration), and would therefore have implications for the adaptive ability of individuals to face changes in food availability at sea.

ii) it has also been demonstrated in several species that personality influenced the use of social information[12]. For instance, Kurvers et al. (2010b) in barnacle geese, *Branta leucopsis*, the use of social information in a foraging context decreased with the level of boldness of the individuals. It has also been shown that the use of social information (including public information[13]) increased the problem-solving ability of a group compared to a single individual (Canonge et al., 2011). In a patchy environment, such as in the Southern Ocean, the use of public information mediated by personality could therefore play an important role in finding food patches (Valone, 1989; Templeton and Giraldeau, 1996; Weimerskirch et al., 2010) and consequently have a strong impact on foraging efficiency of individuals.

iii) Finally, it has been shown in barnacle geese that personality was involved in social foraging strategies through 'producer-scrounger' games (Kurvers et al., 2010a). In animals that forage in groups, such as barnacle geese (Kurvers et al., 2010a; Kurvers et al., 2010b), individuals can either directly search for food by themselves (therefore called 'producers') or use the food discovered by others (therefore called 'scroungers') through social information. Individuals should have the capability to play both roles in a group, but due to differences in personalities, the identities of who are the producers and who are the scroungers are often stable. For instance, Kurvers et al. (2010a) found that shy individuals were more likely to play 'scrounger'. Our results in Adélie penguins could therefore reveal the interplay between personality, social information use, and game-like foraging strategies. Indeed, if we assume foraging durations for 'scroungers' are longer than for 'producers' because they have to wait for 'producers' to find food patches, the high levels of activity on land associated with

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[12] *Social information*: the "monitoring of other's interactions with the environment" to acquire information (Danchin et al., 2004)

[13] *Public information*: a form of indirect social information based on the monitoring of the performances of other individuals or on the monitoring behavioural decisions of other individuals (Valone, 1989)

short foraging trips could reveal individuals that are ‘producers’, and the low levels of activity associated with longer foraging trips could reflect individuals that are ‘scroungers’. To confirm this hypothesis, we would need to gain access to more foraging parameters, such as the distances between the colony and the foraging areas, or diving and feeding behaviours at sea, using bio-loggers.

These last two hypotheses remain untested, as little is known about social interactions between free-ranging Adélie penguins at sea. However, a recent study based on small cameras fixed on the backs of Adélie penguins, demonstrated for the first time interactions between individuals at sea reflected by the amount of time a foraging individual spent closely accompanied by other birds during a dive (Takahashi et al., 2004). Our results linking personality to foraging parameters could therefore have important implications for the field of seabird foraging strategies. Furthermore, personality of individuals (‘scrounger’ or ‘producer’, for instance) contributes to the behavioural pattern of a group, which could in turn have consequences for the adaptive responses of individuals (Michelena and Deneubourg, 2011). Indeed, the adaptive value of adopting one strategy in a theoretical game (such as a 'producer-scrounger' game, Barnard and Sibly, 1981; or the 'Hawk-Dove game' Maynard Smith, 1982) is often conditional on the strategy adopted by other individuals.

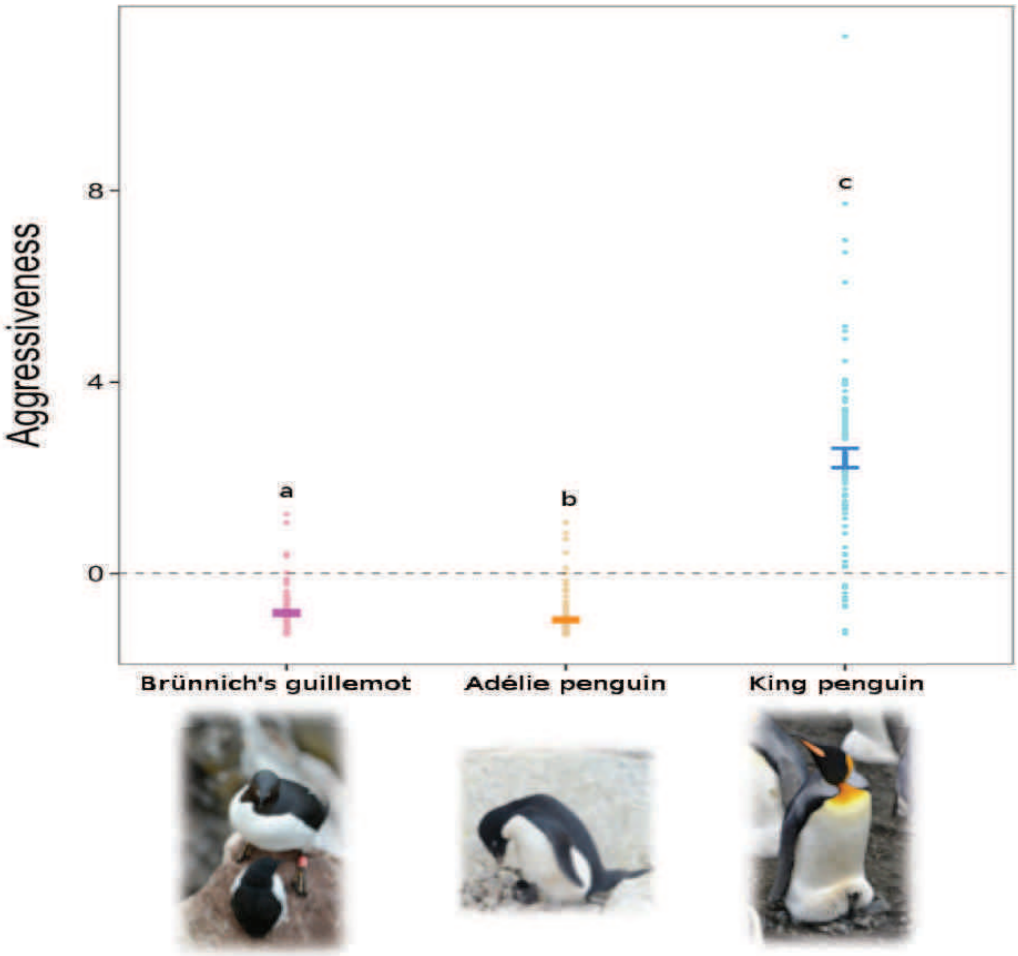
Furthermore, we observed that males and females display the same level of consistency in their foraging trips during the guarding phase. However, males became more variable in their foraging trip durations than female during crèching, which is in accordance with previous studies that demonstrated sex-differences in foraging strategies during chick rearing in this species (Chappell et al., 1993; Clarke et al., 1998). Interestingly, we found that the variance in males’ personality at the nest was correlated with the variance in their foraging trip durations during the crèching phase. These results further emphasize the potential implications of personality in the differences in foraging strategies observed in this species.

Finally, we found that successful Adélie penguins displayed higher levels of aggressiveness and a higher consistency in this behaviour, but also a higher consistency in their foraging trip durations during the crèching phase. Since breeding success is dependent on the capacity of individuals to regularly provision their chicks (Lescroël et al., 2010), these results were anticipated. However, a lower flexibility in their foraging abilities could also mean a reduced ability to react to changes in environmental conditions. Thus, personality may have multiple implications with regards to individual foraging strategies.

4 - Inter-species comparison

The ubiquity of personality traits in the animal kingdom is one of the reasons ecologists and evolutionary biologists gain interests in personality (Dall et al., 2004; Réale et al., 2007). Based on three animal models, this PhD project provides a unique opportunity for an inter-species comparison and the investigation of broad-scale patterns of variations of personality traits. Thus, we ran a Principal Component Analysis using the common behavioural variables measured in the three species (i.e. the proportion of time spent grooming, the proportion of time spent resting/sleeping, and the proportion of time spent in agonistic interactions, and the number of aggressive interactions and the number of bites/flipper hits exchanged during agonistic interactions; values averaged on the individual). The first axis explained 67.5% of the total variance and was mainly loaded with the three variables extracted from agonistic interactions, reflecting therefore the aggressiveness. The second axis explained 19.6% of the total variance and was mainly loaded by the grooming behaviour, reflecting therefore the activity. We found that king penguins were more aggressive than Adélie penguins and Brünnich's guillemots (Figure VI - 1), while Adélie penguins were less aggressive than Brünnich's guillemots. Furthermore, Adélie penguins were less active than king penguins and Brünnich's guillemots (Figure VI - 2), and there was no difference between king penguins and Brünnich's guillemots.

The different levels of aggressiveness displayed by the three species may be related to their territoriality and nesting habits (Figure VI - 1). King penguins establish a breeding territory during each summer with no physical nest structure. Brünnich's guillemots select a breeding site on a cliff also with no physical nest structure, but the boundaries with conspecifics are limited by the cliff edge. In contrast, Adélie penguins build nests out of small stones in rocky outcroppings. According to this breeding behaviour, king penguins physically defend and maintain the boundaries of their breeding territory. Moreover, king penguins do not have a synchronised arrival at their breeding territories, in contrast with Adélie penguins and Brünnich's guillemots. Both of these features select for high degree a aggressiveness in king penguins. Interestingly, Viera et al. (2011) showed that physical agonistic interactions were more costly than non-physical agonistic ones in this species, and that individuals engaged more often in non-physical interactions than in physical ones. They suggested that



Ecological features

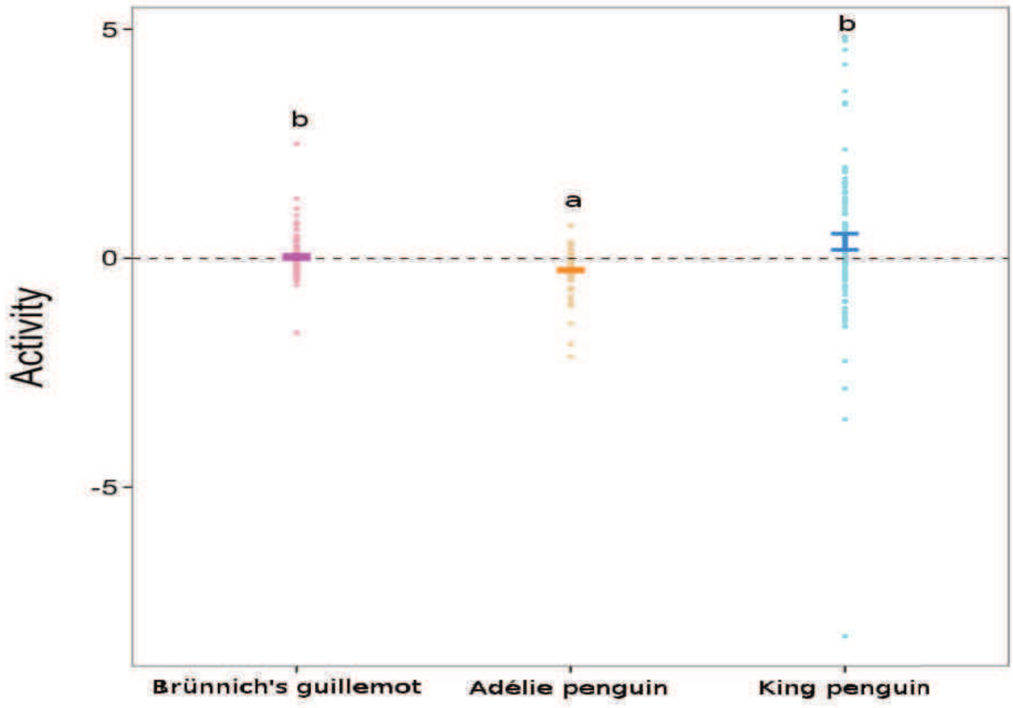
Colony density	High	High	High
Nesting site	Open	Open	Open
Minimal distance between two sites	0 cm	70 cm	50 cm
Nest building	No nest	Nest	No nest
Synchrony	High	High	Moderate
Mobility	Fix in space and time	Fix in space and time	Mobility in space and time
Incubation + Brooding length	*ca.* 56 days	*ca.* 56 days	*ca.* 75 days
Size	~ 40-45 cm	~ 70-75 cm	~ 85-95 cm
Slow/fast gradient	Fast Shorter life Earlier reproduction Higher growth rate	→	Slow Longer life Delayed reproduction Lower growth rate

Figure VI - 1. Aggressiveness and ecological features in Brünnich's guillemots, Adélie penguins and king penguins. Error bars represent mean ± std. error. Species not sharing a letter are significantly different for $p < \frac{0.05}{3}$ according to pairwise Wilcoxon-sum-rank tests.

Figure VI - 1. *Agressivité et caractéristiques écologiques chez le guillemot de Brünnich, le manchot Adélie et le manchot royal. Les barres d'erreur représentent la moyenne ± erreur standard. Les espèces ne partageant pas une lettre diffère significativement au seuil p <* $\frac{0.05}{3}$ *selon les tests de Wilcoxon sur la somme des rangs appariés.*

non-physical agonistic interactions could be an adaptation to reduce the costs of aggressiveness, while still efficiently defending their breeding territory. The level of aggressiveness of an individual might not have the same adaptive value in the three different species and could explain why the relationship between aggressiveness and breeding habitat differ between them. For instance, in the Adélie penguin and Brünnich's guillemot colonies, individuals breeding in high density habitats were less aggressive than those breeding in low density habitats, while in the king penguin colony, birds breeding in high density habitats were more aggressive than in low density habitats (see Table VI - 1). Aggressiveness may confer an even greater adaptive advantage to king penguins breeding in high density habitat because more agonistic interactions are required to defend their territory. On the other hand, in Adélie penguins, although aggressiveness improved breeding performances at the population scale, individuals breeding in high density habitat were less aggressive than low density breeders. In this species, aggressiveness with the surrounding by breeders would have a high cost without additional benefits because territories are physically established and fixed. However, in a nest where individuals are regularly disturbed by the passage of conspecifics that might be pebble thieves (pebbles being an important feature of Adélie nest quality, Ainley, 2002), high aggressiveness would be adaptive, as it could have the benefit of preserving the integrity of the nest no matter what is its density.

The different levels of activity displayed by the three species might be explained by their respective body sizes (see Fig. VI - 2), as we already demonstrated relationships between structural size and activity within the three species through the relationship between body size and specific metabolic rate inferred from allometric equations (Schmidt-Nielsen, 1984). However, the tallest species, the King penguin, displayed the highest level of activity. Therefore, the 'performance model' (see Careau et al., 2008), which provided a good explanation for the higher level of activity displayed by individuals with a higher metabolic rate (i.e. typically smaller individuals) within the Adélie and the King penguin species, does not explain the difference observed between the species. The alternate model, the 'allocation model' (see Careau et al., 2008), does provide a good explanation for the difference observed between the two penguins species. Indeed, this model predicts that individuals with a higher metabolic rate (i.e. typically the smaller species) will have less energy to allocate to activity when their energy budget is limited (Careau et al., 2008), as is the case among fasting breeding penguins. On the other hand, the Brünnich's guillemot has a higher specific metabolic rate as inferred from allometric equations than the two penguin species (which was



Ecological features			
Colony density	High	High	High
Nesting site	Open	Open	Open
Minimal distance between two sites	0 cm	70 cm	50 cm
Nest building	No nest	Nest	No nest
Synchrony	High	High	Moderate
Mobility	Fix in space and time	Fix in space and time	Mobility in space and time
Incubation + Brooding length	*ca.* 56 days	*ca.* 56 days	*ca.* 75 days
Size	~ 40-45 cm	~ 70-75 cm	~ 85-95 cm
Slow/fast gradient	Fast	→	Slow
	Shorter life		Longer life
	Earlier reproduction		Delayed reproduction
	Higher growth rate		Lower growth rate

Figure VI - 2. Activity and ecological features in Brünnich's guillemots, Adélie penguins and king penguins. Error bars represent mean ± std. error. Species not sharing a letter are significantly different $p < \frac{0.05}{3}$ according to pairwise Wilcoxon-sum-rank tests.

Figure VI - 2. *Agressivité et caractéristiques écologiques chez le guillemot de Brünnich, le manchot Adélie et le manchot royal. Les barres d'erreur représentent la moyenne ± erreur standard. Les espèces ne partageant pas une lettre diffère significativement au seuil* $p < \frac{0.05}{3}$ *selon les tests de Wilcoxon sur la somme des rangs appariés.*

confirmed for Adélie penguins by Birt-Friesen et al. (1989) results), but an intermediate level of activity. This may be due to its breeding biology. Indeed, Brünnich's guillemots have shorter incubation/guarding shifts, and more frequent foraging trips, and so shorter fasting periods than the two penguins species. Consequently, the 'allocation' model is less suitable for the guillemots than for the penguins because their energy budgets are less limited. Furthermore, Brünnich's guillemots breed in cliffs and their spatial distribution is vertical. We observed that individuals breeding on lower levels of the cliff are exposed to more guano from individuals breeding in the upper levels (*personal observation*), which lead to higher levels of grooming (and therefore activity) observed in this species despite its smaller size.

In a recent article, Réale et al. (2010b) proposed that personality could be integrated to the 'pace-of-life' syndrome, i.e. the suite of physiological traits that co-evolved with life-history strategies of individuals, populations or species. They therefore predicted that along the 'slow-fast' gradient, 'fast species should display higher levels of aggressiveness and activity as it would facilitate access to resources necessary for high growth and early reproduction. Here, we observed that king penguins, with life-history traits of the 'slow' species, display the highest level of aggressiveness, and higher levels of activity than Adélie penguins (see Fig. VI - 1 and VI - 2). This result suggests that there are strong selective pressures driving this apparent deviation from the expected 'pace-of-life' syndrome. Studying correlations between personality and life-history traits should help us to better understand how populations will respond to global change.

5 - Perspectives

We found indirect evidence for a genetic basis of personality in our 3 species. Yet, our next step is to validate our hypothesis with quantitative genetic methods in order to fully understand the implication of personality in the adaptive potential of a population. Using pedigree information that is currently being tracked in our three seabird colonies, we will estimate the heritability of the personality traits (Kruuk, 2004). Furthermore, cross-fostering experiments (e.g. Merilä, 1997; Kunz and Ekman, 2000) should help us to disentangle genetic effect and common early-life environmental effects, i.e. the proportion of variance from genetic variability and the proportion of variance from developmental plasticity.

In the context of the current global change, gauging the adaptive potentials of populations to face environmental constraints is of crucial interest. The adaptive potential of a population depending on the adaptive capacities of each of its individuals, it is thus important to use both individual-based and population-based approaches to better understand the underlying mechanisms of the impact of environmental variability on populations and evaluate whether and how they may evolve. Next step will be to integrate personality traits into population dynamics models in order to better gauge the adaptive capacity of individuals and populations to cope with the variability of their environment.

Chapter VII – Going further

Chapitre VII – Pour aller plus loin

A – Breeding performances in the Adélie penguin

Impact of sea ice on the breeding phenology and performance of Adélie penguins – *in prep Article 4*

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1 – Introduction

Environmental variability, through its impact on resources available to organisms, is considered as one of the main parameter involved in population regulation (Lack and Gillmor, 1966; Sæther, 1997). More precisely, environment can either directly affect fitness of the individuals, or affect their phenotypic traits, which can then impact their fitness through energy allocation trade-offs (Stearns, 1992). In the context of current global change, numerous studies have already shown effects of climate on populations, highlighting a widespread influence on their phenology, their distribution, and their demography (see Walther et al., 2002). For instance, environmental conditions during winter have shown strong impacts on adult survival through food availability (e.g. Marti and Wagner, 1985; Gates et al., 1986; Robel and Kemp, 1997; Ballerini et al., 2009). Moreover, environmental conditions can also affect the seasonal timing of life-history events related to reproduction in iteroparous species, with consequences for individual fitness. For instance, a change in the phenology of these events could lead, to a mismatch with prey availability necessary to feed the offspring, or to asynchrony with the rest of the population exposing offspring to higher risks of predation (Murphy and Schauer, 1996; Stenseth and Mysterud, 2002; Visser et al., 2004; Both et al., 2006; Durant et al., 2007). These modifications of the phenology of numerous species (e.g. Chmielewski and Rötzer, 2001; Charmantier et al., 2008; Møller et al., 2008; Moyes et al., 2011) have consequently shown strong impacts on individuals' breeding performances (Visser et al., 2004; Dickey et al., 2008; Hipfner, 2008) and ultimately on adults and offspring survival (Festa-Bianchet, 1988; Murphy and Schauer, 1996; Sillett et al., 2000). Any alteration in the phenology of life-history events in a population, because of its effect on vital rates, can therefore have important consequences for its dynamics (see Miller-Rushing et al., 2010).

Populations of Adélie penguins, *Pygoscelis adeliae*, revealed contrasted responses to climate changes due to the fact that changes in environmental parameters are not the same around Antarctica (Smith et al., 1999; Vaughan et al., 2001; Ainley et al., 2005). Adélie penguins are highly dependent on the sea-ice pack to live and to reproduce (Ainley, 2002). Their winter habitat range is defined by the maximal extent of sea-ice pack where they feed (Ainley, 2002). In summer, they reproduce during a short window between the sea-ice retreat and its reformation. Birds are therefore highly synchronous (Ainley, 2002) to adapt to the short period of favourable conditions. Consequently, the timing of the sea-ice retreat is likely to influence the arrival timing at the colony for reproduction, as well as physiological condition upon arrival (Fraser et al., 1992; Croxall et al., 2002; Beaulieu et al., 2010; Emmerson et al., 2011), through its impact on prey availability at the beginning of the breeding season (Trivelpiece et al., 2011). However, Adélie penguins seem to be able to switch diet under unfavourable conditions (Clarke et al., 1998; Ainley, 2002; Beaulieu et al., 2010), and thus compensate for a depletion in their usual preys, but only to some extent. The timing of sea-ice retreat can also affect individuals' breeding performances in other ways. Extensive sea ice later in the breeding season could, for instance, affect food availability and foraging efficiency of individuals during the chick rearing phase (Ainley, 2002; Clarke et al., 2002; Olmastroni et al., 2004; Lescroël et al., 2010). Moreover, the longer distance to walk to reach foraging ground could also increase energy expenditure during this already demanding phase as penguins are better adapted to swimming than walking (Pinshow et al., 1977). A more extensive knowledge on how sea-ice conditions affect breeding parameters is therefore needed to better understand contrasted responses of Adélie penguin populations around Antarctica.

While some studies have shown relationships between environmental conditions and Adélie penguin population trends (e.g. Fraser et al., 1992; Wilson et al., 2001; Kato et al., 2002; Jenouvrier et al., 2006), almost none attempt to identify the underlying mechanisms relating sea-ice conditions and life-history traits, such as phenology and breeding success in this species (only two to our knowledge: Emmerson and Southwell, 2008; Emmerson et al., 2011). In this study, we focused on a colony of Adélie penguins breeding on Petrel Island, Pointe Géologie Archipelago, Antarctica, where almost no information is available on the effects of inter-annual variability in sea-ice extent on this population. Using a long-term automatic monitoring system based on Radio-Frequency-IDentification, we investigated the effects of the inter-annual variability of sea-ice cover around the breeding archipelago on the arrival and laying dates, the number of fledglings and the breeding success of micro-tagged Adélie penguins.

2 – Material and Methods

a) Penguin monitoring

Our study was conducted during eight consecutive austral summers, from 2006/2007 to 2013/2014, on Adélie penguins, *Pygoscelis adeliae,* breeding on Petrel Island (66°40’ S 140°01’ E), Pointe Géologie Archipelago, Adélie Land, Antarctica. The long-term monitoring of a colony (called ‘*ANTAVIA Canyon*’) of *ca.* 300 breeding pairs is carried out using an automatic Radio-Frequency IDentification system (RFID) based on passive transponder tags implanted under birds skin (see Gendner et al., 2005; Le Bohec et al., 2007 for a similar system implemented on king penguins, *Aptenodytes patagonicus*). To date, no known adverse effects of these electronic tags have been found (Froget et al., 1998; Nicolaus et al., 2009). During the study period, all the chicks of the *ANTAVIA Canyon* colony that were still alive mid-February (right upon fledging), were implanted with transponder tags of 0.8 g ($N_{7\ cohorts}$ = 1514 chicks, see Cornet et al. *in prep 3*). The number of chicks micro-tagged each year corresponds to the number of fledglings used later on. In addition, during the summer 2006/2007 and from 2011/2012 to 2013/2014, 170 breeding unknown-aged adults were micro-tagged in order to access adult breeding parameters and to have information on the breeding population before the micro-tagged cohorts reach maturity. The data acquisition system was implemented during austral summer 2008/2009.

b) Breeding phenology and success

Micro-tagged Adélie penguins are detected by double antennas implanted at the usual pathways used by the birds to enter and exit their colony. Thanks to the specific patterns of back and forth between the colony and the sea, we are able to identify the different phases of the breeding cycle of the individuals and to determine their arrival and laying dates, as well as the issue of their breeding cycles (method adapted from our long-term king penguin monitoring system, see Descamps et al., 2002; Le Bohec et al., 2007). Those breeding parameters were obtained from unknown-aged adult birds.

Arrival date was defined as the date an individual was first detected at the beginning of the summer season, as Adélie penguins start to seek a breeding territory and to build a nest as soon as they arrive at the colony, and pairing is fast (Ainley, 2002). Laying date was assessed through the automatic monitoring: for females, the laying date corresponded to the departure date after their first arrival at the colony for the breeding season, and, for males, the laying date was inferred by subtracting the yearly average duration of the first trip at sea of the females from their departure date after their first arrival at the colony for the breeding season. For individuals micro-tagged during the austral summers 2011/2012 and 2012/2013, laying date was inferred through visual daily nest checks (twice a day). The yearly breeding success of the colony was inferred from the number of successful micro-tagged individuals over the total number of micro-tagged individuals that breed a given year.

c) Sea-ice cover

Sea-ice cover (SIC) in the area of the Pointe Géologie Archipelago was extracted from Rayner et al. (2003). Nothing is known about the location of spring foraging grounds of Adélie penguins breeding in this Archipelago prior to their arrival for reproduction. Moreover, prey availability in one area depends on the location of its spawning ground that might occur at a different location, and on the oceanographic conditions between the two locations (Hofmann et al., 1998). We therefore decided to consider two spatial scales representative of the local and the broader regional environmental conditions around the Pointe Géologie Archipelago susceptible of affecting birds' arrival. Consequently, we used the monthly percentage of sea-ice cover on a grid cell of 1° x 1° covering between 66°S and 67°S, and 140° E and 141°E (local scale: right around the breeding archipelago) and on a grid cell of 2° x 2° covering a larger area between 65°S and 67°S, and 139°E and 141°E (regional scale).

d) Statistics

All statistics were computed using the R 2.10.0 statistical environment (R Development Core Team, 2012). Arrival/laying dates or breeding success were modelled using a maximum of likelihood mixed-model approach (GLMM, lme4 package; Bates et al., 2012). Individuals were tracked over multiple breeding seasons, they were thus computed as a random effect, enabling us to account for repeated measures. Models were fitted with Poisson and binomial distributions for arrival/laying dates and breeding success, respectively. Model selection was based on Akaike's Information Criterion (AIC), and on the weights of the models and the number of parameters when ΔAIC < 2. To assess the significance of each variable, we then examined *p*-values calculated using analysis of variance χ^2 tests to compare models with and without the variable. Relationships between sea-ice conditions and the number of fledglings and the breeding success of the colony were assessed using linear models (LM).

In order to compare the arrival and laying dates between years, we tested for normality of the residuals and homoscedasticity of the variables, and consequently used pairwise Wilcoxon sum-rank tests. We therefore applied Bonferroni's correction and differences were considered significant for $p < \frac{0.05}{n}$, with *n* the number of pairwise comparisons performed.

3 – Results

a) Arrival and laying dates

From 2009/2010 to 2013/2014, the average arrival date at the colony to start a new breeding season was November 2nd ± 6 days (Table VII - 1). The annual arrival date was explained by the average sea-ice cover in September at a local scale, i.e. directly around the colony (GLMM – Poisson, χ^2 test with null model: $p < 0.001$, $n = 123$, $N = 265$; Fig. VII - 1a) and independently by the year set as a random effect (GLMM – Poisson, χ^2 test with null model: $p < 0.001$, $n = 123$, $N = 265$; Fig. VII - 2). There was no significant difference between these last two models (GLMM – Poisson, χ^2 test between the two models: $p > 0.5$). The local sea-ice cover negatively affected the arrival date of individuals at the colony, and arrival dates significantly differ between years.

During the same study period, the average laying date was November 24th ± 3 days (Table VII - 1). We decided to exclude laying dates of year 2013/2014 because laying date estimates through automatic monitoring this season might not be reliable. The annual laying date was not explained by sea-ice conditions (all $p > 0.05$), but was explained by the annual arrival date at the colony (GLMM – Poisson, χ^2 test with model null: $p = 0.012$, $n = 162$; Fig. VII - 1b), with the later the arrival date the later the laying date.

Table VII - 1. Mean (± s.d.) annual arrival and laying dates of Adélie penguins breeding in the ANTAVIA Canyon colony.

***Tableau VII – 1**. Dates d'arrivée et de pontes annuelles moyennes (± e.c.) des manchots Adélies se reproduisant dans la colonie du Canyon ANTAVIA.*

Year	**Overall 2009-2014**	**2009/2010**	**2010/2011**	**2011/2012**	**2012/2013**	**2013/2014**
Arrival date (± s.d.)	November 2nd (± 6.2. days)	October 27th (± 3.2 days)	October 29th (± 4.8 days)	November 11th (± 5.8 days)	October 30th (± 4.3 days)	November 5th (± 3.5 days)
Laying date (± s.d.)	November 24th (± 3.2 days)	November 21st (± 2.6 days)	November 23rd (± 3.0 days)	November 26th (± 3.1 days)	November 23rd (± 2.6 days)	-
# of days btw Arrival and Laying (± s.d.)	22.9 (± 5.5 days)	25.4 (± 3.5 days)	24.8 (± 5.8 days)	17.0 (± 3.6 days)	23.7 (± 5.1 days)	-

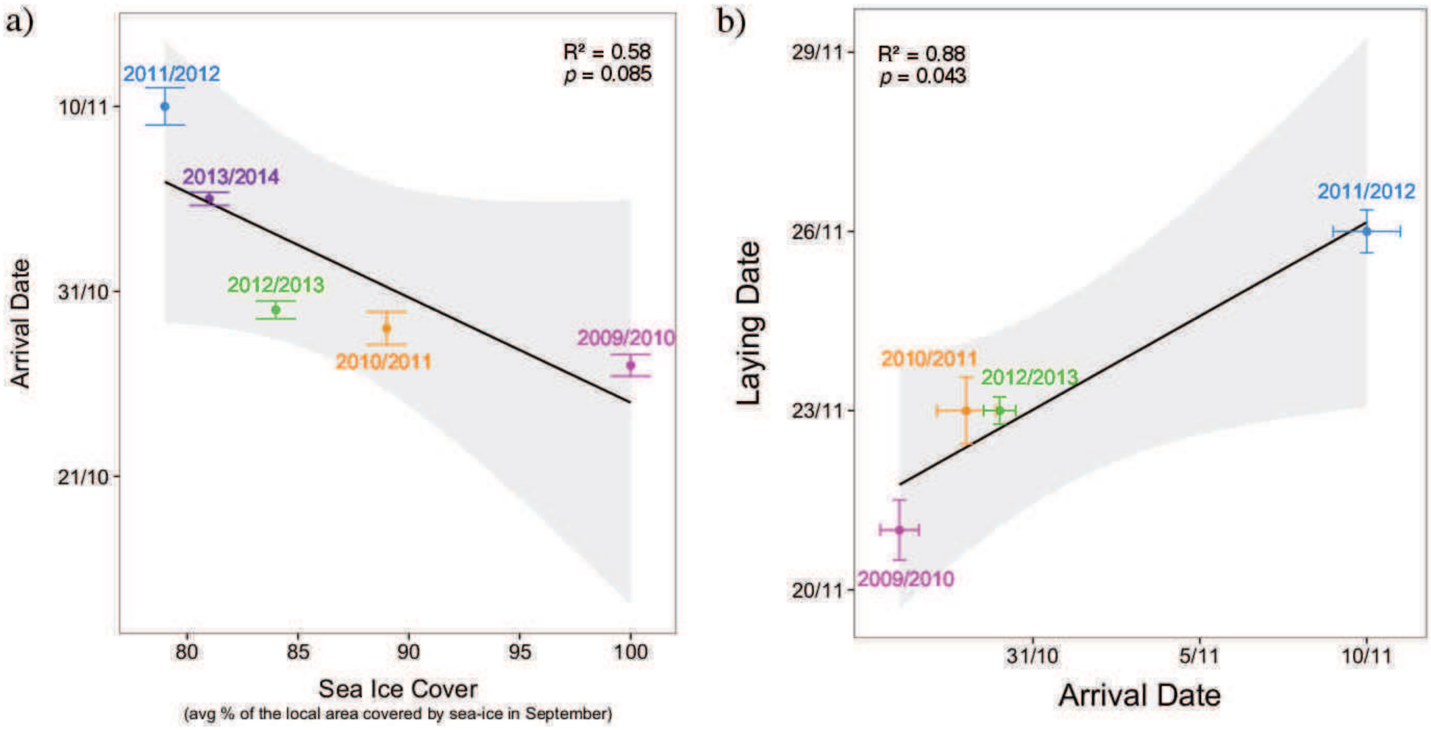

Figure VII - 1. Annual arrival dates according to sea-ice conditions in September, i.e spring, at a local scale (a), and annual laying dates according to arrival date at the colony (b) in Adélie penguins breeding in the ANTAVIA Canyon colony. Bars represent standard errors. Black lines indicate the linear regressions, and shadow the confidence interval based on standard errors.

***Figure VII – 1**. Dates d'arrivée annuelles en fonction des conditions de glace de mer en septembre, i.e. au printemps, à l'échelle locale (a), et dates de ponte annuelles en fonction de la date d'arrivée à la colonie (b) chez des manchots Adélies se reproduisant dans la colonie du Canyon ANTAVIA. Les barres représentent les erreurs standards. Les lignes noires représentent les régressions linéaires, et les ombres les intervalles de confiance basés sur l'erreur standard.*

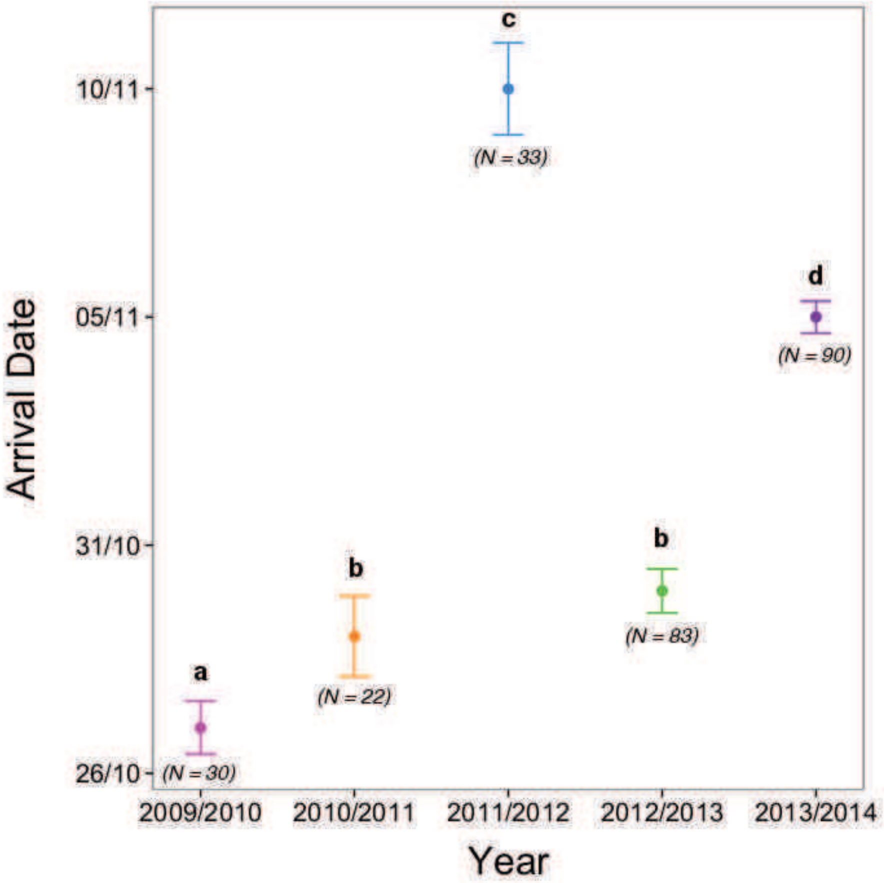

Figure VII - 2. Annual arrival dates of Adélie penguins breeding in the ANTAVIA Canyon colony. Values (mean ± s.e.) not sharing a letter were significantly different.

***Figure VII – 2**. Dates d'arrivée annuelles des manchots Adélie se reproduisant dans la colonie du Canyon ANTAVIA. Les valeurs (moyenne ± e.s.) ne partageant pas une lettre sont significativement différentes.*

b) Number of fledglings and breeding success

From 2006/2007 to 2013/2014, the average number of Adélie penguin fledglings produced in the *ANTAVIA Canyon* colony was 189 ± 205. We found a quadratic relationship between the annual number of fledglings and the average sea-ice cover over the whole breeding season (from October to February) at a regional scale ($LM(N_{fledglings} \sim SIC + SIC^2)$: $R^2 = 0.64$, $p = 0.032$; Fig. VII - 3). The sea-ice cover positively affected the number of fledglings until an average cover of *ca.* 55%, and, above this threshold, the number of fledglings was negatively affected. Note that no chicks survived until fledging, i.e. February, in 2013/2014.

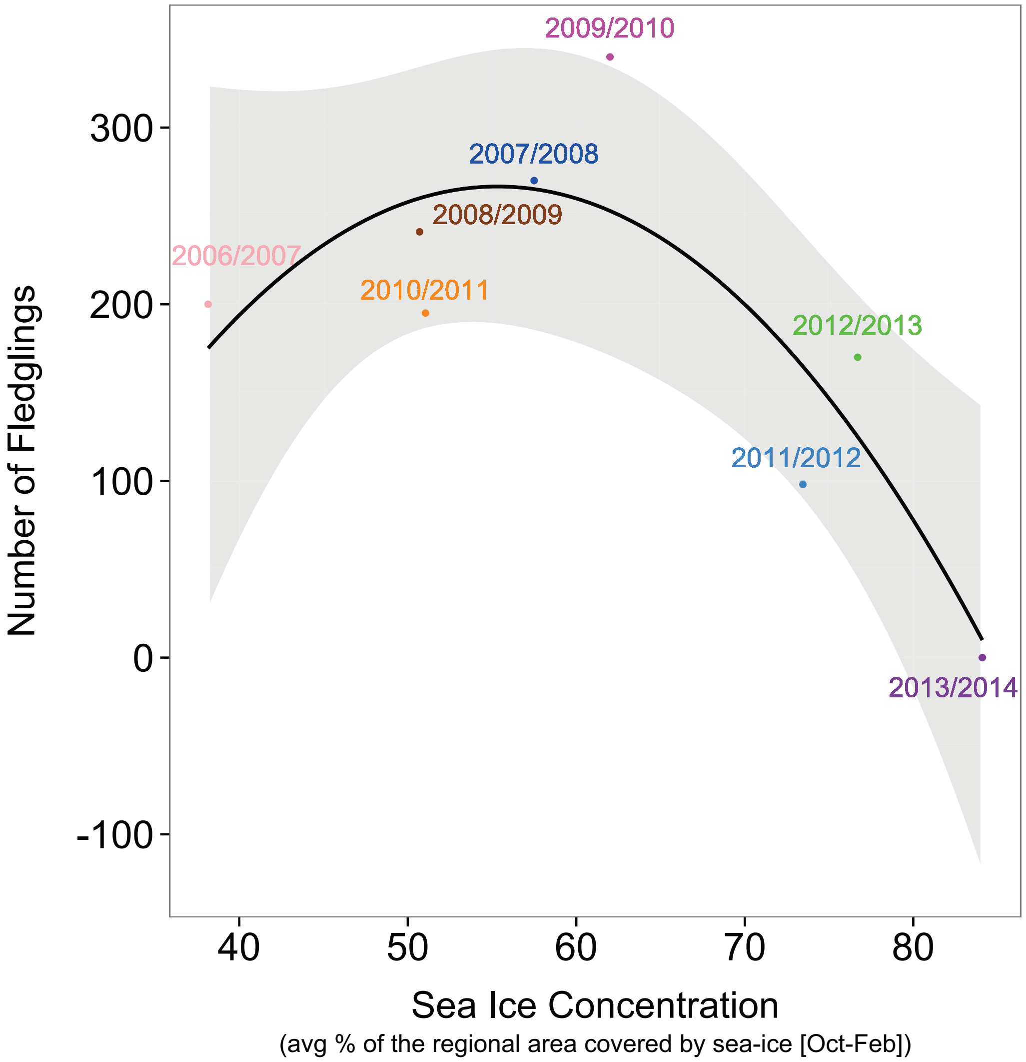

Figure VII - 3. Number of fledglings in the ANTAVIA Canyon Adélie penguin colony according to sea-ice conditions over the whole breeding season at a regional scale. Black line corresponds to the fitted curve of the linear regression $N_{fledglings} \sim SIC + SIC^2$, and shadow shows the confidence interval based on standard error.

Figure VII – 3*. Nombre d'oisillons dans la colonie de manchots Adélie du Canyon ANTAVIA en fonction des conditions de glace de mer sur toute la saison de reproduction à l'échelle régionale. La ligne noir correspond à la courbe ajustée de la régression linéaire $N_{oisillons} \sim SIC + SIC^2$, et l'ombre montre l'intervalle de confiance basé sur l'erreur standard.*

From 2008/2009 to 2013/2014, the average breeding success of Adélie penguins breeding in the *ANTAVIA Canyon* colony was 51.07 ± 18.49%. We also found a quadratic relationship between the annual breeding success of the colony and the average sea-ice cover between December and January at a regional scale (LM(Breeding Success ~ SIC + SIC²): $R^2 = 0.91$, $p < 0.05$; Fig. VII - 4). Below and above a threshold of 53% of sea-ice cover, the breeding success decreased.

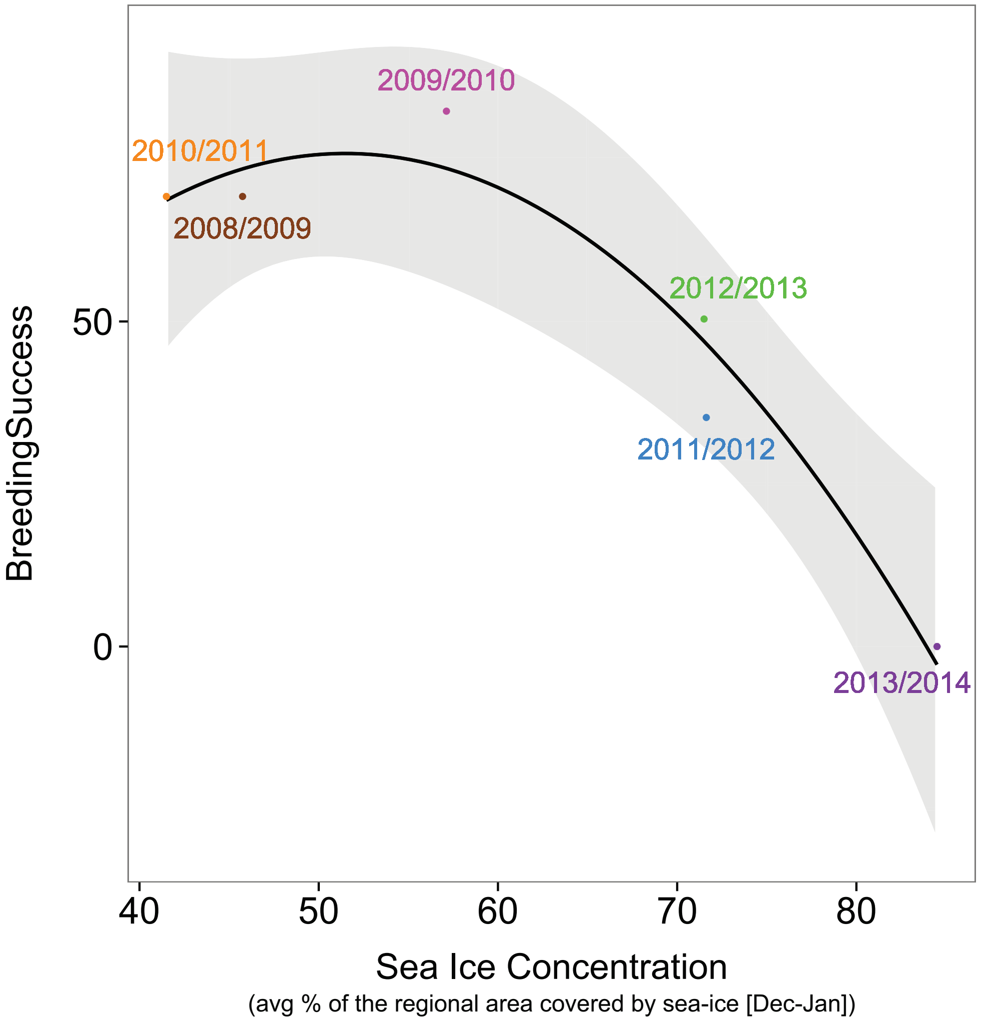

Figure VII - 4. Breeding success of Adélie penguins breeding in the ANTAVIA Canyon colony according to sea-ice conditions between December and January at a regional scale. Black line corresponds to the fitted curve of the linear regression Breeding Success ~ SIC + SIC², and shadow shows the confidence interval based on standard errors.

***Figure VII – 4**. Succès reproducteur des manchots Adélie se reproduisant dans la colonie du Canyon ANTAVIA en fonction des conditions de glace de mer entre décembre et janvier à l'échelle régionale. La ligne noir correspond à la courbe ajustée de la régression linéaire Succès Reproducteur ~ SIC + SIC^2, et l'ombre montre l'intervalle de confiance basé sur l'erreur standard.*

As laying date was explained by arrival date, in a first step we run the full model with either one of the two variables. We then selected the best of the two models, i.e. the model with arrival date (Table VII - 2) to run another model using a larger dataset including individuals for which we had the arrival date but not the laying date, to better explore the effects of phenology and environment. Individual breeding success was explained by the average sea-ice cover between December and January at a regional scale (see model selection in Table VII - 2). Both the sea-ice cover and (sea-ice cover)^2 terms were significant (GLMM-binomial, estimate = 0.918, std. error = 0.215, χ^2 test with model without the term: $p < 0.001$, and estimate = -0.008, std. error = 0.002, χ^2 test with model without the term: $p < 0.001$, respectively). Below and above a threshold of 57% of sea-ice cover, the individual breeding success decreased.

Table VII - 2. Model selection of the generalised linear mixed models explaining the individual breeding success of Adélie penguins of the ANTAVIA Canyon colony.

Tableau VII – 2*. Sélection des modèles linéaires mixtes généralisés expliquant le succès reproducteur individuel des manchots Adélie de la colonie du Canyon ANTAVIA.*

Model	**AIC**	**ΔAIC**	***wj***	***k***	***N***	***n***
$(\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}})^2$ + $\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}}$ + Year + Arrival Date	211	-	-	4	87	162
$(\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}})^2$ + $\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}}$ + Year + Laying Date	214	-	-	4	87	162
$(\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}})^2$ + $\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}}$ + Year + Arrival Date	223	0	0.38	4	123	265
$(\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}})^2$ + $\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}}$ + Arrival Date	223	0	0.38	3	123	265
$(\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}})^2$ + $\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}}$	224	1	0.23	2	123	265
$\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}}$	269	46	< 0.01	1	123	265

AIC: Aikaike's Information Criterion
ΔAIC: absolute difference with lowest AIC
wj: model weight
k: number of parameters in the model
N referred to the number of individuals and *n* to the number of observations
$\mathrm{SIC}_{\mathrm{Dec.-Jan.,\ loc.}}$ referred to the averaged percentage of sea-ice cover at the local scale during December and January
Year referred to the breeding season
Arrival/Laying Date referred to the arrival date or laying date of the individual for the breeding season

Arrival dates at the colony of failed breeders differed significantly between the five breeding seasons (Fig. VII - 5). On the other hand, arrival dates at the colony of successful breeders did not vary much between the four seasons (there were no successful breeders in 2013/2014), except for 2011/2012, for which individuals arrived significantly later than in the other years (Fig. VII - 5).

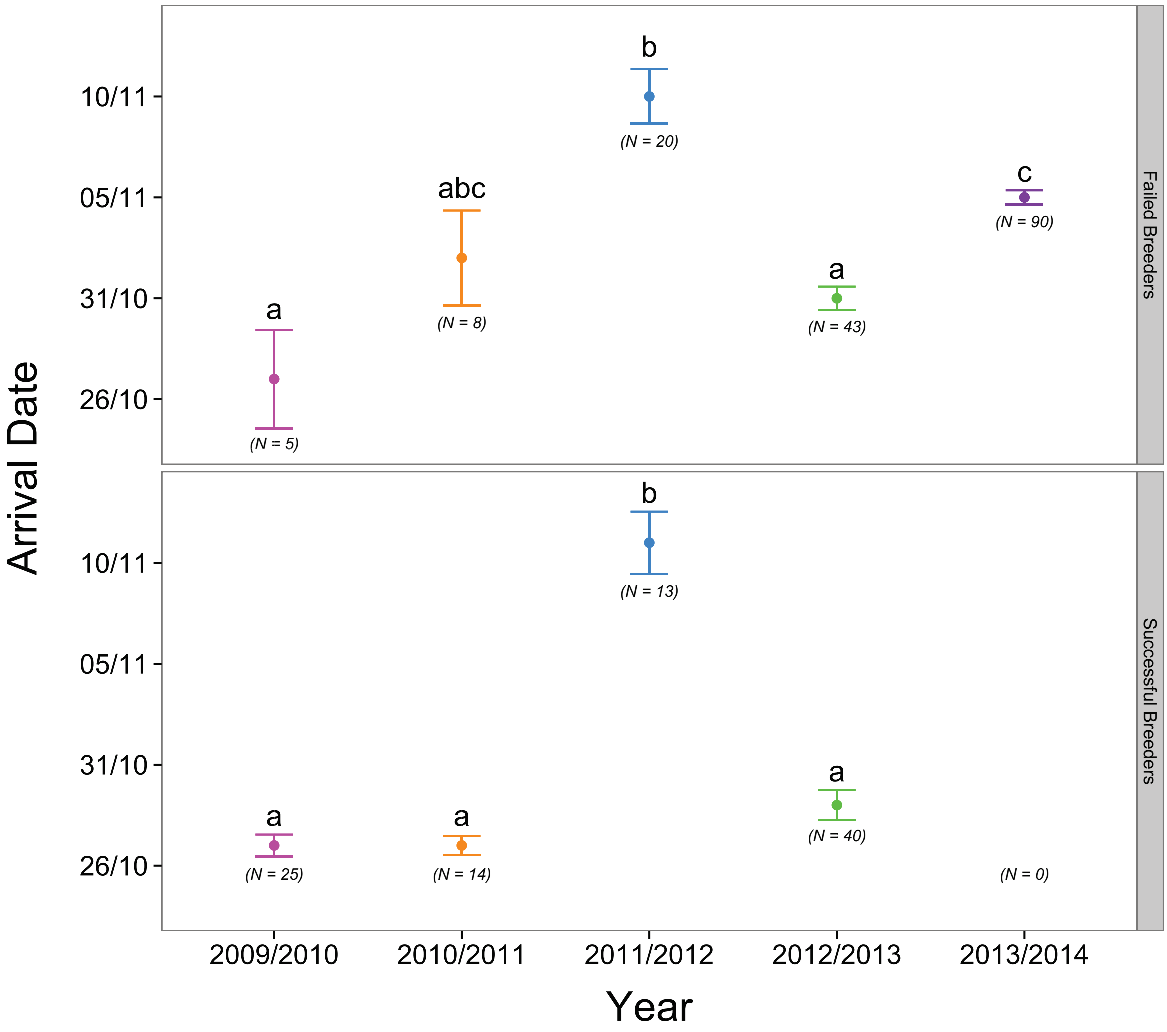

Figure VII - 5. Arrival dates in Adélie penguins breeding in the ANTAVIA Canyon colony according to the breeding output of the individuals. Values (mean ± s.e.) not sharing a letter were significantly different.

Figure VII – 5*. Dates d'arrivée des manchots Adélie se reproduisant dans la colonie du Canyon ANTAVIA en fonction de l'issue de la reproduction des individus. Les valeurs (moyenne ± e.s.) ne partageant pas une lettre sont significativement différentes.*

4 – Discussion

a) Influence of sea-ice conditions on breeding phenology

Our study revealed a high inter-annual variability in the arrival date at the colony of the Adélie penguins to start a new breeding season. This variability appeared to be link to environmental condition variation, as we found an influence of the sea-ice conditions prior to the breeding season (i.e. September) on the arrival date. Indeed, birds arrived later in the season in years where local sea-ice cover was smaller. The main prey of Adélie penguins is the Antarctic krill, *Euphausia superba* (Ainley, 2002; Lynnes et al., 2004). In regions marked with seasonal sea-ice retreat, melting sea-ice and its timing will set the conditions for phytoplankton blooms and their productivity (i.e. iron, light and the stabilisation of the mixed layer; see Smetacek and Nicol, 2005) on which the whole trophic web depend. For instance, an early sea-ice retreat will decrease the areal extent of shallow blooms in favour of deep blooms associated with small phytoplankton (Moline et al., 2004; Smetacek and Nicol, 2005) that would result in lower grazing efficiency of krill (Montes-Hugo et al., 2008) and consequently lower krill recruitment (Moline et al., 2004). However, several studies showed the ability of the Adélie penguin to switch diet when environmental conditions are changing (Clarke et al., 1998; Beaulieu et al., 2010), but the quality of alternative preys, in terms of energetic values, might not be as good as the quality of krill on which they usually feed. Therefore, in years of early sea-ice retreat, it might be more difficult, and thus take more time, for Adélie penguins to reach a good body condition prior to reproduction, leading to delayed arrival dates we observed in our colony. The mean annual arrival date of Adélie penguins we found in this study was very similar to the one observed at the Béchervaise Island (67°35' S) situated at the same latitude than the Petrel Island (November 2nd ± 6.2 days vs. November 1st ± 2.8 days, respectively; Emmerson et al., 2011). This is not surprising, as the pre-migratory hyperphagia and the migration preceding a new breeding season in Adélie penguins are initiated by an increase in day length (Ainley, 2002), which is the same at both study sites. Emmerson et al. (2011) argued, however, that the mean annual arrival date at their colony was delayed compared to what would be expected simply from this relation to latitude. They suggested that environmental conditions might also influence the arrival date. The influence of sea-ice condition we found in our study support this hypothesis. Nevertheless, in contrast with our results on the population of the Point Géologie Archipelago, they found that the sea-ice conditions at the beginning of the breeding season (i.e. the sea ice surface area of more than 15% of sea-ice concentration) influenced positively the arrival date of Adélie penguins breeding in Béchervaise Island. They proposed that an extensive sea-ice prior to the breeding season delayed Adélie penguins arrival because of the greater walking distance to cover to reach the colony, but also because of its potential impact on prey availability. In the Pointe Géologie region, sea ice extended northward between 1979 and 1998 (Zwally et al., 2002), and this tendency appeared to have accelerated in the last 8 to 5 years (data from Rayner et al., 2003). Paradoxically, the percentage of sea-ice cover in the direct vicinity of the colony in

September, which explained the arrival date in our study colony, appeared to have also decreased over the last 8 to 5 years indicating the presence of free water within the ice pack around the Archipelago (data from Rayner et al., 2003). This lower sea-ice cover could therefore be associated to the presence of polynias around the Pointe Géologie archipelago. Polynias are known to allow Adélie penguins to occupy colony sites where extended consolidated pack ice is present over the whole breeding season (Ainley, 2002). Consequently, the presence of polynias around the colony would mean that individuals could arrive early despite sea-ice extending northward. However this is not what we observed here. We would need now to acquire satellite images of the region to elucidate more precisely the changes occurring around the Pointe Géologie Archipelago that may explain the difference observed with Béchervaise Island.

Sea-ice conditions at the beginning of the breeding season did not influence the annual laying date at our study site, and we found no inter-annual variability. However, the laying date of the individuals was explained by their arrival date at the colony. In 2011/2012 individuals arrived on average 12 to 15 days later compared to the average arrival date in the three other breeding seasons (see Table VII - 1). However, in this breeding season there was only 17 ± 3.6 days between arrival and laying date compared to 24.6 ± 0.9 days on average in the three other breeding seasons. These results suggest that when birds arrived later in the season to reproduce, they were able to compress the courtship period for their timing of laying to still match with the timing of prey availability. Emmerson et al. (2011) also found reduced courtship and egg laying periods, when breeders' arrival at the colony was delayed. However, the capacity of the Adélie penguin to compress this period is limited, and it may affect individual physiology (e.g. oxidative stress and/or body condition, Beaulieu et al., 2010; Beaulieu et al., 2011), with consequences on their breeding performances (Angelier et al., 2007; Bize et al., 2008).

b) Influence of sea-ice conditions and breeding timing on breeding performances

The number of fledglings in our Adélie penguin colony of the Petrel Island was explained by the average sea-ice cover over the whole breeding season. We also found a strong correlation between the number of fledglings and the annual breeding success of the colony (LM: adjusted-$R^2 = 0.91$, $p = 0.002$), suggesting that this number was mainly explained by the capacity of the parents to raise their chicks and not dependent on the number of breeding pairs present at the colony in a given year. The capacity of parents to raise their chicks may then have been impacted by sea-ice conditions over the whole breeding season.

Indeed, our study showed that the annual breeding success and the individual breeding success were both affected by an extensive sea-ice cover during the end of the incubation period and the brooding phase, with a decreasing breeding success above a threshold of *ca.* 55% of sea-ice cover. This result, also observed in the Béchervaise Island colony (Emmerson and Southwell, 2008) has multiple and non-exclusive explanations. First, Adélie penguins are well adapted to swimming, but less well to walking (Pinshow et al., 1977). An extensive sea-ice cover means therefore a higher distance to walk before reaching open water and thus accessing foraging grounds compared to usual sea-ice conditions, hence leading to higher energy expenditures in a period already highly energetically demanding (Clarke et al., 1998). Moreover, an extensive sea-ice cover may alter prey availability (Clarke et al., 2002), and, consequently, the quality of the chick meals, as well as the potential for adults to recover from incubation and maintain their body condition (Clarke et al., 1998; Clarke et al., 2002). Finally, an extensive sea-ice cover would also increase the foraging trip length of the Adélie penguin breeders (both consequences of long distances to walk on sea ice and low prey availability), resulting in a reduced chick-feeding frequency (Ainley, 2002; Olmastroni et al., 2004). Interestingly, in a previous paper (Cornet et al. *in prep 3*), we found that breeding adults of this colony were more flexible in the duration of their foraging trip during brooding in a year with extensive sea-ice cover in December-January (i.e. 2011/2012) compared to a year with less extensive sea-ice cover (i.e. 2012/2013). These results could have two implications here. First, if as we hypothesized previously foraging consistency reflects foraging efficiency, individuals might consequently forage less efficiently in years of poor sea-ice conditions (i.e. an extensive sea-ice cover around chicks hatching). This would be congruent with the potential explanations on the effect of sea-ice enumerated above. Secondly, a higher plasticity of the foraging behaviour could mean that individuals responded to the environmental conditions change and were able to cope to some extent with poor conditions. However, the limits of this coping capacity might have been shown in 2013/2014, the year with the more extensive sea-ice cover around hatching when the breeding success of the colony was null.

Our study showed that the breeding success of a colony is the result of a complex combination of direct and indirect effects of environmental conditions at different phases of the breeding cycle and that breeding adults seem to be able to adjust to some extent to changes in these environmental conditions. Interestingly, Jenouvrier et al. (2006) did not find any effect of sea-ice conditions on the breeding success of Adélie penguin colonies from the same archipelago. However, they found that the number of breeding pairs and the population size were negatively correlated with sea-ice extent 6 years before. It is interesting to note that, since their study, sea-ice conditions tremendously change in the region and more particularly at the local scale. The calving of the Mertz glacier tongue in February 2010 altered the oceanography of the region (Tamura et al., 2012; Dragon et al., 2014). This casual extreme event may therefore have a strong impact on Adélie penguin populations breeding in the region, as suggested by our results in Pointe Géologie.

In long-lived species, population dynamics is more sensitive to changes in survival than in breeding parameters (Stearns, 1992; Sæther and Bakke, 2000). Consequently, adult survival (the parameter to which the population growth rate is the most sensitive) should display the less variability to environmental fluctuations (Lebreton et al., 1992; Stearns, 1992; Gaillard and Yoccoz, 2003). Jenouvrier et al. (2006) found no effect of environmental conditions on adult Adélie penguin survival, and neither did Lescroël et al. (2009) which supports this theory. However, several studies argue that traits relating to early-life stages, such as juvenile survival and recruitment, might also have a important impact on population growth rate (Gaillard et al., 1998; Oli and Armitage, 2004). As recruitment depends on both the number of offspring fledged and the sub-adult survival, our results highlighted potential impacts of future changes of sea-ice conditions on Adélie penguin population demography. The next step is therefore to estimate juvenile parameters and their potentialities to cope with rapid changes of sea-ice conditions through phenotypic plasticity and flexibility (Cornet et al. *in prep5*), to evaluate the thresholds of the adaptive abilities beyond which these populations would collapse.

5 – General discussion

The trophic web of the Southern Ocean is relatively simple and short compared to temperate or tropical trophic web (Stevens, 1989). Thus, any alteration at the base of this web has rapid effects on the upper trophic levels (see Chapter I). Consequently, by affecting the distribution and the abundance of the lower trophic-level species, the environmental variability has an indirect impact on species at the apex of this web, through the modification of their foraging strategies and energy allocation trade-offs ('Bottom-Up' control, Frederiksen et al., 2006; Staniland et al., 2006). In this PhD project, we used the Adélie penguin to investigate the mechanisms that might allow individuals and populations to adapt to the rapid alterations of their environment, as predicted by the Special Report on Emissions Scenarios (SRES) of the Intergovernmental Panel on Climate Change (IPCC).

Adélie penguins showed some abilities to adjust their phenotypic traits to changes in environmental conditions at different critical phases of their breeding cycle (Cornet *et al. Article 4*). However, this ability may be limited in the face of current climate changes (IPCC 2013). For instance, Beaulieu et al. (2010) found that Adélie penguins were able to switch diet from Antarctic krill (*Euphausia superba,* preferential) to coastal fish (e.g. Antarctic fish *Pleuragramma antarcticum*) when environmental conditions were poor (i.e. early sea-ice retreat affecting the structure of the trophic web). Although Antarctic fish have a lower energetic value than Antarctic krill, the study showed that this diet shift did not impact individual body condition and breeding success. Our study, based on a greater number of individuals and breeding seasons compared to this previous study, showed that, even though individuals might be able to switch diet under poor environmental conditions, this capacity was limited. Indeed, we observed that individuals arrived later at the colony during years of very poor environmental conditions (i.e. the lowest sea-ice cover during the month before the breeding season). Despite this capacity to switch diet, it might still be more difficult, and thus take more time, for Adélie penguins to reach a good body condition prior to reproduction during these drastic years. Furthermore, the time window for reproduction is very short in this species, as it depends on the timing of sea-ice retreat and its reformation (Ainley, 2002). Such delayed arrival can therefore have a strong impact on the breeding success. However, we found that individuals were able to compress their courtship period to still match the window of food availability (Cornet *et al. Article 4*; Emmerson et al., 2011). However, the capacity of Adélie penguins to compress their courtship period might also be limited for physiological reasons (e.g. minimal time to produce an egg). In addition, we found that harsh environmental conditions during the hatching period had strong effects on the breeding performances of the individuals (Cornet *et al. Article 4*). Indeed, extensive sea-ice at this critical time of the breeding cycle could be associated with an increase in energy expenditure allocated to foraging, as it could affect the trophic web and therefore the food availability, but also the distance to reach the foraging areas (Pinshow et al., 1977; Clarke et al., 1998; Ainley, 2002; Clarke et al., 2002; Olmastroni et al., 2004). Adélie penguins were able to cope to some extent with these harsh conditions, as shown by their higher foraging flexibility during years of poor environmental conditions (Cornet *et al. Article 3*), but this capacity was also limited, as clearly demonstrated by the complete failure of the last breeding season (2013/2014) during which the sea ice was the most extensive.

Our results demonstrated the ability of breeding adult Adélie penguins to adapt to their changing environment. However, the compression of the courtship period could induce physiological stress (e.g. oxidative stress and/or body condition, Beaulieu et al., 2010; Beaulieu et al., 2011), with consequences to their fitness (Angelier et al., 2007; Bize et al., 2008). Furthermore, even if individuals managed to raise a chick during poor environmental conditions, the quality of this chick might also be impacted by these adverse conditions (e.g. energetically poor meals affecting growth, Metcalfe and Monaghan, 2001) and have long-term consequences on the chick's future fitness (Hedgren, 1981; Festa-Bianchet et al., 2000; Cam et al., 2003; Harris et al., 2007; Rödel et al., 2009). Investigating the return rates and the age-specific survival rates of juveniles and their future reproduction could help us unravel these costs.

B – Juvénile parameters in the Adélie penguin

Age-specific return rates and survival in unbanded Adélie penguins (*Pygoscelis adeliae*) *– in prep Article 5*

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1 – Introduction

Population dynamics results from the combination of several life-history variables, such as age-specific survival, age at maturity and age at first breeding, number and size of offspring (Stearns, 1992). These life-history traits are bound by an energy allocation trade-off between three main functions in an organism: growth, reproduction, and maintenance (Stearns, 1989; Roff, 1992). By regulating the resources available for organisms, environmental stochasticity is therefore considered as one of the main parameter involved in population regulation (Lack and Gillmor, 1966; Sæther, 1997). According to the life-history theory, life-history traits should be shaped to optimise the fitness of an organism, that is to say the number of offspring it will produce across its lifespan (Williams, 1966; Roff, 1992; Stearns, 1992). In long-lived species, such as seabirds, adult survival is considered to be the vital rate that should display the least variability, as it may have the largest impact on the population growth rate (Pfister, 1998; Gaillard and Yoccoz, 2003; Gaillard et al., 2005; Oli and Dobson, 2005; Stahl and Oli, 2006). In contrast, lesser contributing life-history traits, such as juvenile survival and age at maturity, are more likely to be impacted by environmental stochasticity. However, it is now recognized that juvenile parameters can still have a major impact on population dynamics (e.g. Gaillard et al., 1998; Oli and Armitage, 2004). Recruitment, defined as the establishment of new individuals in the breeding segment of a population, is indeed crucial for the population turnover (Pradel, 1996; Lebreton et al., 2003). It will depend on the number of offspring produced in the population in a given year, their return and survival rates, and their age at maturity and first breeding. Despite their importance, only a few studies have examined the effects of environmental fluctuations on these early stage life-history traits (e.g. Votier et al., 2008; Emmerson and Southwell, 2011; Saraux et al., 2011b) and their consequences on the population growth. Environmental conditions during the early development period are known to have long-term fitness consequences (Hedgren, 1981; Festa-Bianchet et al., 2000; Cam et al., 2003; Harris et al., 2007; Rödel et al., 2009). Moreover, environmental conditions after fledging or weaning, when individuals are the most vulnerable because inexperienced and in a learning phase, can also affect juvenile body condition and survival (Marchetti and Price, 1989; Wunderle, 1991; Martin, 1995; DeLgiudice et al., 2002; Beauplet et al., 2005). Exploring the complex relationships between environmental variability and juvenile parameters is therefore fundamental to understand the dynamics of a population.

Upper-level predators are known to amplify and magnify changes occurring throughout their trophic webs (Boyd and Murray, 2001). Seabirds, such as penguins, have been therefore identified as good sentinels of the future of their ecosystem (Piatt et al., 2007; Parsons et al., 2008; Grémillet and Charmantier, 2010). The understanding of the mechanisms shaping their populations is thus critical to predict the impact of environmental changes on sensitive ecosystems, such as the Southern Ocean. Although many penguin species have been well studied in the context of climate change (e.g. Croxall et al., 2002; Le Bohec et al., 2008; Jenouvrier et al., 2009), little is still known on their early life parameters due to methodological difficulties to monitor juvenile individuals (but see Saraux et al., 2011b for king penguins *Aptenodytes patagonicus*; and Horswill et al., 2014 for macaroni penguins *Eudyptes chrysolophus*). Moreover, most of the studies on known-aged penguins still rely on the monitoring of flipper-banded individuals, despite their deleterious effects on penguin fitness (Gauthier–Clerc et al., 2004; Dugger et al., 2006; Saraux et al., 2011a). In this study, we focused on a population of Adélie penguins *Pygoscelis adeliae* breeding in the Pointe Géologie archipelago, Adélie land. A colony is continuously monitored since the austral summer 2008/2009 thanks to an automatic monitoring system based on Radio Frequency Identification (RFID), giving us access to the first unbiased dataset (i.e. not based on flipper-banded individuals) in this region of Antarctica. The present study was based on 7 cohorts of Passive Integrated Transponder (PIT) tagged fledging chicks and 6 breeding seasons. We investigated the effects of pre-fledging characteristics (i.e. structural size and body condition at fledging, departure date) and environmental conditions on the return rates of Adélie penguins to their natal colony. The timing of their return and their recruitment to reproductive population was also explored.

2 – Material and Methods

a) Penguin monitoring

The study was carried out on an Adélie penguin *Pygoscelis adeliae* colony of *ca.* 300 breeding pairs settled on Petrel Island (66°40’ S 140°01’ E), Pointe Géologie archipelago, Adélie Land, Antarctica. An automatic Radio-Frequency IDentification system (RFID), based on passive transponder tags implanted under birds’ skin of their leg, ensures the long-term monitoring of this colony, called ‘*ANTAVIA Canyon*’ (see Gendner et al., 2005; Le Bohec et al., 2007 for a similar system implemented on king penguins, *Aptenodytes patagonicus*).

From the austral summer 2006/2007 to 2012/2013, all the chicks of the *ANTAVIA Canyon* colony that were still alive mid-February (i.e. just before fledging), were implanted with transponder tags ($N_{7\ cohorts}$ = 1514 chicks). During tagging, body mass and morphometric measurements (flipper and beak) were taken along with biological samples (feathers or blood) for posterior DNA sexing, with the exception of the first cohort for which only body mass was available. We defined a Structural Size Index (SSI) as the first component (PC1) of the Principal Component Analysis on morphometric measurements (explaining 74% of observed variance), and a Body Condition Index (BCI) as the residuals of the regression of body mass on the SSI (see details in Cornet et al. *in prep. 1*).

Micro-tagged penguins are then automatically detected by double antennas implanted at the usual pathways used by the birds to enter and exit their colony, giving us access to continuous data on their presence/absence in the colony. However, the data acquisition system was only implemented during the austral summer 2008/2009. Considering that no bird returned to their natal colony at one-year old in our study, and that such early returns are extremely rare in Adélie penguins (Ainley, 2002), we could therefore consider our recapture effort constant over the whole study period even including the 2006/2007 cohort.

b) Juvenile parameter survey

Chicks usually moult in the colony before they fledge, but some chicks still with down are observed moving in and out of the colony, before their final departure from the colony. Fledging departure date was therefore defined as the last date a newly micro-tagged bird was automatically detected exiting the colony at the end of the austral summer. Return date was then defined as the date an individual was first detected entering the colony after at least the first winter. Duration of the post-fledging trip outside their natal colony was consequently considered as the difference between the first return date and the fledging date. Arrival dates in subsequent years were defined as the date an individual was first detected entering the colony at the beginning of the following summer seasons.

Return rate was defined as the proportion of fledging birds of a cohort that was detected again during one of the following summer seasons. The global return rate of the colony was determined as the total number of birds detected again after fledging in the colony over the total number of fledged individuals.

We considered an individual as attempting to breed when we observed, at the beginning of a summer season (i.e. October-November), the pattern of presence on land/at sea outlined in red in Figure VII - 6, with consideration also for the time spent in the colony during previous years.

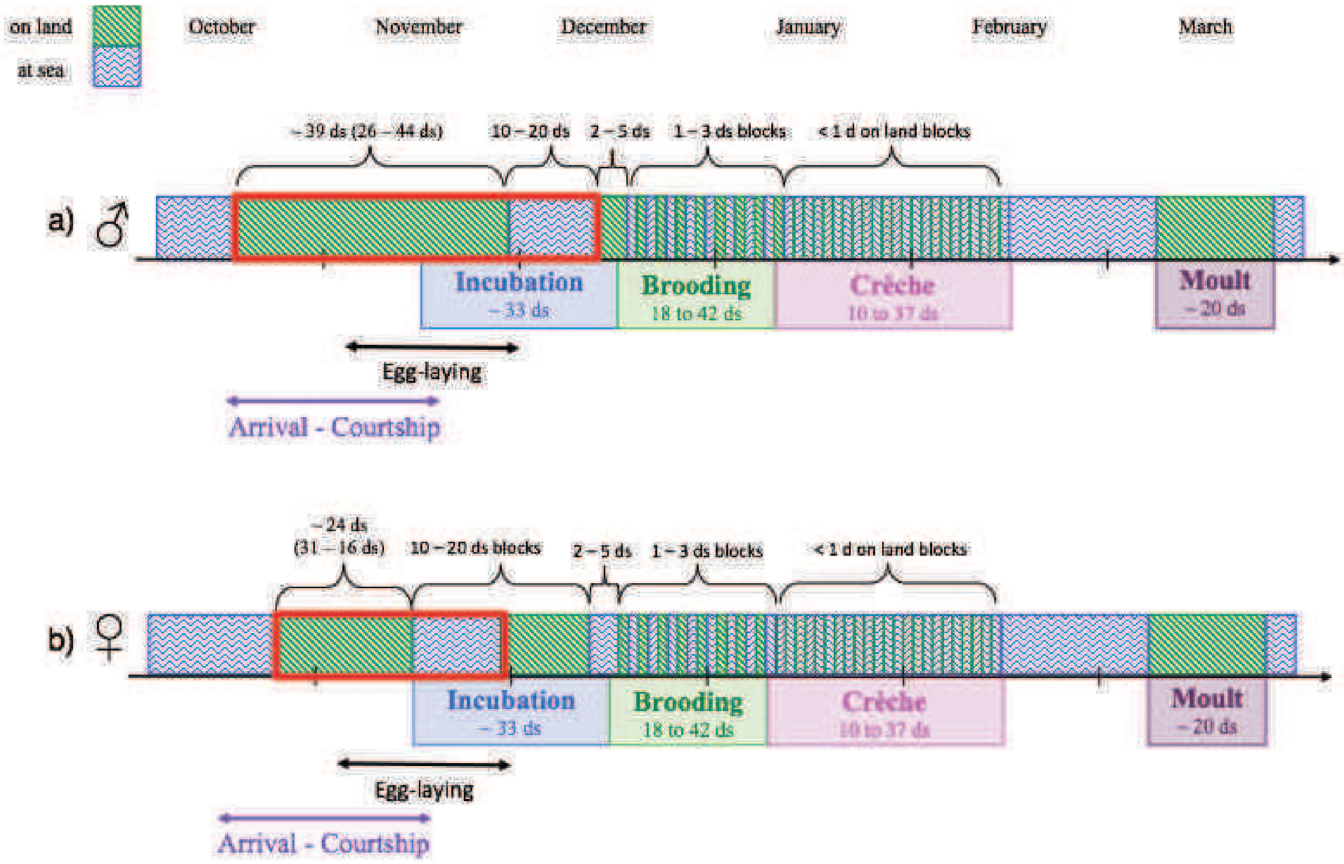

Figure VII - 6. Breeding cycle and its associated pattern of at sea/on land sojourns of experimented a) males and b) females Adélie penguins. The duration of the first on land sojourn is given in days as mean (minimum-maximum) for the *ANTAVIA Canyon* colony. The duration of other sojourns is given in days as minimum-maximum for the *ANTAVIA Canyon* colony. Pattern highlighted in red corresponds to the minimal pattern to be observed to consider that an inexperimented bird attempted to breed.

***Figure VII – 6**. Cycle de reproduction et son motif de séjours en mer/à terre associé pour des a) males et b) femelles manchots Adélie expérimentés. La durée du premier séjour à terre est donnée comme moyenne (minimum-maximum) en jours pour la colonie du Canyon ANTAVIA. La durée des autres séjours est donnée comme minimum-maximum en jours pour la colonie du Canyon ANTAVIA. Le motif souligné en rouge correspond au motif minimal observé pour considérer qu'un oiseau inexpérimenté a tenté de se reproduire.*

c) Ethical statement

All procedures and protocols were approved by the ethical committee of the French Polar Institute (Institut Polaire Paul-Emile Victor, IPEV) in compliance with the French laws on animal experiments and welfare. Authorisations to enter the breeding site (permits n° 2006-67 issued on the 6th of November 2006, n° 2007-149 issued on the 24th of October 2007, n° 2008-98 issued on the 5th of September 2008, n° 2009-57 issued on the 26th of August 2009, n° 2010-79 issued on the 3th of September 2010, n° 2011-107 issued on the 14th of October 2011, and n° 2012-126 issued on the 29th of October 2012) and handle birds (permits n° 2006-73 issued on the 6th of October 2006, n° 2007-157 issued on the 25th of October 2007, n° 2008-71 issued on the 5th of September 2008, n° 2009-59 issued on the 29th of August 2009, n° 2010-67 issued on the 3rd of September 2010, n° 2011-99 issued on the 14th of October 2011, and n° 2012-117 issued on the 29th of October 2012) were delivered by the 'Terres Australes et Antarctiques Françaises' (TAAF). Transponder tags (3.85 mm x 32 mm) weigh 0.8 g, and, to date, no known adverse effects of these electronic tags have been found (Froget et al., 1998; Nicolaus et al., 2009). During manipulations, the birds' heads were hooded with black cloth and the protocol was carried out in silence outside of the colony to reduce the stress of the birds and the disturbance to the colony.

d) Environmental descriptors

Both global and local environmental conditions can affect populations (see review in Stenseth et al., 2002). Large-scale climate indexes integrate variations of several climate factors (also called 'weather packages', see Stenseth and Mysterud, 2005). They have been shown to be good proxies of environmental variability that explain seabird population trends in the Southern Ocean (e.g. Jenouvrier et al., 2005; Le Bohec et al., 2008). We therefore used monthly Southern Oscillation Index (SOI) obtained from the Australian Bureau of Meteorology website (www.bom.gov.au). The SOI is calculated from the monthly fluctuations in air pressure differences between Tahiti and Darwin (Australia). Negative SOI values (i.e. warm phase of El Niño Southern Oscillation; Deser and Wallace, 1987) indicate warmer environmental conditions in the Southern Ocean.

Moreover, Adélie penguins are highly dependent on sea ice to live and reproduce (Ainley, 2002),. The location of winter foraging grounds of juvenile Adélie penguins in this archipelago after fledging is unknown. Moreover, prey availability in one area depends on the location of its spawning ground that might occur at a different location, and on the oceanographic conditions between the two locations (Hofmann et al., 1998). In a previous paper (Cornet *et al. in prep 4*), we already demonstrated that sea-ice conditions at two different spatial scales representative of the local and the broader regional environmental conditions around the Pointe Géologie archipelago had an effect on the breeding performances of adults Adélie penguins of this colony. We therefore decided to consider again these two spatial scales here, as they are also susceptible of affecting fledglings after they departed from the colony for the first time. We thus used monthly percentage of sea-ice cover (SIC, extracted from Rayner et al. (2003)) on a grid cell of 1° x 1° covering between 66°S and 67°S, and 140° E and 141°E (local scale, i.e. direct vicinity of the breeding colony) and on a grid cell of 2° x 2° covering a larger area between 65°S and 67°S, and 139°E and 141°E (regional scale). The Sea Surface Temperature (SST) is also a good indicator of abundance and distribution of prey as it has repercussion on the primary production and therefore on the trophic web of a region (Gregg et al., 2003). We therefore also used monthly SST (extracted from Rayner et al., 2003) on the same grid cells as for SIC.

e) Statistical analysis

All statistics were computed using the R 2.10.0 statistical environment (R Development Core Team, 2012). Data were analysed using a maximum of likelihood generalised linear model approach (GLM) fitted with appropriate distribution (Gamma after examination of the residuals, Poisson or binomial). Model selection was based on Akaike's Information Criterion (AIC, Akaike (1973), but see Symonds and Moussalli (2011) for applications in behavioural ecology). The model displaying the lowest AIC was selected, except when $\Delta AIC \leq 2$, then we selected the model with the smallest number of parameters to avoid overparametrisation. Analyses of variance (χ^2 test) were used to assess the overall significance of categorical parameters (i.e. cohort).

In order to compare body mass, SSI, BCI, fledging departure date, and the duration of the post-fledging trip outside their natal colony between cohorts, we first checked for normality of the variable residuals and for between-group homoscedasticity, and, consequently, used pairwise Wilcoxon sum-rank tests. Pairwise Fisher's exact tests were performed to compare the proportion of resighted individuals between cohorts within each age class. In both cases, a multiple comparison procedure, i.e. Bonferroni's correction, was then applied, and differences were considered significant for $p < \frac{0.05}{n}$ (*n* being the number of pairwise comparisons performed). Finally, we used Fisher's exact test adjusted for r x k contingency tables (i.e. a generalization of the test for 2 row x 2 lines tables) to compare, between cohorts, the proportion of birds that returned for the first time at 2, 3 and 4-year-old to their natal colony. Variables are presented as mean ± standard error unless stated otherwise.

3 – Results

a) Pre-fledging parameters

The body mass at fledging in Adélie penguins varied significantly between years from 3.40 ± 0.03 kg in 2008/2009 to 3.90 ± 0.04 kg in 2012/2013 (GLM – Gamma: χ^2 test with null model, $p < 0.001$, $n = 1509$; Fig. VII - 7a). The Structural Size Index (SSI) and the Body Condition Index (BCI) at departure also showed a significant inter-annual variability (GLM – Gamma: χ^2 test with null model, $p < 0.001$ and $n = 1313$ for both). Interestingly, fledglings of the 2011/2012 cohort, which had a lower SSI compared to the other cohorts (Fig. VII - 7b), also had a higher BCI than the other cohorts (Fig. VII - 7c). Overall, fledging departure dates ranged between February 5th and March 3rd in this colony. Fledging date was explained by the year, the SSI and the BCI of fledglings (GLM – Poisson: AIC = 5393, ΔAIC = 28 with the closest model excluding the BCI, Explained deviance (ED) = 39%, $n = 1008$), with all variables being significant (all $p < 0.001$). The 2011/2012 cohort stood out again with fledglings departing on average significantly later from the colony than the other cohorts (Fig. VII - 7d). Taller fledglings and the ones with a better BCI left the colony earlier.

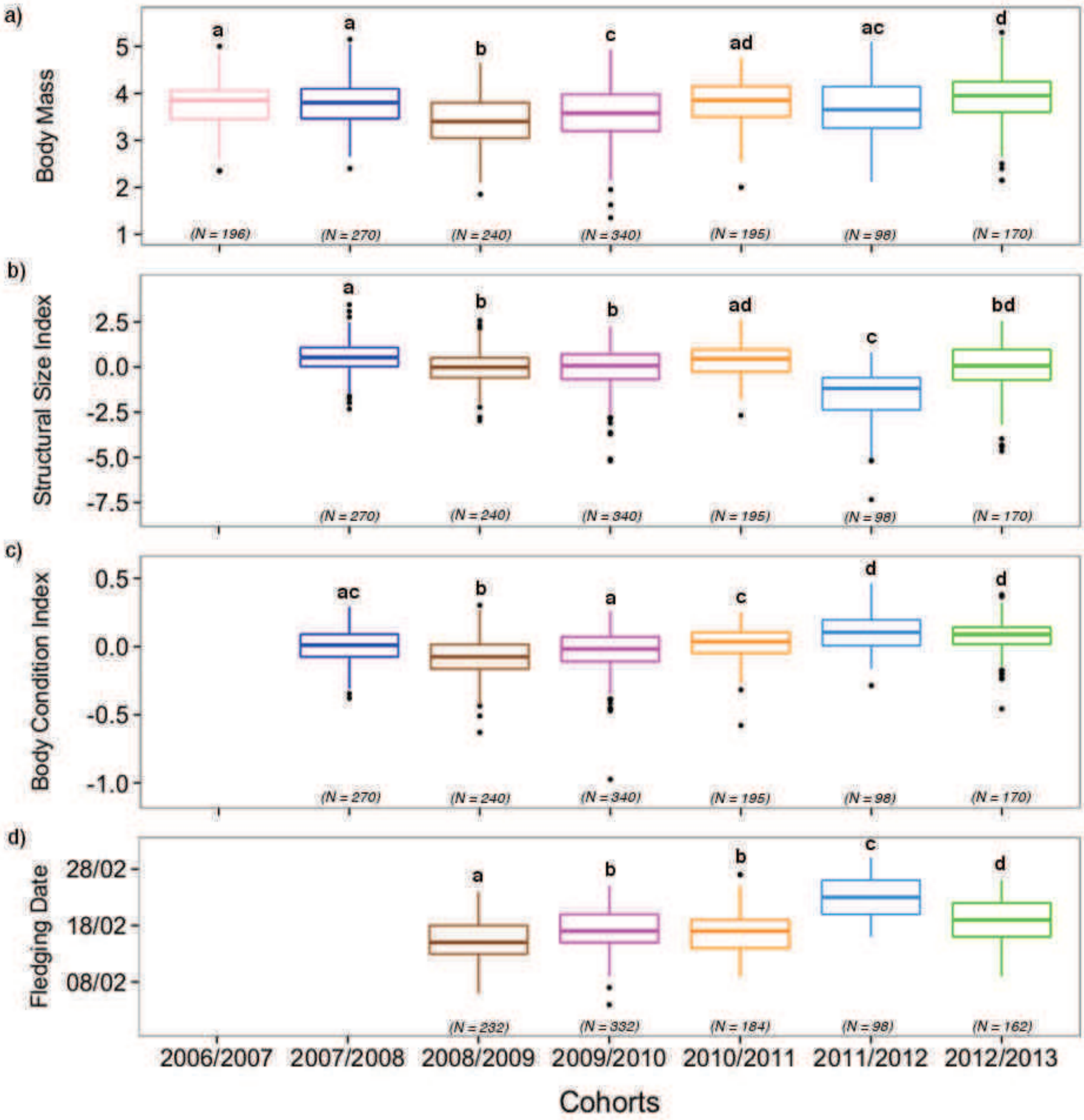

Figure VII - 7. Inter-annual variability of pre-fledging traits in Adélie penguins: a) Body mass (in kg), b) Structural Size Index (SSI), c) Body Condition Index (BCI), and d) Fledging departure date. Values, presented as boxplots, that are not sharing a common letter differ significantly. Sample sizes are indicated into brackets.

***Figure VII – 7**. Variabilité interannuelle des traits pré-envol de manchots Adélie : a) Masse corporelle (kg), b) Indice de taille structurelle (SSI), c) Indice de condition corporelle (BCI), et d) Date de départ à l'envol. Les valeurs, présentées comme des boxplots, qui n'ont pas de lettres en commun diffèrent de façon significative. La taille des échantillons est indiquée entre parenthèses.*

b) Return rates and the influence of individual and environmental parameters

When considering the 4 first cohorts, the global return rate was of 50.7%, ranging from 20.3% to 72.5% (Fig. VII - 8). However, when excluding the fourth cohort (2009/2010 cohort, the lower return rate), the global return rate rised up to 60.9%. Nevertheless, since the probability of resighting 5-year-old and older individuals were low to null for the first cohorts, we do not expect the return rate of the 2009/2010 cohort to improve significanlty in the next years. During the study period, no bird returned for the first time at 1 year old to their natal colony, and, indeed, individuals mainly came back at 2 and 3 years of age (60% and 35%, respectively), while only a few ones came back at 4 and 5 years of age (5% and 0.5%, respectively). No bird was observed to return for the first time to its colony at 6 and 7 years of age. Age-specific return rate was highly variable between cohorts (Fig. VII - 8), especially until 5 years of age.

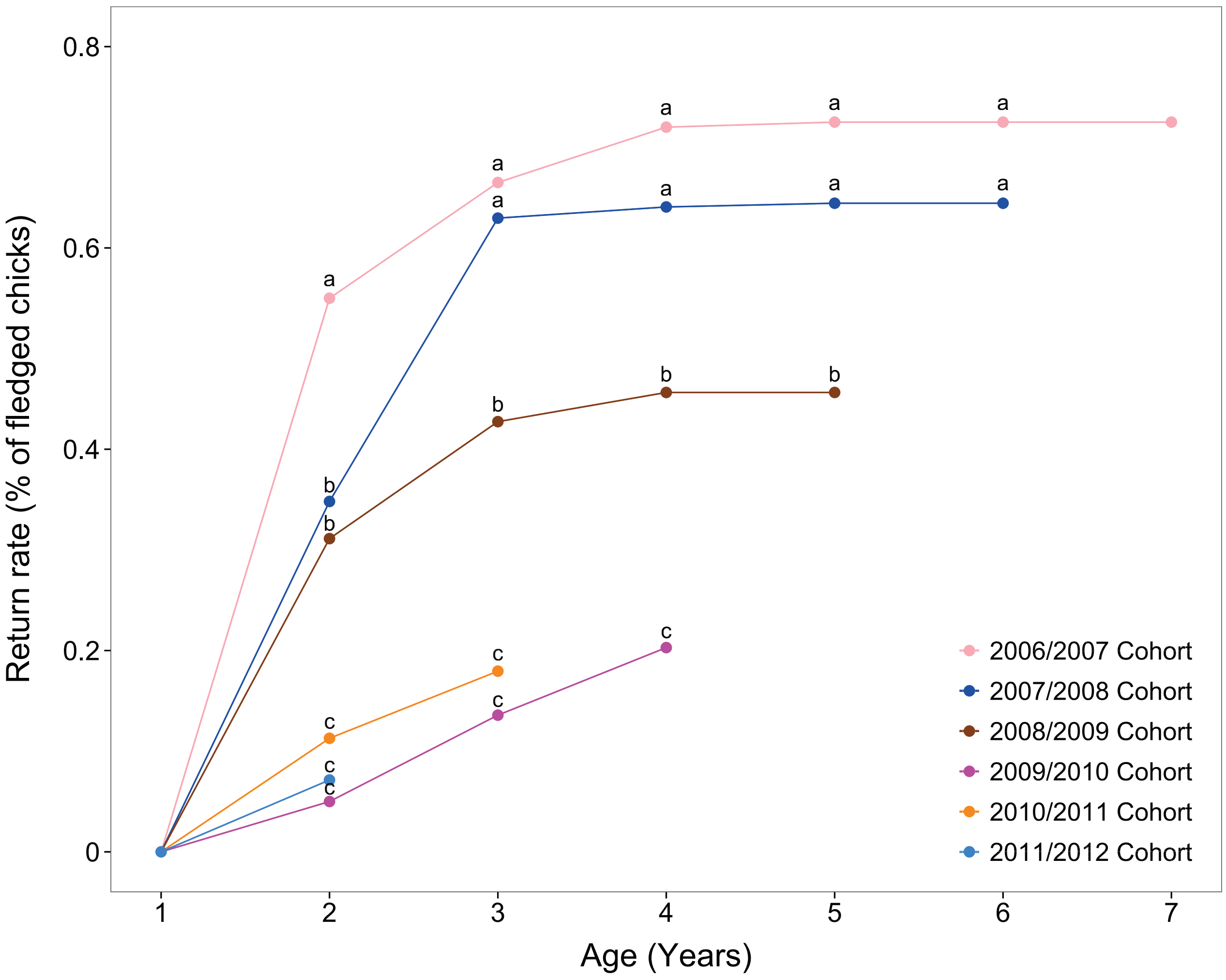

Figure VII - 8. Return rates of Adélie penguins according to their age and their cohort. Values not sharing a letter within an age class were statistically different.

Figure VII – 8*. Taux de retour des manchots Adélie en fonction de leur âge et de leur cohorte. Les valeurs ne partageant pas de lettre en commun au sein d'une classe d'âge sont statistiquement différentes.*

The relative proportion of birds returning for the first time to the colony at 2, 3 and 4 years old differed significantly between cohorts (Fisher's exact test: $p < 0.001$, $n = 496$; Fig. VII - 9). The proportion of birds returning at 2, 3 and 4 years old was explained by the Southern Oscillation Index (SOI) over the post-fledging period (i.e. April-September) (GLM – Poisson: AIC = 1246, ΔAIC = 2 with the closest model including the Sea Ice Cover (SIC) or the Sea Surface Temperature (SST) at a regional scale over the same period, ED = 7%, $n = 498$). The colder (i.e. higher SOI) were the conditions over the post-fledging period, the later was the age at first return.

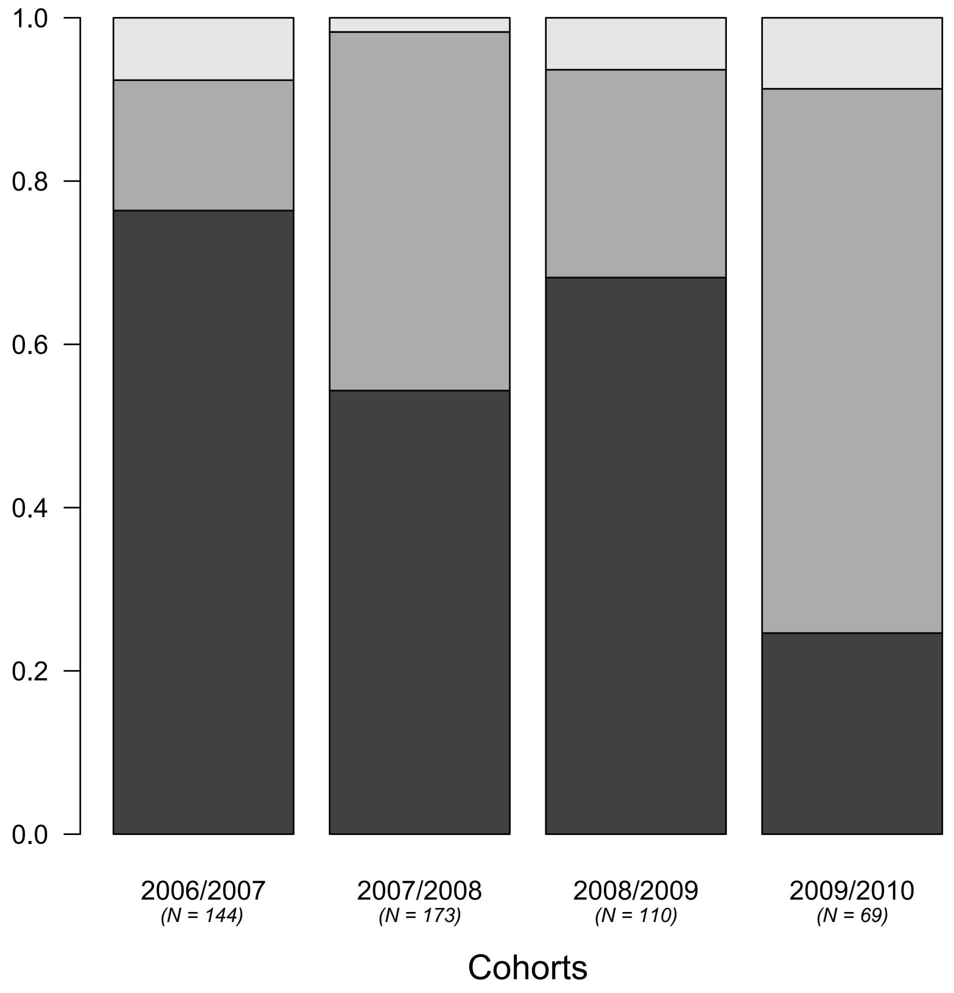

Figure VII - 9. Differences between cohorts in the proportion of Adélie penguins returning for the first time to their natal colony at 2 (dark grey), 3 (medium grey) and 4 years old (light grey).
Figure VII – 9*. Différences entre les cohortes dans la proportion de manchots Adélie retournant pour la première fois à leur colonie natale à 2 (gris foncé), 3 (gris moyen), et 4 ans (gris clair).*

The global return rate was explained by the BCI of the individuals at fledging and by the SST in the direct vicinity of the colony (local scale) during the month following the fledging (i.e. March) (GLM – binomial: AIC = 1027.7, ΔAIC = 0.8 with the closest model including the SSI, ED = 11.4%, *n* = 850). Birds in good condition at fledging were more likely to return to the colony, and the lower was the SST, the greater was the return rate (Table VII – 3-M1). We decided to run another model to better explore the environmental effects, including the 2006/2007 cohort for which the SSI, and thus the BCI, were not available (i.e. excluding those parameters from the model selection). The global return rate was then explained by the SOI and the SIC at the regional scale during month following the fledging (GLM – binomial: AIC = 1269, ΔAIC = 26 with the closest model including the SIC at the local scale during month following the fledging, ED = 13.1%, *n* = 1051). Again, colder conditions (i.e. higher SOI and SIC) positively affected the return rate (Table VII – 3-M2).

Table VII - 3. Estimates of the models explaining the overall return rate of Adélie penguins born in the ANTAVIA Canyon colony. Bold type indicates significant parameters.

***Tableau VII – 3**. Estimations des modèles expliquant le taux de retour global des manchots Adélie nés dans la colonie du Canyon ANTAVIA. Les caractères gras indiquent les paramètres significatifs.*

Model	Variable	Estimate	Std. Error	Z value	***p*** value
M1	Intercept	- 4.409	0.404	- 10.92	< **0.001**
	$SST_{March/Local}$	- 16.097	1.529	- 10.53	< **0.001**
	BCI	1.105	0.543	2.03	**0.042**
M2	Intercept	- 1.927	0.230	- 8.38	< **0.001**
	SOI_{March}	0.057	0.008	6.69	< **0.001**
	$SIC_{March/Regional}$	0.050	0.006	8.38	< **0.001**

$SST_{March/Local}$ referred to the Sea Surface Temperature directly in the vicinity of the colony (local scale) in March
BCI referred to the Body Condition Index
SOI_{March} referred to the Southern Oscillation Index in March
$SIC_{March/Regional}$ referred to the Sea Ice Cover at a regional scale in March

When decomposing the rate of first return, we found that the rate at the age of 2 was explained by the SSI at fledging and the SST at the regional scale during the month following the fledging (GLM – binomial: AIC = 785.7, ΔAIC = 1.3 with the closest model including the BCI, ED = 12.7%, *n* = 850). Birds with a high SSI at fledging were more likely to come back at 2 years old to their colony, and low SST right after fledging positively affected the return rate at age 2 (Table VII - 4-M3). Again, including the 2006/2007 cohort, but excluding the SSI/BCI variables, the return rate at the age of 2 was explained by the SOI and the SIC at the regional scale during the month following the fledging (GLM – binomial: AIC = 1070, ΔAIC = 7 with the closest model including the SIC at the local scale during the month following the fledging, ED = 14.8%, n = 1051). Once again, colder conditions (i.e. higher SOI and SIC) positively affected the return rate at the age of 2 (Table VII - 4-M4). The rate of first return at the age of 3 (including the 2006/2007 cohort, as no individual parameters were found previously selected) was explained by the SST over the winter (i.e. March-September) at the regional scale (GLM – binomial: AIC = 767, ΔAIC = 9.4 with the closest model with the SST over the winter at the local scale, ED = 6.0%, $n = 755$). We found that juveniles that endured cold temperatures during their first winter were more likely to return rate at 3 years of age (Table VII - 4-M5).

Table VII - 4. Estimates of the models explaining the return rates at 2 (M3 and M4) and 3 years old (M5) of Adélie penguins born in the ANTAVIA canyon colony. Bold type indicates significant parameters.

Tableau VII – 4*. Estimations des modèles expliquant les taux de retour à 2 (M3 et M4) et 3 (M5) ans des manchots Adélie nés dans la colonie du Canyon ANTAVIA. Les caractères gras indiquent les paramètres significatifs.*

Model	Variable	Estimate	Std. Error	*Z* value	*p* value
M3	Intercept	- 7.228	0.755	- 9.57	< **0.001**
	$SST_{March/Regional}$	- 37.264	4.515	- 8.25	< **0.001**
	SSI	0.193	0.094	2.04	**0.041**
M4	Intercept	- 3.625	0.275	- 13.19	< **0.001**
	SOI_{March}	0.053	0.010	5.36	< **0.001**
	$SIC_{March/Regional}$	0.069	0.006	10.64	< **0.001**
M5	Intercept	- 55.460	7.770	- 7.130	< **0.001**
	$SST_{Winter/Regional}$	- 35.220	5.040	- 6.990	< **0.001**

$SST_{March\ or\ Winter/Regional}$ referred to the Sea Surface Temperature at a regional scale in March and over the winter (March-September)
SSI referred to the Structural Size Index
SOI_{March} referred to the Southern Oscillation Index in March
$SIC_{March/Regional}$ referred to the Sea Ice Cover at a regional scale in March

The probability for a fledgling of ever being seen again in the colony was explained by the SSI (GLM – binomial: AIC = 1140, ΔAIC = 1 with the closest model also including the BCI, ED = 2%, $n = 850$, χ^2 test with null model, $p < 0.001$).

c) Return dates and first breeding attempts

Individuals from the 2009/2010 cohort had on average a longer post-fledging trip than birds of the 2007/2008 and 2008/2009 cohorts (984 ± 24 days *vs.* 854 ± 15 days and 825 ± 22 days, respectively; Wilcoxon rank-sum tests: $W = 3546$, $N_{2007/2008} = 174$, $N_{2009/2010} = 69$, $p < 0.001$, and $W = 2289$, $N_{2008/2009} = 106$, $N_{2009/2010} = 69$, $p < 0.001$, respectively). Moreover, the longer the birds stayed away from the colony before their first return, the earlier they came back in the season (Table VII - 5).

Table VII - 5. Mean annual return dates of juvenile Adélie penguins coming back for the first time to their natal colony at 2, 3, 4 and 5 years old.

Tableau VII – 5. Dates de retour annuelles moyennes des manchots Adélie juvéniles revenant pour la première fois à leur colonie natale à 2, 3, 4 et 5 ans.

Age (in years)	**2** ($N = 215$)	**3** ($N = 86$)	**4** ($N = 27$)	**5** ($N = 2$)
First return date	January 4th	December 25th	December 20th	December 23rd
[min – max]	[Dec. 6th – Feb. 12th]	[Nov. 7th – Jan. 31st]	[Nov. 9th – Feb. 7th]	[Nov. 19th – Jan. 26th]

We also observed that birds were coming back earlier in the season in subsequent years compared to the year of their first return (Fig. VII - 10). Interestingly, from 4 years old it appears that the distribution of arrival dates shifted to a bimodal distribution.

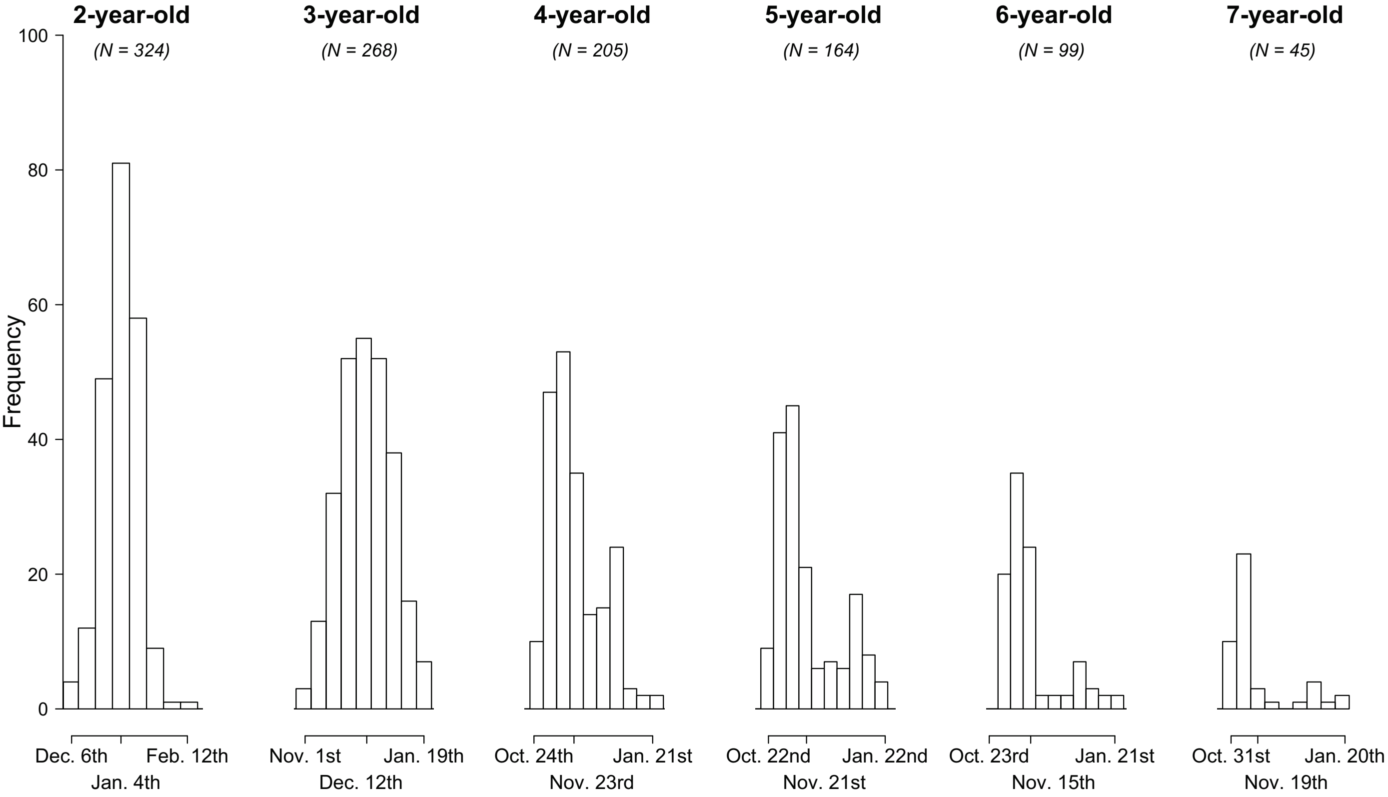

Figure VII - 10. Mean annual arrival dates of Adélie penguins at their first return at 2 years old and in the following years.

Figure VII – 10. Dates de retour annuelles moyennes des manchots Adélie à leur premier retour à 2 ans et dans les années suivantes.

We found that some individuals of each cohort that reached 4 years old started to reproduce between 3 and 4 years old in the *ANTAVIA Canyon* colony. For the two first cohorts that reached the age of 6 years old, more than 40% of the cohort have been seen breeding at least once in the *ANTAVIA Canyon* colony (Fig. VII - 11). The proportion of birds recruited within each age-class into the breeding population of the *ANTAVIA Canyon* colony seemed to vary between cohorts (Fig. VII - 11).

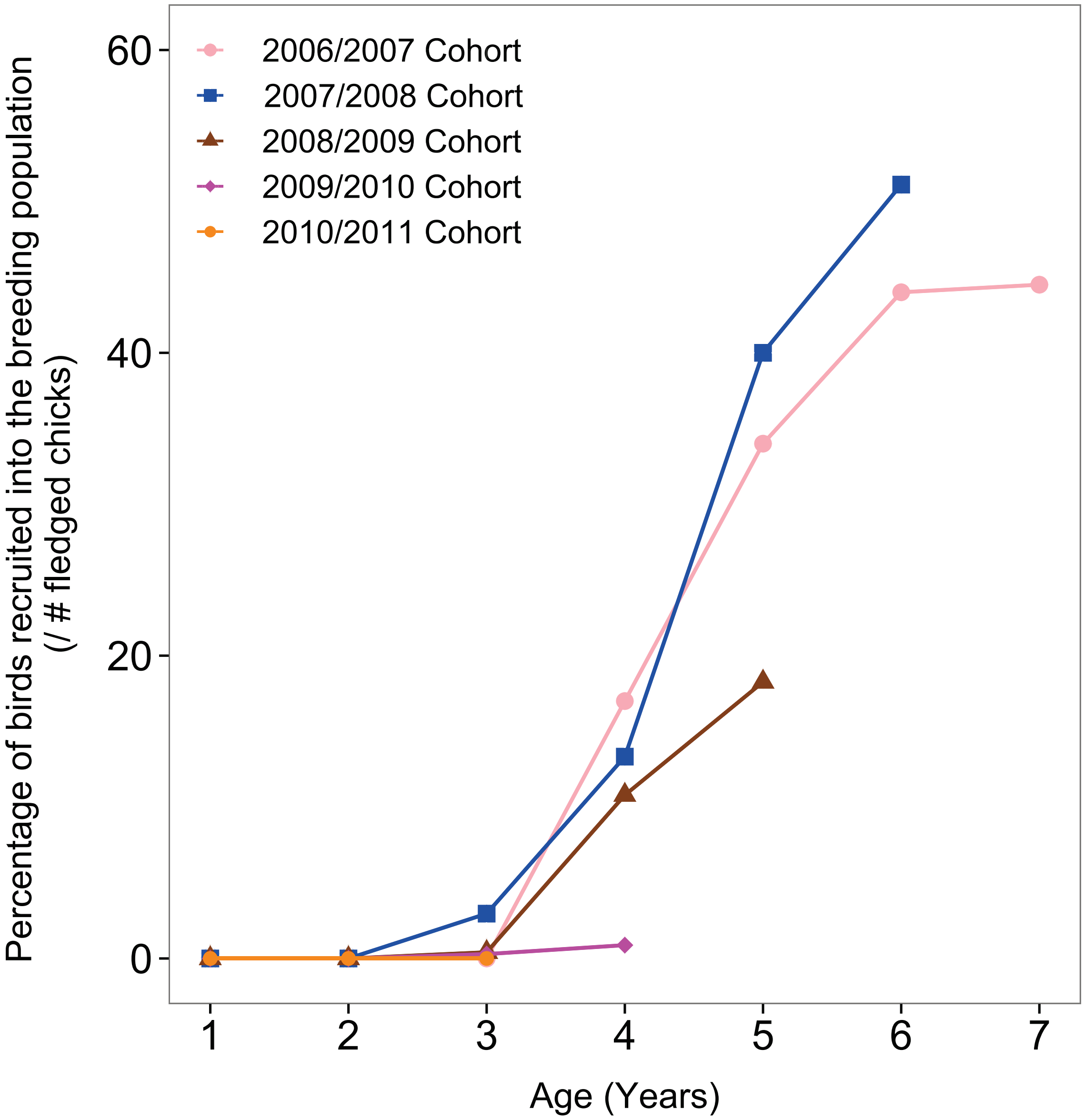

Figure VII - 11. Percentage of Adélie penguins recruited into the breeding population of the ANTAVIA Canyon colony according to age.

Figure VII – 11*. Pourcentage de manchots Adélie recrutés dans la population reproductrice de la colonie du Canyon ANTAVIA en fonction de leur âge.*

4 – Discussion

a) Return rates and age at first return to the natal colony

For the 4 first cohorts (*N* = 1046 individuals) monitored over 7 consecutive years, we found that 51% of fledged Adélie penguin chicks returned within 5 years, with a range of 20% to 73% depending on the cohort. This means that at least more than half of the fledged chicks of this colony of Pointe Géologie survived until 2 years old, in contrast with the estimation of a 0.263 probability of survival until the age of 2 obtained by Ainley (2002) for a non-banded population in Cape Crozier (77°31'S, 169°23'E). Moreover, we found that a higher proportion of birds came back at 2 years old (60%) *vs.* 3 years old (35%), while, in Cape Crozier, individuals came back mostly at the age of 3 (46%, Ainley, 2002). This variability observed between populations in terms of global return rate and patterns of returns can explain the different trends exhibited by Adélie penguin populations around Antarctica (see Forcada and Trathan, 2009). Furthermore, we also observed a high variability between cohorts in the return rates and the proportion of birds returning at the age of 2 and 3 that suggests a strong cohort effect in this population, and therefore highlight the importance of environmental conditions during the early life stages on this demographic parameter.

The Adélie penguin is considered as a highly philopatric species (Ainley, 2002; Dugger et al., 2006). For instance, in Cape Crozier, 96% of the individuals breed within the colony they were born, and up to 77% within an area of less than 200 m^2 around their natal site (Ainley, 2002). Emigration can therefore be considered as low in this species. Nonetheless, the *Antavia canyon* colony is a small colony (~ 300 breeding pairs, < 200 m^2) surrounded by many other close colonies settled in a relatively small archipelago, and dispersal between the colonies of the archipelago should not be neglected when interpreting the return rates of this colony.

b) Influence of environmental conditions on pre-fledging parameters

We observed a strong inter-annual variability in pre-fledging traits in this Adélie penguin colony that can be indirectly linked to the environmental conditions during the breeding season through parents' quality. Indeed, in a previous paper (Cornet et al. *in prep 4*), we found that the environmental variability affected the breeding phenology and success of Adélie penguins, and that only high quality individuals were able to cope with poor environmental conditions. For instance, during the austral summer 2011/2012, extensive sea-ice conditions during chick rearing negatively impacted the breeding success of the colony. Here, we also found that chicks from this cohort were smaller (lower structural size), suggesting that lower food availability may affect their growth. However, we also observed that these fledging chicks from the 2011/2012 cohort had a higher body condition than those of other cohorts. This can be explained by the fact that, during adverse environmental conditions, there should be a strong selection for higher quality individuals, with lower quality chicks being eliminated before fledging (Curio, 1983; Braasch et al., 2009). Another explanation could be that environmental conditions during crèching, for instance, might have become more favourable than they were during brooding, and that chicks were better fed then though still late in their growth. Moreover, we found that body condition had a smaller effect on fledging departure date compared to structural size, with smaller individuals leaving the colony later than larger-size fledglings. Strong effect of pre-fledging body condition and structural size on fledging date was found in other seabird species (Ydenberg et al., 1995; Saraux et al., 2011b). However, an opposite trend to what we observed in Adélie penguins was found in king penguins (Saraux et al., 2011b). King penguin chicks generally fast before fledging to attain an optimal weight. As smaller individuals display higher metabolic rates, their body reserves should deplete faster. Therefore, smaller-size king penguin chicks appeared to reach an optimal body mass sooner and leave the colony earlier than larger ones (Saraux et al., 2011b). On the other hand, in Adélie penguins, timing of reproduction is constrained by the timing of the sea-ice conditions, and the shorter favourable food availability time window associated with it (Ainley, 2002; Emmerson and Southwell, 2008). Chicks may therefore not need to fast before leaving the colony as overfeeding is less likely to happen (Ainley, 2002). The greater are their body reserves, the better are their chances to survive and to be able to forage for themselves later on (Ainley, 2002). Moreover, late hatching chicks have been observed to fledge younger than early hatching chicks (Ainley, 2002), probably to leave the colony before the reformation of the sea ice. Late hatching chicks might still depart a few days later than early hatching chicks, but since they had less time to grow, their structural size upon departure should be lower. This could explain why we observed smaller individuals fledging later than larger ones in this species. Along with this idea, in 2011/2012 breeding season, the timing of the reproduction (i.e. arrival and laying dates) was delayed in our colony because of the sea-ice conditions, and chicks fledged later though with a smaller structural size, suggesting that they may have left the colony younger.

c) Influence of pre-fledging parameters and post-fledging environmental conditions on return rates

We found that return rate at the colony was impacted by the pre-fledging body condition, with individuals in higher body condition having higher chances to return to their natal colony. A higher body condition at fledging means higher body reserves to face cold harsh winter environmental conditions. For instance, young individuals may rely on higher metabolic heat production for their thermoregulation (Whittow, 1987), and higher body reserves could help them sustain such metabolic heat production to face the cold winter temperatures. Furthermore, as we already saw, higher body condition enhances the ability of juvenile to forage for themselves (Ainley, 2002), which is also crucial in winter when food availability should be more scarce (Williams, 1991). In addition, fledglings with a higher body condition left the colony earlier than individuals with a lower body condition, which means they also had more time to improve their foraging skills and to increase their body reserves before winter (Marchetti and Price, 1989; Wunderle, 1991).

Moreover, environmental conditions after fledging showed to influence the return rate of a cohort. Colder environmental conditions around the colony (local scale) during the month following the fledging (i.e. March) influenced positively the return of juveniles to their natal colony. However, it is important to note that since the fourth cohort (austral summer 2009/2010), the return rate at age of 2 and 3 of juveniles is decreasing. This drop may be attributed to the calving of the Mertz glacier tongue in February 2010 that could strongly impact the oceanography of the region (Tamura et al., 2012; Dragon et al., 2014). Indeed, since the calving, a more extensive sea-ice cover is observed around Pointe Géologie archipelago, concomitant with a later sea-ice retreat compared to the years before 2009/2010. Although colder conditions positively affected the return rate, a too extensive sea-ice cover might also have detrimental effect on Adélie penguin survival (Emmerson and Southwell, 2011) by modifying the trophic web of the region and altering food availability, for instance (Clarke et al., 2002; Murphy et al., 2007; Ballerini et al., 2009). This is especially true for young inexperienced individuals (Ainley, 2002) and individuals in poor condition at fledging (Williams and Croxall, 1990). Thus, since the austral summer 2009/2010, fledging chicks probably face detrimental conditions during their first challenging years of life, resulting in a lower return rate compared to the previous cohorts despite an equivalent or higher body condition at fledging.

d) Age of recruitment

Pre-fledging parameters did not explain the proportion of individuals returning at 2, 3 and 4 years old. In contrast, we found that these proportions were explained by environmental conditions, with colder conditions during the first winter (i.e. April-September) leading to a later age at first return. Moreover, we observed that Adélie penguins returning for the first time to their natal colony at an older age also arrived earlier within the breeding season. After their first return, individuals arrived progressively earlier in each subsequent season. Consequently, the earliest birds arrived at the colony early enough to be able to attempt to reproduce from the age of 3. Indeed, the first breeding attempts were observed at 3 years old in our colony. Furthermore, by the age of 6 years old, the majority of the individuals of a cohort arrived early enough in the season to breed. This result was confirmed by the high proportion of birds that already attempted to breed by the age of 6 years old. Individuals starting to breed one or more years after the onset of sexual maturity (i.e. 3 years old in this species) might benefit from a higher survival by avoiding the higher costs of a first breeding attempt while gaining additional experiences at different tasks, such as foraging abilities or predator avoidance. (king penguins, Stonehouse, 1960; black-legged kittiwakes *Rissa Tridactyla*, Wooller and Coulson, 1977; northern fulmars *Fulmarus glacialis*, Ollason and Dunnet, 1978). Foraging efficiency is an important factor affecting survival but also reproductive output (Clarke et al., 2002; Lescroël et al., 2010). By spending more time at sea before starting to breed, individuals may also secure their foraging skills necessary to ensure successful reproduction (Ainley, 2002). Birds returning for the first time at the colony at a younger age might also benefit from learning mating routines and acquiring information on nest site quality before they start to breed (Barrat, 1976). Ainley (2002) observed that Adélie penguins that started to breed earlier had a higher mortality probability, but also a higher number of breeding attempts and a higher number of successful breeding events compared to birds that started to breed later. Interestingly, Ainley (2002) noted that these differences in life-history strategies seemed to be sex specific as he also observed that females tended to reproduce earlier than males and to have a higher fecundity. Consequently, the variability between cohorts in the proportion of birds returning for the first time at a given age and in age at first breeding attempts could reflect the variability of life-history strategies adopted by the different cohorts according the environmental conditions they encountered in their early life.

e) Conclusion

Our results highlight the complex impact of environmental conditions on different sensitive stages of the life cycle in Adélie penguins. As we saw, return rate measured in this study did not reflect only survival, as dispersal in the archipelago is also likely. However, dispersal at the archipelago scale would be more likely triggered by the colony reaching its nesting carrying capacity (Kokko et al., 2004), rather than triggered by environmental conditions that should no vary much at this small spatial scale. Furthermore, even if considered low for this species, emigration to more distant colonies should not be neglected either. Indeed, emigration to further colonies could be triggered by poor environmental conditions through lower breeding success for instance (Boulinier et al., 2008). It would reflect the capacity of individuals to seek elsewhere for more favourable conditions, and thus have implications for the persistence of this population (Taylor, 1990; Berg et al., 2010). Next step would therefore be to investigate the rate of dispersal within this archipelago, and the rate of emigration to further colonies such as the Port Martin colony (66°49'S, 141°24'E), by placing portable antennas around different colonies of the archipelago and of the region. The knowledge of these rates and of the influence of environmental conditions on these rates would help us to better unravel the adaptive potential of this population to face environmental conditions.

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ABSTRACT

The adaptive capacities of seabirds to face environmental variability: the role of heterogeneity within populations.

Cindy Cornet – LIA 'BioSensib' (CNRS-CSM). Under the supervision of Yvon Le Maho and Céline Le Bohec

Population dynamics is driven by several life history traits shaped by population evolutionary history (age-specific survival and/or breeding success, age at maturity, etc.) under environmental constraints. The alteration, direct or indirect, of one of these traits by environmental constraints, through the regulation of resources available for organisms (food and/or habitat), may thus have effects on population persistence (Lack and Gillmor, 1966; Stearns, 1992; Sæther, 1997). However, individual adjustments of some phenotypic traits (behavioural, physiological and morphological) in response to the environment could enable a whole population to track a rapidly changing environment very closely, without the immediate necessity of genetic adaptations (Railsback, 2001; Nussey et al., 2007; Ozgul et al., 2009; Tuljapurkar et al., 2009). In the context of rapid environmental changes, it is therefore important to study the underlying mechanisms of these adjustments, and to do so at both intra- and inter-individual levels.

Until recently, personality or temperament traits in animals have only received little attention mainly because of a lack of framework and a perceived irrelevance, but also because of the difficulty to study them on the field and from an objective point of view (reviewed inRéale et al., 2007). But thanks to a growing interest in those traits, personality has been shown to be common in a wide range of species (e.g. Réale et al., 2000; Martin and Réale, 2008; Michelena et al., 2010; Briffa and Greenaway, 2011; Pinter-Wollman et al., 2012; Twiss et al., 2012), and to have potential implications on how animals respond to ecological and environmental challenges (e.g. Sih et al., 2004; Réale et al., 2007; Biro et al., 2010). Contrary to what has been traditionally hypothesized, behaviour is not fully plastic and animals often exhibit consistent behavioural patterns across time and/or situations (within and between behavioural contexts) which is called personality or temperament (Réale et al., 2007) or behavioural syndrome when these personality or temperament traits are correlated (Sih et al., 2004; Sih et al., 2004). Personality is thus reflected in the behaviour of an animal but also in its ecology (habitat use, interactions with conspecifics, willingness to take risks and to explore new environments for instance) and thus has an impact on the fitness of an individual through its survival and reproduction (Boon et al., 2008; Smith and Blumstein, 2008; Kontiainen et al., 2009; Dammhahn and Almeling, 2012). Moreover, while personality traits are partially genetically determined (Bakker, 1986; Henderson, 1986; Henderson, 1990; Plomin and Caspi, 1999; Fairbanks et al., 2004), they also have a relatively moderate heritability (Drent et al., 2003; van Oers et al., 2004) and are thus likely to be impacted by non-genetic factors such as the environment. They fall therefore into the pool of phenotypic traits that can enable individuals but also populations to cope with changing environmental conditions.

As marine predators at the apex of the trophic web, seabirds integrate and magnify the ecological processes occurring throughout this web, making them good sentinels for the future of their ecosystems (Piatt et al., 2007; Parsons et al., 2008; Grémillet and Charmantier, 2010). Moreover, the pace of changes in polar ecosystems is even greater than for other ecosystems (Clarke and Harris, 2003; IPCC, 2007; Hoegh-Guldberg and Bruno, 2010), and many species of these ecosystems have already been shown to be particularly sensitive to on-going changes (Croxall et al., 2002; Gaston et al., 2005; Irons et al., 2008; Gaston et al., 2009). In addition, despite their importance in evolutionary ecology and their implications in the

adaptive capacities of individuals and populations to adjust to environmental variability, only a few studies sought to identify personality traits in the wild so far (Boon et al., 2008; Kontiainen et al., 2009; Dammhahn, 2012; Dammhahn and Almeling, 2012), and such studies on polar species are even more scarce if not non-existent (to our knowledge only four papers to date: Kazama and Watanuki, 2010; Kazama et al., 2012; Patrick et al., 2013; Patrick and Weimerskirch, 2014). Moreover, while captivity experiments are good tools to study some underlying mechanisms, they probably don't match the behavioural responses of the individuals in their natural environment (Réale et al., 2007; Archard and Braithwaite, 2010). My PhD project was therefore focused on wild populations of 3 species from fragile polar ecosystems: the Adélie penguin *Pygoscelis adeliae* from the Pointe Géologie Archipelago (Adélie Land, Antarctica), the king penguin *Aptenodytes patagonicus* from the Crozet Archipelago (sub-Antarctic region), and the Brünnich's guillemot *Uria lomvia* from the Svalbard Archipelago (Arctic). . My PhD project aimed at a better understanding of how adjustments of individual phenotypic traits can enable wild animal populations to cope with environmental constraints, which is crucial to gauge their adaptive potential to face future ecosystem changes.

In this context, I first evaluated on these three species the intra- and inter- individual differences in personality traits such as activity, aggressiveness, boldness and exploration as defined by Réale et al. (2007) through tests and focal observation in natural environment, as well as the correlation of these traits into behavioural syndromes in order to assess the constraints and independence among them. I also evaluated potential relationships between personality traits and behavioural syndromes and individual characteristics such as sex, morphological and physiological parameters, and other behavioural traits (e.g. parental guarding and provisioning behaviours). Finally, I investigated whether and how the quality of the breeding habitat (local weather and nest characteristics) is related to individual personality and fitness. Then, I investigated the inter-annual variability of several phenotypic traits of unbanded Adélie penguins, and explored their dependence on environmental stochasticity (and its associated consequences on food availability). I investigated the inter-annual variability in the survival rates and the return of juvenile Adélie penguins (ca. 1650 individuals marked as chicks) to their natal colony, but also the plasticity and flexibility in some traits, such as the annual arrival dates at the colony for reproduction or the laying dates (ca. 180 individuals marked as adults) that lead to different breeding outcomes. I also examined how environmental conditions and individual characteristics (i.e. sex, body condition, and structural size), might affect these parameters.

In the framework of life-history theory, this PhD project identified variability in some phenotypic and life-history traits in these three long-lived species. These results allowed us to better understand the associations between these life-history traits and the evolutionary pressures underlying these associations. They also highlight the importance of phenotypic traits such as personality traits in the amount of variability in individuals' fitness that remains unexplained. The integration of these parameters in population models coupled with climatic model projections from the IPCC experts should then allow us to better gauge the adaptive capacity of individuals and their population to face the variability of their environment.

RESUME

Les capacités d’adaptation des oiseaux marins face aux changements environnementaux : le rôle de l’hétérogénéité au sein des populations.

Cindy Cornet – LIA ‘BioSensib’ (CNRS-CSM). Sous la supervision de Yvon Le Maho et Céline Le Bohec

La dynamique d’une population est le résultat de la combinaison de plusieurs traits d’histoire de vie (traits qui sont façonnés par l’histoire évolutive de la population, tels que la survie et le succès reproducteur âge-spécifique, l’âge à la maturité, etc.) soumis à des contraintes environnementales variables. L’altération de l’un de ces traits par des pressions environnementales affectant les ressources disponibles pour les organismes (alimentaires et/ou habitat), peut donc avoir des effets sur la persistance de la population (Stearns, 1992). Cependant, les ajustements individuels de certains traits phénotypiques (comportementaux, physiologiques et morphologiques) pourraient permettre à une population de répondre rapidement aux modifications de son environnement, sans la nécessité immédiate d’adaptations génétiques (Nussey et al., 2007 ; Ozgul et al., 2009). Dans le contexte de changements environnementaux rapides, il est donc important d’étudier les mécanismes sous-jacents de ces ajustements, et ce aussi bien à l’échelle intra- que inter-individuelle.

Jusqu’à récemment, les traits de personnalité (ou de tempérament) chez les animaux n’ont reçu que peu d’attention. En effet, le cadre théorique est quasiment inexistant du fait d’un manque supposé de pertinence de ces traits en écologie et de la difficulté de les étudier en environnement naturel et d’un point de vue objectif (revu dans Réale et al., 2007). Cependant, grâce à un intérêt croissant pour ces traits, il a été montré que la personnalité était commune chez un grand nombre d’espèces (e.g. Martin and Réale, 2008 ; Briffa and Greenaway, 2011 ; Pinter-Wollman et al., 2012), et qu’elle avait de potentielles implications sur la façon dont les animaux répondent aux défis écologiques et environnementaux (e.g. Sih et al., 2004 ; Réale et al., 2007). Contrairement aux hypothèses traditionnellement émises, le comportement n’est pas complétement plastique. Les animaux montrent souvent des schémas comportementaux constants à travers le temps et/ou les situations (au sein de et entre les contextes comportementaux) ce qu’on appelle donc personnalité (Réale et al., 2007) ou syndromes comportementaux lorsque ces traits de personnalité sont corrélés (Sih et al., 2004). La personnalité se reflète ainsi dans le comportement d’un animal, mais aussi dans son écologie (utilisation de l’habitat, interactions avec les congénères, décision de prendre des risques ou d’explorer de nouveaux environnements par exemple), et peut donc avoir un impact sur la valeur sélective d’un individu à travers sa survie et sa reproduction (Boon et al., 2008 ; Smith and Blumstein, 2008 ; Kontiainen et al., 2009). De plus, alors que les traits de personnalité sont partiellement génétiquement déterminés (Plomin and Caspi, 1999 ; Fairbanks et al., 2004), ils ont également une héritabilité relativement modérée (Drent et al., 2003 ; van Oers et al., 2004) et sont donc susceptibles d’être impactés par des facteurs non génétiques tel que l’environnement. Ils tombent ainsi dans le lot de traits phénotypiques qui peuvent permettre aux individus et aux populations de faire face à des conditions environnementales changeantes.

En tant que prédateurs marins au sommet du réseau trophique, les oiseaux marins intègrent les conséquences des modifications affectant ce réseau, ce qui en fait de bonnes sentinelles de leurs écosystèmes (Parsons et al., 2008 ; Grémillet and Charmantier, 2010). De plus, la vitesse des changements observés actuellement dans les écosystèmes polaires semble plus importante que dans les autres écosystèmes (Clarke and Harris, 2003 ; IPCC, 2007 ; Hoegh-Guldberg and Bruno, 2010), et il a déjà été montré que de nombreuses espèces polaires sont particulièrement sensibles à ces changements (Croxall et al., 2002 ; Gaston et al., 2009). Cependant, et malgré leur importance en écologie évolutive et leurs implications dans le potentiel d'adaptation des individus et des populations à s'ajuster aux variations de leur environnement, peu d'études se sont intéressées jusqu'à présent aux traits de personnalité chez des populations dans leur milieu naturel, et de telles études sur des espèces polaires sont encore plus rares si ce n'est inexistantes (à notre connaissance seulement 4 articles parus à ce jour : Kazama and Watanuki, 2010 ; Kazama et al., 2012 ; Patrick et al., 2013 ; Patrick and Weimerskirch, 2014). De même, alors que les expériences en captivité sont de bons outils pour étudier certains mécanismes, les réponses comportementales des individus sont très certainement différentes de celles qu'ils exprimeraient dans leur environnement naturel (Réale et al., 2007 ; Archard and Braithwaite, 2010). Dans le cadre de mon projet de thèse, je me suis donc intéressée à trois populations d'oiseaux marins vivant au sein de ces écosystèmes polaires fragiles : le manchot Adélie *Pygoscelis adeliae* de l'archipel de Pointe Géologie (Terre Adélie, Antarctique), le manchot royal *Aptenodytes patagonicus* de l'archipel de Crozet (région subantarctique), et le guillemot de Brünnich *Uria lomvia* de l'archipel du Svalbard (Arctique). L'objectif principal de mon projet de thèse était de mieux comprendre comment les ajustements individuels de certains traits phénotypiques peuvent permettre à des populations animales sauvages de faire face aux contraintes environnementales, ce qui est crucial pour estimer leur potentiel d'adaptation face aux futurs changements de leurs écosystèmes.

Dans ce contexte, j'ai dans un premier temps évalué chez les trois espèces les différences intra- et inter-individuelles dans les traits de personnalité que sont l'activité, l'agressivité, la témérité et l'exploration tels que définis par Réale et al. (2007) à l'aide de tests et de focales d'observation en environnement naturel. La corrélation de ces traits en syndromes comportementaux a été déterminée dans le but d'évaluer les contraintes et interdépendance parmi eux. J'ai alors exploré les relations potentielles entre traits de personnalité et syndromes comportementaux et caractéristiques individuelles (e.g. sexe, paramètres morphologiques et physiologiques), et d'autres traits comportementaux (e.g. comportements de garde et d'approvisionnement du poussin). Finalement, j'ai examiné si et comment la qualité de l'habitat de reproduction (conditions météorologiques locales et caractéristiques du nid) était liée à la personnalité et pouvait affecter la valeur sélective des individus. Dans un deuxième temps, j'ai cherché à évaluer la variabilité interannuelle de plusieurs traits phénotypiques chez des manchots Adélies non bagués, et leur lien avec les variations environnementales (i.e. leurs conséquences sur la disponibilité des ressources alimentaires). J'ai notamment cherché à déterminer la variabilité interannuelle du taux de retour des juvéniles dans leur colonie de naissance et de leur taux de survie (environ 1650 individus marqués poussins à l'aide de puces électroniques et suivis grâce à un système automatisé), ainsi que la plasticité et la flexibilité de certains traits tels que la date d'arrivée annuelle à la colonie pour la reproduction ou la date de ponte (environ 180 individus adultes marqués électroniquement) qui peuvent affecter l'issue de la reproduction. J'ai ensuite recherché à savoir si les conditions environnementales et les caractéristiques individuelles (i.e. sexe, condition corporelle et taille structurelle) pouvaient expliquer la variabilité de ces paramètres.

Cette thèse, qui se place dans le contexte de la théorie d'histoire de vie, a donc permis d'identifier la variabilité de certains traits phénotypiques et d'histoire de vie chez ces trois espèces longévives. Ces résultats permettent de mieux comprendre les associations entre ces traits d'histoire de vie et les pressions évolutives à l'origine de ces associations. Ils soulignent également l'importance de traits phénotypiques tels que la personnalité dans la part inexpliquée de la variabilité de la valeur sélective des individus. L'intégration dans des modèles populationnels de l'ensemble de ces paramètres couplés aux modèles climatiques projetés par le GIEC devrait permettre à terme de mieux évaluer la capacité d'adaptation des individus et de leur population à faire face à la variabilité de leur environnement.

Cindy CORNET

Les capacités d'adaptation des oiseaux marins face aux changements environnementaux : le rôle de l'hétérogénéité au sein des populations.

Résumé

La dynamique d'une population résulte de la combinaison de plusieurs traits d'histoire de vie qui sont façonnés par l'histoire évolutive de cette population. L'altération d'un de ces traits par des contraintes environnementales peut donc avoir des effets sur la persistance de la population. Les ajustements individuels de certains traits phénotypiques pourraient permettre à cette population de répondre rapidement à ces contraintes sans la nécessité immédiate d'adaptations génétiques. Durant cette thèse, la variabilité de certains traits a été identifiée chez 3 espèces sentinelles des écosystèmes polaires. Ces résultats permettent de mieux comprendre les associations entre ces traits et les pressions évolutives qui en sont à l'origine, ainsi que l'importance de traits tels que la personnalité dans la part inexpliquée de la variabilité de la valeur sélective des individus. A terme, nous pourrions ainsi mieux évaluer la capacité d'adaptation des populations face aux changements globaux.

Mots-clés : *hétérogénéité ; personnalité animale ; plasticité phénotypique ; écologie comportementale ; oiseaux marins; variabilité environnementale ; théorie d'histoire de vie.*

Résumé en anglais

Population dynamics is driven by several life history traits shaped by the evolutionary history of the population. The alteration of one of these traits by environmental constraints may thus have effects on the population persistence. Individual adjustments of some phenotypic traits could then enable this population to rapidly respond to these constraints without the immediate necessity of genetic adaptations. During this PhD project, we identified variability in some of these traits in 3 sentinel species of polar ecosystems. These results allowed us to better understand the associations between these traits and the evolutionary pressures underlying these associations, as well as the importance of traits such as personality in the amount of variability in individuals' fitness that remains unexplained. In the long term, we should then be able to better gauge the adaptive capacity of populations to face global changes.

Key-words: *heterogeneity; animal personality; phenotypic plasticity; behavioural ecology; seabirds; environmental variability; life-history theory.*