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Titre : *Influence du recrutement sur les variations des paramètres démographiques avec l'âge et la vitesse de sénescence chez la mouette tridactyle, Rissa tridactyla*

JURY
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Unité de recherche : *Laboratoire Evolution et Diversité Biologique*
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En Collaboration avec : *Max Planck Institute for Demographic Research, Allemagne*

UNIVERSITÉ PAUL SABATIER

THÈSE DE DOCTORAT DE L'UNIVERSITE TOULOUSE III

Spécialité: Écologie

Présentée par Lise Myriam AUBRY

Pour obtenir le titre de docteur de l'Université Toulouse III

Thèse dirigée par : Prof. Emmanuelle CAM

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Soutenue à Toulouse, le 29 juin 2009, devant un jury composé de :
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Influence of Recruitment on Age-specific Demography and Senescence in a long-lived Seabird, the black-legged Kittiwake, *Rissa tridactyla*

Picture: Lise M. Aubry

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*

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Quel gentleman.

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GENERAL INTRODUCTION

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~ GENERAL INTRODUCTION ~

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"…The tree, the fish, the fly, and the albatross all survived and reproduced. Through their diverse life histories run traces of a general pattern created by a common mechanism that expresses the relationship of age and size to mortality and reproductive performance. To analyze the phenotypic variation that produces selection, the expression of genetic variation that enables a response to selection, and the lineage-specific constraints which selection interacts to produce the observed diversity of life histories is the goal of work on life history evolution" (Stearns 1992).

~

Life history evolution

Evolutionary ecologists are interested in studying the major events that individuals experience in their lifetime. Such events can be demographic (e.g., age at first reproduction, age-specific fertility and survival), physiological (e.g., duration of gestation), and even behavioral (e.g., mate choice), and are referred to as life history traits (Roff 1992). They are either unique or repeated events over the life schedule of each individual, and are the key components of fitness upon which natural selection acts (Stearns 1992). The wide variability within and across life history traits, and the way they combine to define a unique life history, ultimately reflects the diversity of life on earth, and justifies in itself why life history theory has been greatly studied in the last century by behavioral ecologists (Krebs and Davies 1978), evolutionary physiologists (for review see Zera and Harshman 2001), and even anthropologists (e.g., Kaplan 2003).

Trade-offs: the cost of reproduction revisited

Life history traits mainly relate to growth, survival, and reproduction, the main components of fitness. And as there is no such thing as a 'Darwinian demon' (Law 1979), organisms cannot optimize growth, reproduction, and survival simultaneously; they have to make choices and allocate their time and energy (from the resources they acquire) between these fitness components. Such choices are recognized as trade-offs, and are central to life history evolution (Williams 1966). One particular trade-off that has received the most attention in the last decades is the classic ‘cost of reproduction’ (Roff 1992, Stearns 1992). According to ‘the principle of allocation’ (Levins 1968), this trade-off stands for the compromises individuals face by allocating resources towards current reproduction at the expense of future reproduction and (or) survival.

Williams (1966) originally stated that any reproductive investment in a given reproductive episode would decrease “residual reproductive value” (RRV). Reproductive value is the lifetime expectation of reproductive output, a value that combines age-specific fecundity and survival rates (Fisher 1930), and can be broken down into the sum of current breeding value and expected future value (i.e., RRV; Williams, 1966b). Thus, Williams predicted a negative correlation between the intensity of the current reproductive effort and RRV, suggesting that there is a somatic cost to current reproductive investment that inevitably associates with lower reproductive capacity in the future.

More recently, evolutionary ecologists have distinguished between two types of reproductive costs, whereby individuals that increase current reproductive effort will pay a cost either to future reproduction or (and) to future survival (e.g., at the next breeding episode, or in the next season). The most extreme example of the latter trade-off resides in the difference between iteroparous and semelparous organisms (Cole 1954). Iteroparous organisms experience repeated reproductive events during their life course, whereas semelparous organisms only have one opportunity to reproduce and then die. Even though a large body of empirical (e.g., in plants, Metcalf et al. 2003; in reptiles, Bonnet et al. 2003, in fish, Waples 2002; in mammals, Cockbrun and Lazenbycohen 1992) and theoretical work (e.g., Gadgil and Bossert 1970, Takada 1995, Crespi and Roy 2002) has helped us better understand why some organisms would evolve towards semelparity, the selective forces responsible for such an evolutionary transition deserves further study.

Even while considering less extreme cases of reproductive trade-offs, the cost of reproduction amongst iteroparous organisms has received equivocal support. This specific trade-off has largely been investigated via experimental approaches (Linden and Møller 1989), some of which have been criticized (Reznick 1990). Phenotypic manipulation is one type of experimental procedure that has successfully detected reproductive costs in natura (e.g., Gustaffson and Sutherland 1988, Nur 1988). Experimental manipulation studies on birds often increase the number of young before (eggs) or after (chicks) hatching, thus increasing the demand for parental care, and then measure the impact of clutch or brood size manipulation on the parent's survival and reproductive success (or any other fitness component). Results from such studies indicate that there are a variety of short-term costs to the incubating parents and the offspring (Hanssen et al. 2005). Increased physical demand on the parent from increased incubation effort could also lead to delayed reproductive costs such as lower adult survival or reduced future fecundity. Some studies have detected reduced adult survival or reduced future fecundity, but the majority failed to detect such costs (e.g., Dijkstra et al. 1990; Roff 1992; Stearns 1992; Golet et al. 1998). Hanssen et al. (2005) noted that only one study of 'incubation cost' found strong evidence for reduced survival (Visser & Lessells 2001). A cost to offspring condition has been documented in collared flycatchers (Cichón 2000), but no study ever reported a cost of incubation to future fecundity of the parent 'in charge' (e.g., in the blue tit, Pettifor 1993).

Most studies on the regulation of parental effort have been carried out on short-lived passerines. In such short-lived birds, the probability of surviving a reproductive season is so low that an increased investment in current reproduction would be expected regardless of the associated survival costs (Charlesworth 1980). Charlesworth (1980), Curio (1988), and Wooler (1992) all expected long-lived species such as seabirds to limit investment in their offspring because even a small increase in parental investment would lead to a small reduction in future survival, which would in turn reduce lifetime reproductive success (Clutton-Brock 1988). Thus, they suggested that parental effort was approximately fixed in these species, regardless of offspring requirements (Ricklefs 1992). This has been supported by studies on the Leach's Storm-Petrel *Oceanodroma leucorhoa* (Ricklefs and Minot 1991, Hamer and Hill 1994), and the Antarctic Petrel *Thalassoica antartica* (Andersen et al. 1995).

On the other hand, recent studies on geese and other long-lived seabirds that manipulated clutch size have observed increased reproductive effort (Jacobsen et al. 1995, Tombre and Erikstad 1996, Erikstad et al. 1997), even at the expense of parental survival (Reid 1987, Jacobson et al. 1995). In contrast, in a non-experimental study, Cam et al. (2002a) found a positive correlation between reproduction and survival from one year to the next in the long-lived Black-legged kittiwake, suggesting that immediate costs of reproduction are not operating in this population.

They may be two explanations to the lack of detection of short-term costs of reproduction to future fertility or survival in wild populations. i) Heterogeneity in individual quality: individuals differ in their ability to survive and reproduce, but these differences can not always be observed at the population levels if the selective disappearance of 'lower quality individuals' (i.e., individuals that are 'frail' and have a lower chance of surviving for example) is not accounted for (e.g. Vaupel et al. 1979). This phenomenon might lead to erroneous estimates of survival and fertility across ages, often resulting in improved reproductive and survival estimates with age, with thus potential to mask short term reproductive costs (see 'Sources of variability in life history traits' section below). ii) The idea that reproductive costs could be paid much later in life (i.e., delayed cost of reproduction). For example, could early investment (e.g., early recruitment, increased breeding success early in life) be associated with a faster or earlier onset of senescence in reproduction, survival, or both? The latter question has been at the heart of the debate dividing theories of ageing for almost a century.

Senescence theory and reproductive costs

Fisher, Wright, and Haldane's legacy of the modern synthesis in genetics and evolution (Fisher 1930, Wright 1931, Haldane 1941) led to the formulation of two non-exclusive theories of senescence well-known as mutation accumulation ('MA'; Medawar 1952), and antagonistic pleiotropy ('AP'; Williams 1957, refined by Hamilton 1966). These theories have received equivocal support under experimental settings (for review see Monaghan et al. 2008), and can only be distinguished as follows: an increase in additive genetic variance with age may occur under both MA and AP (Charlesworth and Hugues 1996), but only under AP do such mechanisms lead to negative genetic correlations between early- and late-life fitness (Rose 1991, Charlesworth 2000).

Our understanding of how rates of ageing have been shaped by evolutionary forces has greatly improved in the last few decades, especially through the study of laboratory systems such as fruit flies, *Drosophila melanogaster* (Promislow et al. 1996); nematodes, *C. Elegans* (Al-Regaiey et al. 2005); and mice, *Mus musculus* (Lund et al. 2002). By controlling for within-population genetic variation, studies on clonal organisms (e.g., *Daphnia pulex*) have the advantage of exploring plasticity in ageing rates within a controlled range of environments (Dudycha 2003). Thus, important insights into some of the molecular, genetic, and environmental mechanisms that govern rates of ageing have been gained through studies of model organisms under controlled laboratory settings (Kirkwood and Austad 2000, Bonsall 2006). Nevertheless, we do not know if knowledge gained from these studies can be extrapolated to other species (e.g., long-lived vertebrates) and to the natural and variable environmental circumstances that wild organisms must cope with (Nussey et al. 2008).

Evolutionary ecologists studying wild populations have developed statistical models that address the (negative) correlation between early-life and late-life reproduction. Charmantier et al. (2006) found that both age at first and last reproduction in mute swans *Cygnus olor* displayed heritable variation and were under opposing directional selection, suggesting that their evolution is constrained by a strong genetic tradeoff, which is consistent with AP. In red deer *Cervus elaphus,* Nussey et al. (2006) found that females producing more offspring early in life displayed faster senescence rates, thus depicting another trade-off in support of AP in the wild. However, antagonistic trade-offs such as these are not always observed. Environmental effects can induce positive covariance between traits, and mask expected phenotypic expression (i.e., trade-off between early-life and late-life reproduction), even when AP is the genetic mechanism in action (van Noordwijk and De Jong 1986, Wilson et al. 2008). Furthermore, selection on the genetic mechanisms shaping ageing rates can change across environments; for example, when resources are scarce (van Noordwijk and De Jong 1986), when predator concentration increases, or when any other kind of stress is induced (Mangel 2008, Münch et al. 2008, reviewed in Charlesworth and Hughes 1996).

Even though genetically-based studies designed to disentangle environmental from genetic drivers of senescence are greatly needed to push further the debate on ageing across the tree of life, longitudinal studies focusing on senescence patterns experienced by wild organisms are also lacking, as very little is known about senescence *in natura* (Monaghan et al. 2008).

The case of the black-legged kittiwake

Until recently, two main limitations have prevented evolutionary ecologists from studying the evolution of senescence in the wild from a demographic angle. First, adverse conditions and high levels of extrinsic mortality do not allow the large majority of individuals in wild populations to reach senescent ages because most die as juveniles or as young adults (e.g., Ricklefs and Scheuerlein 2001). Second, few studies monitor populations over a long enough period of time for senescence to be detected (but see e.g., in mammals: Nussey et al. 2007; in birds: Cam et al. 2002b, Charmantier et al. 2006; in fish: Reznick et al. 2004), especially in long-lived organisms.

A detailed longitudinal study

Colonies of black-legged kittiwakes (*Rissa tridactyla*, a cliff-nesting seabird) located in Brittany (France) and followed since 1979 offer a great opportunity to address these issues with known life histories for thousands of individuals through mark-recapture techniques (Monnat et al. 1990, Cam et al. 1998, 2000a, 2003, 2005). Breeding events, presence, demographic (e.g., age-specific survival and fertility), behavioral (e.g., courting behavior, formation of breeding pairs), and spatial environmental variables (e.g., nest and cliff location) are recorded every year.

Six colonies located in the Cap Sizun, a few kilometers apart (maximum of 12 Km), are monitored extensively through each breeding season, such that all breeding events are monitored, and presence in the colonies is recorded from January to September, with a peak of field effort from May to the beginning of September. This allows for the identification of the very first reproductive event for each individual returning to the study area. The age of most individuals is known, and each individual's presence is recorded as well as demographic and behavioral information at each resighting occasion. The fieldwork covers each breeding season in its entirety such that the observers do not miss a single reproductive event. Hence, this is a superb dataset to examine delayed costs of reproduction.

Sources of variability in life history traits

In populations of the black-legged kittiwake, as well as in any other population, variability in life-history traits can be observed across individuals and even within individuals over their life course. 'Between individual variability' (e.g. Chesson 1991) can be defined as the diversity of phenotypes within a population. Individuals can differ in their phenotypes even if they possess the same genotype via environmental influences (i.e., phenotypic plasticity). Moreover, individuals can exhibit very different lives because of differences in their ability to collect resources, find a mate, find suitable habitat for reproduction, and maintain their condition while investing in the previously mentioned activities, which ultimately results in fitness differences across individuals (Stearns 1992). ‘within-individual variability’ can change by the hour (e.g., deciding to go find food), the day (e.g., deciding to hide from predators), across seasons (e.g., deciding to migrate), or ages (e.g., deciding to breed), and can be beneficial, costly, or sometimes even lethal. Within-individuals variability is very difficult to measure empirically as it first requires very detailed longitudinal information (both demographic and behavioral) with near-perfect knowledge of the system, as one needs to assess which are the main drivers of within-individual variability.

From a theoretical angle, between-individual variability, defined as “heterogeneity in the endowment for longevity across individuals” by Vaupel and colleagues (1979, 1985), corresponds to differences among individuals whose cause is unknown. In the earliest views of frailty (Vaupel and colleagues 1979, 1985), the differences among individuals were considered as fixed (e.g., at birth or at the onset of reproductive life). Such heterogeneity can result in the selective disappearance of ‘frail’ phenotypes over ages, ultimately leading to erroneous estimates of survival and reproduction that do not reflect the age-specific changes in these fitness components expressed during the individual’s life. To disentangle the genuine pattern of age-specific variation in survival or reproduction during the individual’s life, and the pattern observed at the population level (or sample) when heterogeneity is ignored, statistical models accounting for unobserved (i.e., ‘frailty’) and observed heterogeneity (i.e., observable covariates such as quality of parental care) have been developed. A substantial amount of unobserved heterogeneity has been detected in the studied kittiwake population (Cam et al. 2002b), and thus should systematically be accounted for while estimating reproductive and survival trajectories, especially when addressing hypotheses about senescence.

In addition to intrinsic sources of variability in life history traits such as age-specific reproduction or survival, extrinsic or environmental variability can also have a strong influence on between and within individual variability. Environmental variability in both space and time (e.g., changes in resource availability, in habitat quality, in climate, in local predator concentration) are likely to influence the behavior, physiology, and demography of a given individual within a population, as each individual will have a specific ability to track these changes, and cope with them. In kittiwakes, substantial amounts of individual (between and within) and environmental variability in demographic processes have been documented (e.g., Cam et al. 1998). However, the relative influence of these sources of variation on rates of senescence is not well known in kittiwakes, nor in other wild species.

Objectives of the dissertation

My dissertation focuses on the evolutionary processes shaping age-specific demographic rates, with a particular emphasis on rates of aging. I am interested in the evolution of trade-offs (or lack thereof) between early-life breeding decisions, future reproduction, and survival chances in a long-lived seabird, the black-legged kittiwake.

Chapter I.

Before addressing any long-term reproductive trade-offs, I dedicated the first chapter to the earliest breeding decision, which is the age at which reproduction begins. In black-legged kittiwakes, the *sinequanon* condition to commence reproduction is to hold a nest-site on a reproductive cliff. Thus, recruitment age and habitat selection could be intimately linked.

In situations where habitat quality varies over space and time, where habitat quality influences fitness, and where competition is likely stronger for higher-quality sites, individuals may have to choose between two options: recruiting as early as possible regardless of the quality of the site, or queuing or competing for a higher-quality site and delaying first breeding.

The fitness expectation associated with each option not only depends on fitness in the first breeding event, but also on the long-term consequences of first reproduction, whether age of first reproduction is associated with a given pattern of reproductive senescence (e.g., earlier or stronger senescence), or whether individuals whose first breeding site was of lower quality are able to acquire higher-quality sites later.

I assessed several of these hypotheses using capture-mark-recapture multistate models, and further examined which recruitment tactic was associated with the highest breeding success (BS) at recruitment. Because BS at recruitment is only a snapshot of the age-specific trajectory of an individual's BS, I further investigated how recruitment decisions affect late-life reproduction (Chapter II) and survival (Chapter III).

Chapter II.

Recruitment (i.e., age at first reproduction) is often assumed to initiate mechanisms that impede somatic repair, resulting in a decline in reproductive abilities with age (reproductive senescence). If so, different recruitment tactics, such as early versus delayed recruitment, may lead to contrasting reproductive trajectories (i.e., schedule of reproductive investment over life) and divergent senescence patterns. I examined this 'long-term trade-off' in chapter II, while taking into account the possibility that breeding experience, temporal variation, and heterogeneity in individual quality improve or diminish breeding success across ages. To do so, I used generalized additive mixed models that allow for both flexibility in the estimation of the relationship between age and BS via splines, and for the estimation of individual variability in age-specific BS via random effects.

Chapter III.

In chapter III, I borrowed statistical methods from human demography (i.e., time-to-failure survival analysis) to study age-specific survival trajectories of individuals that recruited at different ages, exhibited variable levels of reproductive investments across ages, and that experienced temporal fluctuations in reproductive investments, all while controlling for unobserved heterogeneity. I then quantified the relative contributions of observed and unobserved heterogeneity to variability in age-specific survival across individuals.

Although the development of statistical techniques allowing incorporation of both unobserved and observed sources of heterogeneity among individuals has considerably enhanced understanding of senescence in humans, the use of such techniques is still rare with data from wild animal populations. Nevertheless, since such tools have become available, this work underlines the relevance of the incorporation of ‘hidden heterogeneity’ in studies of life histories in wild animal populations.

Chapter IV.

Lastly, I combined the results from chapters I-III to estimate individual-based measures of fitness and quantify the costs and benefits associated to each recruitment strategy. Specifically, I developed a detailed matrix-based population-projection model (Caswell 2001) that captured age-specific trajectories of reproductive success and survival conditional on the recruitment ‘state’ (i.e., the age at first reproduction; 87 total stages). I then modified a jack-knifing technique developed by Coulson et al. (2006) to calculate individually based fitness for individuals that recruited at different ages. Based on these results, I calculated selection gradients to determine the mode(s) and strength of selection operating on the age at first reproduction while accounting for its effects on senescence. I conclude by discussing the limitations of estimating selection on the age at first reproduction in populations that are decreasing (i.e., sinks), stable, or increasing (i.e., sources).

~ INTRODUCTION GÉNÉRALE~

Évolution des traits d'histoire de vie

L'écologie évolutive s'intéresse à l'étude des événements majeurs qui jalonnent la vie des individus au sein d'une population donnée. Ces événements peuvent être démographiques (e.g., âge à la première reproduction, fertilité, et survie à chaque âge), physiologiques (e.g., durée de gestation), ou comportementaux (e.g., choix d'un partenaire), et sont appelés traits d'histoire de vie (Roff 1992). Des événements peuvent être uniques ou répétés au cours de la vie, et sont des composantes clés de la valeur sélective (i.e., fitness) sur lesquelles agit la sélection naturelle (Stearns 1992). La grande variabilité des traits d'histoire de vie, et la façon dont ces traits se combinent afin de définir une histoire de vie unique, est une composante de biodiversité de notre planète, et explique la grande popularité de la théorie des traits d'histoire de vie chez les écologistes comportementaux (Krebs and Davies 1978), les chercheurs s'intéressant à la physiologie d'un point de vue évolutif (Zera and Harshman 2001), et même des anthropologues (e.g., Kaplan 2003) au cours de ce dernier siècle.

Compromis évolutifs: le cout de la reproduction revisité

Les traits d'histoire de vie sont principalement liés à la croissance, la survie, et la reproduction des individus, et sont donc les principaux déterminants de la fitness. Et parce qu'à notre connaissance il n'existe pas de 'Démon Darwinien'[1] (Law 1979), les organismes ne peuvent pas optimiser simultanément leur croissance, leur reproduction, et leur survie; ils doivent faire des choix, et allouer leur temps et leur énergie entre les différentes composantes de la fitness. Ces choix sont appelés compromis évolutifs, ou compromis entre traits d'histoire de vie, et sont au cœur de la théorie de l'évolution des traits d'histoire de vie

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[1] Organisme hypothétique qui peut maximiser toutes les composantes de la fitness simultanément, et par conséquent, n'a pas à faire face a des compromise évolutifs.

(Williams 1966). Un compromis évolutif particulier qui a reçu beaucoup d'attention au cours de ces dernières décennies est le classique 'coût de la reproduction' (Roff 1992, Stearns 1992). En accord avec le 'principe d'allocation des ressources' (Levins 1968), ce compromis résulte d'un choix auquel les individus doivent faire face: allouer leurs ressources à la reproduction présente au détriment de leurs chances de reproduction ou de survie future. Williams (1966) précise que l'investissement reproducteur lors d'un évènement de reproduction donné entraine la diminution de la 'valeur reproductive résiduelle' (VRR). La valeur reproductive combine les taux de survie et de fécondité à chaque âge (Fisher 1930), et peut être décomposée en la somme de la valeur reproductive courante et de la valeur reproductive future (Williams, 1966b). Ainsi Williams a fait l'hypothèse d'une corrélation négative entre l'intensité de l'effort de reproduction courant et VRR, ce qui suggère un coût somatique de la reproduction présente associé à une capacité de reproduction plus faible dans le future.

Plus récemment, les « écologistes évolutifs [2]» ont fait la distinction entre deux types de coûts de reproduction: une augmentation de la reproduction courante entraine une diminution de la reproduction future, ou une diminution de la survie future. Le cas le plus extrême de coût de reproduction portant sur la survie future réside dans la différence entre organismes itéropares et sémelpares (Cole 1954). Les organismes itéropares connaissent plusieurs événements de reproduction au cours de leur vie, alors que les organismes sémelpares n'ont qu'une seule opportunité de reproduction et meurent par la suite. Même si un grand nombre d'études empiriques (e.g., chez les plantes, Metcalf et al. 2003; les reptiles, Bonnet et al. 2003, les poissons, Waples 2002; les mammifères, Cockbrun and Lazenbycohen 1992) et théoriques (e.g., Gadgil and Bossert 1970, Takada 1995, Crespi and Roy 2002) nous ont aidés à mieux comprendre les raisons pour lesquelles certains organismes ont évolué vers

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[2] Traduction littérale d' « evolutionary ecologists »

la sémelparité, les forces sélectives responsables d'une telle transition évolutive méritent plus d'attention.

Même dans des cas moins extrêmes de compromis évolutifs, le coût de la reproduction au sein d'organismes itéropares a reçu un soutien mitigé. Ce compromis a été largement étudié par le biais d'études expérimentales (Linden and Møller 1989), même si certaines d'entre elles ont été sévèrement critiquées (Reznick 1990). La manipulation phénotypique est l'une des procédures expérimentales qui a détecté avec succès un coût de reproductions *in natura* (e.g., Gustaffson and Sutherland 1988, Nur 1988). Les manipulations expérimentales faites sur les oiseaux augmentent généralement le nombre de jeunes avant (stade œuf) ou après (stade poussin) l'éclosion, augmentant ainsi la demande en soins parentaux. Ces études mesurent ensuite l'impact de l'augmentation de la taille de ponte, ou de la couvée, sur la survie et le succès reproducteur futurs des parents (et autres composantes de la fitness). Les résultats issus des ces études indiquent une variété importante de coûts de reproduction sur le court terme pour les parents, ainsi que pour leur progéniture (Hanssen et al. 2005). Une sollicitation accrue des parents pourrait aussi aboutir à des coûts de reproduction différés tels qu'une survie et une fertilité adulte réduite, mais rares sont les études qui ont détecté de tels coûts (e.g., Dijkstra et al. 1990; Roff 1992; Stearns 1992; Golet et al. 1998). Hanssen et al. (2005) note que seulement une étude portant sur les coûts associés à l'incubation après manipulation de la taille de ponte soutient l'hypothèse d'une survie diminuée (Visser & Lessells 2001). Un coût portant sur la condition de la descendance issue d'une couvée dont la taille a été artificiellement augmentée a aussi été documenté chez le gobe-mouche à collier (Cichoń 2000), mais aucune étude n'a détecté un coût d'incubation (après manipulation de la taille de ponte) portant sur la fécondité future du parent (e.g., chez la mésange bleue, Pettifor 1993).

La plupart des études portant sur la régulation de l'effort parental ont été conduites sur des oiseaux à faible espérance de vie (i.e., les passereaux). Chez ces oiseaux, la probabilité de survivre à une saison de reproduction est tellement faible, qu'une augmentation de l'effort de reproduction est attendue en cas d'augmentation expérimentale de la taille de ponte ou de couvée, indépendamment des coûts de reproduction associés et portant sur la survie future (Charlesworth 1980). Charlesworth (1980), Curio (1988), et Wooler (1992) s'attendaient tous à ce que les espèces longévives, telles que les oiseaux marins, limitent leur investissement dans leur descendance, car même une légère augmentation de l'investissement parental pourrait entrainer une réduction de la survie future, résultant au final en une réduction du succès reproducteur au cours de la vie (Clutton-Brock 1988). Ainsi, ils suggérèrent que l'effort parental reste approximativement fixe chez ces espèces, indépendamment des demandes énergétiques nécessaires à la bonne croissance de leur descendance (Ricklefs 1992). Cette hypothèse a été appuyée par des études faites sur l'océanite culblanc, *Oceanodroma leucorhoa* (Ricklefs and Minot 1991, Hamer and Hill 1994), et le pétrel antarctique, (Andersen et al. 1995).

A l'opposé, des études récentes de manipulation de la taille de la couvée chez les oies et chez certains oiseaux marins ont observé une augmentation de l'effort reproducteur parental (Jacobsen et al. 1995, Tombre and Erikstad 1996, Erikstad et al. 1997), même au dépend de la survie parentale (Reid 1987, Jacobson et al. 1995). Au contraire, dans le cadre d'une étude non- expérimentale, Cam et al. (2002a) ont observé une corrélation positivée entre reproduction et survie d'une année à l'autre chez la mouette tridactyle, une espèce longévive d'oiseau marin, suggérant que le traditionnel coût de reproduction ne s'exprime pas spontanément dans cette population. Si un coût de reproduction sur le court terme n'est pas toujours observé en milieu sauvage, est-ce qu'un coût de reproduction différé ou cumulé pourrait s'exprimer beaucoup plus tard dans la vie d'un individu? Par exemple, est-ce qu'un investissement reproducteur tôt dans la vie d'un individu (e.g., recrutement précoce, augmentation du succès reproducteur en début de vie reproductrice) est associé à une sénescence[3] plus précoce ou plus rapide, en termes de reproduction ou de survie? Cette question est au cœur du débat divisant les différentes théories du vieillissement[4] depuis presque plus d'un siècle.

Theories de la sénescence et coûts de reproduction

L'héritage que Fisher, Wright, et Haldane nous ont légué via la synthèse moderne de la génétique et de l'évolution (Fisher 1930, Wright 1931, Haldane 1941) a conduit à la formulation de deux théories de la sénescence, théories non exclusives, connues sous le nom 'd'Accumulation des Mutations' ('AM', Medawar 1952), et de 'Pléiotropie Antagoniste' ('PA'; Williams 1957, Hamilton 1966). Ces théories ont reçu un soutien aléatoire dans un cadre purement expérimental (Monaghan et al. 2008), et ne peuvent être distinguées que de la manière suivante: une augmentation de la variance additive génétique avec l'âge peut avoir lieu sous AM et PA (Charlesworth and Hugues 1996), mais les corrélations génétiques négatives entrainant un compromis évolutif entre composantes de la fitness tôt et tard dans la vie ne peuvent être observées que sous AP (Rose 1991, Charlesworth 2000).

Notre compréhension de la façon dont les taux de vieillissement ont été façonnés par certaines forces évolutives s'est beaucoup améliorée ces dernières décennies, surtout grâce à l'étude d'organismes de laboratoire tels que la drosophile, *Drosophila melanogaster* (Promislow et al. 1996); le nématode, *C. Elegans* (Al-Regaiey et al. 2005); et la souris, *Mus musculus* (Lund et al. 2002). En contrôlant la variabilité génétique au sein de la population, les études portant sur des organismes clonaux tels que le daphné (e.g., *Daphnia pulex*) ont l'avantage d'explorer la plasticité phénotypique des taux de vieillissement au sein de toute une gamme d'environnements (Dudycha 2003). Ces études ont ainsi apporté une certaine

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[3] Déclin des capacités de survie et (ou) de reproduction avec l'âge.

[4] Accumulation irréversible de dommages somatiques avec l'âge, entrainant une perte de fonction et éventuellement la mort.

connaissance des mécanismes moléculaires, génétiques, et environnementaux qui gouvernent la sénescence (Kirkwood and Austad 2000, Bonsall 2006). Cependant, nous ne savons pas si cette connaissance peut être extrapolée à d'autres espèces (e.g., vertébrés), et à des conditions environnementales naturelles et variables auxquelles les espèces sauvages doivent faire face (Nussey et al. 2008).

Les écologistes évolutifs qui étudient les populations sauvages ont développé des modèles statistiques spécialisés dans l'étude des corrélations (négatives) entre composantes de la reproduction tôt et tard dans la vie. Charmantier et al. (2006) ont montré que l'âge de première et de dernière reproduction chez le cygne turberculé (*Cygnus olor*) montrent tous deux de la variabilité héritable et sont soumis à des forces de sélection agissant en directions opposées, suggérant que leur évolution est limitée par un fort compromis antagoniste génétique, ce qui est en accord avec PA. Chez le cerf élaphe (*Cervus elaphus*), Nussey et al. (2006) ont montré que les femelles produisant plus de descendants tôt dans la vie souffrent d'une sénescence reproductive plus rapide, ce qui corrobore l'hypothèse sous-jacente à PA. Cependant, les compromis antagonistes tels que ceux-ci ne sont pas toujours observés *in natura*. La variabilité environnementale peut induire de la covariance positive entre traits d'histoire de vie, et peut donc masquer l'expression du phénotype attendu (i.e., compromis entre évènements de reproduction tôt et tard dans la vie), même si AP est effectivement le mécanisme génétique en action (van Noordwijk and De Jong 1986, Wilson et al. 2008). De plus, les pressions de sélection portant sur les mécanismes génétiques qui définissent les taux de vieillissement peuvent changer avec l'environnement; par exemple, lorsque les ressources sont limitées (van Noordwijk and De Jong 1986), lorsque le nombre de prédateurs augmente, ou lorsque d'autres types de stress sont induits (Mangel 2008, Münch et al. 2008, Charlesworth and Hughes 1996).

Même si les études génétiques qui séparent les mécanismes génétiques et environnementaux responsables de l'évolution de la sénescence sont nécessaires au débat portant sur le vieillissement, les études longitudinales focalisées sur les patrons de sénescence en milieu sauvage sont également essentielles, car nous savons très peu de choses sur la sénescence *in natura* (Monaghan et al. 2008).

Cas de la mouette tridactyle, Rissa tridactyla

Deux principales limitations ont empêché les écologistes évolutifs d'étudier l'évolution de la sénescence en milieu sauvage d'un point de vue démographique. Tout d'abord, les conditions défavorables et le haut degrés de mortalité extrinsèque empêche la pluspart des individus d'atteindre des âges avancés, car la pluspart meurt au stade juvénile ou au stade de jeune adulte (e.g., Ricklefs and Scheuerlein 2001). De plus, très peu nombreuses sont les études qui font le suivi de populations en milieu sauvage sur des périodes de temps suffisamment longues pour détecter de la sénescence (mais voir e.g., chez les mammifères: Nussey et al. 2007; chez les oiseaux: Cam et al. 2002b, Charmantier et al. 2006; chez les poissons: Reznick et al. 2004).

Une étude longitudinale détaillée

Les colonies de mouettes tridactyles (*Rissa tridactyla*, un oiseau marin colonial qui niche en falaise) vivant en Bretagne et étudiées depuis 1979, offrent la superbe opportunité d'étudier ces questions sur des milliers d'individus suivis par technique de capture-marquage-recapture (Monnat et al. 1990, Cam et al. 1998, 2000a, 2003, 2005). Les événements de reproduction, la présence de chaque individu, leur démographie (e.g., survie et fécondité à chaque âge), leur comportement (e.g., formation de couples), ainsi que les variables environnementales locales (e.g., localisation du site de reproduction) sont relevés chaque année.

Six colonies localisées au Cap Sizun, à quelques kilomètres de distance (maximum de 12 Km) sont suivies de façon intensive durant chaque saison de reproduction, de manière à ce que tous les événements de reproduction soient répertoriés, et à ce que la présence des individus au sein des différentes colonies soit notée de janvier à septembre, avec un suivi plus intensif entre mai et septembre, afin de couvrir au mieux le pic de reproduction. Ce suivi détaillé permet de connaître le tout premier événement de reproduction pour chaque individu retournant à l'une des colonies après une période plus ou moins longue en mer. L'âge de la plupart des individus est connu, et la présence de chaque individu au sein des colonies est notée à chaque session d'observation. Le travail de terrain couvre entièrement chaque saison de reproduction de manière à ce qu'aucun événement de reproduction ne soit manqué. Ce jeu de données est donc parfait pour examiner l'existence de coût de reproduction différés au sein de cette population.

Pour les populations de mouettes tridactyles, ainsi que pour toute autre population, la variabilité des traits d'histoire de vie peut être observée au sein d'une population, entre individus, et même au cours de la vie d'un individu donné. La 'variabilité inter-individuelle' (e.g. Chesson 1991) peut être définie comme la diversité des phénotypes au sein d'une population. Les individus au sein de cette population peuvent avoir différents phénotypes, même s'ils possèdent tous le même génotype (i.e., plasticité phénotypique[5]). De plus, ces individus peuvent avoir des vie très différentes de part leurs différences de capacités à collecter des ressources, à trouver un partenaire, à trouver un habitat de reproduction, et à maintenir leur condition tout en investissant dans ces autres activités; cela résulte en des différences de fitness 'inter-individuelles' (Stearns 1992). La 'variabilité intra-individuelle' peut s'exprimer d'heure en heure (e.g., décider de rechercher de la nourriture), de jour en jour (e.g., décider de se cacher des prédateurs), de saison en saison (e.g., décider de migrer), d'âge en âge (e.g., décider de se reproduire). Elle peut être bénéfique, coûteuse, et parfois même mortelle. Cette variabilité intra-individuelle est très difficile à mesurer empiriquement car elle nécessite des études longitudinales très détaillées (aussi bien démographiques que

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[5] La capacité d'un individu à changer son phénotype en réponse a des changements environnementaux.

comportementales), et une connaissance parfaite du système étudié, afin d'avoir une idée des principaux déterminants d'une telle variabilité.

D'un point de vue théorique, la variabilité inter-individuelle (Vaupel et al. 1979, 1985), correspond à des différences entre individus qui ne peuvent pas forcement être mesurées. Ces différences sont à l'origine définies comme étant fixes (e.g., définies à la naissance ou au début de la vie reproductrice). Une telle hétérogénéité peut résulter en une disparition sélective précoce des phénotypes les plus 'fragiles' dans les cohortes (individus nés la même année), ce qui au final résulte en une mauvaise estimation des paramètres de survie et de reproduction qui ne reflètent pas les changements âge-spécifiques des composantes de la fitness exprimés au cours de la vie des individus. Afin de séparer les patrons âge-spécifiques de variation de survie et de reproduction au cours de la vie d'un individu, et le patron observé à l'échelle de la population si l'hétérogénéité non-observée n'est pas prise en compte, des modèles statistiques prenant en compte l'hétérogénéité observée (e.g., variable liée à la qualité des soins parentaux) et non-observée ont été développés. Une quantité substantielle d'hétérogénéité non-observée a été détectée au sein des colonies de mouettes tridactyles du Cap Sizun (Cam et al. 2002b), et doit donc être systématiquement prise en compte lors de l'étude des trajectoires de survie et de reproduction, tout spécialement lors de l'étude de la sénescence.

En plus des sources de variabilité intrinsèque des traits d'histoire de vie telles que la reproduction et la survie âge-spécifique, la variabilité environnementale peut aussi exercer une influence profonde sur la variabilité inter- et intra-individuelle. La variabilité environnementale dans l'espace et le temps (e.g., changements de disponibilité des ressources, de qualité de l'habitat, de conditions climatiques, de pressions de prédation) peut sans aucun doute influer sur le comportement, la physiologie, et la démographie d'un individu donné au sein de la population, car chaque individu aura une capacité propre à suivre ces changements, et à s'y adapter. Chez la mouette tridactyle, aussi bien la variabilité individuelle (inter- and intra) que la variabilité environnementale ont été documentés dans les processus démographiques (e.g., Cam et al. 1998). Cependant l'influence relative de ces sources de variation sur les taux de sénescence n'est pas encore connue chez cette espèce, ni chez aucune autre espèce sauvage.

Objectifs de la thèse

Ma thèse s'intéresse aux processus évolutifs qui façonnent les taux démographiques âge-spécifiques, avec une attention toute particulière pour les taux de sénescence. Je m'intéresse aux compromis évolutifs entre les décisions de reproduction tôt dans la vie, la reproduction future, et les chances de survie chez un oiseau marin longévif, la mouette tridactyle.

Chapitre I.

Avant d'étudier dans le détail les compromis évolutifs liés à la reproduction sur le long terme, j'ai dédié mon premier chapitre à l'étude de la première décision de reproduction: 'à quel âge se reproduire pour la première fois ?'. Chez la mouette tridactyle, l'une des conditions s*inequanon* à l'initiation de la première reproduction est d'obtenir un site de reproduction au sein d'une falaise de reproduction. Il semblerait donc que les décisions liées à l'initiation de la reproduction et à la sélection de l'habitat de reproduction soient intimement liées.

Lorsque la qualité de l'habitat varie dans l'espace et le temps, que la qualité de l'habitat peut être corrélée à la valeur sélective, et que la compétition pour l'accès aux meilleurs sites de reproduction est forte, les individus peuvent soit recruter aussi tôt que possible indépendamment de la qualité de leur habitat de reproduction, ou attendre qu'un site de bonne qualité se libère, ou entrer en compétition pour l'accès à ce site (i.e., différé du recrutement).

Les gains de fitness associés à chaque option ne dépendent pas seulement de ce qui se passe lors du premier évènement de reproduction, mais aussi des conséquences de la première reproduction sur le long terme. La première reproduction pourrait donc être associée à un patron particulier de sénescence en termes de reproduction (e.g., sénescence plus ou moins rapide, plus ou moins précoce), et pourrait dépendre de la qualité de l'habitat obtenu à la première reproduction, mais aussi de la capacité d'un individu à acquérir un meilleur site de reproduction au cours de la vie.

J'ai utilisé des modèles de capture-marquage-recapture dits multi-strate afin de déterminer quelle tactique de recrutement est associée à une qualité d'habitat de reproduction plus élevée, et à un plus fort succès reproducteur l'année du recrutement. Mais le succès reproducteur n'étant qu'un aperçu de la trajectoire reproductrice âge-spécifique d'un individu, nous avons également étudié la relation entre âge à la première reproduction, la reproduction (Chapitre II), et la survie future (Chapitre III).

Chapitre II.

Le recrutement (i.e., la première reproduction) est souvent associé à des mécanismes qui diminuent la possibilité de réparation somatique, résultant en un déclin de capacités reproductrices avec l'âge (sénescence reproductive). Si tel est le cas, différentes tactiques de recrutement pourrait aboutir à l'observation de trajectoires de reproduction contrastées. J'ai étudié ce compromis sur le long terme (chapitre II), tout en prenant en compte la possibilité d'une amélioration ou d'une diminution du succès reproducteur au travers des classes d'âges avec l'expérience, la variabilité temporelle, et l'hétérogénéité individuelle. J'ai utilisé des modèles additifs mixtes généralisés afin de permettre une certaine flexibilité dans l'estimation de la relation entre l'âge et le succès reproducteur via l'utilisation de 'splines', et pour l'estimation de la variabilité individuelle j'ai utilisé des effets aléatoires individuels.

Chapitre III.

J'ai utilisé des méthodes statistiques empruntées à la démographie humaine afin d'étudier les trajectoires âge-spécifiques de survie chez des individus qui recrutent à des âges différents, et qui investissent différemment dans la reproduction au travers des classes d'âges. J'ai ensuite quantifié les contributions relatives de l'hétérogénéité observée et non-observée aux variations de survie âge-spécifique.

Si le développement de méthodes statistiques permettant l'incorporation de sources d'hétérogénéité observée et non-observée a considérablement amélioré l'interprétation des profils de sénescence chez l'humain, l'application de telles techniques aux populations sauvages reste très rare. Cependant, ces outils étant maintenant disponibles, ce travail souligne la pertinence de l'incorporation de l'hétérogénéité non-observée lors de l'étude des histoires de vie de populations sauvages.

Chapitre IV.

J'ai combiné les résultats associés aux chapitres I-III afin d'estimer la fitness individuelle, et de quantifier les coûts et bénéfices associés à chaque stratégie de recrutement. Spécifiquement, j'ai développé un modèle matriciel détaillé (Caswell 2001) qui capture la variabilité du succès reproducteur et de la survie au travers des classes d'âges conditionnellement au statut de recrutement (i.e., âge à première reproduction, 87 états au total). J'ai modifié la technique de 'jack-knifing' développée par Coulson et al. (2006) afin de calculer la fitness individuelle associée à chaque individu en fonction de son âge de première reproduction. D'après ces résultats, j'ai calculé des gradients de sélection afin de déterminer l'intensité et la direction de la sélection opérant sur l'âge de première reproduction. Je conclue cette thèse en discutant les limitations de l'estimation des pressions de sélection opérant sur l'âge de première reproduction en fonction de la 'santé' de la population: en décroissance, stable, ou en croissance.

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~ CHAPTER I ~

‘Do you like me for me, or because I have a sweet place?’

Picture: Lise M. Aubry

HABITAT SELECTION, AGE-SPECIFIC RECRUITMENT, AND REPRODUCTIVE SUCCESS IN A LONG-LIVED SEABIRD, THE BLACK-LEGGED KITTIWAKE

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Abstract

Delayed recruitment (i.e. first reproduction) is a key feature of the demography of long-lived species such as seabirds. If physiological, behavioral, and environmental factors are thought to influence age at first breeding, knowledge of the fitness prospects corresponding to different recruitment tactics is needed to get insight into the evolution of delayed recruitment.

Because the age at which an individual recruits may depend on the location chosen to breed, we first investigated the relationship between habitat quality and age of first breeding in a long-lived seabird, the black-legged Kittiwake (*Rissa tridactyla*). We used multi-state mark-recapture approaches to model the transition from non-breeding to breeding status as a function of age and habitat quality. We also investigated whether there was a relationship between age at recruitment and reproductive success in the year of recruitment. We assessed several non-exclusive hypotheses. (i) If experience plays a part in reproductive success per se (e.g. in the quality of parental care), or in acquisition of higher-quality breeding sites (i.e. increased competitive ability), then reproductive success should be lower for early recruits (i.e. age 3) than others. (ii) In the same vein, if delayed recruitment corresponds to a queuing tactic allowing access to higher-quality sites, then late recruits (age 6 or 7) should exhibit higher breeding success than others. Alternatively, delayed recruitment may reflect behavioral inability to access to higher-quality sites; in this case, late recruits should exhibit poorer breeding success than younger ones. (iii) Experience combined with social constraints may lead to an initial increase in breeding success with recruitment age, and a decrease in older recruits.

We found that recruitment probability was highest at intermediate ages (i.e. 5–6 years old), and that recruitment probability was maximal in habitat patches (i.e. ‘cliffs’) of medium quality. This may reflect harsh competition in the most productive cliffs, and avoidance of the least productive ones (i.e. where predation on eggs is high). In accordance with our predictions (i and iii), we found that the youngest recruits experienced poor breeding success at the beginning of their reproductive life, and that breeding success was higher for birds recruiting at intermediate age. In addition, recruitment probability was best predicted by apparent habitat quality the year preceding recruitment. The latter result suggests either that habitat selection takes place the year preceding settlement and first reproduction, or that the information available to individuals at the beginning of a season is temporally auto-correlated to past productivity.

Reproductive choices and/or the constraints met during the pre-reproductive stage of life may influence age at recruitment. Our results show that there is a relationship between age of first breeding and breeding success probability. However, age of first breeding may also have substantial effects on breeding success over life. Future study should examine if reproductive success improves, shows senescent decline, or remains the same over the life course of individuals recruiting at various ages.

Key-words. Age-specific recruitment, Black-legged Kittiwake, Breeding success, Capture-Mark-Recapture, Habitat selection, Habitat quality, Multi-state modeling.

SELECTION DE L'HABITAT, RECRUTEMENT AGE-SPECIQUE, ET SUCCES REPRODUCTEUR CHEZ UN OISEAU MARIN, LA MOUETTE TRIDACTYLE

Résumé

Le recrutement (i.e., passage d'un état pré-reproducteur à un état reproducteur) est un paramètre clé dans la démographie des espèces longévives, telles que les oiseaux marins. Des facteurs physiologiques, comportementaux, et environnementaux sont susceptibles d'influencer l'âge à la première reproduction. Cependant, afin de comprendre comment le recrutement différé a pu être sélectionné d'un point de vue évolutif, nous devons être capables d'associer tactiques de recrutement et valeur sélective.

Nous savons que l'âge auquel les individus recrutent dépend du choix de l'habitat de reproduction ; nous avons donc étudié en premier lieu la relation entre la qualité de l'habitat de reproduction et l'âge de première reproduction chez un oiseau marin longévif, la mouette tridactyle (*Rissa tridactyla*). Nous avons utilisé pour cela des modèles dits 'multi-états' de capture-marquage-recapture afin d'étudier spécifiquement la probabilité de transition d'un état non-reproducteur à un état reproducteur en fonction de l'âge et de la qualité de l'habitat. Nous avons également étudié la relation entre l'âge au recrutement et le succès reproducteur l'année du recrutement. Dans ce cadre, nous proposons plusieurs hypothèses. (i) Si l'expérience influence positivement la performance reproductrice, ou encore l'acquisition d'un habitat de qualité supérieure (par une capacité compétitive accrue), on s'attend à ce que le succès reproducteur soit minimal chez les jeunes recrues (i.e., 3 ans, l'âge minimum de première reproduction). (ii) Selon l'hypothèse du 'queuing' (soit attendre qu'un site de reproduction choisi devienne disponible), on s'attend a que le recrutement soit différé dans le

temps, et permette un accès à des sites de reproduction de meilleure qualité. En d'autres termes, on s'attend à ce que les recrues tardives (recrutement à l'âge 6, 7 ans, ou plus) connaissent un succès reproducteur plus élevé que les recrues précoces. A l'inverse, le recrutement différé pourrait être le reflet d'un manque de capacité à accéder aux meilleurs sites de reproduction. Dans ce cas, les recrues tardives devraient connaître un faible succès reproducteur l'année du recrutement. (iii) L'expérience, combinée à des contraintes d'ordre social, pourrait mener à une croissance initiale du succès reproducteur avec l'âge de recrutement, et à une décroissance chez les recrues les plus âgées.

Nos résultats montrent que la probabilité de recrutement est maximale aux âges intermédiaires (i.e., recrutement entre 5 et 6 ans), et dans des habitats (i.e., falaises de reproduction) de qualité moyenne. Ce résultat pourrait refléter une compétition forte dans les falaises de reproduction les plus productives (i.e., où la prédation sur les œufs est la moins élevée). En accord avec les prédictions (i) et (iii), les jeunes recrues connaissent le succès reproducteur le plus faible l'année du recrutement, c'est-à-dire au début de leur carrière reproductrice. A l'opposé, les individus recrutant à des âges intermédiaires connaissent le succès reproducteur le plus élevé.

La probabilité de recrutement dépend de la qualité de l'habitat l'année précédant le recrutement, et non de la qualité l'année même. Ce résultat suggère que la sélection de l'habitat prend place l'année précédant la première installation sur le site de reproduction, soit un an avant le recrutement, et donc que l'information accessible aux individus au début de la saison reproductrice est auto-corrélée à la productivité passée d'une falaise de reproduction donnée.

Les choix de reproduction et/ou les contraintes rencontrées durant la phase pré-reproductrice semblent être les déterminants de l'âge de première reproduction. Cependant, ce trait d'histoire de vie pourrait lui aussi influencer le succès reproducteur au cours de la vie. Des études plus poussées pourraient examiner si le succès reproducteur augmente, diminue

de façon sénescente, ou demeure le même au cours de la vie des individus qui recrutent à des âges différents.

*Mots-clés : recrutement âge-spécifique, mouette tridactyle, capture-marquage-recapture, sélection de l'habitat, hétérogénéité, modélisation multi-*états, *performance reproductrice.*

Introduction

Age of first breeding (i.e. recruitment) in vertebrates is determined in part by age at sexual maturity, a constraint limiting flexibility in the minimum age at recruitment. However, even within the same population, a wide range of ages at first breeding is observed in many vertebrates, and many seabirds delay first reproduction well beyond physiological maturity. Accordingly, the pre-breeding segment of the population constitutes a significant part of the population. It is important to understand factors influencing the timing of recruitment to the breeding population, as the age of first breeding may have a significant impact on population dynamics and fitness (Caswell and Hastings 1980; Stearns 1992; Charlesworth 1994).

A consistent prediction from models based on life history trade-offs is that early reproduction should be favored by natural selection (Stearns 1992; Charlesworth 1994), except under specific circumstances (i.e. population decline or fluctuating juvenile survival, Charlesworth 1994). Thus, unless one underestimates the importance and evolutionary consequences of temporal variation in juvenile survival, one might expect delayed reproduction to be rare in the wild. Interestingly, empirical observations do not always support this prediction (e.g. in birds: Viallefont et al. 1995; Pradel et al. 1997; Cooch et al. 1999; Lebreton et al. 2003). In a habitat selection framework, delaying recruitment has been suggested to allow individuals to gather information about potential breeding patches before recruitment (Boulinier and Danchin 1997). Reproductive delay might also be beneficial in terms of fitness if reproductive success increases with age, experience (i.e. skill enhancement through learning), or both (Charlesworth 1994), as long as the survival costs associated to such a delay do not exceed its benefits. Furthermore, delayed reproduction can be adaptive (i.e. 'bet-hedging strategy') in environments where reproduction is uncertain (Tuljapurkar 1990).

In the black-legged Kittiwake (*Rissa tridactyla*), a cliff-nesting seabird, reproduction can begin at age two (Cam et al. 2002b, 2003), but the bulk of recruitment takes place between 3 and 6 years of age (Danchin et al. 1991; Cam et al. 2005), and some individuals delay recruitment even longer (e.g., 15 years; Cadiou 1993). In addition to physiological constraints, a certain level of behavioural maturity is required to complete reproduction successfully (Danchin 1987a; Porter 1988). Behavioral maturity is part of the general complex of 'increasing reproductive abillity with age and experience' proposed by Charlesworth (1994), and may explain delayed age of first breeding. A certain level of maturity (e.g. competitive abilities in males to gain ownership on a nest-site), that may require a relatively long learning process, is therefore mandatory before reproduction can begin (Nur 1984; Pickering 1989; Monnat et al. 1990; Danchin et al. 1998).

Environmental conditions may interact with an individual's intrinsic quality and result in a variety of recruitment tactics. Energetic constraints on reproduction are likely to depend on resource acquisition, which is determined by both resource availability (i.e. a feature of the environment) and the individual's ability to harvest them (i.e. intrinsic quality). Only individuals of high quality may be able to recruit early if resource limitation occurs (e.g. in the lesser snow goose, Viallefont et al. 1995; in the blue petrel, Barbraud and Weimerskirch 2005).

Within this framework of constraints setting limits to variation in the age at age at first reproduction, individuals still have 'a decision to make'. For instance, age at first reproduction may directly depend on habitat selection tactics based on optimization of expected fitness (Fretwell and Lucas 1970). Potential recruits may decide either to breed or to wait until the next breeding season based on the quality of potential breeding locations in a given year (Boulinier and Danchin 1997). For example, severe predation events on eggs or chicks in the colonies attended by pre-breeders in a given year (Cam et al. 2004a) may lead some of them to postpone recruitment until the following breeding season. In this view, habitat selection may be one of the main components of the 'selective environment' of the age at recruitment. The decisions of where and when to start breeding may actually be ‘two sides of the same coin’ as Ens et al. emphasized (1995), and delayed recruitment might be the outcome of a specific habitat selection strategy involving:

(1) Information gathering, in order to identify potential habitats and assess habitat quality (e.g., assessment of conspecific reproductive success and predation pressure in different colonies over time, Cadiou 1993; Boulinier and Lemel 1996; Boulinier and Danchin 1997; Danchin et al. 1998);

(2) Gaining ‘ownership’ on a new site via competition or by queuing for an already occupied site to become available (see Wiley and Rabenold 1984; Ens et al. 1995; Cam et al. 2002b).

Obviously, constraints related to the acquisition of a nest-site may influence the timing of recruitment, especially in colonial cliff-nesting seabirds where competition amongst individuals to acquire a nest-site is strong, and may in turn delay accession to the breeding population. In the study-population, nest-site density is stronger in higher-quality patches (i.e. cliffs) than in low-quality ones. Density is part of the environmental features that may in higher-quality patches (i.e. cliffs) than in low-quality ones. Density is part of the environmental features that may influence individual age at recruitment. However, long-term observations (1979–2007) have shown that individuals can always ‘create’ new nest-sites in higher-quality patches if they have the competitive abilities to do so; thus, none of the patches are saturated in the study area. The common observation of individuals competing for specific nest-sites that are already occupied (Cadiou 1993) in higher-quality patches contradicts the idea that density dependence is the main factor influencing settlement decisions. Indeed, these individuals might be more interested in queuing for already occupied nest-sites, or in evicting previous owners of occupied sites, as in both cases they can directly observe how much this site is ‘worth’ (i.e. based on their conspecific’s reproductive success on this particular site). The pays-offs of such behavior might overtake the benefits associated with the creation of a new nest-site, in which case individuals have no information on its potential. Our assumption is that social constraints and competitive abilities, rather than density dependence per se, are the main determinants of the age at first reproduction.

The optimal age at first reproduction, if any, is likely to depend on an individual's phenotype, the environment, and their interaction. It is probably not achievable to fully understand why an individual recruits at a given age without identifying habitat characteristics (nest-site, territory, colony or breeding location) where recruitment takes place. Regrettably, these tend to be treated independently in the literature (but see Ens et al. 1995; Boulinier and Lemel 1996). To circumvent this shortfall, our main objective was to address the relationship between age at objective was to address the relationship between age at first reproduction and habitat selection. Several behavioral tactics of habitat selection characterized by different ages at first reproduction may coexist in populations. For example, age per se may be associated with increased behavioral maturity and competitive ability, which may in turn translate into a higher probability of acquiring a good nest-site in older, more experienced individuals. A non-exclusive hypothesis may explain a similar relationship between age and habitat quality: the queuing hypothesis (Ens et al. 1995). Higher quality individuals may acquire higher quality nest-sites if they wait for a productive site (i.e. site where the current and past reproductive success is high) to become available. Alternatively, individuals with poor competitive abilities may recruit in lower-quality sites, regardless of age, which may lead to a situation where the oldest recruits breed on low-quality sites.

We used capture-mark-recapture (i.e. CMR) multi-state models (Nichols and Kendall 1995; Nichols 1996; Cam et al. 2005) to estimate recruitment probabilities as a function of age, cohort, as well as covariates used as surrogates for habitat quality. We first examined the age at which birds recruit (whether this choice reflects an individual decision or results from constraints), and where they settle at recruitment (in terms of habitat quality) as a function of age, in order to determine whether delayed recruitment results in the acquisition of higher-quality sites within productive cliffs.

Our second objective was to determine how well individuals recruiting at various ages and in habitat patches of different qualities perform in terms of breeding success probability in the year of recruitment. This aims at assessing whether delayed recruitment is associated with higher breeding success than early breeding; more generally, we aim at assessing the importance of habitat selection on breeding success probability in the year of recruitment. This aims at assessing whether delayed recruitment is associated with higher breeding success than early breeding; more generally, we aim at assessing the importance of habitat selection on fitness prospects in the very first breeding event.

Methods

1. Estimation of Recruitment Probabilities as a Function of Habitat Quality Using CMR Multi-State Models

In 1979, a black-legged Kittiwake monitoring program was initiated in Brittany, France, and is continuing today (five colonies located in Cap Sizun a few kilometers apart from each other, 48◦5’N, 4◦36’W; Monnat et al. 1990). Here, we examine the capture–recapture histories of twelve birth cohorts (1986-1997) over 18 years (1986-2003), that is a total of 4030 individuals. The fieldwork covers each breeding season entirely such that observers do not miss a single reproductive event in the study area (Cam et al. 1998). It is therefore possible to identify the very first reproductive event of each individual returning to the study area (Cam et al. 2002b, 2003, 2005). We acknowledge that some pre-breeding individuals may have recruited into another population (e.g. the British Isles or Spain; Cam et al. 2002b) before breeding in Brittany, that is, we may have missed the very first breeding event. However, we believe that such cases are rare as most individuals resighted as recruits attend Brittany colonies in the years preceding recruitment, and the majority of the recruits are sexed through behavior before first breeding. Thus, attending Brittany colonies while breeding in the British Isles is likely to be rare (<1%).

1.1. Habitat Quality

To address the relationship between habitat selection and recruitment probability, we first defined habitat patches as sections of a cliff delimited by topographical discontinuities (e.g. Danchin et al. 1998). In the following, we will use ‘cliff’ and ‘habitat patch’ interchangeably. Only patches hosting at least ten nest-sites were included in our study. Following the approach developed by Danchin et al. (1998), we calculated yearly ‘habitat quality’ (i.e. local productivity) as the percentage of nests in a success situation within each cliff (0–33% for poor quality cliffs, 33–66% for medium quality cliffs, and 66–100% for highly productive cliffs). A ‘success’ was defined as a nest fledging at least 1 offspring. Similar to Danchin et al. (1998), and Cam and Monnat (2000a), the performance of the focal individual was excluded from the calculation of habitat quality in order to maintain independence between measures of individual breeding success and habitat quality. Our measure of habitat (cliff) quality will be referred to as ‘Cliff’ in the statistical analyses.

1.2. Approach to Modeling

Recruitment Probability

We used the definition of recruitment given by Pradel and Lebreton (1999): the probability that a pre-breeder in year t, which survived up to year t+ l, reproduces in year t+ l (i.e. transition probability from pre-breeding to a breeding state; Brownie et al., 1993). Transition probabilities from breeding to non-breeding states were fixed to zero (i.e. impossible transitions). The recapture probability of breeders is ≈1in the study population (Cam et al. 1998, 2005), but previous studies have shown that recapture probabilities for pre-breeders are lower than 1 (Cam et al. 2005). Hence, estimation of transition probabilities conditional on survival (i.e. recruitment probability) requires probabilistic models incorporating recapture probability.

Multi-state (MS) models (Arnason 1973; Nichols et al. 1992, 1993; Nichols and Kendall 1995; Schwarz et al. 1993; Lebreton and Pradel 2002) are designed in such a manner that individuals can move among states (e.g., states can be geographical states, or biological states such as size classes, breeding states, etc.).

Ψ_t is the probability of moving among states between time t and t+ l (in our case, transition from non-breeding to breeding state) conditional on surviving up to time t+l. We used the multi-state models implemented in Program MARK (White and Burnham, 1999) to estimate recapture, survival, and transition probabilities denoted as:

P_t^r : Recapture probability at time *t* for an individual in state *r* at time *t* (*t = 2, 3, ..., k*)

S_t^r : Probability of being alive at time *t l*, for an individual alive and of state *r* at time *t* (*t = 1,2,3, ..., k–l*)

Ψ_t^{rs} : Transition probability from state *r* (non-breeder) at time *t* (*t = 1, 2, 3, ..., k–l*) to state *s* (breeder) at time *t+l*, for an individual surviving between *t* and *t+l*.

Here, age is accounted for by inclusion of both cohort and year (for additional details see Cam et al. 2005)

Influence of Habitat Quality on Recruitment Probability

We modeled the effect of habitat quality on transition probabilities Ψ_t^{rs} (from a non-breeding state *r* to a breeding state *s*) using two different approaches. First, we assigned a covariate corresponding to the quality of the recruitment habitat to each individual. Because previous studies have provided evidence that patch quality the year preceding recruitment (t–l) influences settlement decisions in year t in both dispersers and recruits (Cadiou et al. 1994; Danchin et al. 1998; Cadiou 1999), we considered models with a covariate accounting for habitat quality the year preceding recruitment (covariate q_{t-1}), or the year of recruitment (covariate q_t). The biological hypotheses underlying a model including habitat quality in the year preceding recruitment is that recruits might be prospecting for a high-quality patch. They might make the decision of where they are going to settle and breed for the first time at least a year in advance. We also considered quadratic models including q_{t-1} squared (q_{t-1}^2), and q_t squared (q_t^2), to evaluate possible monotonic relationships between recruitment probabilities and habitat quality. Testing for a positive linear relationship between recruitment probability and cliff quality is testing whether recruitment probability increases as cliff quality increases. A quadratic relationship term may account for higher recruitment probabilities in habitat of medium quality and lower recruitment probabilities in habitats of poor and high quality, or conversely if the sign is switched. We also considered a model without any covariate accounting for habitat quality to address the ‘null’ biological hypothesis that is a lack of influence of habitat quality on recruitment probability.

Since one must assign a covariate value to each individual, we had to dispense a value to individuals that did not recruit and for which recruitment-habitat characteristics did not exist (i.e. individuals that have never reproduced, died before recruitment, or emigrated out of the study area before recruitment). Following Cooch and White’s (2006) two-step solution to the ‘missing-value’ issue, we assigned average covariate values to individuals that did not recruit (i.e. q_t =0.464, q_t^2 =0.215, q_{t-1} = 0.456, q_{t-1}^2 = 0.208). This may artificially skew the estimate of transition probability towards these values (i.e. habitat patches of intermediate quality). To assess the importance of the bias, we compared our results (i.e. models receiving large support) to recruitment estimates obtained in a second set of analyses, where no covariates were involved, but where states were defined differently and accounted for the quality of the recruitment habitat.

The second approach assesses the effect of habitat quality on transition probabilities Ψ_i^{rs} (from non-breeding state *r* to breeding state *s*) by specifying four states. We considered (1) pre-breeders; (2) breeders recruiting in high-quality cliffs (i.e. cliffs where local productivity is between 66 and 100%); (3) breeders recruiting in cliffs of intermediate quality (i.e. local productivity between 33 and 66%); and (4) breeders recruiting in poor quality cliffs (i.e. local productivity between 0 and 33%). Because the previous approach indicated that models including habitat quality the year preceding recruitment performed better than others (according to information criteria, Burnham and Anderson, 1998, see also results), the categorical index of habitat quality used in the second approach to define the states is based on habitat quality the year preceding recruitment.

Our models included covariates (i.e. various measures of habitat quality) or breeding states accounting for habitat quality, as well as age and cohort effects on transition probabilities. We never used interaction terms between age and cohort as it would be equivalent to considering a time effect. However, additive models allowed disentangling age effects on recruitment probabilities from cohort-related effects. The latter may reflect long lasting birth-year effects on age-specific recruitment probabilities (e.g. climatic effects). We also used such additive models (cohort + age) for purely technical reasons, that is to fix some parameters to zero according to the specificity of the distribution of ages at recruitment in the different cohorts (e.g. if in the birth cohort 1992, the minimum transition from a non-breeding to a breeding state occurred between ages 3 and 4, the 'cohort + age' format allowed us to fix the parameters representing the probability of recruitment in younger age classes to zero, such as recruitment probabilities in between age 0 and 1, 1 and 2, or 2 and 3).

Model Selection

Based on prior studies of recruitment probability (Cam and Monnat 2000a; Cam et al. 2002b, 2003, 2005), and movement among colonies of black-legged kittiwakes in Brittany (Danchin and Monnat 1992; Danchin et al. 1998), we were primarily interested in hypotheses pertaining to the relationship between age-specific recruitment probability and habitat selection, conditional on age-and state-specific survival. Accordingly, we designed a general model reflecting all biological processes of interest. Because recapture probability of the youngest pre-breeders is known to be low, sample sizes within age-by-state combinations were assessed to design the most general model (i.e., such model would test for age-specific recapture probabilities for juveniles, e.g. Cam et al. 2002b, 2003, 2005).

Previous studies indicated that adult recapture probabilities have always been ≈1 in the study area (Danchin and Monnat 1992; Cam et al. 1998, 2005), hence we assumed that adult recapture probabilities were independent of time and cohort in all models: p2(.) (state ‘2’ corresponds to adults i.e., after recruitment). On the contrary, we expected recapture probabilities to vary with age amongst pre-breeders: p1(.) (state ‘1’ corresponds to pre-breeders). As the majority of pre-breeders recruit before 7 years old, we pooled data from pre-breeders of age 7 or more (i.e., recapture at age 1, 2, 3, 4, 5, 6, 7 or greater).

Previous work also indicated that apparent survival probability is lower for pre-breeders than for breeders (Cam et al. 2005), as they might be subjected to greater extrinsic causes of death than adults, or have a higher probability of permanent emigration. Therefore, we considered a 7 age-class effect on pre-breeders’ survival as well. Climatic conditions experienced during early development or during the first winter at sea may affect differently each birth cohort justifying why we considered cohort variations in pre-breeders’ survival (i.e. S1(c12, a7), where ‘c12’ stands for the cohort effect and ‘a7’ for the seven age-class effect). We did not consider cohort variation in adult survival, as we were trying to limit model size (i.e. number of estimated parameters). We focussed preferentially on the parameters of interest (i.e. parameters representative of the ‘pre-breeding’ stage, and of ‘first-time breeding’ events). We then considered an age effect on adult survival (denoted as S2(a5)). In the case of adults, we defined only 5 age classes (i.e. a5 defines age classes 2, 3, 4, 5, 6, 7+, where 7 + stands for individuals aged 7 years old and more), as the minimum age to become a breeder is 2 years old.

The last set of assumptions concerns the probability of transition from a non-breeding to breeding state, Ψ . As previous studies have provided evidence of an increase in recruitment probability with age, and in a limited sense, with experience as well (Cam et al. 2002b, 2003, 2005), we considered age effects on transition probabilities. Also, we included an additive cohort effect to account for the influence of annual environmental change (climatic conditions or predation events affecting the proportion of high-quality breeding habitats available to recruits), when individuals belonging to different cohorts reach the age at which transition to the breeding state is theoretically possible. Such environmental factors may influence age-specific recruitment differently from one cohort to another. As our primary objective was to examine the influence of habitat quality on age at first reproduction, we also included the effect of habitat quality, either by using individual covariates (approach 1), or by stratifying the data set into different states, reflecting different combinations of habitat quality and age (approach 2). The initial model accounted for an age effect on recruitment probabilities characterized by 6 age-specific transition probabilities (transition in between 1 and 2 years old, 2 and 3, 3 and 4, 4 and 5, 5 and 6, 6 and 7). Transition probabilities were denoted $\Psi12(c12+a6+q_t+q_t^2+(a6\times q_t)$ in the first approach and $\Psi12(c12+a6)$ $\Psi13(c12+a6)$ $\Psi14(c12+a6)$in the second, where 2, 3 and 4 corresponded to the three different habitat qualities (i.e. poor, medium, high) in which a bird can recruit. As transitions cannot biologically occur in the opposite direction, $\Psi21(.)\Psi31(.)\Psi41(.)$ were fixed to zero. For each approach, our starting model was defined as follows:

Approach 1 (with individual covariates):

$S1(c12+a7)S2(a5)p1(a7)p2(.)\Psi12(c12+a6+q_t+q_t^2)$ $\Psi21(.)$

Approach 2 (discrete states):

$S1(c12+a7)S2(a5)S3(a5)p1(a7)p2(.)p3(.)p4(.)\Psi12(c12+a6)\Psi13(c12+a6)\Psi14(c12+a6)$

We acknowledge that both global (starting) models are not saturated, even though it would be desirable to compare the performance of saturated models and less parameterized ones. A saturated model is defined as the model where the number of parameters equals the number of data points. Such a model is needed to compute the baseline deviance, which is in turn used to estimate the amount of over-dispersion in the data (Cooch and White 2006). However, we had to limit the degree of stratification of the data to make parameter estimation feasible. Furthermore, the large number of biological parameters of interest made it difficult to define a small set of alternative models defined ‘a priori’ (Burnham and Anderson 1998). We sequentially specified models by simplifying the starting model to test for specific biological hypotheses. Nevertheless, we acknowledge that sequential development of models might lead to different conclusions compared to considering a set of models defined a priori.

Unfortunately, formal goodness-of-fit tests for MS models do not allow for treatment of situations with permanent transitions (Pradel 2006). As an alternative approach to a formal goodness-of-fit test, we estimated an overdispersion parameter (i.e. $\hat{c}$) for the global model without individual covariates (approach 2 described above) using bootstrap simulations in MSSURVIV (Hines 1994). We used Akaike’s Information Criterion modified for small sample size, AICc, in the first approach (where no overdispersion parameter $\hat{c}$ can be calculated), and the qAICc modified for overdispersion in the second approach (where q stands for quasi-likelihood; Akaike 1973, see also Sakamoto et al. 1986; Lebreton et al. 1992; Burnham and Anderson 1998). We also used Akaike’s weights, w_i, to select the best models from our set of candidate MS models in both approaches 1 and 2. Only models with an Akaike weight exceeding 0.95 were systematically retained. If the weight was shared among 2 or more models, we discussed the interpretation of each of them.

2. Estimation of Breeding Success in the Year of Recruitment

2.1. Sample Specifications

Only individuals that survived until recruitment and recruited were considered in analyses of breeding success (1450 individuals, 5054 observations). More specifically, we addressed breeding success probability in the year of recruitment and in subsequent breeding occasions.

As emphasized above, for birds recruiting in the Cap Sizun, the probability of recapture is virtually 1 after recruitment (Cam et al. 1998, 2005). Working on the sample of individuals that has recruited allows us to use simple statistical models that do not account for recapture probabilities, such as generalized linear models and mixed models. Individuals whose breeding success in the year of recruitment was unknown or uncertain were excluded from the analyses. Only individuals that fledged at least one chick up to independence were considered ‘successful’, others were considered to have ‘failed’.

2.2. Generalized Linear Models (glm) and Mixed Models (glmmM)

We used generalized linear models (Agresti 1990) to address the influence of two covariates (i.e. age at first reproduction and habitat quality) on breeding success probability, a binary response variable (i.e. success versus failure). Sample sizes incited us to minimize the number of states in the analysis, thus we did not include different levels of failure (e.g. early failure when the chick dies at the nest or late failure when the chick died at fledging) or success (e.g. kittiwakes generally produce 1 or 2 eggs, and occasionally produce up to 3 eggs, and may fledge several chicks).

We built a series of glms (use of the logit link) accounting for cliff quality the year preceding recruitment (found to be a better predictor of the recruitment process than cliff quality the year of recruitment, see Results) and age at recruitment. Age at recruitment was treated either as a continuous or as a categorical covariate. We tested several transformations of cliff quality (i.e. proportions of successful nests within a cliff in a given year):

– the arcsine transformation, suitable for binary data summarized as proportions.

– the square root transformation, suitable for Poisson-distributed covariates where sample means are proportional to the variances of the respective samples; replacing each measure by its square root will often result in homogeneous variances (Neter et al. 1996).

We also built models including a quadratic effect and a cubic effect of age and habitat quality on breeding success probability. A quadratic effect of cliff quality on success probability would mean that maximum (or minimum) success probability is reached in cliffs of intermediate quality. Similarly, a quadratic effect of age on success probability would account for a minimum, or maximum breeding success at intermediate ages. A cubic relationship would account for a bimodal pattern in success probability as a function of covariates.

We accounted for temporal variation in breeding success (possibly resulting from environmental fluctuations; e.g. climatic conditions, predation events, food shortage, etc.) by incorporating a random effect of time (year) only to the best performing model. We modeled year as a random effect for two reasons. First, we had no motive to suspect any specific shape for the influence of year on breeding success probability (e.g. a systematic trend). Second, using a random effect to account for temporal variation in breeding success leads to fewer parameters than a fixed effect model. We viewed this as an advantage (i.e. larger sample sizes) to address the influence of covariates more relevant to hypotheses pertaining to habitat selection (e.g. habitat quality). We used the package ‘glmmML’ (i.e. package ‘MASS’, R version 2.3.1) to implement mixed models.

2.3. Model Selection

First, we compared pairs of models containing the same covariate but parameterized in different ways (e.g. a model containing the age at first reproduction AFR, treated as a continuous covariate, was tested against a model containing AFR treated as a factor). After retaining the best parameterization, we compared models with an additive effect or an interaction term. Each model was created to discriminate between various underlying biological hypotheses. The models selected will be discussed in the results. For model comparison, we only reported model selection based on Akaike’s Information Criterion AIC (Akaike 1973; Burnham and Anderson 1998), as results based on AICc were consistent with results based on AIC.

Results

1. Estimation of Recruitment Probabilities as a Function of Habitat Quality: A CMR Approach Using Multi-State Models

The estimated overdispersion parameter (i.e. variance inflation factor) for the global model without covariates was 1.94 (bootstrap procedure in MSSURVIV, 1000 simulations).

1.1. Analysis with Individual Covariates

The best model, '2-state-model-19', is structured as follow (see Appendix 1; Table 1):

S1(c12+a6)S2(.)p1(a4)p2(.)Ψ(c12+a6+q_{t-1}+q_{t-1}^2)Ψ21(.)

This model includes a cohort effect on survival probability of pre-breeders S1(c12+a6) , and survival probability at a given age varied according to birth year. Pre-breeder survival also varied across ages (i.e. survival probabilities between ages 0-1, 1-2, 2-3, 3-4, and 4-5 years old were significantly different).

Adult survival probability was best accounted for by a model with constant survival across ages and cohorts 'S2(.)'. The recapture probability of pre-breeders did not vary across cohorts, but varied across ages 'p1(a4)''. The best model retained had a 4 age-class structure (0-1, 1-2, 2-3, and 3-4 years old and more) showing a non-negligible difference in recapture probabilities across age groups. Recapture probability of adults was 1, regardless of cohort and age class 'p2(.)' and confirms previous findings (Danchin and Monnat 1992; Cam et al. 1998; 2005). The probability of transition from the 'pre-breeding' to the 'breeding' state varied across cohorts and ages 'Ψ12(c12+a6+q_{t-1}+q_{t-1}^2)'. The model selected included six age classes (transition from 1 to 2, 2 to 3, 3 to 4, 4 to 5, 5 to 6 and 6 to 7+ years old and more). Averaged across cohorts, the recruitment probability between ages 1 and 2 was close to zero (only a handful of individuals recruited at such an early age). Model selection provided support for a model where recruitment probability increased with age at such an early age.

Model selection provided support for a model where recruitment probability increased with age at first breeding up to 5 and 6 years of age, after which it declined (i.e. recruitment probability peaks for the transition occurring in between age 5 and 6; Fig. 1). The model selected also included an effect of cliff quality the year preceding recruitment (i.e. q_{t-l}), largely preferred (according to AICc) over a model with an effect of cliff quality in the recruitment year (i.e. q_t), and over a model without a covariate accounting for cliff quality. Moreover, a quadratic effect of cliff quality in the year preceding recruitment (i.e. $q_{t-l} + q_{t-l}^2$) received more support than a linear effect (Table 1). Thus, for each recruitment tactic, maximum recruitment probability occurred in cliffs that were of intermediate quality in the year preceding recruitment (Fig. 1).

One may argue that this result does not reflect any active individual choice, but rather that the availability of habitat patches of intermediate quality exceeds that of patches of other qualities (i.e. poor and highly productive cliffs). Individuals may simply distribute themselves randomly according to habitat availability. That is true in less than half of the cases (see Table 2, years 1986, 1987, 1991, 1992, 1999, 2000 and 2002). Consequently, a higher recruitment probability in cliffs of intermediate quality cannot be interpreted as resulting exclusively from a spatially random recruitment process. In more than half of the years included in this study, individual choice and/or constraints led recruits to select habitat features different from those that would be obtained by random settlement.

1.2. Analysis Without Individual Covariates

The above results provided evidence that models including an effect of cliff quality in the year preceding recruitment on recruitment proportions (percentage recruited as a function of age at first reproduction and habitat quality) best fit the data. In the second approach (i.e. without individual covariates), we therefore defined three states for breeders (‘2’, ‘3’, and ‘4’, settling in poor, medium, and high quality habitat patch, respectively) according to cliff quality in the year preceding recruitment, as the model including a quadratic form of this covariate was found to perform better than models including cliff quality the year of recruitment (Appendix 2; Table 3).

The best approximating model, ‘4-states-model-21’, had the following structure:

S1(c12+a6)S2,3,4(a3)p1(a5)p2,3,4(.)Ψ12(c12+a6)Ψ13(c12+a6)Ψ14(c12+a6)

This model included a cohort effect on pre-breeder survival, ‘S1(c12)’, showing that birth year influences survival. In addition, pre-breeder survival probabilities changed with age, S1(a6) (i.e. survival probabilities from age 0 to 1, 1 to 2, 2 to 3, 3 to 4, 4 to 5, and from 5 years old to any higher age were significantly different). Adult survival probability did not vary across cohorts or across cliff qualities in the year preceding recruitment. We did however detect an age effect on adult survival (where individuals aged 3, 4, 5 years old and more had different survival probabilities: ‘S2,3,4(a3)’.

Recapture probability of pre-breeders was constant across cohorts, but varied across cohorts, but varied across five age classes: 0, 1, 2, 3, 4 years and more; ‘p1(a5)’. For adults, neither cliff quality, cohort, nor age influenced recapture probabilities.

Recruitment percentages varied according to birth cohort and age (transition probabilities from 1 to 2, 2 to 3, 3 to 4, 4 to 5, 5 to 6, 6 to 7 years old and more were significantly different). Consistent with the results obtained using the previous approach, transition percentages were highest at intermediate ages (i.e. 5 and 6 years old; quadratic age effect on recruitment probability). In addition, age-specific recruitment percentages varied according to cliff quality in the year preceding recruitment, and were higher in habitat patches of intermediate quality Fig. 2).

2. Breeding Success the Year of Recruitment

The best model contained both an effect of age at first reproduction (treated as a factor: AFR = 3, 4, 5, 6, 7 years old and more) and a quadratic effect of cliff quality, on breeding success (Table 4; Fig. 3). Breeding success probability was maximal for individuals recruiting at an intermediate age of 5 years old (Fig. 3). By including a random effect of time in this model, the AIC dropped by 1 unit, down to the value of 1613, providing slight evidence of yearly variation in breeding success over time.

Discussion

In this paper, we first aimed at examining whether habitat selection and age at recruitment were linked, and if so, which recruits gained the best breeding habitats: early recruits or individuals delaying recruitment. We also examined which recruitment tactic led to the highest breeding success in the year of recruitment. Overall, this paper studies (1) recruitment-habitat selection, (2) when and where recruits breed for the first time, and (3) breeding success as a function of the location and the age at which individuals recruit.

1. The Timing of Habitat Selection, Habitat Quality and Age-Specific Recruitment

A number of investigators (Danchin 1988b; Danchin et al. 1991, 1998; Cadiou et al. 1994) have suggested that dispersers actively select their recruitment habitat the year preceding settlement (e.g. the number of prospectors in habitat patches depends on their current productivity; Cadiou 1993). Corroborating their hypothesis, we also observed that models including cliff quality the year preceding recruitment performed better in explaining the recruitment process than models including cliff quality the year of recruitment (Appendix 1; Table 1). Two scenari can be proposed. Habitat selection may take place in the year of recruitment based on information available at the beginning of a breeding season on habitat quality (i.e. information based on social activity and attendance of individuals that bred in that patch the previous year and returned to the same breeding patch). Such information may be strongly autocorrelated to local productivity in the preceding year (Boulinier et al. 1996). However, young recruits (i.e. recruiting at 3 years old) might only benefit from an imperfect knowledge of cliff quality, as they arrive on average 2 months later than individuals delaying recruitment (based on direct observations). Alternatively, settlement decisions may be made the year preceding recruitment. This implies that pre-breeders prospect for a breeding ground at least a year in advance (Danchin et al. 1991). Both scenarii rely on the assumption that habitat quality in a given year t is a reliable indicator of its quality in year $t + l$ (Boulinier and Lemel 1996). If so, temporal autocorrelation in breeding success over 2 consecutive years in a given patch should allow pre-breeders to locate a higher-quality breeding location a breeding season in advance. Although we only considered habitat quality in the year of recruitment and the year preceding recruitment, recruitment probability may depend on past productivity over several consecutive years (with temporal autocorrelation of cliff quality being superior to a year).

In most age classes, recruitment probability in a given year (from 1986 to 2003) was highest in cliffs of intermediate quality the year preceding recruitment (with the exception of individuals recruiting at age 2, for which transition probabilities are not reliable as sample size is very small). According to habitat selection theory, if no constraints are operating (i.e., no competition, no dominance in social hierarchy, and if individuals have information on the range of habitats available), we might expect natural selection to favor habitat selection tactics that maximize selection to favor habitat selection tactics that maximize fitness (Holt and Barfield 2001). That is, recruitment probability should be highest in the most productive cliffs, where the fitness prospects are maximal. Our results do , and therefore suggests the existence of constraints. High-quality cliffs may not be accessible to most recruits (i.e. the youngest). They may be constrained to breed in habitats where competition for nest-sites is lower. Our results also provided evidence that older first-time breeders recruit in habitats of lower quality than intermediate age individuals; therefore, the queuing hypothesis is unlikely to explain the pattern observed in these recruits. Features of individual quality relevant to habitat selection may involve differences in behavioral maturity, social and territorial dominance. These differences could be expressed in terms of the age at recruitment, whereby old recruits (i.e. of low intrinsic quality) can only afford to breed in low-quality patches because of competitive inferiority. However, in the case of young recruits, if they are sometimes assumed to be of high intrinsic quality (Nur 1988), we did not (Nur 1988), we did not find evidence that this translates into access to higher-quality habitat, as they do have the advantage of an early breeding start, but still do not recruit on the best breeding-sites. These individuals may not be of lower intrinsic quality, they may simply lack competitive skills. Behavioral maturation may explain why individuals recruiting at intermediate age have access to higher-quality sites.

These results are valuable only if one assumes that recruits make an active selection of the habitat in which they will breed for the habitat in which they will breed for the first time. One could imagine that individuals breed preferentially in intermediate quality cliffs because these are more abundant than other cliffs type (i.e. cliffs of low or high quality). However, our results suggest that we are observing the outcome of an individual choice involving active habitat selection rather than random settlement. Indeed, over all the years studied, the proportion of cliffs of intermediate quality was not larger than the proportion of cliffs of high or poor quality, as cliffs of low, high, and intermediate quality were equally available in the study area. In addition, we acknowledge that density dependant processes may in cliffs of high or poor quality, as cliffs of low, high, and intermediate quality were equally available in the study area. In addition, we acknowledge that density dependant processes may influence settlement decisions. However, we believe that density dependance alone cannot explain the observed distribution of recruits according to habitat quality. Indeed, behavioral studies have provided evidence that creation of new nest-sites by pre-breeders is possible even in highly productive patches, but that this option is not usually preferred by pre-breeders: they mostly compete for occupied sites (Cadiou 1993; Cadiou et al. 1994).

Both multi-state modeling approaches showed age-related variation in recruitment probability, with highest recruitment probabilities reached at intermediate ages (transition probability in between 5 and 6 years old). Yet, a non-negligible proportion of individuals recruited earlier (i.e. recruitment probability of 0.15 at age 3, and approximately 0.40 at age 4). Age-specific variation in recruitment probability, more specifically the initial increase in recruitment probability, may partly reflect the progressive acquisition of behavioral and physiological maturity of individuals in the population. Whether individuals delaying reproduction do so because they are not sexually mature, or because of a lack of behavioral maturity (in sexually mature individuals), is beyond the scope of this paper: physiological and behavioral data are required to address this question. However, within the framework of physiological and social constraints (e.g. competition), it is possible to address whether there is scope for natural selection processes to operate on age of first breeding by evaluating and comparing fitness components associated with each age-specific recruitment tactic. We addressed whether there was a relationship between each tactic and age-specific reproductive success in the recruitment year to determine which one(s) might yield highest breeding success levels.

2. Breeding Success

We found evidence that birds recruiting at intermediate ages (i.e. recruiting at age 5) experienced the highest reproductive success in the year of recruitment. These results complete our findings regarding age-specific recruitment probability, where again, the highest probability of recruitment was observed at that age. Based on these results, it is tempting to suggest that the age at first reproduction has been shaped by an optimization process. Under this view, recruiting around age 5 (i.e. delaying recruitment up to intermediate ages) would be associated with fitness advantages that offset the direct costs of delayed recruitment (i.e. costs such as ‘missed’ breeding opportunities in comparison with individuals recruiting earlier).

One of the predictions of life history theory is that early reproduction should be favoured by natural selection in stable or increasing populations (Stearns 1992; Charlesworth 1994), except in situations where delayed reproduction is beneficial in terms of fitness. A well-known case explicitly addressed by Charlesworth (1994) is when reproductive success increases with age, experience (or both). In this case, theory suggests that younger individuals may balance the potential benefits of recruiting early (e.g. more breeding events accumulated throughout life compared to recruits delaying first reproduction), with the cost of unsuccessful breeding attempts early in life (Charlesworth 1994), as the youngest recruits lack experience and have a higher probability of breeding failure than others. Also, the time spent prospecting for a site may provide benefits in terms of information gathered on a potential breeding site, despite the costs associated with missing breeding opportunities (Boulinier and Danchin 1997). Early recruitment in this population is indeed associated with low reproductive success in the year of recruitment. Behavioural maturity and competitive abilities gained before breeding may explain why individuals recruiting at intermediate ages exhibit higher breeding success than early recruits (Nol and Smith 1987; Lunn et al. 1994).

Also, it has been suggested that heterogeneity in individual quality contributes to explain the age-specific variation in age at first breeding (Nur 1988; Curio 1983). According to this hypothesis, higher-quality individuals are assumed to be able to invest more into reproduction without incurring as large costs as lower-quality individuals; this may favor early investment into reproduction for higher-quality individuals. At this point, our results concerning breeding success probability are not consistent with this hypothesis. Overall, our results provided evidence that the youngest first-time breeders (the ones that theoretically are assumed to be of highest intrinsic quality: Nur 1988; Pyle et al. 1997), experienced the poorest breeding success probability in the recruitment year, compared to intermediate-age recruits, regardless of the quality of the recruitment habitat. However, it is possible that early recruits improve their breeding success as they age and gain experience; again, they may not be of lower intrinsic quality. Heterogeneity in quality among individuals may explain only partially our results: the decrease in recruitment probability in first-time breeders after age 5 (i.e. individuals delaying recruitment), and the fact that late breeders recruit in lower-quality habitat than birds recruiting at intermediate age. Social inferiority may prevent these individuals from beginning reproduction earlier in life. However, their breeding success probability in the year of recruitment is high: experience gained over a longer pre-breeding period may result in this pattern.

Attempting to explain the evolutionary (dis)advantages of early or delayed recruitment by addressing reproductive success in the first breeding attempt exclusively is too restrictive: first reproduction is only a snapshot of the lifetime profile of reproductive success for individuals recruiting at various ages in each habitat type. However, this first step was crucial in the understanding of the age-specific recruitment process and how it is related to habitat selection theory.

3. Prospects

Regarding habitat selection mechanisms, preliminary analysis conducted in the same study population (Aubry, unpublished; Bled 2006; Bled et al. in prep), suggests that it is critical to work at a much finer spatial scale to address recruitment; that is the nest-site itself, within a given cliff (e.g. it may be disadvantageous to gain ownership on a site of poor quality within the most productive cliff). Using an approach based on the quality of patches, there is no clear hierarchy among age classes in terms of access to habitat of lower, intermediate, or higher quality, but there is a relationship between habitat quality at the patch level and success probability in the year of recruitment. The shape of the relationship between age and success probability (which is highest in birds of intermediate age) cannot be explained by higher recruitment probability in higher-quality habitat: intermediate age first-time breeders do not recruit in higher-quality habitats than others (e.g. the interaction between age and quality was not retained in multi-state models with individual covariates).

Heterogeneity in quality among sites within habitat patches may obscure the relationship between habitat quality, age, and individual success probability. A more detailed study of habitat selection at the site level may help understand the observed in the site level may help understand the observed influence of age on breeding success probability. In this mobile species exhibiting breeding dispersal (Danchin and Monnat 1992; Danchin et al. 1998), it may not be possible to fully understand age-specific variation in fitness components (e.g. variation over life) without considering features of the habitat where each reproductive event takes place. But the very high degree of stratification required by such analysis of age-specific reproductive success as a function of habitat quality may be a major obstacle, and further work is needed to assess whether it is feasible using this data set. The study of reproductive success indicates that reproductive choices and/or the constraints met during the pre-reproductive stage of life may influence age at recruitment, which may in turn have substantial effects on breeding success over life. To address the overall fitness of recruitment tactics, one may consider measures of lifetime fitness such as Lifetime Reproductive Success (Clutton-Brock 1988), or individual lambda (McGraw and Caswell 1996). This would be a first step to assess whether different tactics are associated with a different total number of viable offspring, and if there is scope for natural selection to operate on age of first breeding in a different manner than understood on the basis of breeding success in the first breeding attempt exclusively. However, the same lifetime fitness may be achieved in very different ways in terms of longevity, age-specific reproductive investment, and choices in terms of habitat selection. As for further investigations, an interesting step to take would be to look over the life course of individuals recruiting at different ages (i.e., recruitment tactics), and determine whether breeding success improves, shows senescent decline, or remains the same across ages for the different recruitment tactics identified above. Our results provided evidence that early recruits (i.e. 3 years old) start their reproductive life with a handicap, as their initial breeding success probability is the lowest (Fig. 3). It would be worth addressing whether recruits experiencing poor breeding success in the year of recruitment catch up and perform increasingly better throughout life. One may also assess whether individuals recruiting at intermediate ages (i.e. recruits of 5 years old which show the highest reproductive success in the recruitment year), are the ones performing best overall (i.e. highest r), are the ones performing best overall (i.e. highest fitness prospects). Last, one may determine if recruiting beyond this age leads to the lowest fitness prospects or not. Assessing fitness differences among reproductive tactics and determining the selective advantages of adopting one tactic or the other will require additional work (e.g. Evolutionary Stable Strategy modeling; Maynard Smith 1982).

Moreover, our work suggests that there may be a substantial level of individual heterogeneity in the study population (i.e. variation in age-specific recruitment tactics leading to variation in reproductive success), and highlights the need to develop multi-state models for estimating transition probabilities while properly accounting for unobserved heterogeneity in reproduction (and in survival) in cases where recapture probability is lower than 1. Multi-state CMR models allowed us to address the influence of observable covariates on recruitment probability, but measurable covariates may not account for heterogeneity in a satisfying manner. Heterogeneity in survival (e.g. frailty) has been looked at in human demography starting some 20 years ago (Vaupel and Yashin 1985), and ecologists have long been concerned with heterogeneity as well (e.g. Burnham and Rexstad 1993; Pledger and Schwarz 2002). However, developments regarding heterogeneity in both survival and reproductive success in wild animal population are only fairly recent (Burnham and Rexstad 1993; Cam et al. 2002b; Pledger and Schwarz 2002; Barbraud and Weimerskirch 2005; Crespin et al. 2006; Gordon et al. 2006; Royle 2008), and require additional efforts.

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Table 1. Modelling the influence of habitat quality on the recruitment process I: model selection results based on the first approach (approach with covariates, see Methods).

Model selection	AICc	Δ_i	W_i	Likelihood	NP	Deviance
M19	21374.524	0.00	0.76701	1.0000	42	21290.139
M24	21377.211	2.69	0.20010	0.2609	43	21290.808
M13	21382.499	7.98	0.01422	0.0185	43	21296.096
M18	21838.393	8.87	0.00910	0.0119	44	21294.971
M11	21384.450	9.93	0.00536	0.0070	33	21318.211
M7	21384.959	10.44	0.00416	0.0054	33	21318.720
M12	21395.024	20.50	0.00003	0.0000	50	21294.481
M5	21396.504	21.98	0.00001	0.0000	49	21297.981
M4	21397.035	22.51	0.00001	0.0000	51	21294.470
M3	21401.275	26.75	0.00000	0.0000	40	21320.926
M14	21404.876	30.35	0.00000	0.0000	57	21290.171
M20	21406.687	32.16	0.00000	0.0000	58	21289.957
M6	21408.694	34.17	0.00000	0.0000	59	21289.939
M10	21409.743	35.22	0.00000	0.0000	56	21297.062
M16	21418.584	44.06	0.00000	0.0000	43	21332.181
M22	21420.308	45.78	0.00000	0.0000	43	21333.905
M15	21428.026	53.50	0.00000	0.0000	43	21341.623
M21	21430.071	55.55	0.00000	0.0000	43	21343.668
M9	21449.633	75.11	0.00000	0.0000	45	21359.192
M8	21457.564	83.04	0.00000	0.0000	34	21389.310
M17	21643.402	268.88	0.00000	0.0000	38	21567.087
M23	21643.640	269.12	0.00000	0.0000	38	21567.325
M1	21826.923	452.40	0.00000	0.0000	60	21706.142
M2	22666.039	1291.5	0.00000	0.0000	54	22557.406

Note. NP: number of estimated parameters; AIC : Akaike’s Information Criterion = -2 * log-likelihood + 2 * NP; Wi = exp (-0.5 * AIC) / NP

Table 2. Time series of the proportion of poor, medium, and high quality cliffs from 1986 to 2003.

Year	Cliffs of good quality*	Cliffs of intermediate quality**	Cliffs of poor quality***
1986	29%	45%	26%
1987	32%	39%	30%
1988	16%	35%	49%
1989	6%	34%	59%
1990	11%	39%	50%
1991	35%	40%	26%
1992	33%	35%	33%
1993	23%	28%	49%
1994	10%	23%	67%
1995	26%	21%	53%
1996	19%	19%	62%
1997	24%	34%	41%
1998	7%	22%	7%
1999	15%	54%	31%
2000	21%	62%	17%
2001	41%	32%	27%
2002	20%	44%	36%
2003	62%	35%	4%

Note: Cliff quality was calculated the year preceding recruitment as model selection results indicated that this quantity is the best indicator of recruitment among the predictors tested.

* Proportion of cliffs in a given year, that contain a percentage of nest in a success situation within 66 -100%; ** Proportion of cliffs in a given year, that contain a percentage of nest in a success situation within 33-66%; *** Proportion of cliffs in a given year, that contain a percentage of nest in a success situation within 0- 33%.

Table 3. Modeling the influence of habitat quality on the recruitment process II: model selection results for the second approach (approach without covariates, see Methods).

Model selection	qAICc*	Δ_i	W_i	Model Likelihood	NP	Deviance
Md21	32218.346	0.00	0.99986	1.0000	76	16355.973
Md12	32238.696	20.35	0.00004	0.0000	86	16355.972
Md8	32238.719	20.37	0.00004	0.0000	86	16355.995
Md7	32239.662	21.32	0.00002	0.0000	87	16354.902
Md9	32240.723	22.39	0.00001	0.0000	85	16360.037
Md15	32241.168	22.82	0.00001	0.0000	84	16362.519
Md6	32241.493	23.15	0.00001	0.0000	88	16354.695
Md14	32242.875	24.53	0.00000	0.0000	85	16362.188
Md20	32244.710	26.36	0.00000	0.0000	83	16368.097
Md4	32241.596	33.25	0.00000	0.0000	102	16336.222
Md3	32252.425	34.08	0.00000	0.0000	103	16335.007
Md1	32254.470	36.12	0.00000	0.0000	104	16335.006
Md5	32255.393	37.05	0.00000	0.0000	101	16342.063
Md11	32284.666	66.32	0.00000	0.0000	76	16422.292
Md19	32291.690	73.34	0.00000	0.0000	53	16475.957
Md16	32348.777	130.43	0.00000	0.0000	50	16539.111
Md13	32481.934	263.59	0.00000	0.0000	81	16609.391
Md18	32513.794	295.45	0.00000	0.0000	68	16667.669
Md10	32550.205	331.86	0.00000	0.0000	69	16702.051
Md17	32561.200	342.85	0.00000	0.0000	35	16781.809
Md2	34003.867	1785.5	0.00000	0.0000	98	18096.665

Note. NP: number of estimated parameters.

* We used Akaike's Information Criterion modified for sample size qAICc (where q stands for quasi-likelihood) and for an estimated overdispersion parameter of 1.93 using bootstrap simulations (see section 3.1.2.3. for further explanations).

Table 4. Model selection results: generalized linear models and mixed model testing the effects of age at recruitment and habitat quality on breeding success in the year of recruitment.

Model	NP	AIC	Δ_i	exp(-0.5 * Δ_i)	w_i
AFR.cat + $(\text{Cliff})^2$ + ε (time)*	**7**	**1613.0**	**0.0**	**1.000**	**0.609**
AFR.cat * $(\text{Cliff})^2$	10	1619.6	6.6	0.037	0.022
AFR.cat + $(\text{Cliff})^2$	6	1614.0	1.0	0.606	0.369
Cliff + $(\text{Cliff})^2$	3	1658.4	45.4	0.0	0.0
Sqrt (Cliff)	2	1668.5	55.5	0.0	0.0
$(\text{Cliff})^2$	2	1656.9	43.9	0.0	0.0
Arcsin (Cliff)	2	1661.1	48.1	0.0	0.0
Cliff	2	1659.6	137.3	0.0	0.0
AFR + $(\text{AFR})^2$ + $(\text{AFR})^3$	4	1733.0	120.0	0.0	0.0
AFR + $(\text{AFR})^3$	3	1735.8	122.8	0.0	0.0
AFR + $(\text{AFR})^2$	3	1734.5	121.5	0.0	0.0
AFR.cat	5	1733.3	120.3	0.0	0.0
AFR	2	1750.3	137.3	0.0	0.0

Note. Model selected in bold characters; the model in italics was not retained but had some weight in explaining the biological process that gave rise to the data; we used a mixed model to add a random time effect 'ε(time)' to the best performing glm model; '+' additive effect; '*' interaction; NP = number of estimated parameters; AIC : Akaike's Information Criterion = -2 * log-likelihood + 2 * NP; wi = exp (-0.5 * ΔAIC) / ∑exp(-0.5 * ΔAIC).

Covariates: age at first reproduction (AFR if continuous, AFR.cat if categorical, AFR2 for a quadratic effect); cliff quality (Cliff if continuous, Arcsin (Cliff) if arcsinus transformed, Sqrt (Cliff) if the square root was taken, Cliff2 for a quadratic effect).

Figure 1. Recruitment probabilities as a function of habitat quality and age at first reproduction.

Cliff quality was calculated the year preceding recruitment (continuous covariate). Recruitment probabilities were estimated from the best performing multistate model. Recruitment probabilities were averaged across cohorts (birth cohorts 1986 to 1997, followed from 1986 to 2003).

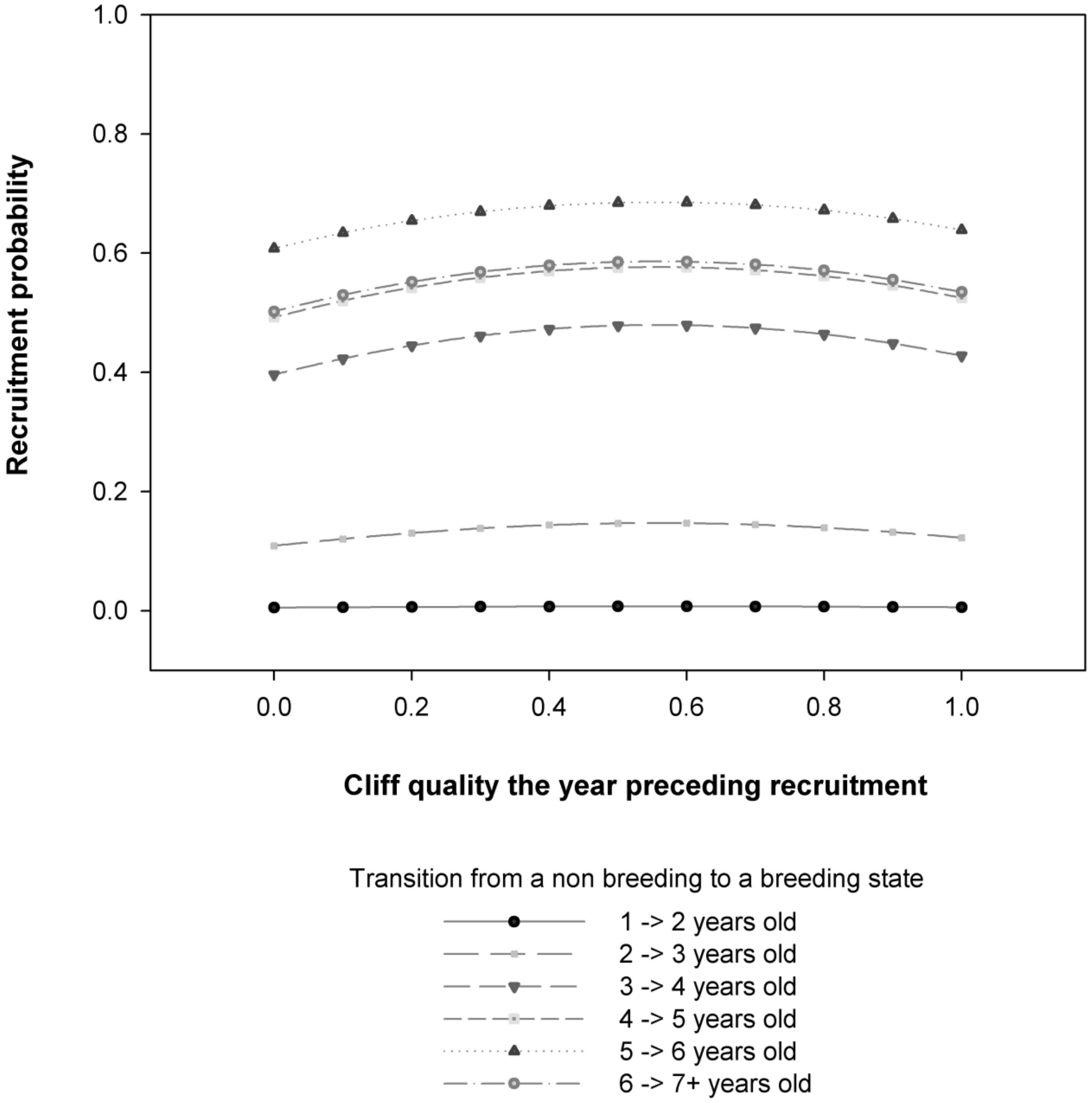


Figure 2. Recruitment probability as a function of habitat quality and age at first reproduction.

Cliff quality was calculated the year preceding recruitment. Three states account for the quality of the recruitment habitat the year preceding recruitment: poor, medium and high quality cliff. A fourth state accounted for the pre-breeding segment of the population. Recruitment probabilities were estimated from the multistate model that received the most support, and were averaged across cohorts (birth cohorts 1986 to 1997, followed from 1986 to 2003).

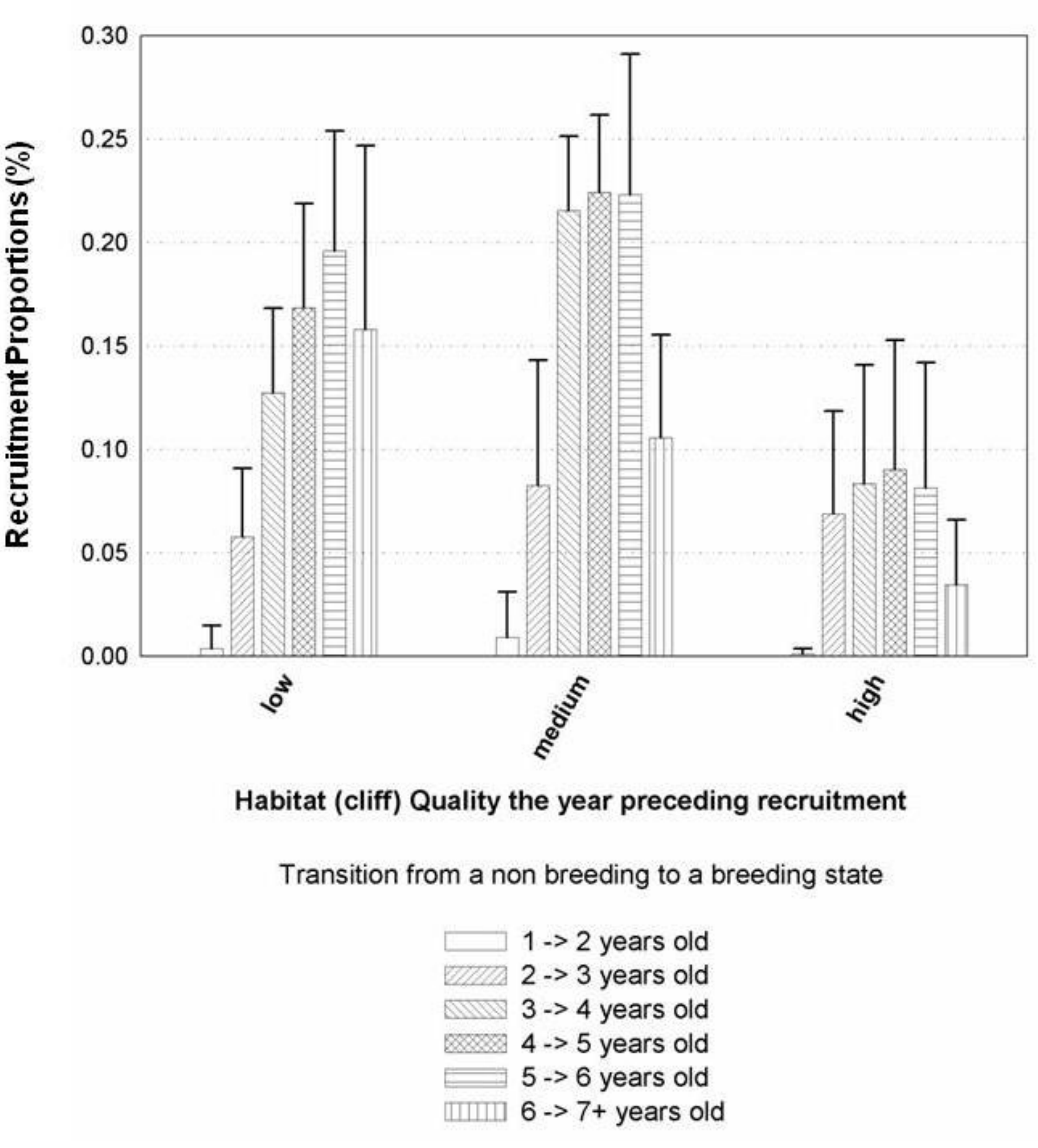
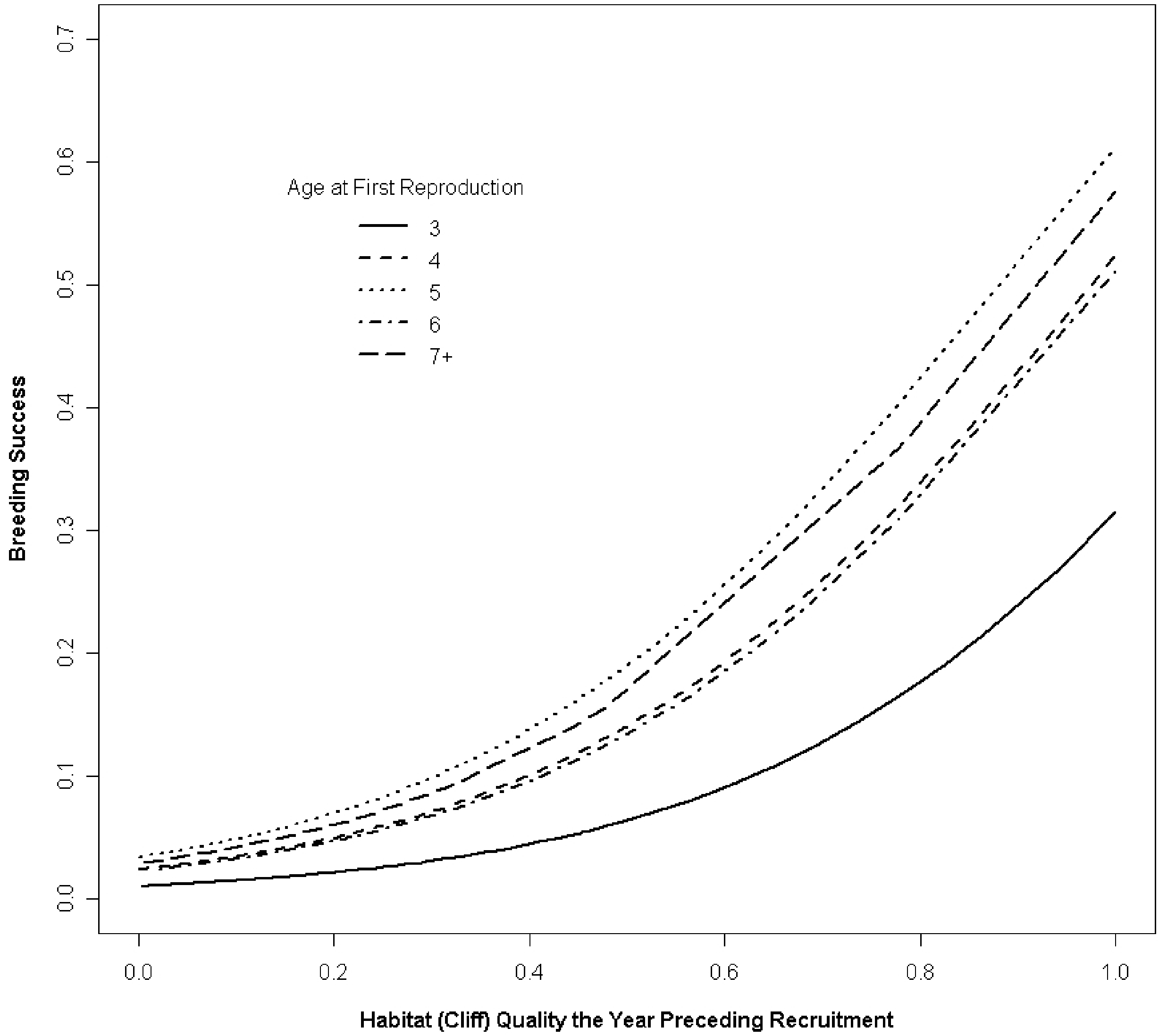


Figure 3. Breeding success the year of recruitment as a function of cliff quality the year preceding recruitment and age at first reproduction.



Appendix A. Multistate models based on biological hypotheses concerning the recruitment process using the first approach (described in section 3.1.2.2.) while accounting for potential sources of variation in recapture and survival probabilities.

Model	Recapture probability	Survival probability	Transition probability
2-state-model-1	p1(a7), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a6+q1+q1c+,(a6*q1)), Ψ21(.)
2-state-model-1bis	p1(a7), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a6), Ψ21(.)
2-state-model-2	p1(.), p2(.)	S1(c12+a7), S2(a5)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-3	p1(a6), p2(.)	S1(c12+a7), S2(a5)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-4	p1(a5), p2(.)	S1(c12+a7), S2(a5)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-5	p1(a4), p2(.)	S1(c12+a7), S2(a5)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-6	p1(a3), p2(.)	S1(c12+a7), S2(a5)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-7	p1(a4), p2(.)	S1(c12+a7), S2(.)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-8	p1(a4), p2(.)	S1(.), S2(.)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-9	p1(a4), p2(.)	S1(c12), S2(.)	Ψ12(c12+a6+q1+q1c+,(a6*q1)), Ψ21(.)
2-state-model-10	p1(a4), p2(.)	S1(a7), S2(.)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-11	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-12	p1(a4), p2(.)	S1(c12+a5), S2(.)	Ψ12(c12+a6+q1+q1c+(a6*q1)), Ψ21(.)
2-state-model-13	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a6+q1+q1c), Ψ21(.)
2-state-model-14	p1(a4), p2(.)	S1(c12+a7), S2(a5)	Ψ12(a6+q1+q1c), Ψ21(.)
2-state-model-15	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a6+q1), Ψ21(.)
2-state-model-16	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a6+q1c), Ψ21(.)
2-state-model-17	p1(a4), p2(.)	S1(.), S2(.)	Ψ12(c12+q1+q1c), Ψ21(.)
2-state-model-18	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a5+q1+q1c), Ψ21(.)
2-state-model-19*	**p1 (a4) p2 (.)**	**S1 (c12+a6) S2 (.)**	**Ψ12 (c12+a6+q2+q2c) Ψ21 (.)**
2-state-model-20	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(a6+q2+q2c), Ψ21(.)
2-state-model-21	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a6+q2), Ψ21(.)
2-state-model-22	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a6+q2c), Ψ21(.)
2-state-model-23	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+q2+q2c), Ψ21(.)
2-state-model-24	p1(a4), p2(.)	S1(c12+a6), S2(.)	Ψ12(c12+a5+q2+q2c), Ψ21(.)

2-state-model-19*: model selected based on its high AIC weight – w_i= 0.767 (Table 4.1.)

Appendix B. Multistate models based on the biological hypotheses concerning the recruitment process using the second approach (described in section 3.1.2.2.) while accounting for potential sources of variation in recapture and survival probabilities.

Model	Recapture probability	Survival probability	Transition probability
4-state-model-1	p1(a7),p2(.),p3(.),p4(.)	S1(c12+a7),S2(a5),S3(a5),S4(a5)	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-2	p1(.),p2(.),p3(.),p4(.)	S1(c12+a7),S2(a5),S3(a5),S4(a5)	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-3	p1(a6),p2(.),p3(.),p4(.)	S1(c12+a7),S2(a5),S3(a5),S4(a5)	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-4	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a7),S2(a5),S3(a5),S4(a5)	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-5	p1(a4),p2(.),p3(.),p4(.)	S1(c12+a7),S2(a5),S3(a5),S4(a5)	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-6	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a7),[S2(a5),S3(a5),S4(a5)]	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-7	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a7),[S2(a4),S3(a4),S4(a4)]	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-8	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a7),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-9	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a7),[S2(a2),S3(a2),S4(a2)]	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-10	p1(a5),p2(.),p3(.),p4(.)	S1(.),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-11	p1(a5),p2(.),p3(.),p4(.)	S1(a7),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12+a7), Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-12	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a6),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-13	p1(a5),p2(.),p3(.),p4(.)	S1(c12),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12+a7), Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-14	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a5),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-15	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a4),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12+a7),Ψ13(c12+a7),Ψ14(c12+a7)
4-state-model-16	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a6),[S2(a3),S3(a3),S4(a3)]	[Ψ12(c12+a7),Ψ13(c12+a6),Ψ14(c12+a7)]
4-state-model-17	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a6),[S2(a3),S3(a3),S4(a3)]	Ψ12(.),Ψ13(.),Ψ14(.)
4-state-model-18	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a6),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12),Ψ13(c12),Ψ14(c12)
4-state-model-19	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a6),[S2(a3),S3(a3),S4(a3)]	Ψ12(a7),Ψ13(a7),Ψ14(a7)
4-state-model-20	p1(a5),p2(.),p3(.),p4(.)	S1(c12+a6),[S2(a3),S3(a3),S4(a3)]	Ψ12(c12+a6),Ψ13(c12+a6),Ψ14(c12+a6)
4-state-model-21*	**p1(a5) [p2(.) p3(.) p4(.)]**	**S1(c12+a6) [S2(a3) S3(a3) S4(a3)]**	**Ψ13(c12+a6) Ψ13(c12+a6) Ψ14(c12+a6)**

4-state-model-21*: model selected based on its high AIC weight – w_i= 0.99986 (see Table 4.3.)

~ CHAPTER II ~

'WJNOP' is a female kittiwake born in 1999 in colony 3. She went on a pelagic foray, and was found hanging-out with another 3 year old in colony 4 in 2002 (but the two being shy, nothing happened). In 2003, she settled in 5O115 (colony 5, cliff O, nest-site 115) with a new partner and had 2 chicks. For a few years she produced chicks with uneven success, and switched partners several times. In 2007, she finally met her match, a younger 3-year old male, JOOBR. Since then, the two have been seen successfully breeding on 5O25.

Picture: Lise M. Aubry

CONSEQUENCES OF RECRUITMENT DECISIONS AND HETEROGENEITY ON AGE-SPECIFIC BREEDING SUCCESS IN A LONG-LIVED SEABIRD

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Abstract

An individual's age at first reproduction and investment in successive reproductive attempts are involved in mechanisms that can impede somatic repair, resulting in a decline of reproductive abilities with age (reproductive senescence). We used long-term data from the black-legged kittiwake, a long-lived seabird, to address the relationship between recruitment age, age-specific breeding success (BS), and reproductive senescence, while accounting for breeding experience and temporal variation in BS. We first detected late-life improvement in BS across all recruitment groups, which we recognized as 'within-generation selection' or the selective disappearance of 'frail' phenotypes. When such heterogeneity was accurately accounted for, we showed that all individuals suffered reproductive senescence.

We first highlighted how different combinations of pre- and post-recruitment experience across recruitment groups resulted in maximal BS at intermediate ages. BS increased in early recruits as they gained post-recruitment experience, whereas late recruits gained pre-recruitment experience which led to high BS at recruitment. Only individuals recruiting at intermediate ages balanced pre-and post-recruitment experience. Consistent with the 'cumulative reproductive cost hypothesis', we also observed a faster decline in BS in early recruits at advanced ages, whereas individuals delaying recruitment experienced the slowest decline in BS with age. Early recruits however, reached the highest levels of BS at intermediate ages sensus stricto (10 to 13 years old), whereas individuals delaying recruitment experienced the lowest at similar ages. These divergent trajectories may reflect a 'delayed trade-off' balancing a maximization of mid-life BS against reproductive senescence at advanced ages.

Additionally, annual variation in BS had a greater effect on individuals early in life, suggesting that experienced individuals were able to buffer out the effects of temporal variation on BS, which can ultimately improve fitness in stochastic environments.

Our findings stress (i) the importance of both observed and unobserved heterogeneity in detecting ‘within individual senescence’. (ii) Short term trade-offs may be rare in long-lived species; thus cumulated reproductive costs should be invoked as an alternative mechanism underlying reproductive senescence.

Key-words. Age-specific recruitment, black-legged kittiwake, breeding success, delayed cost of reproduction, heterogeneity, reproductive senescence, temporal variation, trade-offs.

CONSEQUENCE DE L’AGE DE PREMIERE REPRODUCTION ET DE L’HETEROGENEITE SUR LE SUCCESS REPRODUCTEUR AU COURS DE LA VIE CHEZ UN OISEAU MARIN LONGEVIF

Résumé

La phénologie de la reproduction (e.g., âge à la première reproduction) et l’investissement reproducteur (i.e., investissement dans les événements successifs de reproduction) sont supposés être impliqués dans un mécanisme d’endommagement de la réparation cellulaire qui résulte en un déclin de la capacité de reproduction avec l’âge (sénescence reproductrice). Nous avons utilisé un jeu de données portant sur la mouette tridactyle, un oiseau marin longévif, afin d’étudier la relation entre l’âge au recrutement, le succès reproducteur âge-spécifique (SR), et la sénescence reproductrice, tout en tenant compte de l’expérience post-recrutement des individus, et les fluctuations de SR liées aux conditions environnementales.

Nous avons tout d’abord détecté une amélioration de SR en fin de vie, et cela quel que soit l’âge au recrutement. Ce résultat est sans doute une conséquence de la sélection intra-générationnelle, c’est à dire une disparition sélective des phénotypes de ‘faible qualité’. Une fois cette hétérogénéité prise en compte, nous avons montré que la sénescence reproductrice touche tous les individus, quel que soit leur âge de première reproduction.

Nous avons également mis en évidence que différentes combinaisons d’expérience pré et post-recrutement (i.e., nombre d’années écoulées avant et après le recrutement, respectivement, pour un individu donné) résultent toutes en un SR maximal à des âges intermédiaires. Chez les recrues précoces, plus l’expérience post-recrutement est élevée, plus le SR est élevé. Au contraire chez les recrues tardives, c’est l’expérience pré-recrutement qui est associée un SR maximum l'année du recrutement. Seuls les individus recrutant à des âges intermédiaires parviennent à équilibrer l'expérience pré- et post-recrutement.

En accord avec l'hypothèse du coût de reproduction cumulé, nous avons également observé un déclin plus rapide du SR chez les recrues précoces atteignant des âges avancés, contrairement aux recrues tardives qui connaissent le plus faible déclin de SR avec l'âge (i.e., faible vitesse de sénescence reproductrice). Cependant, les recrues précoces atteignent le plus fort SR à des âges intermédiaires (10 à 13 ans *sensus stricto*), alors que les recrues tardives connaissent le SR le plus faible aux mêmes âges. Ces trajectoires divergentes pourraient refléter un compromis évolutif différé dans le temps, compromis qui maximise le SR à des âges jeunes, contre une sénescence reproductrice aux âges plus avancés.

Nous avons également observé que les variations annuelles de SR affectent plus les jeunes individus que les individus plus âgés, suggérant que les individus expérimentés sont capable de faire face aux changements environnementaux, ce qui ultimement peut augmenter leur valeur sélective en milieu stochastique.

(i) Nos résultats soulignent l'importance de la prise en compte de l'hétérogénéité observée (i.e., variables biotiques et abiotiques) et non-observée (i.e., variation intra-individuelle) dans la détection de la sénescence reproductive. (ii) De plus, les compromis évolutifs sur le court terme (i.e., coût de la reproduction) semblent rare chez les espèces longévives; nous suggérons donc de considérer une hypothèse alternative, celle d'un coût de reproduction cumulé sur le long terme, susceptible de constituer un mécanisme explicatif de la sénescence chez les espèces sauvages longévives.

Mots-clés. Compromis évolutifs, coût de reproduction différé, hétérogénéité, mouette tridactyle, recrutement âge-spécifique, sénescence reproductrice, succès reproducteur, variations temporelles.

Introduction

Within phylogenetic and environmental boundaries, long-lived organisms have to make a series of decisions such as when to breed for the first time, how many times to reproduce, how much and when to devote limited resources away from reproduction towards maintenance or growth (i.e., life history trade-offs). The most widely studied trade-off is the cost of reproduction (for review see Harshman and Zera 2007), where investment in current reproductive effort is expected to decrease subsequent survival and (or) reproduction. However, empirical support for costs of reproduction in wild organisms remains ambiguous (Harshman and Zera 2007). For example, Cam et al. (1997, 1998, 2002a) observed a positive phenotypic correlation between survival and breeding probability in black-legged kittiwakes (*Rissa tridactyla*; a long-lived seabird). Individuals that bred successfully in a given year also survived and reproduced with a higher probability in the following year compared to failed breeders, and non-breeders (individuals that skipped reproduction in a given year). In the latter case, individuals actually experienced a 'cost of non-reproduction', as failure to breed in year t was associated with lower breeding probability in year t+1, and lower chances of surviving up to t+1.

Positive relationships between fitness components are common in observational studies of long-lived species (e.g., Barbraud and Weimerskirch 2005, Nevoux et al. 2007). Three non-exclusive hypotheses may explain positive relationships between fitness components. First, heterogeneity among individuals in their ability to acquire resources may mask trade-offs (van Noordvijk and de Jong 1986). For this reason, it has been argued that trade-offs may not be detectable without using an experimental approach (Partridge and Barton 1983). Second, it has been hypothesized that trade-offs may only be expressed in poor environmental conditions, when resources are scarce (Stearns 1992). Last, the consequences of investing resources into reproduction may not be detectable immediately, and individuals may incur delayed costs (i.e., long-term costs on a lifetime scale).

If costs of reproduction are not demographically evident in the short term, payment could reveal itself later in life, even at advanced ages. For example, an ‘invest now, pay later’ reproductive tactic could culminate in delayed or cumulative costs of reproduction (e.g., Orell and Belda 2002), and could translate into late-life senescence in reproduction. Nevertheless, the literature is heavily weighted towards examination of short-term reproductive costs (Harshman and Zera 2007), for two main reasons. First, adverse conditions and high levels of extrinsic mortality do not allow the large majority of individuals in wild populations to reach senescent ages because most die as juveniles or as young adults (e.g., Ricklefs and Sheuerlein 2001). Second, studies monitoring populations over a long enough period of time for senescence to be detected have only come to fruition in recent years (e.g., in mammals: Nussey et al. 2007b; in birds: Cam et al. 2002a, Charmantier et al. 2006; in fish: Reznick et al. 2004).

Quantifying delayed costs of reproduction would clarify the simultaneous evolution of delayed reproduction and senescence (Lack 1968). Age at first reproduction (i.e., recruitment timing) is often assumed to initiate mechanisms that impede somatic repair, resulting in a decline in reproductive abilities with age, i.e., reproductive senescence (e.g., Charnov 1997). If so, different recruitment tactics, such as early versus delayed recruitment, could lead to contrasting reproductive trajectories (e.g., senescence or improvement in reproductive success with age).

A further complication is that reproductive experience gained throughout life can also have a strong influence on age-specific breeding success (i.e., BS). Increased breeding experience can even lead to improved BS with age (e.g., Nol and Smith 1987, Orell and Belda 2002), obscuring the influence of recruitment timing on reproductive senescence in wild populations. Variable environmental conditions can further affect BS and survival, and must be statistically controlled for in order to detect delayed costs of reproduction in the wild.

Here, we use data from a study of the black-legged kittiwake in which age at recruitment and age-specific BS has been recorded for > 2100 individuals, over almost thirty years. We address the relationship between recruitment decisions and reproductive senescence, while taking into account opportunities for breeding experience and temporal variation in reproductive conditions to improve or diminish BS across ages. Specifically, we propose two contrasting hypotheses:

(1) The cumulative cost hypothesis: early recruitment is associated with acute 'reproductive senescence' (i.e., faster decline in BS at advanced ages), especially for the longest-lived individuals (i.e., those that cumulate a greater number of breeding attempts over life). Recruits delaying first reproduction, on the other hand, are expected to incur a smaller cumulative reproductive cost, especially if short-lived (i.e., delayed recruitment associated to a short reproductive lifespan translates into a low cost of cumulative breeding events over life). Thus, we expect senescence in reproduction for these birds to be subtle, or absent.

(2) The heterogeneity in individual quality hypothesis leads to opposite predictions: individuals of high intrinsic quality recruit early (e.g., Nur 1988) and experience high levels of BS late in life. This hypothesis assumes that higher-quality individuals incur smaller reproductive costs than others for equal reproductive investment. Under this view, we may expect early recruits to incur smaller cumulative costs than others as they age and breed, and senescence to be absent or weak. In contrast, individuals of poor intrinsic quality delay recruitment and the senescent decline in reproduction is expected to be sharper. For an equal number of breeding events, greater cumulative costs of reproduction in lower-quality individuals are expected to translate into a sharper decline in reproductive ability than in high-quality individuals.

These two hypotheses concerning senescence can be combined with the following one (3): lack of pre-breeding experience may translate into poor BS at the beginning of reproductive life in early recruits. Thus, we may expect an initial increase in BS with experience. In contrast, late recruits may exhibit high BS in the year of recruitment and early in reproductive life because they had time to acquire the skills necessary for reproduction (e.g., mate coordination, knowledge of foraging places), and to ‘prospect’ for higher-quality sites. ‘Prospectors’ are assumed to gather local information on their conspecific BS before settling and breeding for the first time (e.g., Danchin et al. 1991, 1998, Cadiou et al. 1994), which, if habitat quality is constant from one year to the next, allows identification of higher-quality habitat, and thus may ensure high BS (e.g., Boulinier and Danchin 1997).

Coulson and Fairweather (2001) also studied late-life reproductive performance in black-legged kittiwakes. They observed a sharp decline in BS at the last breeding event, but did not otherwise find any evidence for senescence. Even though they asserted that ‘terminal illness’ was age-independent and not a reflection of senescence, they did not study the entire breeding history and did not properly account for heterogeneity in individual quality, suggesting that their findings might not be as robust as previously thought. Here, our ultimate goal is to disentangle trade-offs between early-life decisions and late-life BS from heterogeneity in individual quality, in order to identify the demographic mechanisms shaping age-specific breeding trajectories and reproductive senescence.

Methods

Information on the study population, data collection, sample specifications, crude data on BS, and sample size, is given in Appendix A.

Age-related change in breeding success

In this study, only individuals that survived until recruitment, and subsequently recruited, were considered in analyses of BS (2124 individuals, 8335 observations). By working on the sample of individuals that recruited, generalized linear models (GLM, Agresti 1990), generalized additive models (GAM, Hastie and Tibshirani 1986), and generalized additive mixed models (GAMM, Wood 2006b) could be used to estimate the affect of age-related traits on BS from recruitment thereon.

To address the influence of AFR and breeding experience (EXP: time in years elapsed since first reproduction) on the probability of breeding successfully (BS), we treated BS as a binary response variable (i.e., success or failure), and first used GLM (i.e., logistic regression; see Agresti 1990; package 'MASS', procedure 'glm' in R 2.6.0).

We used the term 'experience' in the sense of an opportunity to increase breeding abilities through learning. In this population, 'experience' largely captures the number of breeding attempts over life. Even sabbaticals (i.e., individuals that skipped breeding in a given year and make up only 10% of all breeding events) have the opportunity to gain 'experience' by interacting with other individuals (e.g., Danchin et al. 1998), learning about foraging opportunities, and about 'hot spots' (i.e., cliff locations where breeding pairs are producing viable offsprings). Sabbaticals can thus learn about the quality of breeding sites in which they may try to breed in the future. Sabbaticals were included in the analyses, as we consider them to be part of the population 'at risk': they are able and susceptible to breed, but do not, and can therefore be considered as 'failed breeders'. Thus, the covariate referring to experience is a reasonable reflection of the number of breeding attempts over the life course.

We considered models with linear, quadratic, and cubic effects of EXP on BS (see Table 1 for model list). A quadratic effect translates into minimal (or maximal for negative coefficients) BS for individuals of intermediate experience, whereas a cubic relationship can account for a possible bimodal pattern in BS as a function of EXP. We considered EXP rather than age to investigate the idea of cumulated costs of reproduction, where (along with AFR) only post-reproductive experience matters, and not age sensus stricto. We also considered AFR as either a categorical or continuous covariate in our analysis. When AFR was treated as a categorical covariate, we conducted a cluster analysis (package 'stats', procedure 'hclust' in R version 2.6.0) to choose our cutting points in order to ensure that the selected recruitment groups were statistically meaningful. When performing a cluster analysis, we used Ward's test, which generates clusters minimizing the squared Euclidean distance to the center mean. According to this method, our recruitment groups were defined as: recruitment at age 3, 4, 5, 6 and 7 or older (i.e., 7+).

Because GLMs with continuous covariates assume a specific shape (e.g., linear, quadratic) for the relationship between explanatory and response variables, we compared the fit of our best GLM to the fit of a less constrained GAM (package 'mgcv', procedure 'gam' in R 2.6.0). The generalized additive model (GAM) alleviates constraints of the GLM by fitting nonparametric functions to estimate relationships between the response and explanatory variables. The nonparametric functions are estimated from observed data using spline smoothing, i.e., linear functions of covariates in a GLM are replaced by non-parametric spline functions in a GAM (Hastie and Tibshirani 1986, Wood 2006b). The structure of the best model selected with age-related covariates, whether it was a GLM or a GAM (see 'model selection' below), was then used to further investigate temporal variation in BS as well as possible effects of individual heterogeneity on BS trajectories.

Accounting for heterogeneity in individual quality

Observed (marginal estimates of) age-specific variation in BS depends on whether the correlation between BS and survival probability is taken into account or not (Cam and Monnat 2000a). Heterogeneous survival across individuals leads to changes in the composition of a sample population as 'frail' individuals readily die (and thus exit the sample), leaving only the most 'robust' individuals in a sample at advanced ages (Vaupel and Yashin 1985). As a result, population-level estimates of age-specific BS can reflect patterns resulting from 'within-generation phenotypic selection' (Endler 1986), rather than genuine age-specific variation in BS experienced by individuals (Cam et al. 2002b, Naves 2007).

To account for population-level processes influencing age-specific variation in BS, we first implemented a fixed effect of 'Lifespan' (i.e., breeding lifespan or the time elapsed from first reproduction to death) into our best model (i.e., the best GLM or GAM with AFR and EXP effects). As was done for AFR and EXP, we compared categorical, continuous, and spline-transformed effects of Lifespan on BS. Furthermore, we considered various interactive effects of Lifespan, AFR, and EXP on age-specific BS. As outlined by van de Pol and Verhulst (2006), such an approach can explicitly account for heterogeneity in timing of appearance (i.e., variation in AFR) and disappearance (i.e., variation in Lifespan) from the breeding population. We went one step further by also modeling variation in breeding history (i.e., variation in EXP).

Next, to parsimoniously account for 1) repeated measures on individuals, in which some may be of higher reproductive quality than others, and 2) account for variation in reproductive quality across individuals, we added an individual random effect (denoted as ID) to our best model that included Lifespan and other age-related covariates. The final model thus contained fixed effects of Lifespan, possibly AFR and EXP, as well as an individual random effect, which is necessary to fully account for the effects of individual heterogeneity on estimates of breeding performance (BS in our case; see Cam et al. 2002b, van de Pol and Verhulst 2006).

Temporal change in breeding success

We could not consider a model that simultaneously accounted for both an individual random effect and a random effect of ‘year’ because asymptotic convergence of parameter estimates could not be achieved (despite the use of a super-computer). However, we did include simultaneously a fixed effect of year (i.e., treated either continuously or as a factor in order to control for temporal change in BS) and an individual random effect to control for environmentally driven changes in BS in our best performing model, while controlling for heterogeneity in individual quality.

Separately, we also examined the influence of temporal variation in BS (e.g., resulting from climatic conditions, predation events, food shortages, etc.) on age-specific BS using a random effect of ‘Year’. We modeled Year using a random effect because we had no motive to suspect a specific pattern for the influence of year on BS (e.g., a systematic trend). The random Year effect was implemented into the best performing model with age-related covariates. All random effects were fit using the ‘mgcv’ package in R 2.6.0 (‘gamm’ procedure).

Model selection

Because AFR, EXP, and Lifespan are all linked to age sensus stricto, we calculated a variance inflation factor (i.e., package ‘car’, procedure ‘vip’ in R version 2.6.0) to address the possible issue of multicolinearity prior to model selection (Neter et al. 1996).

To evaluate our predictions laid out in the introduction, we first conducted comparisons of GLMs containing the same biological covariate but parameterized in different ways (e.g., models with AFR or EXP parameterized as continuous linear, quadratic, or cubic covariates, or parameterized as categorical covariates). Throughout, Akaike’s Information Criterion (AIC; Akaike 1973) and Akaike model weights (w_i) were used to compare models and determine which model(s) served as the best approximation(s) to the data. For each estimated slope parameter (β) that appeared in the best approximating model(s), we assessed the precision of each based on the extent to which 95% confidence intervals for each overlapped zero (Graybill and Iyer 1994).

After determining the best parameterization for each covariate, we then used AIC to compare GLMs with additive or interactive effects of covariates with different biological meaning (e.g., AFR, EXP). Using the covariates retained in the best GLM, and the nature of the covariate effects (i.e., additive or interactive, linear, quadratic or cubic, etc.), we then built a less constrained GAM. For example, if the best GLM involved an interaction between a linear effect of AFR and a quadratic effect of EXP, the corresponding GAM would contain an interaction between EXP and AFR; however, the parametric forms would be replaced with a spline function to relax the previous linear or polynomial constraints. The degree of smoothness in modeled spline relationships between BS and explanatory covariates was estimated as part of the GAM procedure. If the GAM outperformed the best GLM, all further modeling was done using GAMs.

Next, we used the best performing model from above (GLM or GAM) to model the effects of individual heterogeneity on age-specific BS. In this endeavor, we considered alternative parameterizations of the Lifespan covariate (e.g., linear, quadratic, categorical, etc.) as well as additive and interactive effects of Lifespan with AFR and EXP on age-specific BS. For reasons laid out above, individual random effects were also included in models designed to account for individual heterogeneity (see ‘Accounting for heterogeneity in individual quality’).

Earlier stages of model selection suggested that GAMs did a better job of explaining our BS data than GLMs. Therefore, random effects were implemented by using generalized additive mixed models (i.e., ‘GAMMs’, as opposed to ‘GLMMs’). When examining GAMMs, one cannot compare them to GLMs or GAMs using AIC because of its reliance on maximization of full likelihoods (Wood 2006b). In such cases, we evaluated the statistical utility of a GAMM, and its effectiveness in accounting for age-specific variation in BS arising from individual heterogeneity, by using graphical diagnostics, assessing the precision of estimated parameters with 95% confidence intervals, and evaluating appropriate test statistics (i.e., we used a plural approach to making inference from models whenever information-criterion methods could not be used; Scheiner 2004). We also compared GAMMs to each other in some cases using AICs (e.g. GAMMs containing different parameterization for temporal change in BS; e.g., fixed versus continuous)

Results

Age-related changes in breeding success

All tests for multicolinearity in models containing AFR, EXP, and Lifespan yielded estimates of variance inflation factors < 7.07. Since all variance inflation factors were < 10, our models did not present any serious issues concerning multicolinearity (Neter et al. 1996). Given these results, we considered models with additive and interactive effect of age-related covariates.

Among GLMs, our top performing model (Table 1, second model from top) indicated that BS changed over life as a function of AFR (treated as a categorical factor), a cubic effect of EXP, and their interaction. Even though many of the coefficients for the AFR and (cubic effect of) EXP interaction were imprecisely estimated (95% C.I.s overlapped 0), ignoring them led to a considerable increase in AICc (Table 1, ΔAICc = 81). The cubic effect of EXP in the best performing GLM implied either 1) the marginal estimate of BS, after an increase early in life, and a decrease at intermediate ages, did indeed improve again late in life (Fig. 1, or 2) the cubic polynomial 'forced' a bimodal pattern between BS and EXP, which might not be an accurate depiction of the underlying relationship between EXP and BS at the population level, but only the closest fit to the data among the set of models examined.

To examine the validity of the parametric constraints in the best GLM, we compared it to an alternative GAM with 'unconstrained' effects of age-related covariates on BS. When added to the set of candidate GLMs, the GAM was a superior fit to the data relative to the best performing GLM described above (top model in Table 1; β_{AIC} =-0.17, 95% CI: -0.16 to -0.18; spline effect of EXP: $\chi2$=100.60, edf=4.23, $p<10^{-3}$; spline effect of EXP and AFR interaction: $\chi2$=220.90, edf=13.26, $p<10^{-3}$). For the sake of conciseness, we did not include the figure associated to the GAM. However, not only was this model a better fit to the data, it also showed that for individuals surviving up to advanced ages, improvement in BS was observed in most recruitment groups. Interestingly, only early recruitment groups (i.e., AFR = 3 or 4) exhibited another decline in BS at very advanced ages (> 20 years old). Yet, only a small sample of individuals existed at advanced ages (Appendix 1). Based on these results, we considered the best performing model (i.e., a GAM) in further analyses of BS as a function of both observed (i.e., AFR, EXP, Lifespan) and unobserved heterogeneity (i.e., random effect of 'ID').

Accounting for heterogeneity in individual quality

When a fixed effect of lifespan was added (last model in Table 2) to the GAM described above (1st model in Table 1), AIC improved by 33.69 units. Since Lifespan (by controlling for the selective disappearance of individuals within the breeding population) led to improvement in model fit, we further considered alternative parameterizations of Lifespan. The top model including Lifespan accounted for 49% of the model weight, and the second best model accounted for 46% (Table 2). In the top model, all interactions were significant (spline effect of AFR and EXP interaction: edf=16.75, $\chi 2$=151.90, $p<10^{-3}$; spline effect of EXP and Lifespan interaction: edf=6.90, $\chi 2$=74.78, $p<10^{-3}$), which was also the case for the second best performing model (spline effect of AFR and EXP interaction: edf=16.75, $\chi 2$=151.87, $p<10^{-3}$; spline effect of EXP and Lifespan interaction: edf=6.89, $\chi 2$=74.80, $p<10^{-3}$; spline effect of AFR and Lifespan interaction: edf=0.03, $\chi 2$=9.35, p=0.002).

To account for (unobserved) heterogeneity in individual quality, we considered an individual random effect and added it to the previously defined best GAM (i.e., generalized additive model). Such a model, a GAMM (i.e., generalized additive mixed model), could not be fit if one of the covariates was included in a spline-transformed interaction more than once (e.g., AFR involved twice in: S(AFR*EXP) + S(AFR*Lifespan) + random effect(ID), where S stands for a spline transformation; see Wood 2006b). However, a model with an individual random effect and a three-way spline-transformed interaction between AFR, EXP, and

Lifespan converged successfully. The triple interaction term was statistically significant (spline effect of AFR, EXP, and Lifespan interaction: edf=9, estimated rank=9, F statistic=29.19, $p<10^{-3}$), and random variation in BS across individuals was detected (individual random effect centered at zero: sd=0.93, residuals=0.87).

Of great importance, this GAMM accounted for all demographic sources of individual heterogeneity in age-specific BS (i.e., selective appearance, selective disappearance, variation in breeding history, correlative structure across repeated measures, and random variation across individuals). According to this model, improvement in BS at advanced ages disappeared across all recruitment groups, and the pattern observed in age-specific BS surfaces was uni-modal for all recruitment groups (Fig. 2) with no detectable late-life improvement in BS. Maximal BS levels decreased as individuals delayed recruitment: BS exceeded 0.6 for individuals recruiting at age 3 (i.e., BS=0.66, 95% CI: 0.45 to 0.87), and 4 (i.e., BS=0.63, 95% CI: 0.50 to 0.76), followed by individuals recruiting at age 5 (i.e., 0.58, 95% CI: 0.47 to 0.69), 6 (i.e., BS=0.53, 95% CI: 0.40 to 0.66), and 7+ (i.e., 0.47, 95% CI: 0.29 to 0.65).

Based on this model, we calculated senescence rates for each recruitment group by calculating the slope between the highest BS and the lowest BS values for each BS surface (Fig. 2). We found that recruits of 4 years old experienced the highest senescence rate (i.e., -0.034), followed by recruits of 3, 6, and 5 years old (i.e., respectively -0.030, -0.029, -0.027). The lowest senescence rate was associated to 7+ year-old recruits (i.e., -0.025).

The model also provided some insights on how BS surfaces shifted as recruitment was delayed, as experience was gained, and as lifespan increased (Fig. 3). Estimated values of BS reached a maximum at 10 years of experience, for a realized lifespan of 20 years old (Fig. 3, top-right), followed by a dramatic decline in BS late in life (Fig. 3, top-left). Recruitment at age 3 was associated to a slightly higher maximal BS given that an individual lived up to 15 years old (Fig. 3, center). The confidence bounds associated to each BS surface confirm the uni-modal shape of BS surfaces across recruitment groups (Fig. 3).

Temporal changes in breeding success

A GAMM accounting for both individual effects and for temporal variation in BS (i.e., individual and temporal random effect) failed to converge. Simultaneous estimation of multiple random effects in GAMMs is known to be computationally intensive (Wood 2006b).

We first examined temporal variation in BS (i.e., random effect of 'YEAR') using a GAMM with a spline-transformed triple interaction of AFR, EXP, and Lifespan. The interaction term was statistically significant (spline effect of AFR, EXP, and Lifespan interaction: EDF=9, estimated rank=9, F statistics=41.24, $p<10^{-3}$) and the temporal random effect was non-negligible (temporal random effect centered at zero: SD=0.34, residuals=0.99). Most of the temporal variation in BS took place early in life, but decreased with AFR, and as an individual gained experience (Appendix B).

We also considered two similar GAMM (i.e., with a spline transformed triple interaction between AFR, EXP, and Lifespan), accounting for heterogeneity in individual quality (i.e., random effect of 'ID'), and controlling for temporal change in BS by adding a fixed effect of 'YEAR' either treated as a continuous covariate or as a factor. Models controlling for both individual differences in BS (i.e., random effect of 'ID') and for environmental stochasticity (i.e., random effect of 'YEAR'), did converge successfully. However, in a GAMM considering a fixed effect of 'YEAR', the estimated effect was not significant and the confidence bounds overlapped zero (i.e., YEAR=3.6 10^{-3}, 95% CI: -1.1 10^{-3} to 8.3 10^{-3}, p=0.442). As AIC is comparable across GAMM models, adding a fixed effect of 'YEAR' did not improve model fit (i.e., AIC=36530.82 for the GAMM without a fixed effect of 'YEAR', versus AIC=36531.03 for the GAMM with the fixed effect of 'YEAR'). A GAMM with 'YEAR' as a factor did not improve model fit either (AIC=36949.05). Moreover, none of the factorial levels were significant, and all estimates overlapped 0. Therefore, it seems that most of the unobserved heterogeneity is a reflection of heterogeneity in individual quality rather than temporal change in BS.

Discussion

In this study, we addressed which recruitment tactics (i.e., early versus delayed recruitment) yield the highest BS across ages, and whether recruitment tactics led to contrasting reproductive senescence profiles. We knew from past work (Aubry et al. 2009) that pre-breeders reaching age 4 had the highest probability of recruiting in the following year if they survived (i.e., reach age 5), and also experienced the highest BS in the year of recruitment. However, fitness prospects and life history consequences of individual decisions in terms of recruitment age are more completely understood by studying variation in BS throughout life; BS in the first breeding attempt is only a snapshot of the age-specific reproductive profile. We addressed this while accounting for heterogeneity in individual quality, a key component of the apparent influence of age on demographic parameters (e.g., Cam et al. 2002a, van de Pol and Verhulst 2006).

In accordance with hypothesis (3), we consistently found that early recruits (i.e., 3 years old) experienced low BS at recruitment, and thus started their reproductive life with a handicap (Fig. 1, Fig.2), perhaps as a consequence of a lack of ‘pre-breeding experience’. We also found that individuals delaying recruitment exhibited higher BS in the recruitment year than early recruits (Fig. 1, Fig.2). These results, consistent throughout all analyses (i.e., GLM, GAM, GAMM), confirm that pre-recruitment experience matters in determining levels of BS early in the reproductive career of individuals. Such pre-recruitment experience is likely to allow for an increase in skills related to reproduction (e.g., mate coordination, foraging abilities, nest construction, etc) through prospection. It has been shown in the Kittiwake that most individuals ‘prospect’ for higher-quality sites (e.g., Danchin et al. 1991, 1998, Cadiou et al. 1994). Before reproduction begins, ‘prospectors’ gather local information based on the performance of their conspecifics, which permits selection of more productive habitats the following year(s), likely to ensure high levels of BS in the recruitment year (e.g., Boulinier and Danchin 1997). Individuals that delayed recruitment forewent early-life breeding opportunities and achieved high BS at first reproduction. Potentially, they might have queued for high-quality sites, and obtained a favorable breeding ground necessary to achieve such high levels of BS at recruitment. To test this, one would have to simultaneously examine the relationship between habitat selection, individual quality, and age-specific BS.

Following recruitment, improvements in BS were observed for all individuals that gained breeding experience, including early recruits (Fig. 1, Fig. 2), suggesting that individuals can catch-up for early-life deficits and perform increasingly better throughout life. The most rapid increase in BS was observed in early recruits, as their initial BS at recruitment year was so low, there was scope for substantial improvement later in life. On the other hand, individuals that delayed recruitment, experienced a less impressive improvement, as they initially experienced high levels of BS, leaving little room for enhancement.

Following the initial increase in BS across all recruitment groups, the different set of analyses provided different results. Under a GLM (Fig. 1) modeling framework, we did not detect senescence in BS in any of the recruitment groups, and an improvement in BS was even observed late in life (Fig. 1). We improved model fit by considering unconstrained relationship between the selected covariates and BS (see GAM, Table 1) which highlights the utility of spline transformations in obtaining realistic age-specific trajectories of demographic parameters such as BS.

These models however, did not account for individual heterogeneity, and all showed late-life improvement in BS (in all recruitment groups under the best GLM, Fig. 1; and in most recruitment groups under the GAM, figure not presented here for the sake of conciseness). Recruitment-level increases in BS may only represent a handful of ‘robust’ individuals that survive to advanced ages, and might not accurately reflect variation in BS within individuals, if individuals within recruitment groups do not die at the same rate (i.e., heterogeneity in individual quality can bias group level estimates of BS, survival, etc; Vaupel and Yashin 1985). Even though the inclusion of Lifespan in our best GAM did improve model fit (table1, table 2), we were concerned that defining frailty a priori with 'lifespan' might not fully distinguish between 'robust' and 'frail' individuals. Such an approach might only take into account 'within-cohort phenotypic selection' (Ender 1986), but not other unobserved components of heterogeneity among individuals (e.g., Lewis et al. 2006). Therefore, we used an approach explicitly accounting for variation in reproductive quality across individuals (i.e., individual random effect), and for variability in recruitment age, lifespan, and breeding experience. According to this approach, there was a noticeable difference in the observed peak in BS across recruitment groups (Fig. 2, Fig. 3), which occurred earlier in individuals delaying recruitment. However, across all recruitment groups, maximal BS levels were attained by individuals reaching intermediate experience levels. Interestingly, the balance between pre- and post-recruitment experience differed across recruitment groups, but resulted in similar timing of maximal BS (i.e., age 10 to 13 sensus stricto). Assuming that individuals were physiologically mature at age 2: maximum BS was attained at high levels of post-breeding experience (i.e., 10 years of experience) in early recruits (i.e., AFR = 3), and at high levels of pre-recruitment experience (i.e., 5 years of pre-recruitment experience) in individuals delaying recruitment (i.e., AFR = 7+). Individuals recruiting at intermediate ages (i.e., AFR = 5), demonstrated balanced pre- and post-recruitment experience (2 and 3 years respectively) when BS reached its maximal value As a follow up, it would be worth testing which 'recruitment tactic' (e.g., cumulating pre-recruitment, or post-recruitment experience) is associated to the highest fitness pay-off (Maynard Smith 1982), BS being only a component of fitness. It would also be worth testing whether such tactics relate to differences in phenotypic quality. This would allow us to assess if low quality individuals, suspected to delay recruitment, improve BS by cumulating pre-recruitment experience, and if higher quality individuals (i.e. early recruits) increase BS by gaining breeding skills post-recruitment.

While focusing on the second half of BS trajectories, individuals delaying recruitment showed slightly lower senescence rates (i.e., lowest senescence rate observed in 7+ year-old recruits) than ‘early recruits’ (i.e., highest senescence rates observed in 4 year old recruits). In accordance with the cumulative cost hypothesis (1), early recruits showed strong senescence decline in BS at advanced ages, when heterogeneity was properly accounted for. Individuals delaying recruitment on the other hand, showed weaker senescence in BS. The idea of delayed costs of reproduction that could be expressed later in life, in terms of either reproductive senescence, actuarial senescence, or both, has only emerged recently in empirical studies of long-lived species, even though it has been a central idea in senescence theory for more than 70 years. If costs of reproduction are not demographically evident in the short term, payment could reveal itself later in life, even at advanced ages. For example, an ‘invest now, pay later’ reproductive tactic could culminate in delayed or cumulative costs of reproduction (e.g., Orell and Belda 2002), and could translate into late-life senescence in both reproduction and survival. We still need to address whether these trade-offs also underlie senescence in survival. Such delayed trade-offs should be of special interest to evolutionary ecologists, since they have the potential to clarify the simultaneous evolution of reproductive strategies and senescence.

BS also varied across years, but annual effects primarily affected individuals early in life (Appendix B), suggesting that experienced individuals were able to buffer out the effects of temporal variation in environmental conditions on BS, which can substantially improve fitness in stochastic environments (Lewontin and Cohen 1969, Tuljapurkar 1982). Thus, in addition to bet-hedging (e.g., Slatkin 1974), iteroparity (e.g., Orzack and Tuljapurkar 1989), and longevity (e.g., Metcalf and Koons 2007), a stochastically changing environment may also select for the devotion of resources toward acquiring reproductive experience. Temporal change however, only contributed to subtle changes in BS early in life.

In accordance with Cam et al. (2002b), our work suggests that most of the changes in BS across ages in the population were accounted for by an interaction between age-related covariates (i.e., observed heterogeneity), and an individual random effect (i.e., unobserved heterogeneity). Heterogeneity in survival (e.g., frailty models) was first looked at in human demography starting some twenty years ago (Vaupel and Yashin 1985). But developments and applications regarding heterogeneity in demographic rates such as BS in wild animal population are fairly recent (e.g., Cam et al 2002b, Barbraud and Weimerskirch 2005, Van de Pol and Verhulst 2006, Fox et al. 2006, Royle 2008). We found that in addition to unobserved heterogeneity, one should also consider interactions between observable age-related covariates to account for the multiplicity of life-course events that define individual differences in BS. The triple interaction between recruitment age, experience, and lifespan seemed to account for the selective appearance and disappearance of individuals, and for the diversity of possible ‘breeding lives’ (i.e., number of breeding attempts in the life course).

Even though a flurry of scientific papers have been studying trade-offs between a variety of traits and late-life reproduction (e.g., Bérubé et al. 1999, Reid et al. 2003, van de Pol and Verhulst 2006, Reed et al. 2008), only a handful used proxies for differences in individual quality (e.g., lifespan). To our knowledge, Balbontin et al. (2007), along with Reed et al. (2008), are the only ones relating senescence in BS to age-related traits while accounting for heterogeneity in individual quality by using mixed models. However, we went one step further by using models (i.e., GAMMs) accounting for both random effects controlling for heterogeneity in individual quality, and splines to examine unconstrained relationship between BS and age-related covariates (see Ezard et al. 2007 for similar models applied to age, phenology, and individual fitness relationships). By doing so, we explicitly show how to obtain individually-based estimates of BS by simultaneously accounting for the fact that individuals recruit, breed (successfully or not), and die at various ages, without constraining the relation between BS an age-related covariates (i.e., smooth splines).

We next aim at explicitly measuring the relative contributions of observed and unobserved heterogeneity to age-specific trajectories of survival in the kittiwake, then develop appropriate models for integrating all life-cycle parameters and measuring forces of natural selection on life history decisions (e.g., Coulson et al. 2006).

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Table 1. Selection results for models testing the effects of age at first reproduction (AFR if continuous, AFRc if categorical), and experience (EXP if continuous, EXP2 if quadratic, EXP3 if cubic) on age-specific breeding success. The top model is a GAM as it involves a spline function 'S', all other models are GLMs.

Models	AIC	EDF	Δ_i	$e^{-0.5*\Delta_i}$	w_i
S(AFRc * EXP)	10969	18	0	1	0.96
AFRc * (EXP + EXP2 + EXP3)	10976	20	6	0.05	0.04
AFRc * (EXP + EXP2)	10984	15	14	0	0
AFRc + EXP + EXP2 + EXP3	11057	8	87	0	0
AFRc + EXP + EXP2	11061	7	91	0	0
AFRc * EXP	11068	10	98	0	0
EXP + EXP2 + EXP3	11093	4	123	0	0
EXP + EXP2	11097	3	127	0	0
AFRc + EXP	11111	6	141	0	0
EXP	11149	2	179	0	0
AFRc	11297	5	327	0	0

'+' denotes an additive effect, '*' an interaction; EDF: Estimated Degrees of Freedom; AIC = -2*log-likelihood + 2*EDF; Δ_i = AIC$_{\text{model i}}$ - AIC$_{\text{min}}$; $w_i = e^{-0.5*\Delta_i} / \sum_i e^{-0.5*\Delta_i}$

Table 2. Selection results for models testing the effects of age at first reproduction and experience on age-specific breeding success, while accounting for heterogeneity in survival chances (Lifespan effects). All models considered are GAMs.

Models	AIC	EDF	Δ_i	$e^{-0.5*\Delta i}$	w_i
S(AFRc * EXP) + S(EXP * Lifespan)	10913.29	24.65	0	1	0.49
S(AFRc * EXP) + S(EXP * Lifespan) + S(AFRc * Lifespan)	10913.4	24.67	0.11	0.95	0.46
S(AFRc * EXP) + S(Lifespan)	10919.01	20.52	5.72	0.06	0.03
S(AFRc * EXP) + S(AFRc * Lifespan)	10920.08	21.97	6.79	0.03	0.02
S(AFRc * EXP) + Lifespan	10936.71	19.11	23.42	0	0

Figure 1. Trajectories of age-specific breeding success (BS) in relation to age at first reproduction (AFR) and breeding experience (EXP). Estimates obtained from the best performing Generalized Linear Model (GLM) before potential sources of individual and temporal heterogeneity were accounted for (see 2nd model, Table 1).

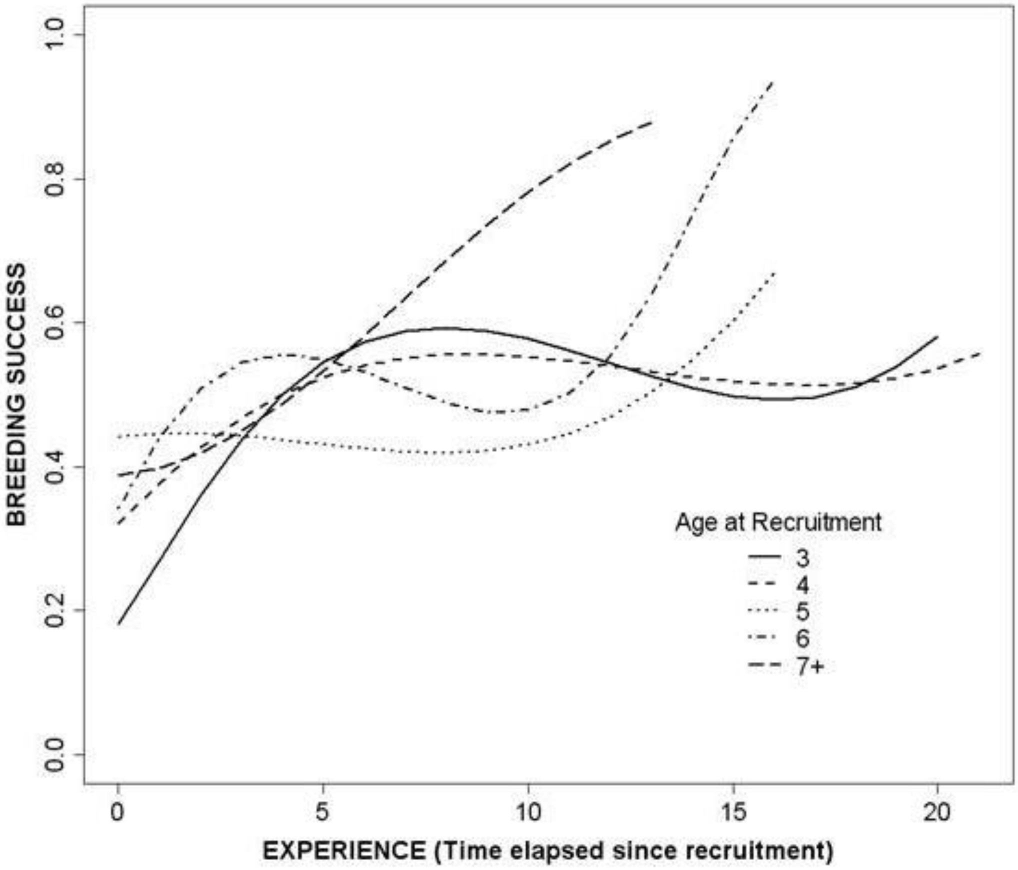


Figure 2. BS surfaces across recruitment groups (AFR) as a function of experience (EXP) and Lifespan, once all potential sources of heterogeneity were accounted for (individual heterogeneity is accounted for by an individual random effect, ‘ID’). Estimates obtained from the following GAMM: BS ~ spline (AFR * EXP * Lifespan) + random effect (ID).

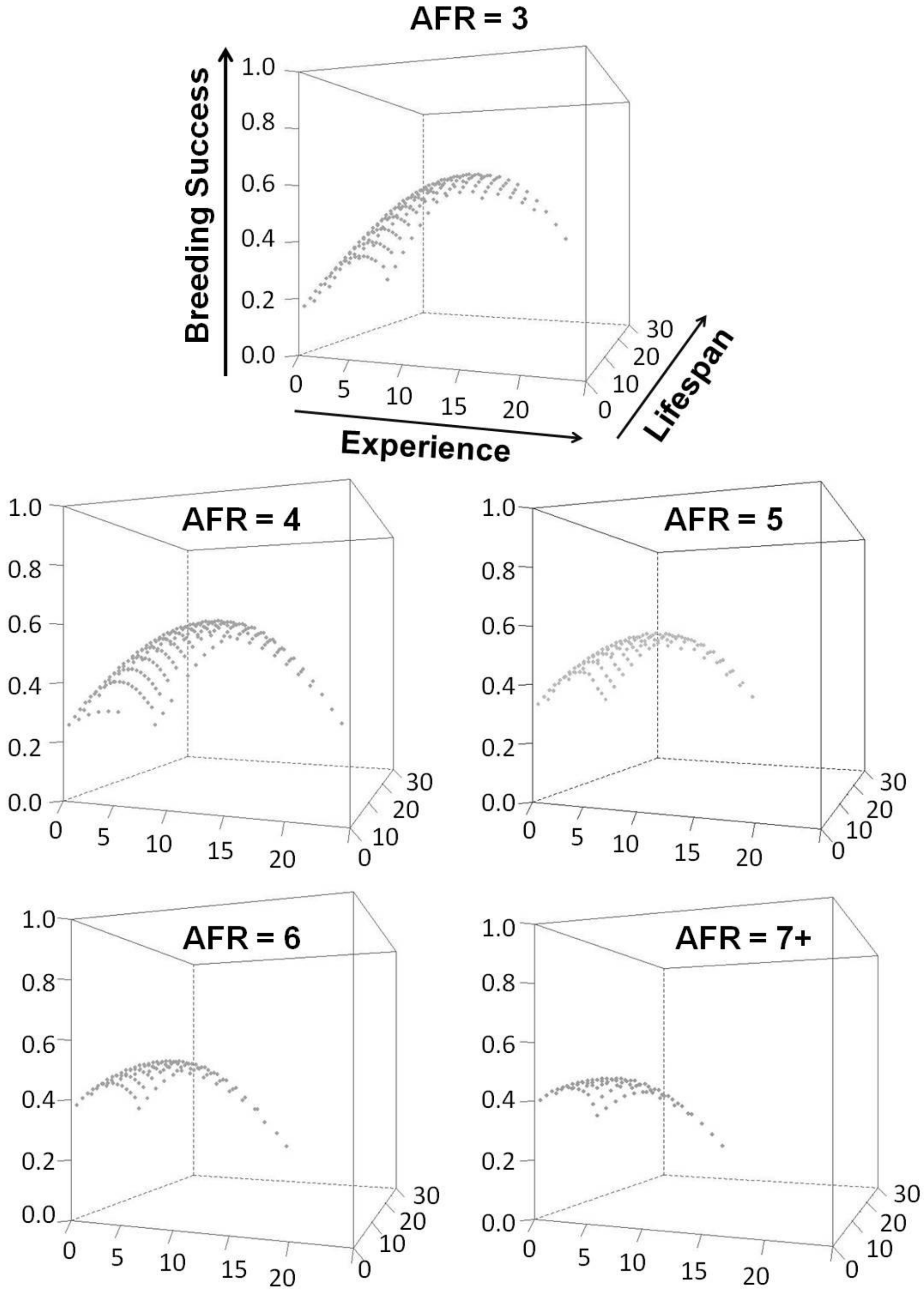
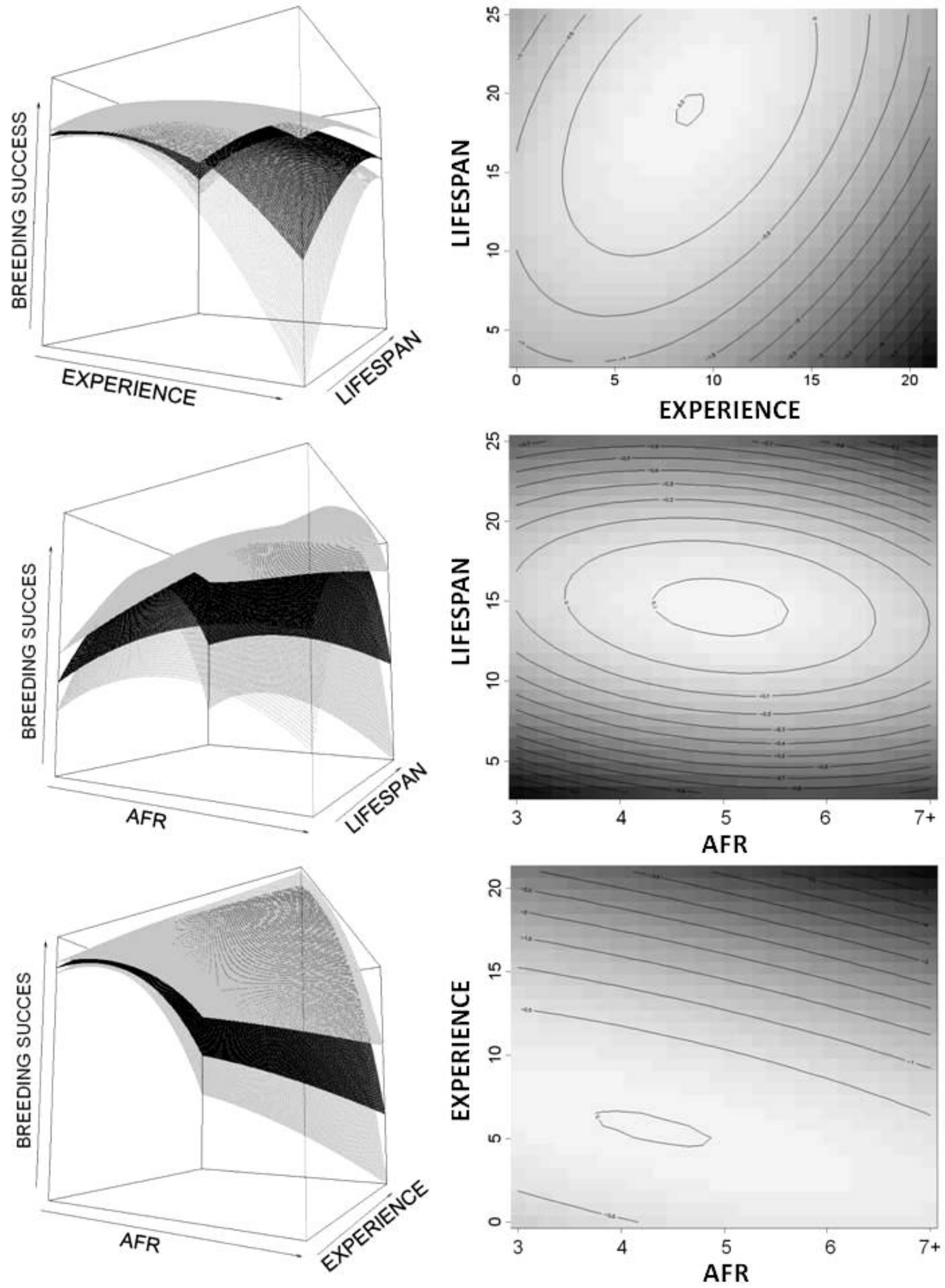


Figure 3. Depictions of the influence of paired covariates (AFR and EXP, AFR and Lifespan, EXP and Lifespan) on BS. Estimates obtained from the GAMM defined in figure 2. The 95% confidence bounds associated to each BS surface are based on spline-transformed estimates. The contour plots serve as an alternative to 3D plots, display BS peaks more accurately, and show how they change as a function of age-related covariates.



Appendix A.

Study population, data collection, and sample specifications

The Kittiwake project in Brittany (France) provides long-term data (beginning in 1979) on large numbers of color-marked individuals. Five colonies located in the Cap Sizun (48°5’N, 4°36’W), a few kilometres apart, are followed extensively through each breeding season (Monnat et al. 1990), such that all breeding events are monitored (Cam et al. 1998). This allows for the identification of the very first reproductive event for each individual returning to the study area (Cam et al. 2002b, 2003, 2005). The age of most individuals is known, and each individual’s presence is recorded throughout January to September, as well as demographic and behavioral information at each resighting period.

Because recapture probabilities for pre-breeders are inferior to 1 (Cam et al. 2005), estimation of recruitment probabilities conditional on survival requires mark-recapture probabilistic models (Aubry et al. 2009b). However, as we are only interested in the influence of age-specific recruitment decisions on future reproduction (i.e., individuals belonging to the breeding population), and since recapture probability for breeders is virtually equal to 1 ($p = 0.9964$, 95% CI: 0.9925 to 1; Cam et al. 2003), we do not have to account for detectability in our models of variation in breeding success (BS) over life.

The sample consists of individuals that recruited in between 1982 and 2007. Only 7 individuals recruited at the minimum age of 2 years old. Therefore, we pooled individuals recruiting at 2 with individuals recruiting at age 3, and will further refer to this pool of individuals as 3 year-old recruits for the sake of simplicity (i.e., Age at First Reproduction, or AFR = 3). The maximum observed lifespan in the study was 25 years and concerned two individuals recruiting at age 4 (i.e., 21 years of breeding experience). Sample sizes across both recruitment and lifespan groups were very reasonable (see table below), and allowed us to study breeding success trajectories within each recruitment group (i.e., age at first reproduction, AFR = 3, 4, 5, 6, or 7+).

Sample size across recruitment and lifespan groups

Lifespan groups (years old)	Recruitment groups (years old)				
	3	4	5	6	7+
Group 1 (AFR - 7)	1054	1164	339	70	5
Group 2 (8 - 9)	358	622	339	124	15
Group 3 (10 -13)	437	903	529	201	63
Group 4 (14 - 17)	210	353	122	61	59
Group 5 (18 -19)	109	124	60	38	24
Group 6 (> 20)	56	134	52	17	0

Since we are interested in reproductive senescence, individuals that were still alive at the end of the study (i.e., 2007) were systematically excluded from the sample, and only ‘known-fate individuals’ were included (i.e., individuals that bred at least once and were not resighted in a year can be considered as permanently absent from the study area because recapture probability is almost 1 after recruitment; Cam et al. 1998, 2005). Here, death and permanent emigration from the study area are confounded.

Individuals whose BS in a given year was unknown or uncertain were excluded from the analyses. ‘Sabbaticals’ (adults skipping at least one breeding occasion) were included in the analyses, as we consider them to be part of the population ‘at risk’: they are able and susceptible to breed, but do not, and can therefore be considered as ‘failed breeders’.

Because of sample size issues, we minimized the number of reproductive states in the analysis of BS. Consequently, we did not include different levels of failure (e.g., early failure when the chick died before fledging or late failure when the chick died after fledging) or success (e.g., kittiwakes generally produce 1 or 2 eggs, and occasionally up to 3 eggs, and may fledge several chicks). Individuals that fledged at least one chick up to independence were considered 'successful', whereas other breeding events were considered as 'failures'.

A plot of breeding success profiles as a function of age showed a bimodal pattern in BS accompanied by a late life improvement in BS at advanced ages (fig. 1).

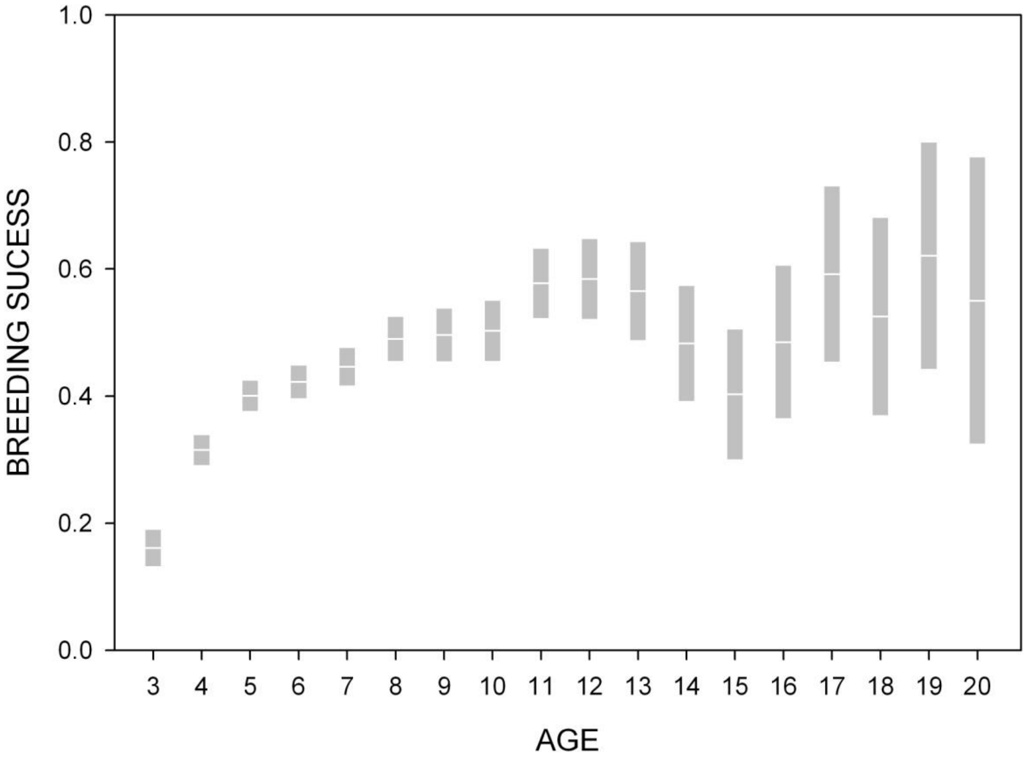


Figure 1. Breeding success as a function of age (based on the overall population). White lines indicate means and grey bars indicate 95% confidence intervals).

Our aim is to determine whether this late-life improvement in BS is a mere artefact of selection, whereby only 'robust' individuals survive up to advanced ages, showing an improvement in BS at advanced ages (i.e., heterogeneity); or if this late-life improvement is a realistic trend in this population, when heterogeneity is controlled for.

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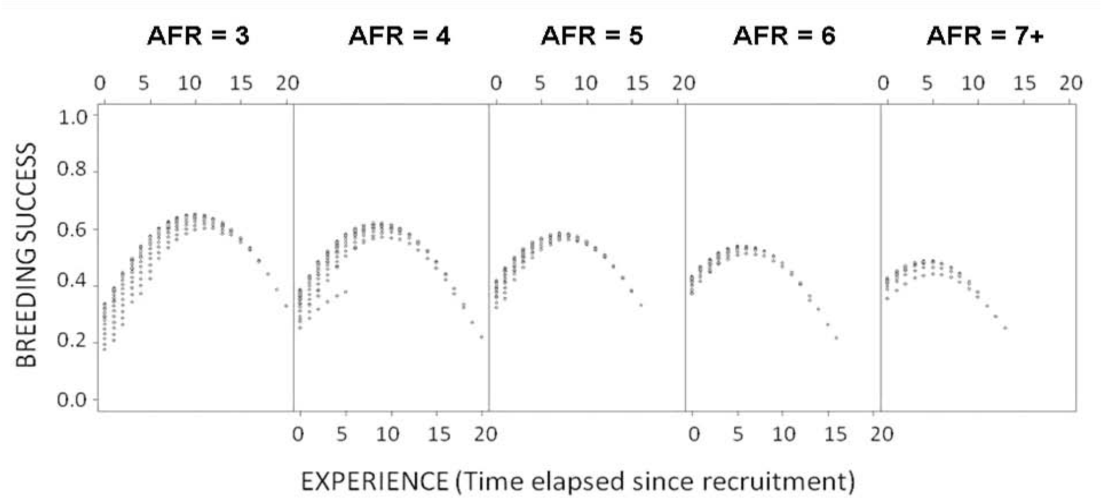
Appendix B.

Trajectories of age-specific BS in relation to spline transformed effects of age at first reproduction ‘AFR’, experience ‘EXP’, and ‘Lifespan’, once temporal variation was accounted for via a random effect of ‘YEAR’. Estimates were obtained from the following GAMM:

BS ~ spline (AFR * EXP * Lifespan) + random effect (YEAR).



Both the triple interaction (EDF = 9, estimated rank = 9, F statistics = 41.24, $p < 10^{-3}$), and the temporal random effect of ‘YEAR’ (temporal random effect centered at zero: SD = 0.34, residuals = 0.99) had a significant effect on BS. Most of the temporal variation in BS took place early in life, especially in younger recruits, but disappeared has individuals gained experience. However, the observed temporal changes in BS were subtle even early in life.

~ CHAPTER III ~

‘Will he remember Jean-Yves when he will be 23? Probably.’

Picture: Lise M. Aubry

DRIVERS OF AGE-SPECIFIC SURVIVAL IN A LONG-LIVED SEABIRD: CONTRIBUTIONS OF OBSERVED AND HIDDEN SOURCES OF HETEROGENEITY

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Abstract

1. We assessed the relative influence of variability in recruitment age, dynamic reproductive investment (time-specific reproductive states) and frailty (unobserved differences in survival abilities across individuals) on survival in the black-legged kittiwake. Furthermore, we examined whether observed variability in survival trajectories was best explained by immediate reproductive investment, cumulative investment, or both.

2. Individuals that delayed recruitment (< age 7) suffered a higher mortality risk than early recruits (age 3), especially later in life, suggesting that recruitment age may be a surrogate for individual quality. Although recruitment age helped explain variation in survival, time-varying reproductive investment had a more substantial influence.

3. The dichotomy of attempting to breed or not explained variability in survival across life better than other parameterizations of reproductive states such as clutch size, brood size, or breeding success. In the kittiwake, the sinequanon condition to initiate reproduction is to hold a nest site, which is considered a very competitive activity. This might explain why attempting to breed is the key level of investment in this species, independent of the outcome (failure or success).

4. Interestingly, the more individuals cumulate reproductive attempts over life the lower their mortality risk, indicating that breeding experience may be a good indicator of parental quality as well. In contrast, attempting to breed at time t increased the risk of mortality between t and t+1. We thus detected an immediate trade-off between attempting to breed and survival in this population, however, the earlier individuals recruited, and the more breeding experience they accumulated, the smaller the cost.

5. Lastly, unobserved heterogeneity across individuals improved model fit more (1.34 times) than fixed and dynamic sources of observed heterogeneity in reproductive investment,

demonstrating that it is critical to account for both sources of individual heterogeneity when studying survival trajectories. Only after simultaneously accounting for both sources of heterogeneity were we able to detect the ‘cost’ of immediate reproductive investment on survival and the ‘benefit’ of cumulative breeding attempts (experience), a proxy to individual quality.

Key-words: age at first reproduction, Breslow estimator, frailty, individual quality, reproductive investment, senescence, survival analysis, trade-offs.

TRAJECTOIRES DE SURVIE: CONTRIBUTION RELATIVE DE L'HETEROGENEITE NON-OBSERVÉE ET DE L'INVESTISSEMENT REPRODUCTEUR

Résumé

Nous avons étudié l'influence de l'investissement reproducteur et de l'hétérogénéité non-observée sur la survie âge-spécifique de la mouette tridactyle, un oiseau marin longévif. Les individus qui recrutent après 5 ans connaissent une sénescence forte en termes de survie, reflétant la plus faible qualité intrinsèque de ces individus qui recrutent tardivement. Les non-reproducteurs (individus s'étant déjà reproduit mais ne le faisant pas l'année courante) connaissent une mortalité plus faible que les reproducteurs en échec (i.e., individus qui ne produisent ni œuf ni poussin). Ce résultat suggère que les individus engagés dans la reproduction, mais en échec de reproduction avant même de pouvoir ponde, au 'stade œuf' ou au stade 'poussin' subissent un coût en termes de survie, ou alors que la disparition de l'adulte en cours de saison de reproduction est la cause de l'échec (par accident, ou parce qu'ils succombent à l'effort de reproduction avant de l'avoir menée à son terme). Leur mortalité est alors supérieure à celle des individus qui ne s'engagent pas du tout dans la reproduction. Les individus capables d'élever au moins un poussin jusqu'à l'envol, connaissent une mortalité plus faible que les non-reproducteurs et les reproducteurs en situation d'échec; une interprétation possible est que les oiseaux en situation de succès de reproduction sont de plus forte qualité intrinsèque. L'hétérogénéité dynamique observée (i.e., investissement reproducteur annuel) explique en grande partie la variabilité de survie âge-spécifique observée. Cependant, elle explique moins de variabilité que l'hétérogénéité non-observée (prise en compte à travers un terme de « fragilité » (i.e., « frailty ») modélisée par un effet aléatoire individuel). Ainsi, aussi bien l’hétérogénéité observée que l’hétérogénéité non-observée sont des sources de variabilité individuelle qui doivent être prise en compte lors de l’étude de la relation entre investissement reproducteur et survie.

Mots-clés : âge de première reproduction, hétérogénéité, ‘frailty’, investissement reproducteur, analyse de survie.

Introduction

Organisms must eventually face trade-offs, and allocate limited time and energy amongst growth, reproduction, and survival (Williams 1966). One particular trade-off that has received great attention is that between investment in current reproduction at the expense of future reproduction and (or) survival. Although a large number of experimental and correlative studies have examined this trade-off (Stearns 1992), empirical support for it in wild organisms remains ambiguous (Harshman and Zera 2007), especially in long-lived species where some seemingly escape trade-offs and appear to be ‘Darwinian demons’ (i.e., hypothetical organism that can maximize all aspects of fitness simultaneously; Law 1979).

A number of factors might limit our ability to detect trade-offs between reproduction and survival in long-lived species. First, reproductive investment early in life might not bear its effect until much later in life as a result of subtle costs accumulating over time. In long-lived species ‘cumulative costs of reproduction’ might be the norm rather than the exception (Aubry *et al.* 2009b). Moreover, reproductive traits can be fixed (e.g., age at first reproduction), or can fluctuate over an individual’s life in a stochastic manner (changes in egg production, chick production, number of offsprings fledged, etc.) in response to environmental conditions, competition, and previous life experiences (Tuljapurkar *et al.* 2009). It is thus crucial to account for all of the above sources of variation, whether they are fixed (e.g., age at first reproduction) or dynamic (time or age-varying reproductive states), in order to detect the true relationship between survival and reproductive investment.

Second, ecologists often encounter the problem of limited data. High levels of extrinsic mortality in the wild can prevent most individuals from reaching old age, which constitutes the key sample in senescence studies, i.e., a decline in survival at advanced ages (e.g., Ricklefs and Sheuerlein 2001). Thus, long-term monitoring is essential for studying senescence in survival.

Third, a variety of genetic, maternal, and environmental factors can lead to variation in survival abilities amongst individuals of the same population (Wilson and Nussey 2010). When difficult or impossible to measure directly, these unobserved differences in survival abilities across individuals (commonly called ‘frailty’) lead to underlying changes in the composition of a sample population. According to Vaupel and Yashin’s definition (1985), ‘frail’ individuals readily die and thus exit the sample, leaving only the most ‘robust’ individuals in the sample at advanced ages. As a result, population-level estimates of age-specific survival can reflect patterns resulting from ‘within-generation phenotypic selection’ (Endler 1986), rather than genuine age-specific variation in survival experienced by individuals (Vaupel and Yashin 1985; for an application see Fox *et al.* 2006).

The black-legged kittiwake (*Rissa tridactyla*) is a long-lived seabird that exhibits substantial variability in reproductive traits across individuals (Cam and Monnat 2000b, Cam *et al.* 2002a, 2002b, Aubry *et al.* 2009 a, b), some of which are fixed (e.g., the age at first reproduction) and some of which are dynamic over life (age or time-specific reproductive investments). Such sources of observed individual heterogeneity in reproductive investment may help explain variation in survival trajectories, but if so, trade-offs are not readily apparent in kittiwakes. Aubry et al. (2009b) found that the cost of early-life reproductive investment on future reproduction was delayed, and not born out until late life. Furthermore, age at recruitment, sometimes a proxy to individual quality (Forslund and Pärt 1995), had a large influence on the age trajectory and rate of senescence in breeding success (Aubry et al. 2009b). We suspect that any potential trade-off between reproduction and age-specific survival in kittiwakes would also be delayed, and tempered by variation in individual quality.

In addition to observed sources of individual heterogeneity, substantial amounts of unobserved heterogeneity have been detected in this population, both in survival and reproduction (Cam *et al.* 2000b, Cam *et al.* 2002a, Aubry *et al.* 2009b). Kittiwakes thus serve as an ideal biological model to evaluate the relative contributions of observed (i.e., reproductive traits) and unobserved individual heterogeneity (i.e., frailty) to variation in survival trajectories, and elucidate possible trade-offs between reproductive investment and future survival.

We propose to examine whether (i) trade-offs exist between survival trajectories and immediate or cumulative levels of reproductive investment. On one hand, individuals that accumulate several years of reproductive investment might incur long-term somatic costs that could translate into a decline in survival later in life (i.e., senescence in survival). On the other hand, individuals that breed successfully for several consecutive breeding seasons might be of higher intrinsic quality or benefit from breeding experience, which could translate into maintaining high levels of survival even later in life. (ii) While investigating these trade-off, we account for the potential importance of individual variability in recruitment age on survival trajectories. Recruitment age might be another proxy to individual (parental) quality (Aubry et al. 2009b) and temper the trade-offs defined in objective (i). (iii) We implement these effects in parallel with a frailty variable to quantify the relative contributions of observed heterogeneity and frailty to variability in survival trajectories. Doing so may also help elucidate underlying trade-offs between reproduction and survival in a long-lived species that could go undetected if frailty were not accounted for.

Methods

The population of interest has been under intense monitoring for 30 years (2046 individuals, 8279 observations), and all individuals are detected and observed every year from the age at first reproduction until death (here, inferences about mortality are necessarily restricted to the study area; Cam *et al.* 2005). Classical survival models used in human demography (e.g., Kleinbaum and Klein 2005) are therefore appropriate for estimating trajectories of survival across life (e.g., Wintrebert *et al.* 2005). Various extensions to the non-parametric Kaplan-Meier (1958) estimator, such as the Cox Proportional Hazard model

(CPH; Cox *et al.* 1972a) further allow identification of the measurable (i.e., observed) covariates associated with patterns in survival trajectories while accounting for frailty (Klein 1992). Information about the study population and site can be found in appendix A. All analyses were conducted in R (Development Core Team 2008; version 2.10.1).

Modeling observed heterogeneity

To address objectives (i) and (ii), we used CPH models (library 'survival' in R, procedure 'coxph') that are semi-parametric and have the advantage of making no assumption regarding shape of the underlying mortality hazard (a.k.a. the force of mortality) over life. Each covariate within the model is assumed to act multiplicatively (i.e., proportionally) on the baseline mortality hazard at each time step (e.g., Bradburn *et al.* 2003), such as $h(t, X_i) = h_0(t) \times \exp(\Sigma_{i=1}^{p} \beta_i X_i)$ where h_0 refers to the baseline hazard (i.e., hazard's value when all covariate values are null), p denotes the number of parameters in the model, the βs denote a set of estimated parameters, and the Xs represent the data, or series of covariate values for each individual i such as $X = (X_1, X_2, \ldots X_i)$, and t denotes time (in our case, time elapsed since recruitment rather than actual age). X_i can either consist of one unique value per individual (e.g., the age at first reproduction), or can be a vector of values (i.e., one value per year lived for each individual; e.g., time-specific reproductive investment).

The study is particular in that individuals that did not attempt to breed at least once were not a part of it. Individuals enter the 'risk set' at first reproduction (e.g., age 3, 4, 5, 6, 7 or more), which in our study is considered time 0. Thus, time in the above-defined CPH models is a correlate to age, and is equivalent to the number of years elapsed since first reproduction. For example, if a bird starts to breed at age 3, time step 1 corresponds to the interval between age 3 and age 4, time step 2 to the interval between age 4 and age 5, for such an individual.

CPH models are widely used to assess the effect of covariates on survival, whereas Accelerated Failure Time models are usually used to assess the underlying form of the mortality hazard, which was of less interest. To test the validity of using CPH models, we used the 'coxzph' procedure in the 'survival' library of R (Therneau and Grambsch 2000) to assess whether each covariate modality within the best performing CPH model acted proportionally on the mortality hazard. If so, the *p*-value associated to each covariate's proportionality test would be > 0.05. Using interactions between covariates can help relax the assumption of proportional covariate effects, since covariate effects may not only vary across covariate modalities, but can also be tempered by time or age (Martinussen & Scheike 2006).

To examine the relationship between recruitment age, reproductive investment, and future survival (objective *i*), we used 4 biological covariates (see Appendix B for graphical representation of these covariates). We used a single time-varying reproductive covariate 'REP' treated as a factor to capture effects of immediate reproductive investment at time t on survival from t to $t+1$. We first considered 11 different levels of reproductive investment (REP_1) that included not attempting to breed (reproductive level 1), attempting to breed but failing to produce any eggs (level 2); producing 1 egg (level 3), 2 eggs (level 4), or 3 eggs (level 5) but no chick; producing 1 egg (level 6), 2 eggs (level 7), or 3 eggs (level 8) but only fledged a single chick; producing 2 eggs (level 9), or 3 eggs (level 10) and successfully fledged 2 chicks, and producing 3 eggs that all fledged (level 11). If most levels of reproductive investment were straight forward, 'attempting to breed' had a particular meaning. We considered that an individual was attempting to breed if it completed nest construction (Maunder and Threlfall 1972), since only individuals that are truly involved in reproduction are able to complete the structure (Cam et al. 1998).

We progressively collapsed the different levels of reproductive investment into fewer categories to examine alternative hypotheses regarding the most relevant levels of reproductive investment that affect survival trajectories (Table 1). For example, we distinguished between individuals that failed to breed successfully (level 1 and 2) and individuals that bred successfully (level 3 to 11) and indexed the covariate as REP_3. Table 1 lists all of the biological sub-hypotheses tested (models 1 to 10).

We also considered a cumulative version of REP (i.e., CREP) and investigated the effects of CREP cumulated from the age at first reproduction 'AFR' to time *t* on survival from time *t* to *t*+1 (Table 1; models 11 to 20). For CREP, we also progressively collapsed the different levels of cumulative reproductive investments and indexed CREP accordingly from $CREP_{11}$ to $CREP_{20}$ (Table 1).

To assess if both immediate and cumulative reproductive investment affects survival, we developed a lagged cumulative reproductive investment covariate that only included investment from AFR up to time x-1, and its effect on survival from time *t* to *t*+1 (and called it 'LCREP'; App. B). This covariate allowed us to examine independent additive effects of cumulative (LCREP) and immediate (REP) reproductive investment on future survival (i.e., it avoids the qualms of colinearity between covariates). Again, we considered progressively collapsed levels of cumulative reproductive investment and indexed LCREP as above (Table 1; models 21 to 30).

Finally, we considered a series of models accounting for interactions between REP and LCREP (Table 1; models 121 to 220), since they could account for the effect of individual differences in reproductive investment on survival better than additive models. We controlled for differences in AFR across individuals when examining the influence of cumulative reproduction on survival (i.e., by modeling interactions between AFR and CREP, or between AFR and LCREP). We also systematically considered an additive effect of year ('YEAR') in each CPH model to account for environmentally driven changes in survival over time.

Overall, we compared the fit of the above-defined CPH models (Table 1) using Akaike's information criterion adjusted for sample size (AIC_c; Akaike 1973). We based our inference on the top performing model and any model that was within 2 AICc units of the top model (Burnham and Anderson 2002).

Modelling frailty

Vaupel and Yashin (1985) introduced the idea of a frailty component '*z*' that acts multiplicatively on the hazard rate at each time step to correct for unobserved individual heterogeneity. Such frailty terms were later implemented into CPH frailty models: $h(t \mid X_i(t)) = z \times h_0(t) \times \exp(\beta_i X_i(t))$, also denoted as $h(t \mid X_i(t)) = h_0(t) \times \exp(\beta_i X_i(t) + \varepsilon)$ with the error term $\varepsilon = log(z)$(Klein 1992). The frailty term is generally assumed to have a gamma distribution such that frailty values are positive, whereas a normal distribution ranges from - ∞ to + ∞. The expected value of a gamma-distributed frailty for the i^{th} subject exiting at time y_i, and experiencing an event of type δ_i is given by: $E(Z \mid y, \delta, \alpha) = \dfrac{1+\sigma^2\delta}{1+\sigma^2 H_0(y)\exp^{\beta X}}$, where *i* is the individual, *y* is the exit time (i.e., time at which the individual left the study either because it died, or because the study ended), *α* is the right-censoring indicator ('0' if right-censored, i.e., the individual was still alive at the end of the study; '1' if death is observed), and *β* is the covariate profile (β_t in the case of a time-varying covariate). We maximized Breslow's maximum likelihood estimator (Breslow 1972) with the E-M algorithm to estimate the variance σ^2 of the frailty term *z* with mean 1 (Klein 1992, Lin 2007).

We calculated AIC_c values for a model accounting only for observed heterogeneity (i.e., reproductive covariates; top performing model) (model a), a model accounting for both observed heterogeneity and frailty (model b), and a model accounting for frailty only (i.e., frailty) (model c). Models a, b, and c accounted for a categorical effect of 'YEAR' (see above) as a baseline source of environmental variability in survival. A reference model accounting only for temporal changes in survival was also considered (model d; YEAR effect only).

We used Adler and HillRisLambers' approach (2008) to calculate the relative contribution of observed heterogeneity (i.e., reproductive covariates) and frailty to individual variation in survival. According to this approach, if A is the R^2 of model a, B is the R^2 of model b, and C is the R^2 of model c, then $D = A + C - B$, where D is the overlap of A and B. We were particularly interested in the relative proportion of the variance that is explained only by observed sources of heterogeneity ($A - D$) and unobserved sources ($C - D$). However, because the use of R^2 is not appropriate for CPH models with random effects (Adler and HillRisLambers 2008), we used Zheng's goodness of fit measure (Zheng 2000), which we renamed: $Dev_x' = 1 - \frac{Dev_x}{Dev_y}$, where *Dev* stands for deviance, x is the model of interest (either a, b, or c), and y is the reference model (d). We obtained a log-likelihood estimate for model a, b, and c, then calculated deviances for each model according to the following formula: $Dev_x = -2 \times \ln \ Likelihood_{\mathrm{model}(x)}$. We then calculated Dev_x' for each model, and replaced those values in Adler and HillRisLambers' equation to obtain the 'relative percentage reduction in the deviance' attributable to the reproductive covariates on one hand, and frailty on the other hand. We then took the ratio of these % reductions to identify whether observed reproductive covariates or frailty led to a greater reduction in overall deviance. We note that it is not appropriate to think of Dev_x' as a direct surrogate for R^2 statistics. A 100% reduction in Deviance is impossible, and thus these percentage reductions should not be thought of on a 0 to 100% scale (Zheng 2000).

Results

To appropriately account for temporal changes in time-specific survival, we investigated the fit of a fully year-varying CPH model ($df = 26$), then used the model's estimates to cluster years that had a similar effect on time-specific survival (i.e., similar β estimates). Accordingly, we found that categorizing 'YEAR' into 4 groups explained annual changes in survival in the most parsimonious fashion (group 1: 2003, 2005, 2006, 2007; group 2: 1983, 1992, 1993, 1996, 1997, 2002, 2004; group 3: 1987, 1988, 1990, 1998, 1999, 2001; group 4:

1984, 1985, 1986, 1989, 1991, 1995, 2000), where group 1 represents the baseline group with lowest mortality, and in order, group 4 represents the years with highest mortality. Naturally, years are not necessarily consecutive within each group because environmental conditions (e.g., storms, massive predation events, pollution, etc.) change stochastically.

Among the set of models testing for trade-offs between reproductive investment and survival, only two models were supported by the data (top model: model 132, Table 2). These top models retained the same covariates, but only the best ranked model (model 132) included interaction terms. We thus focus our inference on the top ranked model because nearly all covariates, including interactive effects, were statistically significant. Moreover, frailty improved model fit (larger reduction in deviance) more than observed reproductive covariates. Therefore, we present here the estimates associated with the best performing model containing both reproductive covariates and frailty.

The best performing model retained an effect of YEAR treated as a factor, additive and 2 by 2 interactive effects of AFR, REP_2, and $LCREP_{2,}$ as well as a triple interaction between AFR, REP_2, and $LCREP_2$ (see Table 3 for parameter estimates). Positive coefficient estimates for the 'YEAR' effect ($\beta > 0$ or $\exp(\beta) > 1$; Table 3) indicate higher mortality risk and lower survival than the baseline YEAR group (i.e., group 1), and negative parameter coefficients indicate the opposite. Thus, YEAR groups 2, 3, and 4 were years in which mortality risk was higher than in the baseline group (Table 3).

We found that individuals that delay recruitment had lower survival after recruitment than those that began reproduction earlier in life (Table 3, $\exp(\beta) = 1.246$: 24.6% higher mortality risk per year of delayed age at first reproduction).

The $LCREP_2$ and REP_2 parameters in the top model indicate that two key levels of reproductive investment accounted for variability in kittiwake survival better than other parameterizations: not attempting to breed (Table 1, reproductive level 1) versus attempting to breed regardless of clutch size and breeding success (reproductive levels 2 to 11 treated the same). We found that individuals who accumulated more reproductive attempts up to time *t*-1 experienced higher subsequent survival from time *t* to *t*+1 (Table 3; exp(β) = 0.449). Increasing the number of lagged cumulative breeding attempts by 1 unit decreased the risk of dying by more than half. Moreover, the interaction terms including LCREP_2 and AFR indicated that the negative influence of delayed recruitment may be somewhat counter-balanced by the accumulation of breeding attempts over life (Table 3, Fig. 1).

Only after variation in recruitment age (AFR) and breeding experience (LCREP_2) were accounted for, could the 'immediate' impact of reproductive investment on survival be revealed. The effect of REP_2 in the top model indicated that attempting to breed at time *t* quadrupled the risk of dying between time *t* and *t*+1 (Table 3; exp(β) = 4.207; Figs. 1. b and d) relative to individuals that did not attempt to breed (Figs. 1. a and c). However, the interaction terms indicated a lesser impact of immediate reproduction in experienced individuals (greater LCREP_2), which was further tempered by recruitment age (Table 3, Fig. 1).

Our results further indicated that once individuals cumulated more than 4 lagged breeding attempts ($\mathrm{LCREP}_2 > 4$), their predicted probability of survival over their remaining life was nearly constant and extremely high (Fig. 1), yet only 27.61% of the sample cumulated > 4 breeding attempts; mostly young recruits. Thus, the stabilization of the predicted survival surfaces at high survival (Fig. 1) did not apply to many individuals in our population, especially those with delayed recruitment.

On the other hand, 72.39% of the population cumulated < 5 breeding attempts over life ($\mathrm{CREP}_2 < 5$), and within this sub-group, most individuals recruited at ages 3, 4, or 5, and cumulated 2 or less breeding attempts overall (App. C). For individuals with < 5 lagged accumulated breeding attempts, survival estimates exhibited substantial variation across reproductive covariate combinations and across life (Fig. 1. a-d). For example, an individual that recruited early and did not subsequently breed, experienced fluctuations in annual survival between 0.7 and 1.0 throughout much of life (age 3-16), but then experienced rapid senescence to an annual survival probability of 0.31 at age 20 (Fig. 1. a). Attempting to breed led to an immediate cost of reproduction on one hand (Fig. 1. b), but on the other hand, increased breeding experience (i.e., greater $LCREP_2$) later improved annual chances of survival up to age 16, and reduced the severity of senescence thereafter (and little senescence at all after $LCREP_2 > 4$; Fig. 1. a). The same patterns in age-specific survival related to reproductive attempts were also observed in individuals with delayed recruitment (Fig. 1. c & d). Attempting to breed and delayed recruitment have similar dramatic effects on survival, and the two combined result in the lowest survival chances across life (Fig. 1.d.).

Residual plots for the best performing model including frailty did not indicate signs of large departure from proportional effects across recruitment groups (AFR; *Rho* = -0.025, χ^2 = 0.898, p = 0.343; plots are not presented for the sake of conciseness). The main effect of immediate reproductive investment on the hazard was not proportional (REP_2, *Rho* = -0.058, χ^2 = 4.871, p = 0.027), nor was the lagged (main) effect of cumulative reproductive investment ($LCREP_2$, *Rho* = 0.103, χ^2 = 16.717, $p < 0.05$). However, the triple interaction between all of the covariates of interest corrected for the occasional lack of proportionality of single covariates (AFR * REP_2 * $LCREP_{22}$, *Rho* = -0.047, χ^2 = 3.823, p = 0.051), indicating that the proportionality assumption was reasonable as long as the triple interaction was accounted for.

The estimated variance of the frailty term in the top ranked model that accounted for both sources of heterogeneity was large (3.02). We found that unobserved heterogeneity (i.e., frailty) contributed 1.34 times more to the overall reduction in deviance than observed (fixed and dynamic) heterogeneity in reproduction relative to the reference model with only temporal variation in survival (model d).

Discussion

Variation in kittiwake survival was related to both fixed (recruitment age) and dynamic (time-varying reproductive investments and temporal effects) covariates, as well as unobserved individual differences (frailty).

Age at first reproduction had an important impact on survival and senescence. In the black-legged kittiwake, we suspect that early recruits might possess inherent reproductive, survival, and competitive abilities that could allow them to start breeding earlier, senesce slower, and attain higher fitness than individuals that delay recruitment (e.g., Cam and Monnat 2000a, Cam *et al.* 2002a, Aubry et al. 2009b). That said, recruiting at the earliest possible age may not be the best strategy either.

Pre-breeding experience can help achieve high levels of reproductive success through ‘prospection’. For example, black-legged kittiwakes are known to prospect for breeding sites in order to gain information on reproductive success within a reproductive colony, and increase chances of successful settlement and reproduction the following year (e.g., Boulinier et al. 1996). Because chicks are often left unattended by their parents at the nest, ‘squatters’ (Cadiou 1993) often visit these nests, not to experience parenthood (i.e., squatters often kill the left-alone chicks by beating them, sitting on them, or even re-building nests on them), but to acquire a social status (i.e., squatters become familiar with neighbors whose aggressiveness progressively decreases) while the parents are gone at sea to find food.

Post-recruitment experience on the other hand is the experience gained through previous breeding opportunities. Aubry *et al.* (2009b) showed that individuals recruiting at intermediate ages maintained high levels of breeding success over their lifespan, balanced pre- and post-recruitment experience in an advantageous way (i.e., highest levels of breeding success at first reproduction), and seemed to balance the level, onset, and speed of reproductive senescence compared to earlier and later recruits (Aubry *et al.* 2009b). Future work will thus aim at estimating individual fitness (e.g., Coulson *et al.* 2006), and measure the force of selection on recruitment age operating through its impact on lifetime trajectories of reproductive success (Aubry *et al.* 2009b) and survival (presented here).

Although recruitment age helped explain variation in survival, dynamic reproductive investment had a more substantial influence. The effects of different levels of reproductive investment (i.e., attempting and not attempting to breed) on survival demonstrated that dynamic sources of reproductive investment should not be neglected while studying the effects of reproduction on survival (Tuljapurkar *et al.* 2009, Steiner *et al.* 2010), especially in long-lived species that have more opportunities to display variation in reproductive investment. We found that both immediate and cumulative reproductive investment influenced kittiwake survival. On one hand, breeding at time *t* had a large negative effect on survival between time *t* and *t*+1 (i.e., the classic immediate cost of reproduction). One the other hand, the more breeding attempts were cumulated up to time *t*-1, the lower the chance of dying from time *t* to time *t*+1. Thus, it seems that immediate costs of reproduction on survival do exist in this population, but in the long run, they could be tempered by the number of cumulated breeding attempts, which may indicative of environmental experience, innate individual (parental) quality, or quality determined by developmental conditions before recruitment. In part, this reinforces the findings of Cam *et al.* (2002a) who observed a positive correlation between breeding probability (analogous to breeding attempts in our study) and survival.

Kittiwakes also experienced significant temporal stochasticity in survival. In recent years (2003, 2004, 2006, 2007) the mortality hazard was lower than in the past (Table 3); however, we know very little about the causal drivers of temporal variation in age-specific or cohort-specific survival. Frederiksen *et al.* (2007) found that kittiwake survival in England and Ireland was negatively correlated with sea-surface temperature and breeding productivity, but positively correlated with an increase in abundance of their principal prey, *Calanus* copepods.

Knowledge about changes in resource availability, climatic conditions, and the frequency of predation events is accruing for locations near our study area. In the future, we hope to investigate how these variables influence temporal variation in survival for different birth cohorts.

In accordance with Cam *et al.* (2002b), our work also indicates that there is a significant amount of unobserved individual heterogeneity in survival chances. In fact, our most interesting finding was that frailty (Vaupel and Yashin 1985) reduced the relative model deviance (i.e., improved model fit) 1.34 times more than observed heterogeneity in reproductive investment. The approach usually taken in demographic studies is to try and explain as much variability as possible *via* measured covariates (e.g., Wintrebert *et al.* 2005). Reproductive covariates alone, however, were not sufficient to explain individual variability in adult survival. There is a large amount of individual variation in survival that we cannot explain with the measured covariates, which may be related to genetic differences, micro-habitat variability, or traits that we simply did not record. Because it is impossible to capture all of the individual heterogeneity in survival chances with measured (i.e., observed) covariates, we recommend always considering the contribution of unobserved heterogeneity while studying age-specific demographic trajectories (Vaupel and Yashin 1985).

Survival analyses with frailty parameters are rarely used in population and evolutionary ecology (but see for e.g., Fox *et al.* 2006), despite their growing popularity in human demography (Hougaard *et al.* 1991). In large part, this is likely driven by the requirement of perfect detectability, a condition that has recently been relaxed in capture-mark-recapture methods (e.g., Royle 2008, Gimenez and Choquet 2010). Moreover, identifiability of frailty in Cox proportional hazard models can potentially be confounded with a lack of proportionality (K. Wachter, pers. com.). Given that the observed covariates in the top model satisfied the assumption of proportionality, we do not think this was of great significance in our study, but careful attention should be paid to this issue until better statistical methods are developed. Development of mixed models accounting for fixed and dynamic covariates, as well as dynamic frailty (Tuljapurkar et al. 2009), is also needed. Such models might be able to explain even more variability in age-specific reproduction and survival for long-lived species, and could thus be critical in efforts to learn more about long-term trade-offs in the wild.

Additional questions regarding frailty and key life history traits involved in trade-offs remain. For example, how heritable is an individual's risk of mortality? In human demography, correlated gamma-frailty models of bivariate survival in pairs of twins are used to decompose frailty into genetic and environmental components, allowing for estimation of heritability in frailty (e.g., Iachine et al. 1998). In wild animal populations, animal models are also used to understand evolutionary mechanisms underlying variation in key life history traits (Kruuk 2004). Quantitative genetics is providing a fertile research framework to understand the evolution of life histories that we intend to use in future research on kittiwakes (e.g., Hadfield 2010, Papaix et al. 2010).

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Table 1. Cox proportional hazard models testing for the effects of various levels of immediate (i.e., ‘REP’; models 1 to 10), cumulative reproductive investment (i.e., CREP; models 11 to 20), or both (i.e., REP + LCREP; models 21 to 120), as well as the effect of interactions (i.e., between REP and LCREP; models 121-220) on age-specific survival. For each model defined below, additive year effects (i.e., ‘YEAR’) were systematically included to account for environmental variability in survival. Moreover, interactions between the age at first reproduction (i.e., AFR) and CREP, LCREP, or REP * LCREP were considered to account for potential differences in individual quality reflected by the timing of first reproduction.

Different levels of reproductive investment are defined for each of the covariate defined above: REP, CREP, and LCREP. For example, model 2 addresses the effect of two levels of investment (i.e., not breeding or breeding) at age x, on survival from age x to x+1 (i.e., REP_2). Model 13 addresses the effects of 1) not breeding, 2) breeding but failing to produce eggs, and 3) laying at least 1 egg, cumulated from the age at first reproduction up to age x, on survival between age x and x+1 (i.e., $CREP_3$). Model 117 addresses both the immediate and cumulative effect of 4 levels of reproductive investment: 1) not breeding, 2) breeding but laying no eggs, 3) producing at least 1 eggs, 4) fledging at least 1 chicks) up to age x, on survival between age x and x+1 (i.e., REP_4 + $LCREP_4$).

Note. n: number of observations per level of reproductive investment.

<table>
<tr><td colspan="2">Model Covariates</td><td colspan="10">Models</td></tr>
<tr><td colspan="2">Immediate effect of reproductive investment on survival ‘REP’</td><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td>6</td><td>7</td><td>8</td><td>9</td><td>10</td></tr>
<tr><td colspan="2">Cumulative effect of reproductive investment on survival ‘CREP’</td><td>11</td><td>12</td><td>13</td><td>14</td><td>15</td><td>16</td><td>17</td><td>18</td><td>19</td><td>20</td></tr>
<tr><td colspan="2">Immediate and lagged cumulative effects of reproductive investment on survival ‘REP + LCREP’</td><td colspan="10">21-120</td></tr>
<tr><td colspan="2">Interactions between immediate and lagged cumulative effect of reproduction on survival ‘REP * LCREP’</td><td colspan="10">121-220</td></tr>
<tr><td colspan="12">Partitioned levels of reproductive investment used to define the models above</td></tr>
<tr><td><i>n</i> = 989</td><td>Level 1. does not breed</td><td>x</td><td>x</td><td>x</td><td rowspan="5">x</td><td>x</td><td rowspan="2">x</td><td>x</td><td rowspan="2">x</td><td>x</td><td rowspan="2">x</td></tr>
<tr><td><i>n</i> = 872</td><td>Level 2. bred but did not lay eggs</td><td>x</td><td rowspan="10">x</td><td>x</td><td>x</td><td>x</td><td>x</td></tr>
<tr><td><i>n</i> = 1635</td><td>Level 3. produced 1 egg but no chick</td><td>x</td><td rowspan="9">x</td><td rowspan="3">x</td><td rowspan="3">x</td><td rowspan="3">x</td><td rowspan="3">x</td><td rowspan="3">x</td><td rowspan="3">x</td></tr>
<tr><td><i>n</i> = 2068</td><td>Level 4. produced 2 eggs but no chick</td><td>x</td></tr>
<tr><td><i>n</i> = 61</td><td>Level 5. produced 3 eggs but no chick</td><td>x</td></tr>
<tr><td><i>n</i> = 638</td><td>Level 6. produced 1 egg, fledged 1 chick</td><td>x</td><td rowspan="6">x</td><td rowspan="6">x</td><td rowspan="6">x</td><td rowspan="3">x</td><td rowspan="3">x</td><td rowspan="3">x</td><td rowspan="3">x</td></tr>
<tr><td><i>n</i> = 2004</td><td>Level 7. produced 2 eggs, fledged 1 chick</td><td>x</td></tr>
<tr><td><i>n</i> = 95</td><td>Level 8. produced 3 eggs, fledged 1 chick</td><td>x</td></tr>
<tr><td><i>n</i> = 1200</td><td>Level 9. produced 2 eggs, fledged 2 chicks</td><td>x</td><td rowspan="3">x</td><td rowspan="3">x</td><td rowspan="2">x</td><td rowspan="2">x</td></tr>
<tr><td><i>n</i> = 79</td><td>Level 10. produced 3 eggs, fledged 2 chicks</td><td>x</td></tr>
<tr><td><i>n</i> = 27</td><td>Level 11. produced 3 eggs, fledged 3 chicks</td><td>x</td><td>x</td><td>x</td></tr>
</table>

Table 2. Test of hypotheses pertaining to the effect of immediate (i.e., REP_{1-10}), cumulative (i.e., AFR * $CREP_{1-10}$), or both cumulated and immediate reproductive investment (REP_{1-10} + AFR * $LCREP_{1-10}$) on survival from one age to the next (i.e., models in table 2). We only present the top 10 models (out of 220 models) since only the top two models were at all supported by the data (shaded models).

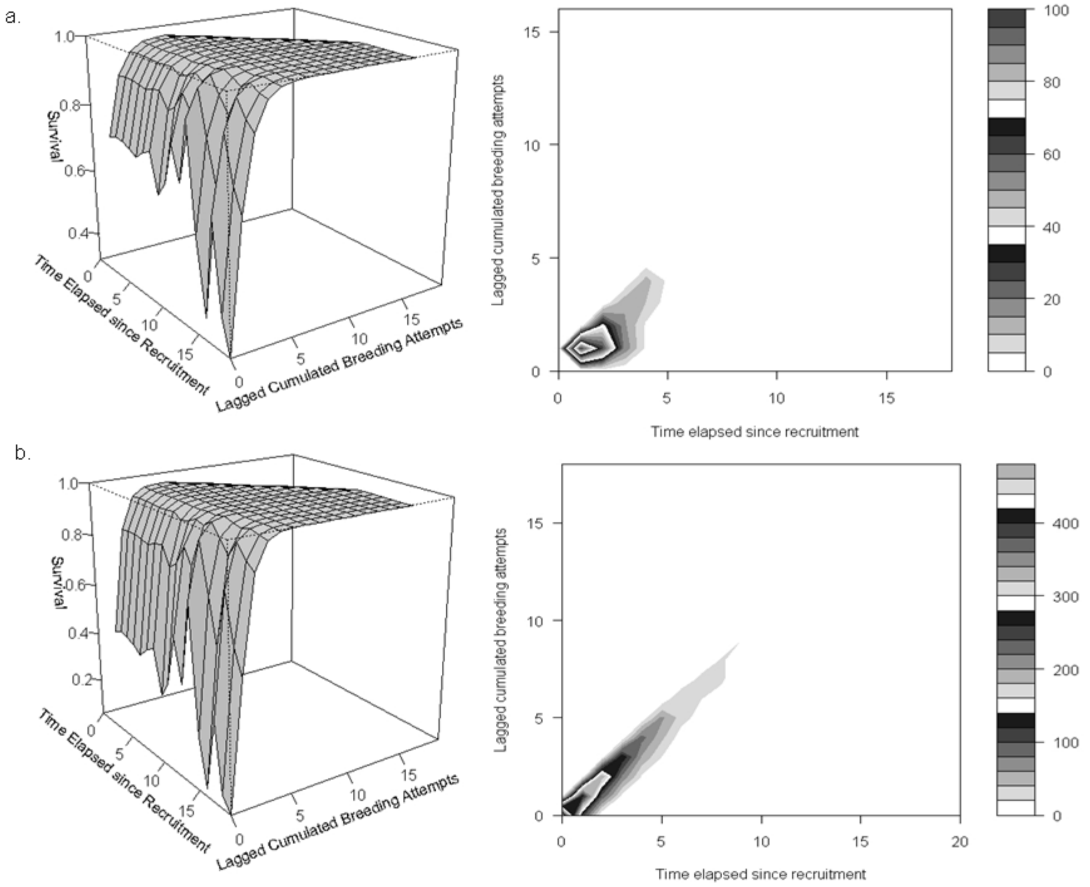
Models	K	AICc	ΔAICc
132	10	16587.25	0.00
32	6	16587.66	0.41
42	6	16610.33	23.08
142	10	16611.15	23.90
62	6	16639.54	52.29
162	10	16640.96	53.71
82	6	16645.04	57.79
102	6	16645.08	57.83
202	10	16645.41	58.16
182	10	16645.42	58.17

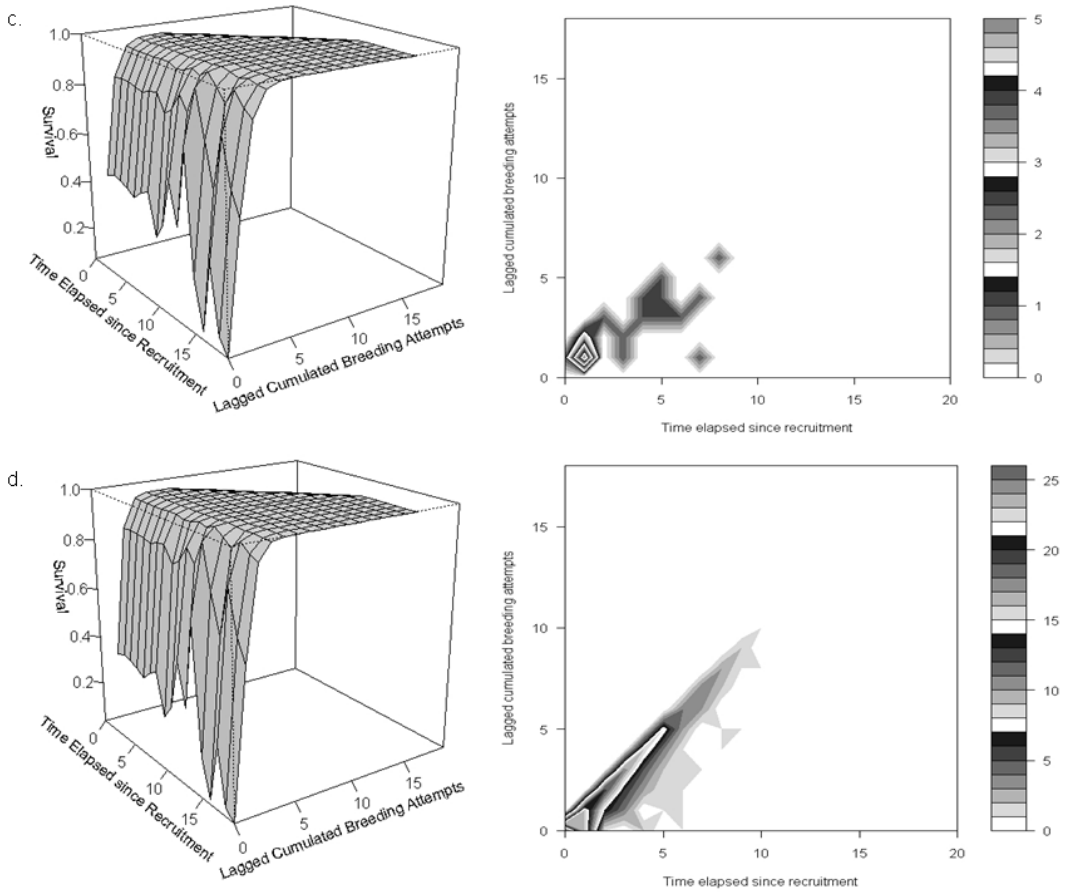
† K: number of parameters in the model.

Table 3. Coefficient estimates (β) for the top-performing model including a frailty term; exp(β) is the associated mortality risk (i.e., a value superior to 1 indicates an increased mortality risk compared to the baseline coefficient, and vice versa, a value inferior to 1 indicates a lower mortality risk). We also provide standard errors (i.e., s.e. (β)), 95% confidence intervals, as well as test statistics.

Covariates	β	exp(β)	s.e.(β)	CI-lower	CI-upper	z-values	p-values
$YEARC_2$	0.138	1.148	0.076	0.062	0.214	1.815	0.070
$YEARC_3$	0.340	1.405	0.081	0.258	0.421	4.171	< 0.001
$YEARC_4$	0.260	1.297	0.076	0.184	0.336	3.418	< 0.001
AFR	0.220	1.246	0.106	0.114	0.326	2.084	0.037
REP_2	1.437	4.207	0.474	0.963	1.911	3.031	0.002
$LCREP_2$	-0.800	0.449	0.127	-0.927	-0.673	-6.320	< 0.001
$AFR*REP_2$	-0.166	0.847	0.113	-0.280	-0.053	-1.464	0.143
$AFR*LCREP_2$	-0.110	0.896	0.030	-0.140	-0.080	-3.720	< 0.001
$REP_2*LCREP_2$	-0.465	0.628	0.133	-0.598	-0.331	-3.484	< 0.001
$AFR*REP_2*LCREP_2$	0.110	1.116	0.032	0.078	0.142	3.473	< 0.001

Figure 1. Predicted surfaces of survival, averaged across all years, from the best performing CPH model accounting for both observed heterogeneity and frailty. Survival is presented across ages and lagged cumulated breeding attempts (i.e., $LCREP_2$) for various combinations of recruitment age (i.e., AFR) and immediate reproductive investment (i.e., REP_2). We selected 4 combinations of AFR and REP_2 representing the extremes within each trait: AFR = 3 (panels a & b) and AFR = 7 (panels c & d) (earliest and latest possible recruitment respectively), and $REP_2 = 0$ (panels a & c) or 1 (panels b & d) (no attempt or attempt to breed at age *x*). For each combination for AFR and REP_2, we presented contour plots representing sampling sizes as a function of the time elapsed since recruitment and the number of lagged breeding attempts cumulated over a lifetime ($LCREP_2$).




c.
Survival
0.2
0.4
0.6
0.8
1.0
Time Elapsed since Recruitment
Lagged Cumulated Breeding Attempts
Lagged cumulated breeding attempts
Time elapsed since recruitment
0
5
10
15
20
d.
Survival
Time Elapsed since Recruitment
Lagged Cumulated Breeding Attempts
Lagged cumulated breeding attempts
Time elapsed since recruitment
25

Appendix A.

Study site and sample specifications

Five colonies of black-legged Kittiwakes (*Rissa tridactyla*) breeding in Brittany, France (Cap Sizun, 48°5’N 4°36’W) have been studied since 1979, which provides us with 30 years of data on thousands of individuals. Each individual’s presence is recorded at each resighting occasion during the breeding season, currently ranging from January to September (Monnat *et al.* 1990). All breeding events are observed for all marked individuals, along with behavioral and demographic information such as age, identity of the partner, age at first reproduction, number of chicks hatched, number of chicks fledged, nest attendance, etc. Additional details on data collection and field work can be found in Cam *et al.* 2002a, 2002b, 2003, 2005, Naves *et al.* 2007, and Aubry *et al.* 2009a.

Since detectability is virtually equal to 1 for the breeding segment of the population ($p = 0.9964$, 95% CI: 0.9925 to 1; Cam *et al.* 2003), this dataset is ideal for examining the influence of recruitment age, breeding history, and unobserved heterogeneity on survival trajectories. We were only interested in breeding individuals (i.e., individuals that have bred at least once, successfully or not), and working on such a sample allowed us to consider models free of nuisance parameters (i.e., recapture probabilities) because all breeding individuals are observed (Cam *et al.* 2003, Aubry *et al.* 2009a).

The sample consisted of 2046 individuals that recruited between 1982 and 2007 (8279 observations in total). Minimum recruitment age was 2 years old and only concerned 7 individuals, thus we pooled them with individuals that recruited at age 3 (i.e., recruitment group 3-). Only 13 individuals recruited after 7 years of age. We pooled these individuals with 7 year-old recruits, and will further refer to this group as 7+ year-old recruits (i.e., Age at First Reproduction, or AFR = 7+). The maximum observed lifespan in the study was 25 years and concerned one individual that recruited at age 4 in 1986 that was still alive in 2007.

Intense monitoring efforts (i.e., daily observations) are not always sufficient to track egg and chick production (due to predation, siblicide, etc), especially given limited viewing access to the nests (i.e., seashore cliffs). Since we were studying the potential influence of various levels of reproductive investment on survival, we had to deal with some measurement uncertainty in both egg (290 out of 8279 observations) and chick production (58 out of 8279 observations). Removing these observations from the dataset or replacing them with zero, however, did not change any of the results. Thus, we included uncertain measures in our sample.

Since we were interested in age-specific survival and senescence, individuals that were still alive at the end of the study in 2007 were ‘right-censored’ (see e.g. in Kleinbaum and Klein 2005). Some individuals died after the study period but still contributed partly to the likelihood function underlying each survival model tested. Right-censoring takes into account these partial individual contributions to the likelihood to ultimately obtain unbiased estimates of survival (e.g., Kleinbaum and Klein 2005). We did not have to consider cases of left-truncation, as individuals that did not make it to recruitment age (and that should have been left-truncated) were not of interest.

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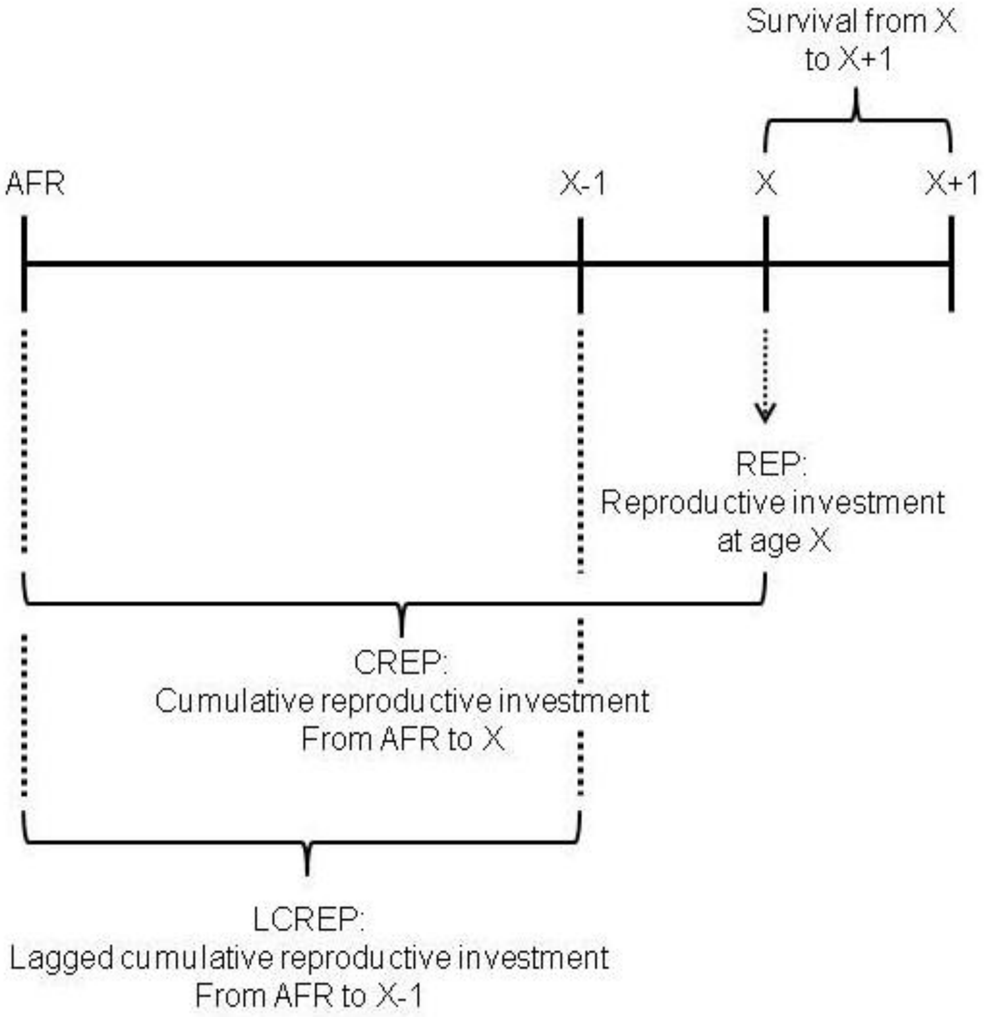
Appendix B.

Representation of the 4 reproductive covariates of interest: AFR (i.e.., recruitment age), REP (i.e., reproductive investment at age *x*), CREP (i.e., cumulative reproductive investment from AFR to age *x*), and LCREP (i.e., lagged cumulative reproductive investment from AFR to age *x*-1) and their effects on survival from age *x* to *x*+1. *Note*. According to our approach (see methods), 'age *x*' is equivalent to 'AFR + time *t*', since *t* denotes the time elapsed since recruitment rather than actual age. Thus, time *t* is a correlate to age *x* in this study, and we often use them interchangeably in the text.



Appendix C.

Percentage of individuals within the population recruiting at ages 3, 4, 5, 6, 7 or more, and cumulating 1, 2, 3, 4, or more than 5 breeding attempts over life (CREP = 1, 2, 3, 4, ≥ 5). Note: CREP is similar to LCREP except that the latter is lagged by 1 unit (see Appendix B for graphical representation of CREP and LCREP).

	Age at first reproduction							
Number of breeding attempt cumulated over life	3	4	5	6	≥ 7	(%)	*N*: number of individuals	*n*: number of observations
1	8.65	11.44	6.55	2.15	0.83	29.62	431	1884
2	4.45	7.58	3.81	1.47	0.24	17.55	302	1249
3	3.96	5.87	2.64	1.03	0.20	13.69	248	896
4	3.67	4.74	2.10	0.78	0.24	11.53	171	629
≥ 5	7.43	12.07	5.52	1.86	0.73	27.61	419	1575
(%)	28.15	41.69	20.63	7.28	2.25			
N: number of individuals	576	853	422	149	46			
n: number of observations	2414	3537	1565	571	192			

~ CHAPTER IV ~

'One can choose to work hard, or to chill in the sun.

But if you chose the latter, don't complain about your fitness.'

Picture: Lise M. Aubry

SELECTION ON THE AGE AT FIRST REPRODUCTION IN A LONG-LIVED SEABIRD: ESTIMATING INDIVIDUAL FITNESS FOR VARIOUS RECRUITMENT STRATEGIES

Lise M. Aubry, Emmanuelle Cam, Jean-Yves Monnat, and David N. Koons

In Preparation

Abstract

We used a known statistical approach to estimate individual fitness (i.e., jack-knifing) in order to study selection on delayed recruitment in a long-lived seabird, the black-legged Kittiwake. However, we expanded on the jack-knifing approach to estimate individual fitness by utilizing formal statistical estimators (rather than crude proportions) that accounted for observed and unobserved (e.g., frailty) heterogeneity in fertility and survival across individuals. We found that the studied population (scenario 1) was declining ($\lambda = 0.8916$), and jack-knifed estimates of individual fitness (w_i) were measured relative to the log of this value. We observed a slight directional change favoring earlier age at first reproduction (age 3). However, the selection gradient was weak (slope of the regression between individual fitness estimates and recruitment age) and indicated that delaying recruitment for two or three years (age 5, 6, or 7) might not be as costly as previously thought. Theory suggests that selection on recruitment age can be different in declining versus growing populations. The estimated population growth rate might be biased low because the estimation of mortality and permanent emigration are confounded in this population that has been persisting at stable levels for years. Thus, we developed two other scenarios by multiplying the matrix population model by a constant such that average population growth rates were either $\lambda = 1$ (scenario 2), or $\lambda = 1.1084$ (scenario 3; mirror image of scenario 1). However, the direction and strength of the selection gradient was virtually equivalent across all scenarios. We next aim to apply this novel approach to examine selection on the age at first reproduction in a stochastic setting.

Key-words: age at first reproduction, individual fitness, jack-knifing, recruitment strategy, Rissa tridactyla, selection gradient.

SÉLÉCTION SUR L'ÂGE À LA PREMIÈRE REPRODUCTION CHEZ UN OISEAU MARIN LONGÉVIF : ESTIMATION DE LA FITNESS INDIVIDUELLE POUR DIVERSES STRATÉGIES DE RECRUTEMENT

Résumé

Nous avons utilisé une approche statistique connue afin d'estimer la fitness individuelle (i.e., jack-knifing) et d'étudier la force et la direction des processus de sélection opérant sur l'âge à la première reproduction chez une population d'oiseaux marins longévifs (la mouette tridactyle). Cependant, nous avons étendu cette approche à l'utilisation d'estimateurs statistiques (plutôt qu'à la simple utilisation d'information démographique 'brute') qui prennent en compte l'hétérogénéité observée et non-observée au sein de la population.

Nos résultats indiquent que la population étudiée (scenario 1) est en déclin ($\lambda = 0.88916$); les estimateurs de fitness individuelle (w_i) ont été mesurés sur une échelle logarithmique de cette valeur. Nous avons également observé un faible changement directionnel en faveur d'un recrutement précoce (âge 3). Néanmoins, le gradient de sélection montre une pente de régression faible entre fitness individuelle et âge à la première reproduction, et semble indiquer que différer le recrutement pour 2 ou 3 ans (âge 5, 6, or 7) n'est pas aussi couteux que cela.

La théorie des traits d'histories de vie prédit que les forces de sélection opérante sur l'âge à la première reproduction peuvent être différentes dans le cas d'une population en déclin ou en croissance. Nous pensons que le taux de croissance de la population pourrait être sous-

estimé, car la mortalité et la dispersion permanente sont des processus confondus dans cette étude. Ainsi, nous avons développé deux autres scenarios démographiques: en multipliant le modèle matriciel par une constante, nous avons pu fixer le taux de croissance moyen de la population à $\lambda = 1$ (scenario 2), et à $\lambda = 1.1084$ (scenario 3; λ miroir du scenario 1). Cependant, la direction et le sens du gradient de sélection sont restés inchangés.

Nous proposons d'utiliser cette nouvelle approche d'estimation de la fitness individuelle en milieu stochastique, afin d'étudier les processus de sélection sur l'âge à la première reproduction dans un contexte plus réaliste.

Mots-clés: âge à la première reproduction, fitness individuelle, gradient de sélection, jack-knifing, stratégie de recrutement, Rissa tridactyla.

Introduction

Age at first reproduction is a central trait to life history evolution (e.g., Stearns 1992), and is known to be one of the main determinants of fitness in species that show variability in recruitment age (Cole 1954, Lewontin 1964, Brommer et al. 1998, Kruger 2005). Delayed recruitment was first thought to be maladaptive in nature, as early recruitment should be favored by natural selection (Cole 1954, Charlesworth 1994). Indeed, early recruitment expedites investment in the next generation, maximizes the potential number of reproductive events in a lifetime, and is associated to a higher probability of surviving to adulthood (Bell 1980). However, within a species that displays variability in recruitment; individuals that recruit at the earliest possible age are rare (see Stearns 1992 for review).

Delayed recruitment occurs in both semelparous and iteroparous organisms. In semelparous monocarpic plants for example, the advantage of delayed flowering (an event that occurs once in a lifetime) comes from increased fertility as a result of growth (Metcalf et al. 2003). In iteroparous organisms such as birds, the advantage of delayed recruitment mainly results from an increase in reproductive abilities with age, experience, or both (Charlesworth 1994, Forslund and Pärt 1995). For example, delayed recruitment permits one to gather information on suitable habitats for reproduction (e.g., Ens et al. 1995, Boulinier and Danchin 1997, Aubry et al. 2009), foraging (e.g., Machetti and Price 1989), and allows for improved social skills (e.g., Danchin and Wagner 1997, Danchin et al. 1998), all of which can improve fitness. Pre-recruitment activities such as these can result from learning via pre-recruitment experience (e.g., Cam et al. 2002b, Aubry et al. 2009), or from observing conspecific activity (e.g., Danchin et al. 1998). Thus, delayed recruitment could be beneficial if the survival cost associated to such delay does not exceed its benefits (Cody 1971, Weimerskirch et al. 1992). Even in the absence of fitness benefits acquired by growth or experience, environmental variability alone can select for delayed reproduction (Tuljapurkar

1990a, Wilbur and Rudolf 2006, Koons et al. 2008), which might further help explain why delayed reproduction is common in vertebrate populations experiencing natural (i.e., stochastic) conditions.

Age at first reproduction is also a key trait in evolutionary theories of ageing such as ‘mutation accumulation’ (i.e., “MA”, Medawar 1952) and ‘antagonistic pleiotropy’ (i.e., “AP”, Williams 1957, refined by Hamilton 1966), as it can further influence senescence in age-specific reproduction and survival. Charmantier et al. (2006) found that both age at first and last reproduction in mute swans displayed heritable variation and were under opposing directional selection, suggesting that their evolution is constrained by a strong genetic tradeoff, which is consistent with AP. In red deer, Nussey et al. (2007) found that females producing more offspring in early life displayed faster senescence rates, thus depicting another tradeoff in support of AP in the wild. However, environmental effects can induce positive covariance between traits, and mask expected phenotypic expression (i.e., trade-off between early-life and late-life reproduction), even when AP is the genetic mechanism in action (Wilson et al. 2008). Indeed, many have empirically assessed the relationship between age at first reproduction and fitness (e.g., Newton 1988, Weimerskirch 1992, Viallefont et al. 1995, Oli et al. 2002, Kruger 2005); however, the patterns remain ambiguous because of the use of disparate measures of fitness (Oli et al. 2002, Kruger 2005).

Use of rate-insensitive measures of fitness, such as Lifetime Reproductive Success ‘LRS’ (Clutton-Brock 1988), have mainly produced results favoring selection for delayed reproduction (e.g., Fitzpatrick and Woolfenden 1988, Newton 1988); whereas the use of rate-sensitive measures of individual fitness (e.g., Arnold and Wade 1984, de Jong 1994, McGraw and Caswell 1996) have produced results favoring selection for early recruitment (e.g., Ribble 1992, Oli et al. 2002). Rate-sensitive measures of individual fitness, such as λ measured from individually-based matrices (McGraw and Caswell 1996) are more likely to reveal the true relationship between age at first reproduction and fitness because they account for the ‘timing’ of investment into the next generation as well as fertility and survival schedules (Brommer et al. 2002). LRS, on the other hand, only accounts for the number of offspring produced in a lifetime, which is a component of fitness amongst others (Clutton-Brock 1988). However, several concerns have been raised regarding fitness measured from individually-based matrices. For example, fitness estimates are based on a sample size of 1. Link et al. (2002) thus proposed estimating ‘latent individual fitness’ as an “a priori summary of parameters governing potential realizations of an individual’s life history” rather than the ‘realized individual fitness’ proposed by McGraw and Caswell (1996). The latent approach, however, may be difficult to implement, and Coulson et al. (2006) proposed a more direct method by 1) calculating the growth rate of an entire population, 2) excluding the demographic performance of a focal individual between time *t* and *t*+1 (a statistical method called jack-knifing, renamed “de-lifing” by Coulson et al. 2006), 3) re-calculating the population growth rate with an individual removed, and 4) measuring an individual’s relative fitness by subtracting the growth rate from step three from that for the entire population.

However, the Coulson et al. method makes use of only crude demographic rates and the annual jack-knifed measurements are not consistent with ‘long-term’ notions of Darwinian fitness. Here, we develop an alternative version of the jack-knifing approach that combines concepts put forth by both Link (2002) and Coulson et al. (2006), and employ robust statistical estimators that account for observed and unobserved (e.g., frailty and random effects) heterogeneity amongst individuals. We then apply this method to a longitudinal study of black-legged Kittiwake (*Rissa tridactyla*) known to show important variability in recruitment age (e.g., Cadiou et al. 1994, Cam et al. 2002b, Aubry et al. 2009) that has consequences on senescence in both breeding success and survival (Aubry et al. in press). Our goal is to determine which recruitment tactic (i.e., early, intermediate, or delayed recruitment) is most advantageous in this population by estimating the strength and direction of selection operating on recruitment age using spline regression (Ezard et al. 2007).

Methods

Study Area and Data collection

The black-legged kittiwake (i.e., a cliff-nesting seabird) study takes place at Cap Sizun, Brittany, France (48°5’N, 4°36’W). Five colonies have been extensively followed since 1979 (Monnat et al. 1990), such that all breeding events are monitored (Cam et al. 1998), and the first reproductive event is recorded for each individual returning to the study area (Cam et al. 2002b, 2003, 2005). The age of most individuals is known, and each individual’s presence is recorded throughout January to September, as well as demographic (e.g, age at first reproduction, age, number of breeding attempts, number of eggs and chicks produced), spatial (i.e., location of the nesting-site, within a given reproductive cliff), and behavioral information (social and reproductive interactions, identity of the partner, etc) at each resighting period. Resighting is imperfect before recruitment (e.g., Cam et al. 1998, 2005), as juveniles often stay at sea for a few years before first reproduction. Individuals belonging to the breeding segment of the population, however, are observed with virtually perfect detection (e.g., Cam et al. 2002a, Aubry et al. 2009). More information on the studied population can be found in Danchin et al. 1998 and Cam et al. 1998, 2002b, 2003, 2005.

The sample used here consisted of 2046 individuals that recruited between 1982 and 2007 (8261 observations in total). Minimum recruitment age (i.e., Age at First Reproduction; AFR) was 2 years old and only concerned 7 individuals, thus we pooled them with individuals that recruited at age 3 (i.e., recruitment group 3-). Maximum age at recruitment was 7 years old (AFR=7). The maximum observed lifespan in the study was 25 years and concerned one individual that recruited at age 4 in 1986 and that was still alive in 2007. However, because of small sample size beyond age 20, we defined an open age category, ‘20+’, for individuals that reached ages≥20.

Demographic estimates

To build population projection matrices, we used demographic information on age-specific recruitment (Aubry et al. 2009) breeding attempt, egg production, chick production (unpublished data), breeding success (i.e., the probability of raising at least one chick up to fledging; Aubry et al. in press) and survival (Aubry et al. 2009, submitting). These demographic parameters were primarily estimated in previous studies, but are briefly described below.

Juvenile survival

In Aubry et al. 2009, we used Multi-State (MS) Capture-Mark-Recapture (CMR) models implemented in Program MARK (White and Burnham, 1999) to estimate both age-specific juvenile survival and age-specific recruitment (Aubry et al. 2009). From the best performing model, we extracted juvenile survival from age 0 to age 1 (0.633), 1 to 2 (0.607), 2 to 3 (0.789), 3 to 4 (0.738), 4 to 5 (0.782), 5 to 6 (0.683), and 6 to 7 (0.687).

Age-specific recruitment estimates

Using the same MS CMR model, we could have obtained age-specific recruitment probabilities (Aubry et al. 2009). However, these probabilities cannot easily be used in a jack-knifing approach because available multi-state modeling programs (e.g., MARK, ESURGE, etc.) do not provide individually based predicted values. Thus, we calculated γ, the fraction of individuals recruiting at each age unconditional on survival, and $(1-\gamma)$, the fraction of individuals that remain non breeders at each age. For example, we calculated γ_3 (i.e., the fraction of individuals recruiting at age 3) as: ———, and so forth for $\gamma_4, \gamma_5, \gamma_6,$ and γ_7 where x in the denominator summation begins at the focal age category. Calculated values of age-specific γ were: $\gamma_3 = 0.281$, $\gamma_4 = 0.581$, $\gamma_5 = 0.684$, $\gamma_6 = 0.764$ and $\gamma_7 = 1$. These fractions were then multiplied by juvenile survival estimates (see previous section) at the corresponding ages, in order to ensure that we accounted for the probability of recruiting or not, conditional on survival.

Fertility

We obtained fertility estimates by combining several fertility components according to: $F(x) = 0.5 \times BA(x) \times EP_1(x) \times BS(x) \times (CP_2(x) / EP_2(x)) \times JS(x)$

where $BA(x)$ is the probability of attempting to breed or not at age x, $EP_1(x)$ is the average number of eggs produced given that breeding is attempted (subscript 1), $BS(x)$ is the probability of successfully breeding at age x (i.e., successfully fledging at least 1 chick), $CP_2(x)$ and $EP_2(x)$ are respectively the mean number of chicks and eggs produced at each age for an individual that bred successfully (i.e., that fledged at least one chick) (subscript 2), $CP_2(x) / EP_2(x)$ is the average chick to egg ratio for individuals that successfully fledged at least 1 chick, and $JS(x)$ is the probability of offspring surviving from fledging to age 1 (see section on 'juvenile survival'). $BS(x)$ was obtained from our best generalized additive mixed model (gamm) that accounted for age-specific information (i.e., age at first reproduction, time elapsed since first reproduction, and breeding lifespan) and unobserved individual heterogeneity (modeled via an individual random effect; Aubry et al. in press). Different patterns of age-specific improvement and senescence in $BS(x)$ were found across the recruitment groups. Of key importance for later use in the jack-knifing steps (see below), the gamm also provided individually-based predicted estimates of age-specific breeding success. Average $BA(x)$, $EP_1(x)$, and $CP_2(x) / EP_2(x)$ were calculated as crude rates based on unpublished data. However, detailed statistical modeling of these fertility components is the focus of future research.

Adult survival estimates

Because adults in this study are resighted every year (resighting probability > 0.99), we developed Cox Proportional Hazard models (CPH, Cox et al. 1972a) to estimate survival while accounting for sources of both observed (i.e., progressive levels of time-varying reproductive investment, including breeding attempt, egg production, chick production, and breeding success) and unobserved individual heterogeneity (i.e., frailty; Vaupel and Yashin 1985) (Aubry et al. 2009). Both sources of heterogeneity were found to significantly influence adult survival, and thus it was crucial to account for both in order to attain unbiased estimates of age-specific survival (Aubry et al. submitted). We were also able to extract predicted estimates of individually-based survival from our best CPH model for all adults in the sample. To do this we used the CPH equation for our best model:

, where is a vector of individually-based (i) age-specific (x) linear predictors (β is a set of coefficients which associated time-varying covariate values X to the mortality hazard), is the age-specific baseline mortality hazard, and z is the frailty component centered around 1. Survival from age x to $x+1$, $p_i(x)$, was extracted from the previous equation as follows: , where $h_i(x)$ denotes the individually-based, age-specific hazard over a year (re-sightings recorded over annual intervals).

Modeling framework

Step 1. Development of the average population projection matrix.

There were significant differences in age-specific patterns of the adult demographic parameters described above (with ages ranging maximally from 3 to 20+) across the various recruitment groups (i.e., AFR = 3, 4, 5, 6, or 7; Aubry et al. 2009, in press). Thus, averages were calculated for each age-AFR category. Adding these categories to the pre-breeding stages of life yielded a complex life cycle with 86 unique life-cycle stages (Fig. 1). We then used the life-cycle diagram to parameterize a stage-classified projection matrix **A** that describes the average demographic performance of kittiwakes in our study population assuming a pre-breeding census (Fig. 2; Caswell 2001). The top row of **A** depicts stage-specific (age-AFR categories) fertilities (see fertility section above) and the other non-zero entries depict stage-specific survival probabilities as well as recruitment transition probabilities (Fig. 2). The dominant eigenvalue of **A** yields the long-term geometric rate of population growth λ_{POP}. We defined mean fitness as the natural log of λ_{POP}: $\log(\lambda_{POP})$

Step 2. Jack-knifing of the dataset.

The individually-based data for each demographic parameter (e.g., attempted to breed (1) or not (0), eggs produced (0, 1, 2, or 3), predicted value of $BS(x)$ for each individual *i*: $BS_i(x)$, $p_i(x)$, etc.) was stored in a 635 (i.e., adult age- and recruitment-specific demographic parameters, and the 5 gamma values) by 2046 (i.e., number of individuals in the dataset) matrix. To 'jack-knife' the dataset (Efron and Gong 1983) we created a loop that removed individual *i* from the data storage matrix (i.e., 1 row) and calculated the sample means for each demographic parameter with individual *i* 'completely removed' from the population as if it never existed. Individual *i* was then re-entered into the population and the jack-knifing procedure was repeated for a new individual (e.g., $i = 2$) until the procedure had been performed for all 2046 individuals.

Step 3. Calculation of individual contributions to mean fitness.

At each step of the jack-knifing procedure described in Step 2, we updated the population projection matrix $\boldsymbol{A}_{JACK,i}$ which depicts the average demographic performance of kittiwakes in our study population from which individual *i* was removed. The dominant eigenvalue for each $\boldsymbol{A}_{JACK,i}$ was used to measure the jack-knifed population growth rates, $\lambda_{JACK,i}$. Individual contributions to mean fitness (i.e., relative individual fitness) were then defined as

Positive values of w_i reflect an individual that outperformed the mean individual, whereas a negative value reflects an individual that underperformed (Coulson et al. 2006). Our approach differs from that of Coulson et al. (2006), however, in that we removed an individual's entire life history and computed the impact on long-term fitness. Coulson et al. (2006) jack-knifed an individual's life history in a single year and computed the impact on short-term population growth rate (N_{t+1}/N_t), which nicely accounts for temporal variation but does not reflect the impact on an accepted measure of long-term fitness. In the future we plan to extend our approach of jack-knifing an individual's entire life history and computing the impact on temporal variation in the demographic parameters and the long-term stochastic growth rate λ_s (Tuljapurkar 1990b) to attain measures of w_i in a stochastic environment.

Step 5. Calculating selection gradients under different demographic scenarios

We used the 'qsreg' function (i.e., 'robust spline regression', package 'fields' in R) to fit a regression between individual fitness estimates (w_i) and recruitment age to assess the direction and strength of selection on the age at first reproduction. This approach smoothes the robust regression by using an iterative algorithm (i.e., weighted least squares cubic splines) (Oh et al. 2002). We then used the 'lowess' function in package 'stats' (Cleveland 1979) to draw a smooth regression 'curve'.

Demographic scenarios

Based on the average population projection model **A**, we estimated a growth rate $\lambda \approx 0.8916$ (see results below). Because it is theoretically predicted that, all else being equal, the strength and direction of selection on recruitment age can be different for populations that are declining, stable, or increasing (Charlesworth 1994), we conducted the same analysis on the true declining population (i.e., scenario 1), on the same population for which λ was adjusted to 1 (i.e., stationary population, scenario 2), and on the same population for which λ was adjusted to 1.1084 (i.e., increasing population, the mirror image of the declining population, scenario 3). To adjust the growth rate under scenarios 2 and 3, we used a quasi-Newton optimization procedure in R to estimate the value of a constant c needed to multiply **A** in order to obtain $\lambda = 1$ (scenario 2), or a lambda = 1.1084 (scenario 3). This constant was then multiplied to both **A** and each $\mathbf{A}_{JACK,i}$.

Results

The average population projection matrix **A** provided a mean λ of 0.8916 (scenario 1) with an associated $\log(\lambda)$=-0.1147 (i.e., value used as a basis for individuals fitness comparisons to the mean individual fitness). To set the average population projection matrix **A** to a mean λ of 1 (scenario 2), we multiplied **A** by 1.1216 (constant obtained from the optimization procedure described in the methods). We found that the associated log (λ) was almost 0 ($-4.9172\ 10^{-7}$), which is expected as $\log(\lambda)$ as if $\lambda=1$, $\log(\lambda)=0$. Finally, under demographic scenario 3, we had to multiply **A** by 1.243 to set $\lambda=1.1084$. The associated $\log(\lambda)$ was =0.1029.

The three demographic scenarios produced very similar results. We found evidence for slight directional selection favoring earlier age at maturity (figure 3); however, the slope (or strength of selection) decreased as AFR increased past age 4 (figure 3), suggesting that the costs associated to delayed recruitment might not be as substantial as previously thought.

Discussion

A population in decline?

The detailed age-specific average population projection matrix **A** yielded a $\lambda < 1$ (λ = 0.8916). As this population has been persisting over time, we suspect that $\lambda < 1$ is an artifact for several reasons. First, it is important to acknowledge that observed mortality in this study is confounded with permanent emigration (Williams et al. 1992). Further, it is interesting to note that the individuals that are the more likely to disperse to other cliffs within the study area, also suffer the highest local mortality (e.g., Danchin et al. 1998). Studies combining recaptures and recoveries (Williams et al. 1992), as well as the use of small GPS units could potentially help estimate the current level of bias in survival estimates, if any, and provide more accurate estimates of λ.

To delay or not to delay

In an increasing population early recruitment should be favored, and if heritable, the frequency of such a trait would be expected to increase over time (Caswell 2001). We, however, found directional selection for early recruitment under all three demographic scenarios (figure 3; differences in individual fitness under the 3 different scenarios were < 10^{-15}). That said, the strength of selection (as indicated by the regression slope) was small, indicating that the inherent costs of waiting to invest in the next generation may be somewhat offset by improved fertility and adult survival (Aubry et al. in press, submitting). However, the true environment experienced by this population is stochastic, and our deterministic analysis may not reveal the actual direction and strength of selection on AFR in kittiwakes. Environmental stochasticity alone can select for delayed reproduction (Tuljapurkar 1990b, Koons et al. 2008), which could provide enough of an added fitness advantage (in addition to improved BS and survival) to make delayed reproduction evolutionarily stable in our population. Adding temporal stochasticity to our jack-knifing approach will be the topic of future study..

A novel estimation procedure for individual fitness

LRS (e.g., Clutton Brock 1988) and λ_{IND} (McGraw and Caswell 1996) can lead to contrasting conclusions while studying the evolution of delayed reproduction in wild populations. LRS is rate-insensite and does not account for the timing of the repeated reproductive events (e.g., breeding attempt, egg production, chick production) over life. λ_{IND} defined by McGraw and Caswell(1996) has been shown to overestimate the advantage of early reproduction while neglecting other parts of the life cycle (Brommer et al. 2002). Both measures are also highly sensitive to the moment at which progeny are counted as dead or alive and attributed to the parent's fitness (Brommer at al. 2004), which ultimately has profound effects on the measurement of fitness. For example, one can account for a chick produced, one that fledged successfully, that survived the first winter at sea, or one that survived and recruited when measuring an adult's fertility in the McGraw and Caswell approach. Instead of studying the fitness characteristics of an isolated individual in the population, Coulson and colleagues (2006) proposed to apply a jack-knifing procedure to calculate individual fitness, and to decompose fitness into yearly contributions for each individual, in order to account for the impact of environmental change on individual fitness.

The measure of individual fitness we propose here is inspired by Coulson et al.'s idea (2006), but uses finer demographic information via a very detailed population projection matrix **A** constructed from estimates of juvenile survival (multi-state Mark-recapture model; Aubry et al. 2009), breeding success (generalized additive mixed model; Aubry et al. in press), and adult survival (Cox proportional hazard frailty model; Aubry et al. submitting). We did not decompose individual fitness into yearly contributions, however, the advantage of this method is that one can associate to individual fitness any measure of environmental variation, or individual information. We only kept track of recruitment age at this stage, but we could potentially decompose fitness contributions by age, year, cohort, or any other information that can be associated to the age-specific life of an individual.

Perspectives

We made use of age-specific estimates that were calculated under various modeling settings (i.e., CMR multi-state models, gamms, and Cox proportional hazard frailty models); thought to be the best estimates possible for our kittiwake population, as they accounted for both observed and unobserved sources of heterogeneity. However, some fitness components used in the fertility equation were still crude demographic values. For example, breeding probabilities were calculated as an average of binary events (0 or 1); egg and chick production were calculated as averages of raw numbers. We next aim to the crude demographic information with estimates attained from in-depth statistical analyses (Cam et al. in prep).

Ideally, we would like to be able to re-estimate each demographic component of our model when removing one individual at a time via the jack-knifing procedure. In our case, this would include reiterating the estimation procedures for juvenile survival, adult survival (already implemented), and each fertility components (breeding attempt, egg and chick production, breeding success (already implemented)). From a technical standpoint, it seems feasible to jointly re-estimate most of these components; however, it seems unwieldy to apply such a procedure to the estimation of juvenile survival and recruitment at this stage. These processes were estimated with program MARK, which does not yet allow for individual random effects, nor does the program provide individually-based predicted values.

Because environmental stochasticity can favor the evolution of delayed reproduction in long-lived organisms (Tuljapurkar 1990a, Wilbur and Rudolf 2006, Koons et al. 2008), one of our next goals is to conduct the same analysis under a stochastic setting. However, before doing so, we would like to incorporate (limited) information on dead-recoveries and GPS tracking systems in order to obtain an unbiased measure of the growth rate for the kittiwake population located at Cap Sizun.

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Figure 1. Black-legged Kittiwake life cycle providing age-specific (age 0 up to age 20) and recruitment specific (recruitment age = 3, 4, 5, 6,7 or more) demographic information (i.e., fertility, juvenile survival, and adult survival components)

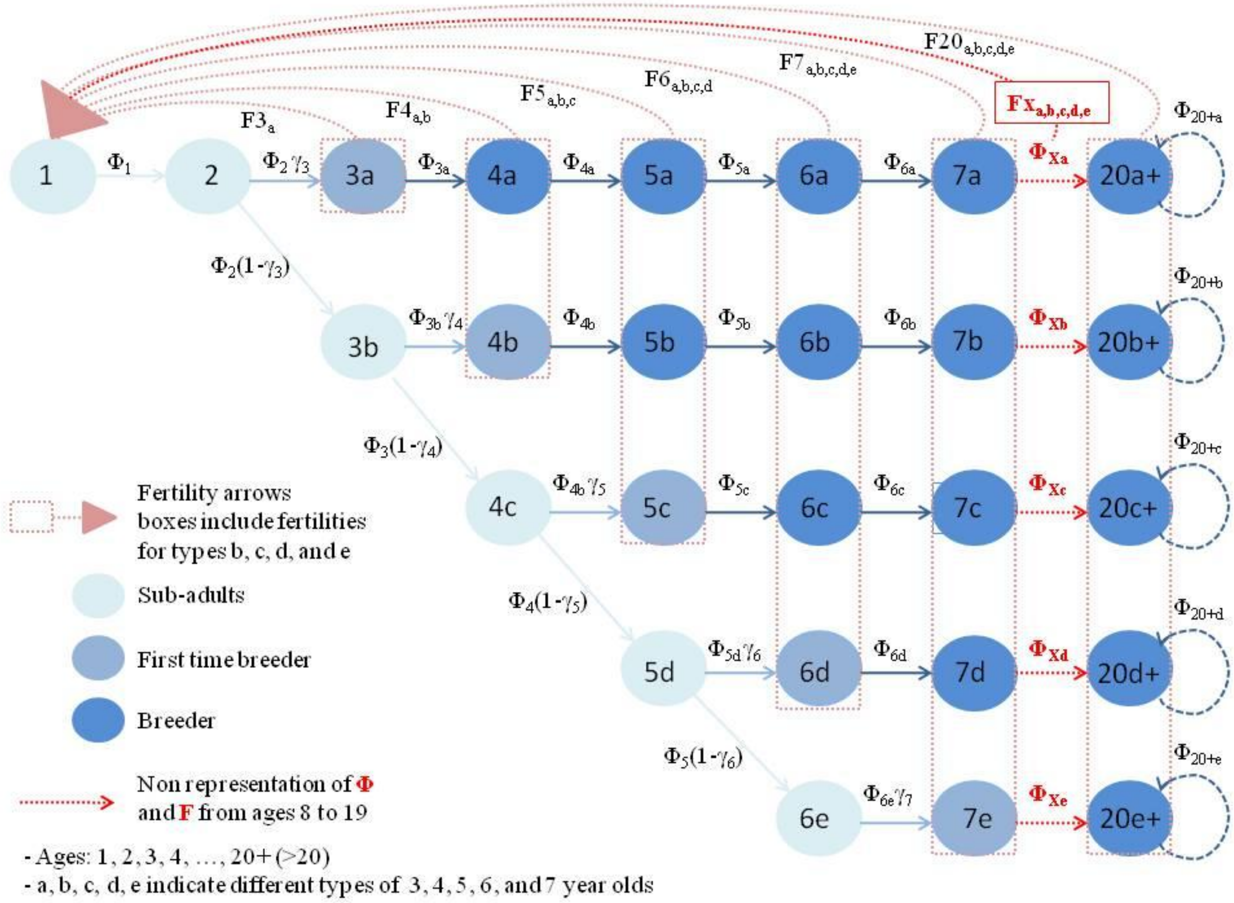


Figure 2. Graphical representation of the average projection matrix A (86 * 86) symbolizing the kittiwake life cycle described in figure 1.

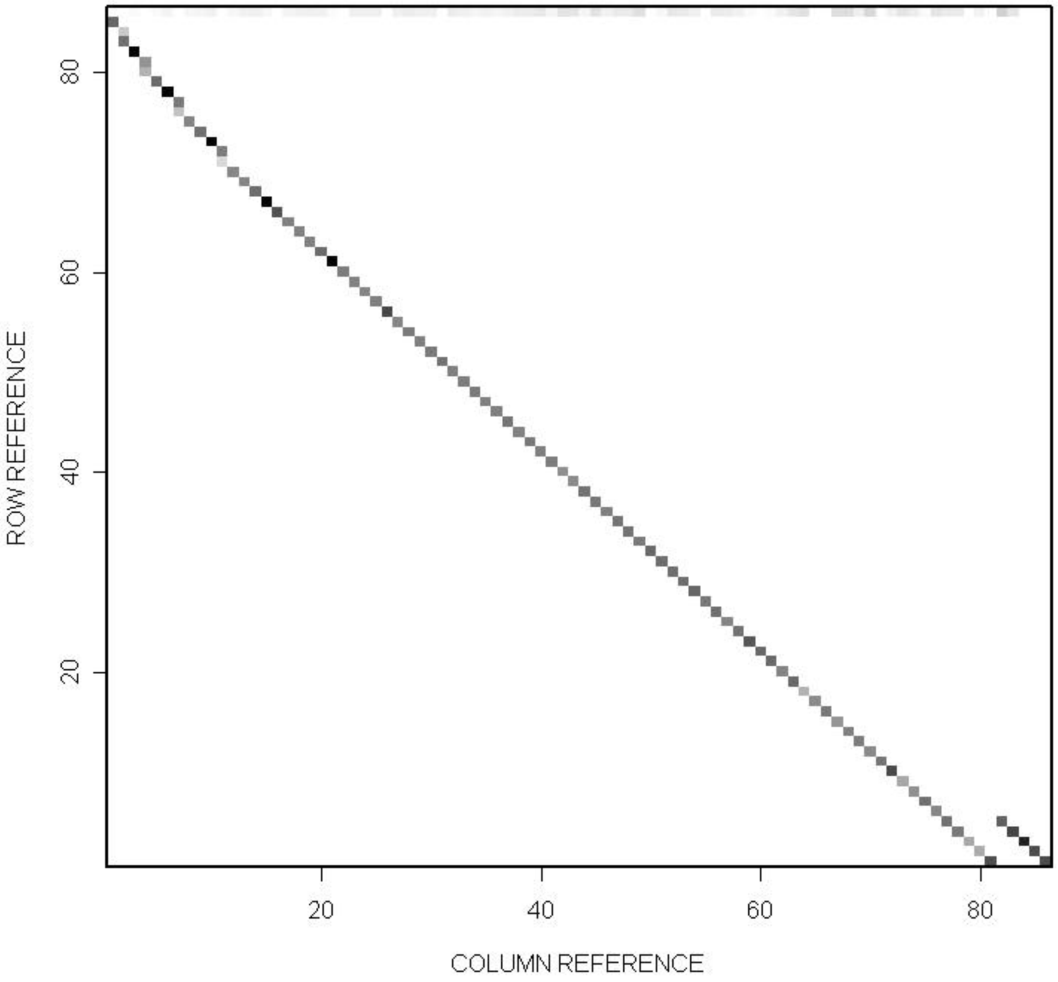
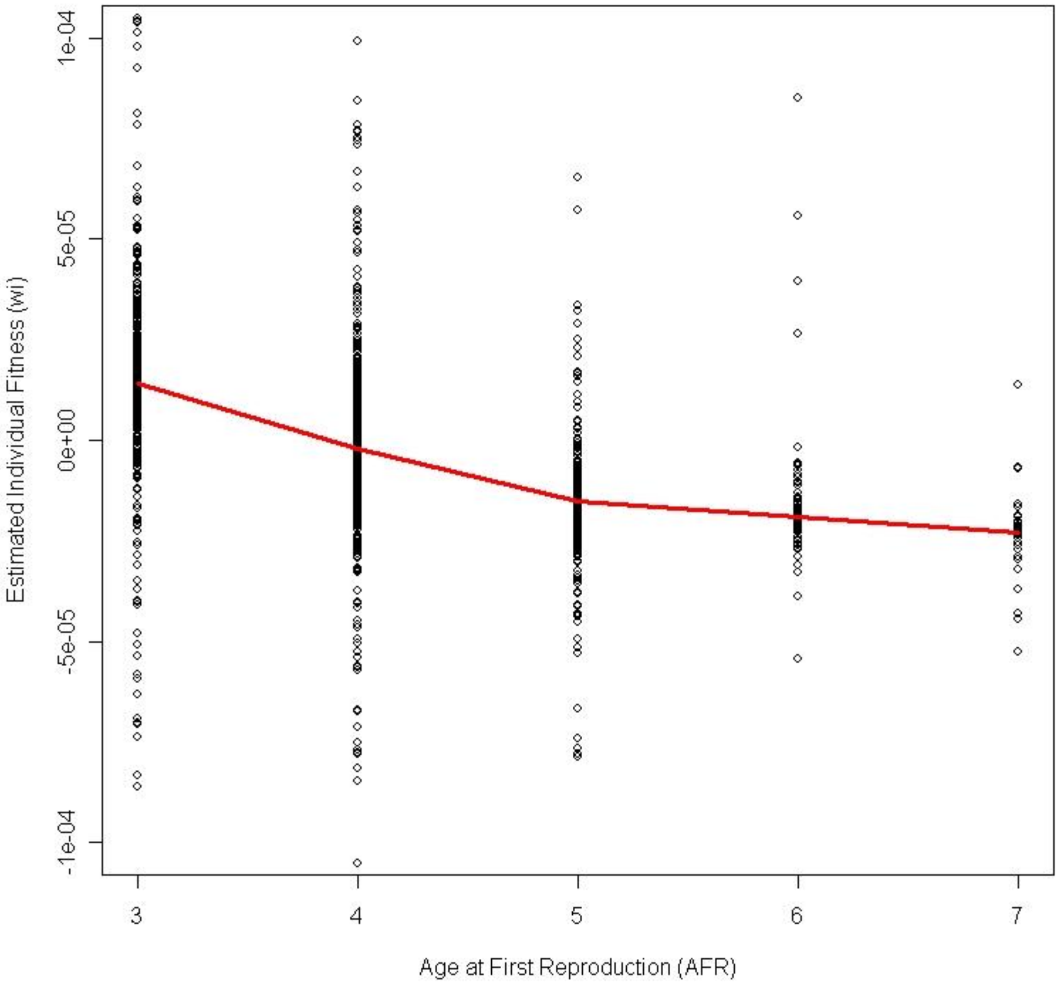


Figure 3. Direction and strength of selection on the age at first reproduction: robust spline regression between estimated individual fitness and recruitment age.



~ GENERAL DISCUSSION ~

'The reality of the field'

Picture: Lise M. Aubry

Age at first reproduction (i.e., AFR or recruitment age) is often assumed to initiate mechanisms that impede somatic repair, resulting in a decline of reproductive and survival abilities with age (i.e., reproductive and actuarial senescence; Charnov 1997). If true, different recruitment tactics, such as early *versus* delayed recruitment, could lead to contrasting reproductive and survival trajectories (e.g., senescence or improvement in breeding success and, or, survival with age). Along with a number of collaborators, I examined this 'long-term trade-off' between early-life reproductive decisions and future reproductive and survival chances from a demographic perspective, while taking into account the potential for (1) breeding experience, (2) temporal variation, and (3) heterogeneity (i.e., phenotypic differences across individuals; Vaupel and Yashin 1985) to improve or diminish reproduction and survival chances across ages. I have also linked recruitment strategies to individually-based fitness measures, and have measured selection on recruitment age in a deterministic framework.

Because delayed recruitment (i.e. first reproduction) is a key feature of the demography of long-lived species such as kittiwakes, I studied (Chapter I) variables related to observed variability in the age at first reproduction with models that accounted for imperfect detectability (i.e. Capture-Mark-Recapture Multi-State models: CMR MS; Williams et al. 2002). Based on previous work by Danchin and colleagues (e.g., Danchin et al. 1998), we had the strong intuition that variability in recruitment age and habitat selection processes where intimately linked, i.e., that AFR and habitat selection were ‘two sides of the same coin’ (Ens et al. 1995). Indeed, habitat selection theory predicts that recruits should settle on territories (e.g., potential nest-sites) where expected fitness is the highest (Frewell et Lucas 1970). However, a habitat that leads to a high probability of successfully reproducing also means that the competition for such type of habitat is likely to be fierce. Thus, it is possible that individuals that display superior competitive abilities could establish themselves on such superior quality territories. Two hypotheses come to mind: either individuals of higher ‘intrinsic quality’ do possess superior competitive abilities which allow them to recruit earlier and acquire higher quality territories, or only time and experience allow for the acquisition of such competitive abilities. Indeed, territorial conflict can lead to costs (injuries, energetic investments, etc), especially for males, the ‘territorial sex’. Another tactic could also allow individuals to acquire a good nesting-territory: the ‘queuing tactic’ (Ens et al. 1995), which consists of waiting for a good quality habitat to become available because of the death of the previous owner(s). I found that recruitment probability was highest at intermediate ages (i.e. recruitment at age 5) in habitat patches (i.e. “cliffs”) of medium quality (chapter I, figures 1 and 2).

The first finding contradicts the idea that recruitment should take place as early as possible in order to maximize fitness (Stearns 1992), but is in partial agreement with the assumption that delayed recruitment could be advantageous if it conveys higher breeding success with age, experience, or both (Charlesworth 1994). I found that the youngest recruits experienced poor breeding performance at the beginning of their reproductive life. However, Charlesworth was referring to post-recruitment improvement in breeding success, not to advantages in the recruitment year. Most individuals recruited at intermediate age, and because these individuals experienced higher reproductive success at recruitment, I could only ascertain that a few years of pre-recruitment experience ‘might’ convey fitness benefits. If so, what sorts of information and experience are gained during a prolonged sub-adult life?

Delayed recruitment could allow for prospection to take place, a common phenomenon in seabirds (e.g., Jenouvrier et al. 2008), and in black-legged kittiwakes in particular (e.g. Danchin et al 1991, 1998, Cadiou et al. 1994, Boulinier et al. 2008). In fact, I found that recruitment probability was best predicted by apparent habitat quality the year preceding recruitment. This suggests that either habitat selection takes place the year preceding settlement and first reproduction, or that the information available to individuals at the beginning of a season is temporally auto-correlated to past productivity. If temporal autocorrelation spans over several years, additional work will be needed to assess whether prospection occurs over several years preceding AFR. If true, prospection would be a very efficient way of increasing the probability of identifying higher-quality habitat, and ultimately future breeding success and survival chances.

Delayed recruitment does not imply that the individual is not investing into territorial activities and couple formation. Indeed, being a part of the very dense social network in a kittiwake colony requires working for it, for example via ‘squatterism’ (i.e., sitting on a nest-site that contains chicks while the owners are gone at sea). Numerous pre-breeders are of known sex before recruitment, which implies in this study that they have attempted to breed, or have fed a female, and to have initiate the formation of a couple (sexing in this study relies on very particular behavioral displays). Some pre-breeders are also clearly settled on given location within a reproductive cliff, which implies that they have accomplished territorial activities, and even sometimes have displayed reproductive behaviors such as nest construction. It is reasonable to hypothesize that delayed recruitment is associated with the acquisition of real experience explicitly linked to reproduction (e.g., formation of a breeding pair, nest construction), but also with knowledge of the location of feeding zones close to the reproductive cliffs.

Our latter finding contradicts habitat selection theory (Holt and Barfield 2001), whereby it is expected that selecting a habitat of the highest quality should be associated with the highest fitness prospects. I found that recruitment primarily took place in habitats of intermediate quality, and that reproductive success in the recruitment year what highest for recruits that chose such breeding cliffs compared to recruits that chose more productive cliffs (chapter I, figure 3). The term ‘choice’ reflects that fact that the distribution of habitats of various qualities was different from the distribution of habitats available that they would have obtained by settling randomly. This distance between theoretical and observed distribution of individuals across breeding cliffs reflect either an active choice, or constraints. By constraints, I mean harsh competition in the most productive cliffs (i.e., where density is high), and avoidance of the least productive ones (i.e., where predation on eggs is high). From field observations it is obvious that fitness prospects are dismal in low-quality habitats where most nests fail (i.e., rare successful production of at least one chick). This could be due wave disturbance (likely to wash away a nest), to the rough topography of the cliff (inhibiting large nests from staying in place), or to the proximity of predators such as corvids (*Corvus corone and Corvus Corax*), other seagulls (mostly *Larus argentatus*), and peregrine falcons (*Falco peregrinus*). Predation on eggs by corvids have led to complete failure in two colonies and, temporary desertion of a colony early in the 1980's, and permanent desertion of the largest colony at the end of the 1990's (Cam et al. 2004). Herring gulls have also caused complete failure at the chick stage in kittiwake breeding on small islets by the cost. However, additional field work would be needed to disentangle the relative importance of these variables in causing cliffs, (probably specific sections of cliffs) to have low overall productivity.

The criterion of habitat quality chosen here has its limits. The colonies studied are located in a bay, and are close to one another, which is likely indicating that all birds have access to the same feeding zones (mainly out of the bay). But reproductive sites on the other hand, are probably not of similar quality. As I did not have at disposal a quality criterion describing the nest-site itself, I used a criterion developed by Danchin and collegues (1998): the proportion of failed nests within a reproductive cliff that contains most than 10 nests. This criterion has the advantage of integrating within a single metric all the determinants of habitat quality, however, it's impossible to disentangle the site's quality from the quality of individuals holding the site. The idea that individuals breeding in very dense cliffs (> 200 nests) all own a site of similar quality seems unrealistic, but this assumption cannot be disregarded *a priori*.

The other disadvantage of this criterion is that it is currently impossible to work on a smaller spatial scale. The 'quality' or a reproductive cliff is estimated based on all the active nesting sites within the cliff, which create differences across cliffs of various densities (e.g., 10 versus 200 nesting-sites). Also, within some of the larger cliffs, it is likely that individual habitat selection choices are focused on a group of nest-sites, even on a particular nest-site (Cadiou 1994), and not on the entire cliff. Spatial analyses are currently being done to study habitat selection mechanisms at a much finer spatial scale, the nest-site itself (e.g., Bled 2006). We also would like to combine spatial analyses with our knowledge of each recruits' reproductive performances (as recruits never bred before, these individuals did not yet influence the quality of the nesting-site they own).

I found interesting relationships between AFR and breeding success in the year of recruitment. However, AFR may also have substantial effects on breeding success and survival over life. In chapters II and III, I examined whether reproductive success and survival increased, showed senescent decline, or remained the same over the life course of individuals recruiting at various ages.

I have found that individuals delaying recruitment experience an earlier onset of reproductive senescence, a faster, but less steep decline in reproductive success, their pic RS at intermediate ages being lower (chapter II). Besides, they suffered a faster decline in survival chances with age (i.e., slower increase in the cumulative hazard, chapter III), compared to younger recruits (AFR < 6), and their life expectancy declined much faster with age than in early recruits (chapter III). These results suggest that individuals might differ in their ability to recruit early or late (i.e., heterogeneity in intrinsic quality), and that the decision of when to start breeding has consequences on both late-life reproduction and survival.

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In chapter II, I addressed the relationship between recruitment age, age-specific breeding success (BS), and reproductive senescence, while accounting for breeding experience, individual heterogeneity, and temporal variation in BS. To do so, I used GAMM models which are new to such applications, but I believe will become extremely popular in the future (e.g., Ezard et al. 2007). GAMMs allow for unconstrained relationships between covariates and the response parameter (i.e, splines) while accounting for heterogeneity in e.g., individual quality, a key component of the apparent influence of age on demographic parameters (e.g., Cam et al. 2002a, van de Pol and Verhulst 2006).

Individuals that delayed recruitment forewent early-life breeding opportunities, but achieved high BS (chapter I). To examine the relationship between AFR and breeding success in greater detail, I focused chapter II on the influence of AFR on the trajectory of age-specific breeding success over the lifespan. Simple models revealed late-life improvement in BS across all recruitment groups (chapter II, figure 1), which I recognized as ‘within-generation selection’ (i.e., phenotypic selection; Endler 1986) or the selective disappearance of ‘frail’ phenotypes (Vaupel and Yashin 1985). When such heterogeneity was accurately accounted for, I showed that all individuals suffered reproductive senescence (chapter I, figures 2 and 3), thus indicating how crucial it is to account for unobserved sources of heterogeneity while studying demographic trajectories (e.g., Cam et al. 2002a). However, unobserved heterogeneity alone did not explain the true shape of the reproductive trajectory: one should also consider interactions between observable age-related covariates to account for the multiplicity of life-course events that define individual differences in BS. The triple interaction between recruitment age, experience, and lifespan best accounted for the selective appearance and disappearance of individuals, and for the diversity of possible ‘breeding lives’. Thus, not only is unobserved heterogeneity crucial in explaining age-specific variability in demographic traits, but so are dynamic (i.e., experience) and fixed sources (i.e., recruitment age and lifespan) of observed heterogeneity.

Although breeding success trajectories all exhibited a concave shape, there were important differences in age-specific trajectories across recruitment groups (chapter II, figures 2 and 3). Different combinations of pre- and post-recruitment experience across recruitment groups resulted in maximal BS at intermediate ages, but BS increased most rapidly amongst early recruits as they gained post-recruitment experience, whereas late recruits gained more pre-recruitment experience leading to high BS at recruitment. Individuals recruiting at intermediate ages apparently balance pre-and post-recruitment experience. These findings thus suggest that individual recruiting at different ages manage to maximize their BS at intermediate ages, via different experience 'routes'.

Even if this dataset allows for a very detailed follow up of life histories, it presents some limitations which I could not overcome. Indeed, if reproductive cliffs show to any observer a true heterogeneity in terms of reproductive success, more global sources of productivity differences exist across colonies within the same year (e.g. Danchin et al. 1998), mainly caused by massive predation events on some of the colonies. A predation episode can sometimes lead to the total extinction of the colony through massive dispersion of breeders (Cam et al. 2004). Thus, if the degree of temporal autocorrelation of the cliff or the colony's global performance is positive, the moment at which a predation episode occurs is stochastic. How important is stochasticity in affecting the reproductive trajectory of an individual (AFR, age-specific RS)? The tools being developed to study the relation between nest-site quality, stochasticity within the colony, and age-specific (e.g., Bled 2006) are unfortunately not yet available.

This nevertheless prompts additional life-history questions, such as: 1) does recruitment age, and other components of age-specific reproductive investment, also influence age-specific survival, and 2) is recruitment at an intermediate age (i.e., AFR = 5) an optimal recruitment tactic in terms of evolutionary fitness (chapter IV)?

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In chapter III, I used time-to-failure survival analysis to estimate individually-based age-specific survival while accounting for fixed (i.e., recruitment age) and dynamic (e.g., time-varying egg and chick production) sources of observed heterogeneity, unobserved individual heterogeneity (i.e., frailty), and environmental variability (i.e., year effect).

I found that individuals recruiting at different ages experienced different age-specific survival, and life expectancies (chapter III, figures 1 and 2). More specifically, recruitment past the age of 5 was associated with acute senescence in survival, whereas early (AFR < 5) and intermediate age (AFR = 5) recruitment was associated to higher life expectancy, even at advanced ages. Recruitment age might thus be a reasonable indicator of the individual's intrinsic quality (Stearns 1992, Forslund and Pärt 1995, Becker et al. 2008) as age at first reproduction is unambiguously associated with differences in survival. Moreover, the competitive abilities of individuals might not only allow them to start breeding earlier and to senescence slower, but also to attain higher fitness than 'low-quality individuals' that delay recruitment (e.g., Cam and Monnat 2000, Cam et al. 2002a, Hadley et al. 2006). However, I have found so far that intermediate-age recruits perform better at first reproduction (chapter I), and that they seem to balance pre- and post-recruitment experience in a way that maximizes BS across ages (chapter II). Yet, I still did not know whether early or intermediate recruitment age conveyed higher overall fitness (currently being addressed in chapter IV).

I also found that observed age-specific reproductive investment and success had a substantial influence on survival (Orell and Belda 2002). For example, failed breeders suffered higher mortality than non-breeders (chapter III, figure 3). On the other hand, individuals that fledged at least 1 chick experienced the lowest mortality at each age. This suggests that unsuccessful birds experience a cost of reproduction whereas successful kittiwakes may be of higher intrinsic quality (e.g., Forslund and Part 1995) allowing them to avoid such costs (Cam et al. 2002a). The higher mortality of failed breeding will require additional work. Death of the individual during the breeding season may result in breeding failure, as well as death of the mate. Death may reflect reproductive costs in individuals in poor condition that started the breeding process, but this may also simply be accidental death (caused by fisheries for example, or small oil spills). Also, it is likely that some of the mortality of failed breeders reflects permanent emigration out of the study area. Indeed, it is important to acknowledge that observed mortality in this study is confounded with permanent emigration (Williams et al. 1992). Besides, it is interesting to note that the individuals that are the more likely to disperse within the study zone, also suffer the highest local mortality (e.g., Danchin et al. 1998). Studies combining recaptures and recoveries (Williams et al. 1992), as well as the use of GPS units could potentially bring some answers to these questions.

Even after accounting for observed sources of individual heterogeneity in survival chances there was still a substantial amount of unobserved individual variability, which is consistent with studies of other demographic processes in this population (Cam et al. 2002a, Aubry et al 2009b). For the first time, I assessed the relative contribution of observed and unobserved sources of heterogeneity (Vaupel et al. 1979, Vaupel and Yashin 1985) in explaining variability in age-specific survival. Unobserved heterogeneity explained 6 times more of the reduction in deviance than covariates describing fixed and time-varying reproductive investment, once again confirming the need to account for both observed and unobserved sources of individual heterogeneity while studying demographic trajectories (chapter II).

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In the last chapter, My collaborators and I were interested in using all the age-specific demographic information estimated in each of my dissertation chapters to build a detailed matrix population model (chapter IV, figures 1 and 2) for the black-legged kittiwake population studied in order to i) estimate the population growth rate with the best demographic information available for this study; ii) assess whether delayed recruitment was an advantageous recruitment strategy by assessing the direction and the strength of selection on recruitment age under different demographic scenarios (i.e., declining, stationary, or increasing population); iii) establish a new approach to estimate individual fitness in a deterministic framework, which we wish to adapt to a stochastic context in the near future.

i) We have found the growth rate was inferior to 1 ($\lambda = 0.8916$), suggesting a decline of population abundance (i.e., declining population, demographic scenario 1). This population however has been persisting in Cap Sizun over decades, and even though some colonies have disappeared (Cam et al. 2004), others have appeared over time, and the overall population has maintained itself. The fact that permanent emigration is confounded with death in this population could explain why we obtained a $\lambda < 1$ even though this population is stationary or even growing, depending on the year considered. GPS information along with dead recoveries within the study area, and live recoveries in other kittiwake colonies could potentially help us assess the true survival and population growth rates.

ii) We used an optimization procedure to assess by how much the population projection matrix has to be multiplied by in order to correct the growth rate and fix it equal to either 1 (i.e., stationary population, demographic scenario 2), or 1.1084 (i.e., increasing population, scenario 3, mirror image of scenario 1). However, whatever the demographic scenario considered (decreasing, stationary, or decreasing population), the conclusion remained unchanged: early recruitment was slightly favored as we observed a slight directional selection favoring earlier age at maturity (chapter IV, figure 3); however, the strength of selection decreased as AFR increased past age 4 (chapter IV, figure 3), suggesting that the costs associated to delayed recruitment might not be as substantial as previously thought.

iii) We develop an alternative version of the jack-knifing approach that combines concepts put forth by both Link (2002) and Coulson et al. (2006), and employ robust statistical estimators that account for observed and unobserved (e.g., frailty and random effects) heterogeneity amongst individuals. The measure of individual fitness we propose thus used finer demographic information via a very detailed population projection matrix. However, this procedure could be improved by first using estimated fitness components exclusively. We did use estimates for age-specific survival and fertility such as breeding success for example. However, we could still model components such as breeding attempt, egg and chick production and include those estimates into the population projection matrix rather than crude demographic values. Ideally we would like to re-estimate each component each time an individual is removed, which is possible for fertility components that are modeled in R via gamms, but will require advancements in program MARK (for the estimation of juvenile survival) that are not yet available.

We next aim at using the same procedure for the estimation of individual fitness in relation to recruitment age in a stochastic framework, in order to assess whether our conclusions will change.

~ CONCLUSION AND PERSPECTIVES ~

I have found that recruitment age is intimately linked to the quality of the habitat where recruitment takes place (chapter I), depends on heterogeneity across individuals in their ability to recruit (chapter I), and affects late-life reproduction (chapter II), and survival (chapter III). However additional sources of variability, fixed (i.e., recruitment age, lifespan) or dynamic (e.g., time-varying reproductive investment, experience), observed (e.g., reproductive and temporal covariates), or unobserved (i.e., frailty), also explain substantial variability in demographic trajectories. Interestingly, I also found that temporal variation in environmental conditions had a large influence on age-specific survival (chapter III) and reproduction (chapter II), especially in young adults (chapter II). Additional work could help assess whether increased environmental stochasticity influences selection on recruitment age, age-specific reproductive investment, and rates of ageing.

The long-term study of black-legged kittiwakes is ideal for disentangling the genetic and environmental components that shape ageing patterns in both reproduction and survival to gain a better understanding of how the environment interacts with the genome (i.e., phenotypic plasticity[6]), and ultimately affects rates of senescence. In wild populations, poor environmental conditions early in life can impede development and affect late-life reproduction and survival (Metcalf and Monaghan 2001, Reed et al. 2003, Keller et al. 2008). For this reason, I am further interested in studying the plasticity of ageing in response to environmental effects, rather than attempting to discriminate between the major theories of senescence (i.e., antagonistic pleiotropy, Williams 1957; and mutation accumulation, Medawar 1957) that are often not mutually exclusive.

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[6] Expression of different phenotypes by a single genotype under different environmental conditions

To formally estimate the genetic and environmental components of senescence and rates of ageing in the wild, I could perform a quantitative-genetic study using available pedigree information (i.e. the animal model; Lynch and Walsh 1998). The main advantage of the ‘animal model’ is that it goes beyond classic parent-offspring regression (Kruuk and Hadfield 2007) and uses all information available on relatedness across individuals, which increases statistical power in the estimation of genetic and environmental determinants of any trait under study and reduces bias introduced by family effects (i.e., shared environments; in the kittiwake the male feeds the female during the production of eggs, shares parental care with the female, and often takes care of the chicks until the very end of the breeding season, even after the female takes off by the end of august). Moreover, the animal model can handle missing data, which is an ordinary issue when studying wild animal populations.

The animal model, however, only allows for the estimation of a genetic and an environmental basis for ageing rates. Multivariate random regression models (Kirkpatrick et al. 1990) can explicitly examine how genetic values of survival and breeding success change across both age and environmental conditions (i.e., density dependence, climate variation, parasite abundance) simultaneously.

I aim to address these objectives in the future, as a follow-up to this dissertation. Monitoring populations and their response to contemporary environmental changes is fundamental towards understanding how demographic and evolutionary changes operate in wild systems. Long-term studies such as this one are needed to monitor the impact of environmental change on the demography and evolution of wild populations. This project is a first step towards further investigations into the heritability and evolution of a wide range of age-specific traits. I ultimately hope to shed light on the relative contribution of environmental (e.g., population density) and genetic factors (e.g. inherited differences in survival and reproductive abilities) in shaping senescence profiles in the wild. Such research will add to interdisciplinary research in the fields of gerontology, demography, evolutionary ecology, population biology, and conservation.

~ DISCUSSION GÉNÉRALE~

L’âge à la première reproduction (APR) est supposé être impliqué dans un mécanisme d’endommagement de la réparation cellulaire qui résulte en un déclin de la capacité de reproduction et de survie avec l’âge (i.e., sénescence; Charnov 1997). On peut donc supposer que différentes tactiques de recrutement, précoce ou tardif, pourraient résulter en des trajectoires de survie et de reproduction contrastées (e.g., sénescence ou augmentation du succès reproducteur ‘SR’ ou de la survie avec l’âge). Avec l’aide de mes collaborateurs, nous avons examiné la possibilité d’un compromis évolutif sur le long terme entre les décisions de reproduction tôt dans la vie (e.g., recrutement, choix du première habitat de reproduction) et les chances de survie et de reproduction futures d’un point de vue démographique, tout en prenant en compte (1) l’expérience reproductrice (i.e., nombre d’années écoulées depuis la première reproduction) (2) la variation temporelle, et (3) l’hétérogénéité (i.e., différences phénotypiques entre individus; Vaupel and Yashin 1985). Ces paramètres sont susceptibles d’augmenter ou de diminuer les chances de survie et de reproduction au cours de la vie de chaque individu. J’ai également fait le lien entre chaque stratégie de recrutement et des mesures de fitness individuelle appropriées par le biais d’une approche statistique dite de ‘jack-knifing, mais différente de celle proposée par Coulson et al. 2006, afin de calculer des gradients de sélection portant sur APR en fonction de différents scenarios démographiques (population stationnaire, en croissance, ou en décroissance).

Parce que l’APR est un élément clé de la démographie des espèces longévives telles que la mouette tridactyle, nous avons étudié certaines variables susceptibles d’influencer l’âge au recrutement par le biais de modèles de marquage-recapture prenant en compte une détectabilité imparfaite des individus avant la première reproduction (i.e., modèles de Capture-Mark-Recapture Multi-State: CMR MS; Williams et al. 2002). D’après le travail de

Danchin et des ses collègues (e.g., Danchin et al. 1998), et les observations faites sur le terrain, nous avions la forte intuition que la variabilité observée de l'APR et la sélection de l'habitat étaient 'les deux faces d'un même pièce' (Ens et al. 1995). En effet, la théorie de sélection de l'habitat prédit que les individus devraient s'installer dans les endroits (territoires ou sites) où la fitness attendue est la plus forte (Frewell et Lucas 1970). Pourtant, qui dit habitat à forte probabilité de produire des descendants par exemple (fitness attendue), dit potentiellement habitat pour lequel la compétition est plus forte. Ainsi, il est possible que seuls les individus présentant des capacités compétitrices particulièrement fortes puissent s'établir sur les sites de meilleure qualité.

Deux hypothèses peuvent alors être mises en avant : soit les individus de bonne qualité ont des capacités compétitrices leur permettant de recruter tôt dans la vie, soit seuls l'expérience et le temps permettent d'acquérir de telles capacités. En outre, les conflits territoriaux peuvent entraîner des coûts, notamment chez le mâle de mouette tridactyle, le sexe territorial (batailles, blessures, dépense énergétique, etc.). Une autre tactique pourrait alors permettre aux individus d'acquérir de bons sites : la file d'attente (Ens et al. 1995), qui consiste à attendre qu'un site se libère par mort d'un, ou des deux propriétaires. Les principaux résultats montrent que la probabilité de recrutement était plus forte à des âges intermédiaires (i.e., recrutement à l'âge 5) dans des habitats (falaises) de qualité intermédiaire, suggérant une relation entre qualité de l'habitat de recrutement et âge à la première reproduction.

Le premier résultat contredit l'hypothèse d'un recrutement précoce associé à une fitness maximale (Stearns 1992), mais cette idée reste en accord partiel avec l'hypothèse que le différé du recrutement pourrait être avantageux s'il est associé à une augmentation du succès reproducteur avec l'âge, l'expérience, ou les deux (Charlesworth 1994). De plus, les résultats obtenus montrent que les recrues les plus jeunes font l'expérience d'un succès reproducteur faible en début de vie reproductrice. Cependant, Charlesworth faisait référence à une augmentation du recrutement post-recrutement, et non pas à des avantages l'année du recrutement. La plupart des individus recrutent à des âges intermédiaires, et parce que ces individus connaissent le succès reproducteur le plus élevé l'année du recrutement, il semble que quelques années d'expérience pré-recrutement pourraient mener à une augmentation de la fitness par rapport à ceux qui ne bénéficient pas de ce type d'expérience. Si tel est le cas, quel genre d'information pourrait être acquis pendant une vie pré-reproductrice prolongée?

Le différé du recrutement pourrait permettre à la prospection d'avoir lieu, un phénomène très commun chez les oiseaux marins (e.g., Jenouvrier et al. 2008), et chez la mouette tridactyle en particulier (e.g. Danchin et al 1991, 1998, Cadiou et al. 1994, Boulinier et al. 2008). En effet, dans le cadre des modèles de capture-marquage, recapture multistrates, la probabilité de recrutement est associée à la qualité de l'habitat de recrutement l'année précédant le recrutement. Ce résultat suggère que la sélection de l'habitat de recrutement prend place l'année précédant l'installation sur un site et la première reproduction, ou bien que l'information disponible pour les individus en début de saison reproductrice est auto-corrélée à la productivité l'année précédente. Si l'auto-corrélation temporelle dure plusieurs années, une autre étude serait nécessaire afin d'évaluer si la prospection a lieu sur une ou plusieurs années précédant le recrutement. Si cela s'avère être vrai, la prospection pourrait être une façon très efficace d'augmenter la probabilité d'identification d'un habitat de meilleur qualité, et en dernier lieu, d'améliorer les chances de survie et de succès reproducteur future.

En outre, que le recrutement (reproduction effective) soit différé n'implique pas que l'individu ne s'investisse pas dans des activités territoriales ou de formation de couple. En effet, s'insérer dans un réseau social dense tel que celui des colonies de reproduction de mouettes tridactyles réclame également de s'imposer dans un tel réseau, par exemple par le biais du « squattérisme » (le fait de se poser sur des sites dont les propriétaires sont absents, mais contenant des poussins, e.g. Monnat et al. 1990). De nombreux pré-reproducteurs sont en outre de sexe connu avant le recrutement, ce qui implique dans le cadre de cette étude de s'être accouplé, ou d'avoir nourri des femelles, donc d'avoir initié la formation d'un couple (le sexage repose en effet ici sur l'observation de comportements précis). Certains sont également clairement cantonnés sur un site et y construisent des ébauches de nids, ce qui implique d'y accomplir des activités territoriales et même de montrer des comportements de propres à la reproduction tels que la construction d'un nid. Il est raisonnable d'émettre l'hypothèse que le différé de reproduction est associé à l'acquisition d'une réelle expérience (Cam et al. 2002b) explicitement liée à la reproduction (formation de couple, construction de nid), mais également une expérience liée à la connaissance des zones d'alimentation proches des colonies, etc.

Le second résultat contredit la théorie de la sélection de l'habitat (Holt and Barfield 2001), théorie qui stipule qu'un habitat de plus forte qualité devrait être préférentiellement sélectionné, car ce type d'habitat est potentiellement associé à une plus forte fitness. Les résultats indiquent que la plupart des individus ont recruté 'par choix' dans des habitats de qualité intermédiaires (choix indépendant de la disponibilité de falaises de faible, moyenne, ou forte qualité), et que le succès reproducteur l'année du recrutement était plus élevé chez les recrues qui avaient choisi ce type de falaise de reproduction. Ce terme de 'choix' reflète ici le fait que la distribution des qualités d'habitats choisis est différente de la distribution de qualités qu'ils auraient obtenues par le fait de s'installer au hasard, simplement au pro rata de la proportion d'habitats de qualité donnée disponible. Cette distance entre distribution théorique et observée reflète soit un choix actif, soit des contraintes. Ces résultats reflètent sans doute la forte compétition dans les falaises très productives (i.e., où la densité est très élevée) d'une part, et un comportement d'évitement des falaises de très faible qualité d'autre part (i.e., où la prédation est très forte). D'après les observations de terrain, il est évident que le potentiel en termes de fitness dans des falaises de faible qualité est faible, car une forte proportion de nids est en situation d'échec. Cela pourrait être le résultat de la violence et de la proximité des vagues (qui peuvent balayer les nids situés le plus bas dans les falaises par jour de tempête), ou une topographie difficile pour l'installation d'un nid (e.g., pan de roche pentue trop lisse, ou trop vertical), ou encore la proximité de prédateurs tels que certains corvidés (corneille noire *Corvus corone* et grand corbeau *Corvus Corax*), autres oiseaux marins (surtout le goéland argenté *Larus argentatus*), et quelques rares faucons pèlerins (*Falco peregrinus*). La prédation sur les œufs par les corvidés a entrainé l'échec complet d'une colonie de reproduction au début des années 80 (celle qui à l'époque hébergeait la plus grande proportion de reproducteurs du Cap Sizun), et la désertion permanente de la colonie la plus importante à la fin des années 90 (Cam et al. 2004). Les goélands argentés ont également causé l'échec total de plusieurs petites sous-colonies insulaires par prédation sur les poussins. Cependant, des études complémentaires seraient nécessaires afin de séparer l'importance relative de ces différentes variables (tempêtes, topographie, prédation) dans la détermination de la qualité des falaises concernées.

Il faut également noter les limites du critère de qualité de l'habita choisi ici. Les colonies étudiées sont situées dans un baie, à faible distance les unes des autres, et il est raisonnable de penser que toutes les mouettes ont accès aux mêmes habitats d'alimentation (situés principalement en dehors de la baie). Par contre, les sites de reproduction, eux, ne sont probablement pas de même qualité. En l'absence de critère de qualité des sites proprement dits (e.g., critères physiques) dans des falaises denses, nous avons utilisé un critère développé par Danchin et al. (1998) : la proportion de sites en échec dans les falaises de plus de 10 sites. Ce critère a l'avantage d'intégrer 'en une seule métrique' les divers déterminants de la qualité objective des habitats, mais il est impossible à séparer la performance reproductrice de 'la falaise' de la qualité des individus eux-mêmes. Que tous les individus se reproduisant dans des falaises comptant parfois plus de 200 couples soient tous de même qualité me semble une hypothèse irréaliste, mais qui ne peut être complètement écartée *a priori*. L'autre désavantage de ce critère est qu'il est actuellement impossible de travailler à une échelle spatiale fine. La ‘qualité’ des falaises est estimée en prenant en compte tous les sites actifs l’année donnée, ce qui crée des disparités entre falaises de taille très différente (10 versus 200 sites). Enfin, dans ces grandes falaises, il est suspecté que le choix de l’individu se porte sur un groupe de site, voire un site particulier (Cadiou 1994), et que l’échelle ‘falaise’ est bien trop grossière. Des analyses spatiales plus poussées sont actuellement en cours (e.g., Bled 2006). Il serait intéressant de ‘croiser’ ces approches spatiales fines avec la performance des recrues ; ne s’étant jamais reproduits, ces individus n’ont pas influencé la ‘performance des sites’ sur lesquels ils s’installent, ni bien entendu celle des nouveaux sites qu’ils peuvent créer.

La relation établie entre âge de première reproduction et succès reproducteur est également un résultat intéressant. L’âge de première reproduction (APR) pourrait aussi être associé à des variations substantielles sur le succès reproducteur (SR) et la survie au cours de la vie. Dans les chapitres II et III, j’ai tenté de déterminer si le SR, et la survie augmentent, demeurent constant, ou diminuent au cours de la vie des individus qui recrutent à des âges différents.

Nos résultats indiquent que les individus qui diffèrent le recrutement (APR > 5) font l’expérience d’un déclin plus précoce mais moins marqué du SR (i.e., sénescence reproductrice ; chapitre II), sans doute car le SR de ces recrues ‘ne tombent pas de bien haut’. De plus, ils souffrent d’un déclin plus rapide de la survie avec l’âge (i.e., sénescence en termes de survie ; chapitre III) comparé à des recrues plus jeunes (APR < 6), et leur espérance de vie décline plus rapidement que celle des individus qui recrutent tôt (chapitre III). Ces résultats suggèrent que les individus doivent sans doute être dissemblables dans leur capacité à recruter plus ou moins tôt (i.e., hétérogénéité de qualité individuelle), et que la décision de se reproduire pour la première fois a des conséquences sur la reproduction et la survie future.

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Dans le second chapitre, je me suis intéressée à la relation entre âge au recrutement, SR, et la sénescence reproductrice, tout en prenant en compte l’expérience reproductrice, l'hétérogénéité individuelle, et la variabilité temporelle. Pour cela, j'ai utilisé des modèles généralisés additifs mixtes (i.e., gamm) qui n'ont pas encore été utilisés pour ce genre d'applications, mais qui deviennent de plus en plus populaires (e.g., Ezard et al. 2007). Les gamm permettent d'étudier des relations sans contraintes entre covariables et la variable réponse (SR dans note cas) par l'utilisation de splines, tout en prenant en compte des sources d'hétérogénéité non-observée, e.g., la qualité individuelle, un élément susceptible d'influencer la relation entre l'âge et les paramètres démographiques (e.g., Cam et al. 2002a, van de Pol and Verhulst 2006).

Les individus qui diffèrent le recrutement ont manqué quelques opportunités de reproduction, mais réalisent un succès reproducteur élevé à la première reproduction (chapitre I). Afin d'examiner la relation entre APR et SR au cours de la vie des individus, le chapitre II porte sur l'influence de APR sur les trajectoires de SR âge-spécifique. Les modèles ne prenant pas en compte l'hétérogénéité non-observée ont tous révélé une augmentation du SR avec l'âge, et cela quelque soit APR, sans doute le résultat d'une 'sélection intra-générationnelle' (i.e., 'sélection phénotypique'; Endler 1986), ou d'une disparition sélective des phénotypes les plus 'faibles' (Vaupel and Yashin 1985). Lorsqu'une telle hétérogénéité était prise en compte, il a été mis en évidence que tous les individus connaissaient une sénescence reproductrice marquée, indiquant ainsi à quel point il est crucial de prendre en compte toutes les sources d'hétérogénéité lors de l'étude des trajectoires démographiques (e.g., Cam et al. 2002a). Cependant, l'hétérogénéité non-observée seule n'explique pas la véritable trajectoire de reproduction observée. Nous avons également considéré des interactions entre covariables âge-spécifiques afin de prendre en compte la multiplicité des histories de vie qui définissent les différences de SR entre individus. L'interaction triple entre APR, l'expérience (i.e, nombre d'années écoulées depuis la première reproduction), et la durée de vie semble avoir prise en compte l'apparition sélective (variabilité de APR), la disparition sélective des individus (i.e., variabilité dans la durée de vie reproductrice), et la diversité des ‘vies reproductrices’ possibles (i.e., variabilité dans l’expérience acquise). Ainsi, non seulement l’hétérogénéité non-observée explique la variabilité âge-spécifique de certains traits d’histoire de vie, mais des sources d’hétérogénéité dynamique (i.e., expérience) et fixes (i.e., recrutement âge et durée de vie) le peuvent également.

Même si les trajectoires de SR ont toutes une forme concave, des différences importantes dans les trajectoires âge-spécifiques au travers des différent groupes de recrutement ont été observées. Différentes combinaisons d’expérience pré- et post-recrutement résulte en un SR maximal à des âges intermédiaires, et ce quelque soit l’âge de recrutement (APR). Cependant, SR augmente plus rapidement chez les jeunes recrues au fur et à mesure qu’elles gagnent en expérience post-recrutement, alors que les recrues tardives connaissent un fort SR l’année du recrutement, sans doute grâce à une accumulation d’expérience pré-recrutement. Les individus qui recrutent à des âges intermédiaires voient probablement leur expérience pré- et post-recrutement s’équilibrer. Ces résultats suggèrent que les individus, en fonction de leur APR, maximise leur SR à des âges intermédiaires, via différentes ‘voies’.

D’une manière générale, même si ce jeu de données permet un suivi fin des trajectoires reproductrices au cours de la vie, il présente des limites qu’il m’a été impossible de dépasser. En effet, si les falaises de reproduction montrent à tout observateur un peu familier une hétérogénéité de succès de reproduction évidente, il existe des différences de productivité globale très substantielles entre colonies la même année (e.g. Danchin et al. 1998), principalement causées par l’activité de prédateurs ayant une influence massive sur quelques colonies. Une fois l’épisode de prédation commencé, cela continue parfois jusqu’à l’extinction totale de la colonie par dispersion des reproducteurs (Cam et al. 2004). Ainsi, si le degré d’autocorrélation temporel de la performance globale de grandes unités spatiales (falaises ou colonies) n’est pas nul, le moment où survient le premier événement de prédation est stochastique. Quel est le poids de cette stochasticité dans les trajectoires reproductrices des individus (e.g., âge de recrutement, variation de la performance avec l’âge par la suite)?

Les outils analytiques étant actuellement en cours de développement (e.g., Bled 2006), il m'a été impossible d'étudier la relation entre qualité des sites, stochasticité de la qualité de plus grandes unités spatiales, et trajectoires individuelles de reproduction.

Ces résultats cependant, posent des questions additionnelles, telles que: 1) est-ce que l'APR, et autres composantes âge-spécifiques de l'investissement reproducteur, influencent également la survie âge-spécifique (chapitre III), et 2) est-ce que le recrutement à un âge intermédiaire (i.e., AFR = 5) est une tactique de recrutement optimale en termes évolutifs (i.e., individuelle fitness; chapitre IV)?

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Le chapitre III fait appelle a une approche appelée 'analyse de survie' (i.e., 'time-to-failure survival analysis') afin d'étudier la survie âge-spécifique individuelle tout en prenant en compte des sources fixes (i.e., APR) et dynamiques (e.g., production âge-spécifique d'œufs et de poussins) d'hétérogénéité observées, non-observées (i.e., 'frailty'), et de variabilité environnementale (i.e., effet année).

Les individus qui recrutent à des âges différents connaissent des chances de survie et des espérances de vie âge-spécifiques contrastées. Plus spécifiquement, recruter après 5 ans est associé à une sénescence plus forte en termes de survie, alors que les individus recrutant à 5 ans ou avant cet âge ont une espérance de vie plus élevée, même à des âges avancés. APR doit donc être un bon indicateur de la qualité intrinsèque des individus (Stearns 1992, Forslund and Pärt 1995, Becker et al. 2008), la variabilité de l'APR étant indubitablement associée à différentes chances de survie. De plus, les différences de capacités compétitives entre individus pourraient permettent à certains de commencer à se reproduire plus tôt, mais également de « sénescer » plus lentement, et également d'atteindre une fitness plus élevée que les individus de plus 'faible qualité' qui diffèrent le recrutement (e.g., Cam and Monnat 2000, Cam et al. 2002a, Hadley et al. 2006). Cependant, les recrues d'âge intermédiaire connaissent un SR plus élevé à la première reproduction (chapitre I), et semblent équilibrer expérience pré- and post-recrutement de façon à maximiser le SR au cours de la vie (chapitre II). Reste encore à déterminer laquelle des tactiques de recrutement est la plus rentable en termes de fitness (chapter IV): le recrutement précoce ou à un âge intermédiaire?

L'investissement reproducteur âge-spécifique influence de manière substantielle la survie à chaque âge (Orell and Belda 2002). Par exemple, les reproducteurs en situation d'échec connaissent une mortalité plus élevée que les non-reproducteurs. D'un autre côté, les individus qui élèvent au moins un poussin jusqu'à l'envol connaissent une mortalité plus faible que les non-reproducteurs et le reproducteurs en échec. Ce résultat suggère que seuls les reproducteurs en situation d'échec accusent un coût de reproduction, et que les individus en situation de succès sont plus performants (e.g., Forslund and Part 1995) ce qui leur permet d'échapper à un tel coût (Cam et al. 2002a). La mortalité plus élevée observée chez les reproducteurs en échec est un fait qui mérite plus de travail. La mort de l'individu pendant la saison reproductrice pourrait aboutir à un échec à la reproduction, mais la mort du partenaire pourrait aboutir au même résultat. Dépouiller le jeu de données afin de déterminer le devenir du partenaire chez les couples doublement marqués ferait l'objet d'une étude à part entière. La mort pourrait refléter le coût reproducteur chez les individus de faible condition qui ont initié la reproduction cette saison là (i.e., mortalité intrinsèque), mais cela pourrait également être expliqué par un mort accidentelle (i.e., mortalité extrinsèque, e.g., pêcherie, dégazages sauvages). Enfin, il n'est pas impossible qu'une partie de la mortalité des individus en échec reflète une dispersion permanente en dehors de la zone d'étude. Il est en effet important de garder à l'esprit que la mortalité observée dans la zone d'étude combine la mortalité vraie et l'émigration permanente (Williams et al. 1992). Or il est pour le moins intéressant de noter que ce sont les individus qui par ailleurs montrent la plus forte propension à disperser à l'intérieur de la zone d'étude (e.g., Danchin et al. 1998), qui montrent également la mortalité locale la plus élevée. Des études combinant reprises et recaptures (Williams et al. 1992), voire l'utilisation de dispositifs GPS pourraient peut-être apporter des éléments de réponses à ces questions.

Même après avoir pris en compte l'hétérogénéité fixe et dynamique expliquant une certain quantité de variabilité individuelle en terme de chance de survie à chaque âge, il demeurait une certaine variabilité individuelle non-observée, ce qui est en accord avec plusieurs études démographiques menées sur cette population par le passé (e.g., Cam et al. 2002a, Aubry et al 2009b). Pour la première fois, la contribution relative de l'hétérogénéité observée et non-observée (Vaupel et al. 1979, Vaupel and Yashin 1985) responsable de la variabilité âge-spécifique de survie observée au sein de cette population a pu être calculée. L'hétérogénéité non-observée explique 6 fois plus de réduction de la déviance que l'hétérogénéité observée (i.e., fixe et dynamique) ce qui encore une fois confirme l'importance de la prise en compte de l'hétérogénéité non-observée lors de l'étude des trajectoires démographiques de survie et de reproduction (chapitre II).

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Dans le dernier chapitre, nous avons voulu utiliser toute l'information démographique âge-spécifique estimée dans chacun des chapitres précédents et construire un model matriciel le plus détaillé possible (chapitre IV, figures 1 and 2) afin i) d'estimer le taux de croissance de la population; ii) déterminer si le différé du recrutement est une stratégie de recrutement avantageuse en étudiant le direction et la force de sélection opérant sur l'âge à la première reproduction sous différents scenarios démographiques (i.e., population en déclin, stationnaire, ou en croissance); iii) établir une nouvelle méthode d'estimation de la fitness individuelle dans un contexte déterministe, que nous voudrions étendre à un contexte stochastique dans un futur proche.

i) Nos résultats indiquent que le taux de croissance de la population est inferieur à 1 (λ = 0.8916), suggérant un déclin de la population important (i.e., population en décroissance, scenario démographique 1). Cependant, cette population persiste au Cap Sizun depuis des décennies, et même si certaines colonies ont disparus au cours du temps (Cam et al. 2004), d'autres se sont formées, et la population dans son ensemble semble se maintenir en nombre. Dans cette population, la mort et l'émigration permanente hors du site d'étude sont confondus, expliquant sans doute pourquoi $\lambda < 1$ même s'il est très possible que cette population soit stationnaire ou en croissance, selon l'année considérée. Des suivis par GPS, des informations concernant des cas d'oiseaux morts au sein de la zone d'étude, ainsi que des informations concernant les oiseaux qui ont dispersé et sont vus hors de la zone d'étude pourraient nous aider à estimer le véritable taux de croissance de la population.

ii) Nous avons utilisé une procédure d'optimisation afin de determiner par combien le modèle matriciel doit être multiplier afin d'obtenir un taux de croissance corrige à une valeur de 1 (i.e., population stationnaire, scenario démographique 2), et de 1.1084 (scenario 3, population en croissance, image miroir du scenario 1). Quelque soit le scenario considéré, la conclusion demeure la même : un recrutement précoce est légèrement préféré à un différé du recrutement (chapitre IV, figure 3); cependant, la force de sélection diminue au fur et à mesure que le recrutement est différé au delà de l'âge 4 (chapitre IV, figure 3), suggérant que les coûts associés au différé du recrutement ne sont pas aussi substantiels que précédemment suggéré.

iii) Nous avons développé une nouvelle version du jack-knifing qui combine des concepts propres aux travaux de Link (2002) et de Coulson (2006), et qui utilise des estimateurs statistiques robustes qui prennent en compte des sources d'hétérogénéité observée et non-observée (e.g., effet aléatoire individuel) au sein de la population. La mesure de fitness individuelle que nous proposons utilise une information démographique détaillée. Cependant, cette procédure pourrait être améliorée si l'on pouvait par exemple n'utiliser que des estimateurs des composantes de la fitness. Nous avons utilisé des estimateurs pour la survie et certaines mesures de fécondité âge-spécifique. Cependant, nous pourrions également modéliser d’autres composantes de la fitness telles que la production d’œufs et de poussins, que nous avons considéré jusqu’a présent comme des valeurs démographiques brutes. En outre, nous voudrions ré-estimer chaque composante de la fitness à chaque fois qu’un individu est ôté de la population par ‘jack-knifing’, ce qui est faisable pour certaines composantes, mais qui nécessiterai une amélioration du programme MARK qui ne permet pas de faire du faire du jack-knifing lors de l’estimation de la survie juvénile.

Nous aimerions utiliser cette même procédure pour l’estimation de la fitness individuelle en relation avec l’âge à la première reproduction dans un contexte stochastique, afin de déterminer si nos conclusions restent ou non inchangées.

~ CONCLUSION AND PERSPECTIVES ~

APR est intimement lié à la qualité de l'habitat où le recrutement a lieu (chapitre I), et sa variabilité reflète l'hétérogénéité individuelle: différences inter-individuelles en terme de compétence reproductrices permettant l'initiation de la première reproduction (chapitre I), elle influence la reproduction âge-spécifique (chapitre II), et la survie (chapitre III). Cependant, des sources additionnelles de variabilité, fixe (APR, durée de vie) et dynamique (e.g., investissement reproducteur âge-spécifique, expérience), observée (e.g., covariables reproductrices ou temporelles), et non-observée (i.e., 'frailty') sont également responsable de la variabilité âge-spécifique des trajectoires de reproduction et de survie.

La variabilité temporelle des conditions environnementales exerce également une forte influence sur la survie âge-spécifique (chapitre III) et la reproduction (chapitre II), spécialement chez les jeunes adultes (chapitre II). Des études supplémentaires pourraient aider à établir si une augmentation de la stochasticité environnementale et à le pouvoir de modifier la direction et la force de sélection sur APR, la reproduction âge-spécifique, et les taux de sénescence (i.e. survie et reproduction).

Cette étude sur le long-terme est idéale pour séparer les composantes génétiques des composantes environnementales susceptible de façonner les patrons de sénescence aussi bien en termes de reproduction qu'en termes de survie, afin d'accroire notre compréhension de la plasticité phénotypique[7], susceptible de modifier les profiles de sénescence. Chez les populations sauvages, des conditions environnementales défavorables tôt dans la vie pourraient endommager le développement, et potentiellement la reproduction et les chances de survie plus tard dans la vie des individus (Metcalf and Monaghan 2001, Reed et al. 2003, Keller et al. 2008). Pour cette raison, je suis plus intéressée par l'étude de la plasticité de la

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[7] Expression de différents phénotypes par un unique génotype sous différentes conditions environnementales.

sénescence en réponse aux variations de l'environnent, que par l'étude de la discrimination entre les différentes théories majeures de la sénescence (i.e., pléiotropie antagoniste, Williams 1957; accumulation des mutations, Medawar 1957), théories qui ne peuvent vraisemblablement pas être distinguées par des travaux (même en génétique quantitative) sur des espèces sauvages.

Afin de formellement estimer les composantes environnementales et génétique de la sénescence *in natura*, nous pourrions potentiellement mener une étude de génétique quantitative, en utilisant l'information disponible sur les pedigrees (i.e., modèle animal multivarié; Lynch and Walsh 1998). Le principal avantage du modèle animal est qu'il va au-delà de la régression classique 'parent-enfant' (Kruuk and Hadfield 2007) et utilise toute l'information disponible sur les relations entre individus de la même famille. Idéalement, ce modèle devrait être adapté à des situations de détectabilité imparfaite, afin de nous permettent d'étudier tout le cycle de vie la population de mouettes tridactyles étudiée, pré-reproducteurs inclus (i.e., $p < 1$).

J'espère pouvoir répondre à ces objectives dans la continuité de cette thèse. Le suivi des populations sauvages et leur réponse aux changements environnementaux contemporains est un aspect fondamentale de la dynamique des populations et de l'écologie évolutive. Ces suivis sont nécessaires à la compréhension des changements évolutifs et démographiques qui opèrent sur les systèmes sauvages. Ce travail est une première étape vers une plus profonde compréhension de l'héritabilité et de l'évolution d'une variété de traits âge-spécifiques, tel que APR. Le but de ses travaux serait d'approfondir les connaissances actuelles sur l'influence relative de l'environnement (e.g., densité de population) et de la génétique (e.g., différences de survie et de capacités reproductrices héritables) sur les profiles de sénescence in natura. Cette recherche apporterait à un domaine très porteur et interdisciplinaire qui réunit les sciences gérontologique, démographique, l'écologie évolutive, la biologie des populations, et la conservation.

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Influence du recrutement sur les variations des paramètres démographiques avec l'âge et la vitesse de sénescence chez la mouette tridactyle, *Rissa tridactyla*

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Directeur de Thèse : Emmanuelle CAM

Spécialité : Écologie

J'ai utilisé une étude de 30 ans portant sur une espèce d'oiseau marin longévif (la mouette tridactyle) afin d'étudier les compromis évolutifs entre recrutement, reproduction, et survie. Mes résultats indiquent que l'âge à la première reproduction et la sélection de l'habitat sont intimement liés, et que l'âge au recrutement influence également les trajectoires de survie et de reproduction. D'autres sources d'hétérogénéité observée (investissement reproducteur) et non-observée ('frailty') agissent également sur la survie et la reproduction au cours de la vie. Les recrues d'âge intermédiaire (âge = 5) maintiennent un succès reproducteur élevé au cours de la vie et minimisent le déclin des chances de survie avec l'âge par rapport aux autres recrues. Même si les mesures de fitness individuelles indiquent que le recrutement précoce est la plus avantageuse des stratégies, les coûts associés au différé du recrutement semblent minimes.

Mots-clés: âge à *la première reproduction, évolution des traits d'histoire de vie, fitness individuelle, hétérogénéité, model additif mixte, model matriciel, model multi strate, mouette tridactyle, sélection, sénescence, succès reproducteur, survie.*

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Influence of Recruitment on Age-specific Demography and Senescence in a long-lived Seabird, the black-legged Kittiwake

I used a 30-year study of long-lived seabirds (black-legged Kittiwakes) that breed in Brittany to study the evolution of trade-offs between early-life breeding decisions, future reproduction, and survival. I first found that recruitment age and habitat selection were intimately linked. Recruitment age further influenced breeding success and survival trajectories. Furthermore, sources of observed (reproductive covariates, experience) and unobserved heterogeneity (frailty) explained substantial amounts of variability in breeding success and survival. Overall, intermediate age recruits (age 5) seemed to maintain high breeding success over life and minimized senescence in survival compared to other recruits. Even though individual fitness showed that earlier recruitment was the most beneficial recruitment strategy, the costs associated to delayed recruitment seemed minimal.

Key-words: age at first reproduction, black-legged Kittiwake, breeding success, generalized additive mixed models, heterogeneity, individual fitness, life history evolution, matrix population model, multi-state models, selection, senescence, survival, time-to-failure survival analyses.