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# The determination of seasonal declines in breeding success in seabirds

Juan Moreno
Museo Nacional de Ciencias Naturales, J. Gutiérrez Abascal 2, E-28006 Madrid, Spain
e-mail: jmoreno@mncn.csic.es

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**Abstract.** Variables related to fecundity or reproductive success like clutch size, egg size, chick growth and survival, etc., are subject to seasonal declines in numerous species of seabirds breeding in temperate or polar areas. Several hypotheses have been proposed to explain this phenomenon: 1) food availability decreases throughout the breeding season (food supply hypothesis); 2) late nests suffer higher predation risks due to the diminishing dilution effect (predation hypothesis); 3) young or inexperienced breeders, or individuals less efficient in finding food, will breed late (parental quality hypothesis), and 4) late reproducers do not invest as much as early ones (reproductive restraint hypothesis) because a) chicks hatched late in the season have a lower reproductive value, and/or b) an increasing need to invest in the adults' own survival as the season advances. Here, I elucidate the generality of seasonal declines in fecundity or breeding success in seabirds. Further, the impact of age and breeding experience on reproductive performance is shown to be important, as predicted by the 'parental quality' hypothesis. A search of the seabird literature shows scant evidence on the importance of seasonal trends in food availability or predation risk for eggs and chicks. Further, the basic tenets of the 'restraint' hypothesis are discussed in full and its underpinnings in life-history theory formally presented. This hypothesis has not received its due share of attention in the seabird literature, although it appears especially suitable for such long-lived animals. Finally, the scarce experimental evidence testing the different hypotheses is fully reviewed. Several experiments are shown to be flawed in their design and statistical analysis. The two clearest experiments do not support the 'parental quality' hypothesis, and in one case are in accordance with the 'restraint' hypothesis. There is an urgent need for further experimental work.

**Key words:** Seasonal declines, Reproductive success, Seabirds, Life history, Parental quality.

**Resumen.** *La determinación de descensos estacionales del éxito reproductor en aves marinas.* Las variables relacionadas con la fecundidad o éxito reproductor como tamaño de puesta, tamaño de los huevos, crecimiento y supervivencia de pollos, etc., están sometidas a descensos estacionales en numerosas especies de aves marinas que se reproducen en zonas templadas o polares. Se han propuesto varias hipótesis para explicar este fenómeno: 1) la disponibilidad de alimento decrece a lo largo de la temporada (hipótesis del alimento); 2) nidos tardíos sufren un mayor riesgo de depredación debido a una disminución en el efecto de dilución (hipótesis de la depredación); 3) reproductores jóvenes o inexpertos, o individuos menos eficaces en localizar alimento, crían más tarde (hipótesis de la calidad parental), y 4) reproductores tardíos no invierten tanto como los tempranos (hipótesis de la restricción reproductora) por que a) los pollos nacidos tarde en la temporada tienen un menor valor reproductor, y/o b) los adultos tienen una mayor necesidad de invertir en su propia supervivencia según avanza la temporada. Aquí dilucido la generalidad de los descensos estacionales en fecundidad o éxito reproductor en aves marinas. Además, se demuestra la importancia de la edad o experiencia reproductora en el rendimiento reproductor, como predice la hipótesis de la calidad parental. Una revisión de la bibliografía sobre aves marinas muestra escasa evidencia sobre la importancia de tendencias estacionales en el alimento o en el riesgo de depredación sobre huevos o pollos. También se discuten los supuestos básicos de la hipótesis de la restricción y se presenta formalmente su entronque con las teorías sobre evolución de historias vitales. Esta hipótesis no ha recibido la atención que se merece en la bibliografía sobre aves marinas, aunque parece especialmente indicada para animales tan longevos. Finalmente, la escasa evidencia experimental que pone a prueba las diferentes hipótesis es revisada. Varios experimentos han resultado estar afectados por problemas de diseño y análisis estadístico. Los dos experimentos más claros no apoyan la hipótesis de la calidad parental, y en un caso están más de acuerdo con la hipótesis de la restricción. Hay una necesidad urgente de más trabajo experimental en este campo.

## Introduction

In temperate and polar areas, seasonal declines in different components of fecundity and breeding success of seabirds are prevalent. Clutch size, egg size, hatching success or fledging success decrease frequently with laying date, although there are exceptions to this ubiquitous pattern. Several hypotheses have been proposed to explain seasonal declines in reproductive success in temperate species (Klomp, 1970; Perrins, 1970; Daan et al., 1988), which all can apply to seabirds. The most important are: 1) there are seasonal deteriorations in food supply or food availability (food supply hypothesis: Lack, 1968; Perrins, 1970; Martin, 1987); 2) pairs breeding outside the peak of breeding in the population suffer a higher predation pressure due to a reduced dilution of predation risk (predation hypothesis: Birkhead, 1977); 3) young or inexperienced pairs or low-quality breeders lay late and suffer impaired success due to their poor breeding proficiency (parental quality hypothesis: Coulson & White, 1956); and 4) late breeders have a lower breeding drive, i.e. are less willing to invest in reproduction than early breeders (restraint hypothesis: Curio, 1983; Moreno et al., 1997). To elucidate the relative applicability of the different hypotheses for different species remains a challenge. It is important to ascertain their validity as it has important implications for life history theory. The basic question can be framed in the dichotomy between 'reproductive constraint' and 'reproductive restraint' models (Curio, 1983). While hypotheses (1)-(3) can be said to express different constraints acting on the breeding performance of individuals, hypothesis (4) can be thought of as expressing prudence in current reproduction (Drent & Daan, 1980) in order to be able to reproduce in the future (Roff, 1992). This last hypothesis seems eminently suitable for seabirds, given their long life expectancies.

In the present paper, I will elucidate the generality of seasonal declines in fecundity or breeding success in seabirds. Further, the impact of age and breeding experience on reproductive performance will be explored, as it is a basic prerequisite for the 'parental quality' hypothesis. The seabird literature will be scanned for evidence on the importance of seasonal trends in food availability or predation risk for eggs and chicks to test the 'food supply' and 'predation' hypotheses. Further, the basic tenets of the 'restraint' hypothesis will be discussed in full and its underpinnings in life-history theory formally presented. This hypothesis has not received its due share of attention in the seabird literature, although it appears especially suitable for seabirds. Finally, the scarce experimental evidence testing the different hypotheses will be fully reviewed. The suitability of the different experimental protocols will be discussed in this context. I will end with conclusions derived from this short review and a plea for further experimental work.

## Evidence of seasonal declines in reproductive performance

Table 1 summarises the evidence of seasonal declines in reproductive performance in seabirds. The cases of absence of significant trends and of positive trends have been pooled. It becomes apparent from Table 1 that negative trends in reproductive output are common in four orders of seabirds, and clearly more prevalent than positive or nonexistent trends. Except for egg size, for which the evidence is mixed, there is ample evidence of seasonal declines in reproductive variables. Thus, seasonal decreases are frequent with respect to clutch size, hatching success, chick size at fledging, fledging success (relative success of hatched eggs) and breeding success (relative success of laid eggs and/or number of fledged young), with less available information for parental care variables, chick growth rate, probability of clutch replacement, survival of fledged young, delay to breed in the next season or lifetime reproductive success.

## Evidence of effects of age and experience on reproductive performance

Table 2 summarises the evidence of improvements with age or experience in reproductive performance. It is evident from this review that age and to a lesser degree breeding experience determine significant changes in breeding success variables. It is especially noteworthy that age affects breeding date in 15 of 18 species studied. If young or inexperienced birds breed later and have a lower reproductive success, the seasonal declines reported in Table 1 may be just a consequence of age-dependent trends in breeding performance. However, breeding date appears to be consistent and repeatable in many species studied (Table 3).

This consistency from year to year suggests that some components of breeding date variation may not be strictly related to age but to age-independent variation in parental quality related to condition (Perrins, 1970; Daan et al., 1988) and health state (Gustafsson et al., 1994; Moreno et al., 1998). In any case, the evidence of individual variation in reproductive performance associated to breeding date is strong, supporting the plausibility of the parental quality hypothesis.

## Evidence of seasonal changes in food availability

Lack (1968) proposed that chicks were normally raised during the time of maximum food availability. Thus, if individuals for some reason delayed breeding, they would raise chicks after the peak in food abundance. Perrins (1970) suggested that energy requirements for egg formation prevent most females from laying at the optimal date, explaining the general observation that the earliest clutches were frequently

**Table 1.** Evidence of seasonal declines in fecundity, breeding success or breeding effort in seabirds. In parentheses are studies in which both early and late nesters had less fecundity/success/effort than peak nesters. Question marks denote studies in which the trend was detected in less than half of the years of study. Numbers refer to references in Appendix.

| **Variable** | **Family** | **Seasonal declines** | **No seasonal declines** |
|---|---|---|---|
| Clutch size | Sphenisciformes | *Pygoscelis antarctica* [pers.obs.] | |
| | Pelecaniformes | *Phalacrocorax atriceps* ? [30] | *P. neglectus* [34] |
| | | *P. aristotelis* [32] | |
| | | *P. auritus* [33] | |
| | Charadriiformes | *Larus delawarensis* [39] | *Sterna striata* [63] |
| | | *L. occidentalis* [42] | *S. sandvicensis* [69] |
| | | *L. argentatus* [45, 49] | |
| | | *L. fuscus* [45] | |
| | | *Rissa tridactyla* [59] | |
| | | *Sterna paradisea* [67] | |
| | | *S.dougallii* ? [69] | |
| | | *S. hirundo* ? [69] | |
| | | *Cepphus grylle* [83] | |
| Egg size | Sphenisciformes | *Eudyptes chrysolophus* [15] | *Pygoscelis papua* [6] |
| | | | *P. antarctica* [12] |
| | Procellariiformes | | *Puffinus puffinus* [27, 46] |
| | | | *P. lherminieri* [46] |
| | | | *Oceanodroma castro* [46] |
| | Pelecaniformes | *Sula bassana* [28] | |
| | | *Phalacrocorax aristotelis* [35] | |
| | Charadriiformes | *Larus delawarensis* [39] | *Creagrus furcatus* [46] |
| | | *L. argentatus* [46, 49] | *Larus argentatus* ? [48] |
| | | *L. novaehollandiae* [63] | *L. marinus* [46] |
| | | *Rissa tridactyla* [57, 58] | *L. fuscus* [46] |
| | | *Sterna fuscata* [69] | *Sterna striata* [63] |
| | | *Uria lomvia* [80, 81] | *S. hirundo* [65] |
| | | *Alca torda* [82] | |
| Hatching success (prop. of hatched eggs or no. of hatched eggs) | Sphenisciformes | *Pygoscelis antarctica* [pers. obs.] | |
| | Pelecaniformes | *Phalacrocorax atriceps* [30] | |
| | Charadriiformes | *Larus delawarensis* [37, 38] | |
| | | *L. occidentalis* [42] | |
| | | *L. argentatus* ? [48] | |
| | | (*L. argentatus*) [49] | |
| | | *Uria aalge* [75] | |
| | | *U. lomvia* [79] | |
| | | *Alca torda* [82] | |

**Table 1** (Continued). Evidence of seasonal declines in fecundity, breeding success or breeding effort in seabirds.

| **Variable** | **Family** | **Seasonal declines** | **No seasonal declines** |
|---|---|---|---|
| Incubation shifts (duration) | Charadriiformes | *Sterna fuscata* [70] | |
| Courtship feeding (rate) | Charadriiformes | *Sterna hirundo* [65] | |
| Provisioning (rate) | Charadriiformes | | *Sterna hirundo* [66] |
| | | | *Uria aalge* [73] |
| Chick guarding (duration) | Sphenisciformes | *Pygoscelis antarctica* [13, 14] | *Larus glaucescens* [41] |
| | | *P. adeliae* [8] | |
| Chick growth (rate) | Sphenisciformes | *Pygoscelis antarctica* [13, 14] | |
| | | *P. papua* [7] | |
| | Procellariiformes | | *Pachyptila desolata* [23] |
| | Charadriiformes | *Larus glaucescens* [41] | *Sterna paradisea* [67] |
| Fledging size | Sphenisciformes | *Aptenodytes patagonica* [2] | |
| | | *A. forsteri* [4] | |
| | | *Pygoscelis papua* [7] | |
| | | *P. antarctica* [13, 14] | |
| | Procellariiformes | *Puffinus puffinus* [26] | *Pachyptila desolata* [23] |
| | Charadriiformes | *Sterna fuscata* [70] | *Fratercula arctica* [85] |
| | | *Uria aalge* [72] | *U. lomvia* ? [80, 81] |
| | | *Alca torda* [82] | *Cepphus grylle* [83] |
| | | *Synthliboramphus antiquus* [84] | |
| | | *Cerorhinca monocerata* ? [87] | |
| | | *Aethia pusilla* [88] | |
| Fledging success (survival until fledging or proportion of chicks that fledge) | Sphenisciformes | | *Megadyptes antipodes* [17] |
| | Procellariiformes | | *Pachyptila desolata* [23] |
| | Pelecaniformes | *Sula bassana* [28] | |
| | | *Phalacrocorax atriceps* [30] | |
| | | *P. auritus* [33] | |
| | Charadriiformes | *(Larus delawarensis)* [38, 39] | |
| | | *L. occidentalis* [42, 44] | |
| | | *L. argentatus* ? [48, 49] | |
| | | *Sterna paradisea* [67] | |
| | | *S. fuscata* [70] | |
| | | *Uria aalge* [75, 77] | |
| | | *U. lomvia* [79] | |
| | | *Alca torda* [82] | |
| | | *Fratercula arctica* [83] | |

**Table 1** (Continued). Evidence of seasonal declines in fecundity, breeding success or breeding effort in seabirds.

| **Variable** | **Family** | **Seasonal declines** | **No seasonal declines** |
|---|---|---|---|
| Replacement (prop. of failed | Pelecaniformes | *Phalacrocorax neglectus* [34] | |
| clutches that are replaced) | Charadriiformes | *Sterna fuscata* [70] | |
| | | *Uria aalge* [75] | |
| | | *U. lomvia* [79] | |
| | | *Alca torda* [82] | |
| Breeding success | Sphenisciformes | *Aptenodytes patagonica* [1,3] | *Pygoscelis papua* [6] |
| (prop. of eggs that fledge or | | *Pygoscelis adeliae* [8, 10] | |
| no. of fledged young) | | *P. papua* [7] | |
| | Procellariiformes | *Pterodroma macroptera* [22] | |
| | | *Fulmarus glacialis* [21] | |
| | Pelecaniformes | *Phalacrocorax aristotelis* [32] | *P. auritus* [33] |
| | Charadriiformes | *Larus argentatus* [45, 48] | *Larus argentatus* [46] |
| | | *L. fuscus* [45] | *Sterna hirundo* [69] |
| | | *(L. ridibundus)* [56] | |
| | | *Sterna sandvicensis* [69] | |
| | | *S. paradisea* [69] | |
| | | *S. dougallii* [69] | |
| | | *(S. fuscata)* [70] | |
| | | *Uria aalge* [71, 76] | |
| | | *Alca torda* [82] | |
| | | *Cepphus grylle* [83] | |
| | | *Fratercula arctica* [86] | |
| Recruitment | Sphenisciformes | | *Megadyptes antipodes* [17] |
| (survival of fledged chicks) | Procellariiformes | *Puffinus puffinus* [25] | |
| | Pelecaniformes | *Phalacrocorax aristotelis* [31] | |
| | Charadriiformes | *Larus occidentalis* [44] | *Uria aalge* [74] |
| | | *L. argentatus* ? [47, 52] | *Alca torda* [82] |
| | | *Uria aalge* [78] | *Synthliboramphus* |
| | | | *antiquua* [84] |
| Breeding delay | Sphenisciformes | *Aptenodytes patagonica* [3] | |
| (delay in breeding next year) | | *Pygoscelis papua* [7] | |
| LRS (lifetime reproductive | Charadriiformes | *Larus novaehollandiae* [55] | |

**Table 2**. Evidence of effects of parental age/experience on fecundity/breeding success. In parentheses are studies in which breeding success variables attained a peak in mid-age or with intermediate experience. Underlined are changes with experience. An improvement in breeding date refers to an advancement. Success variables as in Table 1. The letters m and f denote male and female respectively.

| Variable | Family | Improvements | No improvements |
|---|---|---|---|
| Breeding date | Sphenisciformes | *Pygoscelis adeliae* [11] | *Pygoscelis adeliae* [11] |
| | | | *P. papua* [6] |
| | Procellariiformes | *Diomedea immutabilis* [9] | |
| | | *Fulmarus glacialis* [21] | |
| | | *Puffinus puffinus* [27] | |
| | Pelecaniformes | *Sula bassana* [28] | *Phalacrocorax atriceps* [30] |
| | | *Phalacrocorax aristotelis* [29] | |
| | Charadriiformes | *Catharacta skua* [36] | *Larus occidentalis* [43] |
| | | *Larus delawarensis* [37] | *Sterna paradisea* [68] |
| | | *L. occidentalis* [42, 43] | |
| | | *L. argentatus* [48, 51] | |
| | | *L. novaehollandiae* [55] | |
| | | *Rissa tridactyla* [60] | |
| | | *Rissa tridactyla* [60] | |
| | | *Sterna striata* [63] | |
| | | *S. hirundo* [64] | |
| | | *Alca torda* [82] | |
| | | *Cepphus grylle* [83] | |
| Clutch size | Sphenisciformes | *Pygoscelis adeliae* [11] | |
| | | *Megadyptes antipodes* [17] | |
| | Pelecaniformes | *Phalacrocorax atriceps* [30] | |
| | Charadriiformes | *Larus delawarensis* [37] | *Catharacta skua* [36] |
| | | *L. californicus* [40] | |
| | | *Sterna striata* [63] | |
| | | *L. occidentalis* [42, 43] | |
| | | *L. occidentalis* [43] | |
| | | *L. argentatus* [51] | |
| | | *L. novaehollandiae* [53] | |
| | | *Rissa tridactyla* [59] | |
| | | *R. tridactyla* [60, 63] | |
| | | *Sterna hirundo* [64] | |
| | | *(S. paradisea)* [68] | |
| | | *Cepphus grylle* [83] | |
| Egg size | Sphenisciformes | *Megadyptes antipodes* [17] | |
| | | *Pygoscelis papua* [6] | |
| | | *P. papua* [6] | |
| | Procellariiformes | *(Diomedea exulans)* [20] | |
| | | *Puffinus puffinus* [27] | |
| | Pelecaniformes | *Sula bassana* [28] | *Phalacrocorax atriceps* [30] |

**Table 2** (Continued). Evidence of effects of parental age/experience on fecundity/breeding success.

| Variable | Family | Improvements | No improvements |
|---|---|---|---|
| Egg size | Charadriiformes | *Larus argentatus* [48] | |
| | | *L. novaehollandiae* [54] | |
| | | *Rissa tridactyla* [61] | |
| | | *Sterna striata* [63] | |
| | | *(S. paradisea)* [68] | |
| | | *Alca torda* [82] | |
| Hatching success | Sphenisciformes | *Megadyptes antipodes* [17] | |
| | | *Pygoscelis papua* [6] | |
| | Pelecaniformes | *Sula bassana* [28] | |
| | | *Phalacrocorax atriceps* [30] | |
| | Charadriiformes | *Catharacta skua* [36] | *Larus novaehollandiae* [53] |
| | | *Larus occidentalis* [42, 43] | |
| | | *L. occidentalis* [43] | |
| | | *L. californicus* [40] | |
| | | *L. delawarensis* [37] | |
| | | *Rissa tridactyla* [61] | |
| Chick growth | Charadriiformes | *Rissa tridactyla* [62] | |
| Fledging size | Sphenisciformes | *Pygoscelis adeliae* [9] | *Pygoscelis adeliae* [9] |
| Fledging success | Sphenisciformes | *Megadyptes antipodes* [17] | *Pygoscelis adeliae* [9] |
| | | *P. papua* [6] | |
| | Procellariiformes | *Diomedea immutabilis* [19] | |
| | Pelecaniformes | *Phalacrocorax atriceps* [30] | |
| | Charadriiformes | *Larus occidentalis* (m.)[42] | *Larus occidentalis* (f.)[43] |
| | | *L. californicus* [47] | *L. novaehollandiae* [62] |
| | | *Rissa tridactyla* [61] | |
| Breeding success | Procellariiformes | *(Diomedea exulans)* [20] | |
| | | *(Diomedea exulans)* [20] | |
| | | *Fulmarus glacialis* [21] | |
| | | *Puffinus tenuirostris* [24] | |
| | | *P. tenuirostris* [24] | |
| | Pelecaniformes | | *Phalacrocorax aristotelis* [29] |
| | Charadriiformes | *Catharacta skua* [36] | |
| | | *Larus argentatus* [51] | |
| | | *Rissa tridactyla* [60] | |
| | | *R. tridactyla* [60] | |
| | | *Sterna. hirundo* [64] | |
| | | *S. paradisea* [68] | |
| | | *Alca torda* [82] | |
| | | *Cepphus grylle* [83] | |
| Recruitment | Charadriiformes | *Larus novaehollandiae* [53] | |

**Table 3.** Evidence of individual consistency in breeding time.

| | Individual consistency | No individual consistency |
|---|---|---|
| Sphenisciformes | *Megadyptes antipodes* [17] | *Pygoscelis papua* [6] |
| | *Pygoscelis antarctica* [13] | *P. adeliae* [11] |
| | *P. adeliae* [10] | |
| | *Eudyptes chrysolophus* [15] | |
| Procellariiformes | *Diomedea exulans* [20] | |
| | *Fulmarus glacialis* [21] | |
| | *Puffinus puffinus* [27] | |
| | *P. tenuirostris* [89] | |
| Pelecaniformes | *Sula bassana* [28] | |
| | *Phalacrocorax atriceps* [30] | |
| Charadriiformes | *Larus argentatus* [48] | |
| | *L. novaehollandiae* [55] | |
| | *Rissa tridactyla* [60] | |
| | *Uria aalge* [77] | |

the most successful. Thus, the prediction would be that most young are in the nest after, rather tan during, the food peak (Drent & Daan, 1980). This, in turn, would mean that food availability for nestlings would decline throughout the breeding season, which would explain the seasonal declines in breeding success observed. Food availability for seabirds is difficult to measure, but the few attempts indicate that timing of the nestling period does not always coincide with peak food availability (Drent & Daan, 1980; Safina & Burger, 1988; but see Vermeer, 1981). This raises the possibility that food supplies are really declining throughout the chick-raising phases of many seabirds. Few studies have to my knowledge clearly related declines in breeding success to deterioration in food supply (e.g. Lemmetyinen, 1973). In some cases, the evidence for food restrictions invoked is indirect. Thus, as the hatching and fledging success of replacement eggs is similar to that of first eggs laid at the same date in some studies (Feare, 1976; Gaston & Nettleship, 1981), it is argued that the decline in breeding success for late eggs is probably due to environmental deterioration. The opposite happens in other studies (Lloyd, 1979; Mills, 1979), in which case the reason for the decline cannot be attributed to environmental conditions. However, in the first case, a date-dependent reluctance to invest in reproduction can also be invoked (see below). In some studies, it is the breeding date relative to neighbours, and not as absolute date, which affects breeding success (Wanless & Harris, 1988). This also argues against a decline in food availability being involved in seasonal declines in performance.

## Evidence of seasonal changes in predation risk

Birkhead (1977) showed that breeding density and breeding synchrony within groups markedly affected the reproductive success of Guillemots due to the difficulties of predators in approaching dense concentrations of nests and the greater risk of predation of nests out of phase with the rest. This effect of breeding synchrony within groups of neighbouring nests may be due not only to joint nest defense by neighbours (Birkhead, 1977), but also to the dilution of predation risk when all nests are in the vulnerable phase at the same time (Daan & Tinbergen, 1979; Nisbet & Welton, 1984). This effect presupposes that the number of predators remains constant throughout the season. The strongest evidence in favour of the predation hypothesis derives from studies showing that relative breeding date in groups and not absolute breeding date is important for reproductive success (Patterson, 1965; Parsons, 1975; Birkhead, 1977; Wanless & Harris, 1988; Hatchwell, 1991). This would explain the synchronization of breeding within groups of neighbouring nests (e.g. Seddon et al., 1991). The evidence of a seasonal peak in breeding success (Table 1), with both early and late nests being less successful, could also be cited in favour of the predation hypothesis (dilution effect). However, the possibility that food availability experiences a similar peak cannot be disclaimed without experiments.

## Reproductive restraint by late breeders

Curio (1983) suggested that young birds could be restraining their effort in order to improve their chances of reproducing in the future, i.e. they were being prudent (Drent & Daan, 1980). He proposed that idea as an alternative based on life-history theory to the frequent assumption that young individuals were constrained in their ability to find food (Nelson, 1989), and had therefore an impaired reproductive capacity compared to older individuals. A similar argument can be made for late breeders based on two deletereous consequences of delayed breeding: 1) the frequently observed seasonal decline in the reproductive value of young, and 2) the negative consequences of moult-breeding overlap and the time restrictions imposed by seasonality in temperate and polar areas (Moreno et al., 1997). According to this idea, there is a seasonal decline in the disposition to invest in reproduction in long-lived birds such as most seabirds due to a seasonal change in the trade-off between the value of present and future reproduction (Figure 1). The waning of parental attention near the end of the season or a reluctance of parents to feed were earlier invoked by Nelson (1966) and Parsons et al. (1976) as possible explanations for seasonal declines in reproductive performance, but, to my knowledge, no study had envisaged reproductive restraint of late breeders as a general explanation for these trends.

Daan et al. (1988) reviewed the evidence of seasonal declines in offspring reproductive value, and found them to be a general phenomenon in single-brooded species. However, they referred both to offspring survival during the dependence period in the nest and to chances of survival after fledging. However, chick survival in the nest cannot be invoked both as a cause and as a consequence of reduced parental investment (Daan et al., 1988). Only survival after the dependence period can be considered as a factor modulating parental investment, as it does not directly depend on reproductive investment by parents itself. If late-hatched chicks survive poorly, independently of what the parents do, their value decreases relative to that of future offspring. Data on postfledging survival and recruitment probability of young raised early or late in the season still show a negative trend with date (Daan et al., 1988; Table 1), supporting the contention of the restraint model that the value of present reproduction declines throughout the season (Figure 1). Thus, the decreasing value of present young could prompt parents to reduce investment, so detracting even more from that value.

One of the possible costs of delayed breeding may be an impaired postnuptial moult process due to a greater moult-reproduction overlap (Nilsson & Svensson, 1996; Svensson & Nilsson, 1997). This may be especially important at high latitudes and/or for migratory species, for which there is only a short period after reproduction in which to moult (Viñuela et al., 1996; Moreno et al., 1997). A plumage of lower quality or a delayed moult as consequences of moult-breeding overlap may jeopardise survival during the impending winter or delay premigratory fattening and migration with possible negative repercussions on survival (Moreno, 1993: Nilsson & Svensson, 1996). A way of avoiding these risks is to reduce investment in reproduction, given the low reproductive value of offspring. Thus, both the need to avoid risks for survival and the low offspring value may restrain the reproductive investment of late breeders independently of their age. However, age may affect the shift in the life-history trade-off as young birds may be less willing to sacrifice future reproduction than old breeders (Curio, 1983). For very old breeders, so-called 'terminal investment' processes (Pärt et al., 1992) may impede reproductive restraint. Seabirds as long-lived species should be especially sensitive to changes in their future reproductive potential (Saether et al., 1993).

## Experimental evidence

While descriptive studies can discard some hypotheses in some cases (see above), the best way to test the predictions derived from the different hypotheses is by performing experiments (Table 4). The parental quality hypothesis can be tested by subjecting individuals with the same original laying date to breeding conditions at different times (see below). The predation hypothesis can be preferably tested by excluding predators from certain colonies or breeding groups. No study of seabirds has to date excluded predation to specifically test the predation hypothesis. The food availability and restraint hypotheses are difficult to separate as both predict a decreasing trend in food transfer to chicks, but in the first case due to unavoidable constraints and in the second to a declining disposition to feed the chicks. If food is supplemented to both early and late-hatched chicks, the absence of differences in growth and survival between early and late supplemented broods may result from food supplements exceding the needs of the chicks. However, a difference between early and late supplemented broods in growth and survival despite food supplementation would argue in favour of the restraint hypothesis, as parents of late-hatched chicks could be improving their own condition at the cost of the well-being of their offspring. Some supplementation studies of seabirds (e.g. Harris, 1978; Bolton, 1995) have not considered date-dependent effects, although Bolton et al. (1993) detected a significant seasonal decline of clutch size in unfed pairs of lesser black-backed gulls *Larus fuscus*, which was absent in supplemented pairs. This argues in favour of food supply limiting the clutch size laid by late pairs.

Only 8 experimental tests of hypotheses explaining date-dependent breeding success in seabirds have been conducted to date, all testing the parental quality hypothesis by subjecting individuals to breeding commitments at different times. Nisbet & Drury (1972) forced pairs of herring gulls *Larus argentatus* in certain colonies to relay by destroying their clutches. They were able to delay breeding for these pairs with 3-4 weeks. They showed a 10-20% reduction in the survival rate during the first winter of chicks from delayed broods. However, recovery rates were very low making a comparison between delayed and simultaneous control pairs difficult. Parsons (1975) performed a similar experiment also with herring gulls by removing eggs in certain areas, thus forcing pairs to relay. Experimental birds laid similar clutches to simultaneous control pairs, so clutch size was directly affected by date, not by parental quality. However, he obtained that at a time when hatching success of control clutches was decreasing, repeat clutches were being more successful. Also, the seasonal decline in breeding success was delayed in experimental compared with control areas.

**Table 4**. Experimental methods to determine the causes of seasonal declines in breeding success

**Food availability:** Supplementary food offered at certain nests with different phenologies

Prediction: Late experimental nests will improve their success more with respect to simultaneous controls than early experimental nests with respect to their own controls

**Predation:** Predation will be excluded at certain nests with different phenologies

Prediction: Late experimental nests will improve their success more with respect to simultaneous controls than early experimental nests with respect to their own controls

**Parental quality:** Individuals with the same laying date (and therefore of the same quality) will be forced to breed on different dates

Prediction: Individuals with the same laying date will have a similar success independently of actual breeding date

**Reproductive restraint:** Breeding date of late breeders will be advanced and of early breeders delayed

Prediction: Advanced late breeders will invest as much as their simultaneous controls and more than late controls, while delayed early breeders will invest as much as their simultaneous controls and less than early controls

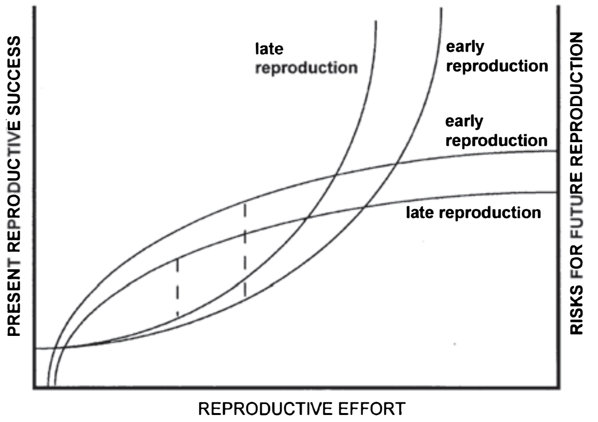

**Figure 1**. The 'reproductive restraint' model as based on the differences between early and late breeders in the fitness benefits and costs derived from variation in parental effort. The function representing the benefits of present reproduction is lower for late breeders than for early breeders due to the reduction in the reproductive value of offspring with date, while the function representing the risks for future reproduction is higher for late breeders due to their higher probability of molt-breeding overlap. The optimal reproductive effort is obtained when the difference between benefits and costs is maximal, and is higher for early breeders. The form of the functions is based on the reasonable assumptions that the benefits in terms of offspring fitness derived from parental effort reach an asymptote, and that the costs increase exponentially due to cummulative physiological effects of exertion.

Both results support the parental quality hypothesis. Feare (1976) destroyed clutches of sooty terns *Sterna fuscata* in certain areas, and observed that the success of replacement clutches declined seasonally. However, he did not compare experimental broods with simultaneous controls, a necessary condition to test the parental quality hypothesis. Hedgren & Linnman (1979) used the same approach with guillemots *Uria aalge*, and showed that experimentally delayed broods grew less well than controls, but again, given the long delay provoked (3 weeks), could not compare experimental broods with simultaneous controls. Another egg removal study on guillemots was performed by Hatchwell (1991), who was able to compare the productivity of experimental broods in a certain part of the colony where all pairs were forced to renest with that of simultaneous controls. He obtained a higher success in experimental broods than in simultaneous control broods, a result which he attributed to the effect of breeding synchrony among neighbours being more important than date. According to this interpretation, late broods are less successful due to their lack of synchrony with the breeding peak in the colony (predation hypothesis). If you remove all eggs from a certain part of the colony, forcing all individuals in that group to relay, you are affecting date but not within-group synchrony. An alternative interpretation is that experimental pairs have a higher parental quality than late controls. However, Hatchwell (1991) disclaimed this possibility by comparing experimental broods with simultaneous natural replacement broods. As experimental nests were more productive, he argued that only the higher within-group synchrony of experimental nests could determine this difference. This is arguable since natural replacement broods are not a random sample of the population, but probably the result of failures determined partly by parental quality. Thus, the higher parental quality of experimental pairs could also be involved in explaining the difference. He convincingly disclaimed the food availability hypothesis, by showing that feeding rates were similar or even higher at delayed nests than at control nests for the same age of the chicks. His results are the strongest experimental evidence in favour of the parental quality hypothesis, although he interpreted them in the light of the predation hypothesis. Another evidence of the importance of parental quality is the natural experiment effected by a gale on parts of a large colony of shags *Phalacrocorax aristotelis* (Aebischer, 1993), where many pairs whose nests were destroyed or damaged relayed. Irrespective of breeding experience, delayed early breeders produced more chicks than late breeders nesting at the same time, showing that the seasonal decline in shag productivity could be due to the poorer parental quality of late breeders.

However, forcing birds to relay has the problem of creating an unwanted difference between treatments, namely the additional cost of producing a new clutch for the experimental females. This cost can be considered slight depending on the species, although this is arguable (Carey, 1996). However, it may represent a problem when delayed birds suffer reductions in breeding success. Still, the main problem of these experiments is that experimental pairs were on different areas than control pairs, as egg removals performed in whole areas, without local interspersion of treatments (see Hurlbert, 1984 for the need of interspersion). This invalidates the statistical analyses performed, as the proper comparison is using areas and not nests as data points (Hurlbert, 1984; Kamil, 1988). Areas may differ in certain respects, introducing confounding variables in the analysis (Kamil, 1988). Only in the case of Hedgren & Linnman (1979) is this uncertain, as they did not fully report on the local assignment of experimental nests.

Two experimental studies have avoided these two possible sources of error by exchanging eggs or chicks between nests without forcing parents to relay and by interspersing treatments locally and homogeneously. Hunt & Hunt (1976) exchanged eggs between nests in the Glaucous-winged Gull *Larus glaucescens*, so chicks hatched at the same time were reared by pairs having laid at different times (early, middle or late pars of the laying season). Independently of the laying date of the pairs raising them, chicks hatched in the same period survived to the same degree. This would disqualify parental quality as a possible explanation for the seasonal trends observed. However, the problem with the survival data is that three are no clear indications of a seasonal decline in the year of the experiment. Another result was that growth rates were more clearly associated with hatching date than with laying date. As parental quality is probably involved in laying date determination, the authors concluded that date-dependent food availability was restricting breeding performance late in the season. They disclaimed the possibility that the results could be affected by differing incubation durations for different pairs (e.g. early pairs receiving eggs to hatch in the middle period had prolonged incubation periods), by stating that the behaviour of parents was normal and that chick survival was unaffected by treatment. However, the similarity in chick survival could itself be partly an artifact of the shortening or prolongation of the incubation period.

The other experiment exchanged chicks between pairs having laid one week apart in the Chinstrap Penguin *Pygoscelis antarctica* (Moreno et al., 1997). This was done by assigning treatments randomly in the same colony, by using only nests hatching during the peak of hatching in the population and by using a short interval to delay or advance the breeding schedule of pairs having laid simultaneously. This ensured the required inter-spersion of treatments (Hurlbert, 1984), the avoidance of extreme phenotypes in the tails of the distribution, and also reduced the plausibility of effects of changes in food availability (one week is too short a period in the two-month chick-raising period to allow large changes in food supply). This experimental design assumes that parents can respond flexibly to changes in chick demand as effected by chick exchanges. This flexible response to chick nutritional needs has been observed in other seabirds (Harris, 1983; Johnsen et al., 1994; Wernham & Bryant, 1998). By comparing the growth and fledging size of chicks and the duration of their guarding periods (chicks left unguarded at young ages suffer fitness losses), this study was able to show clearly that something related to date itself and not to parental quality was behind the seasonal trends observed (Viñuela et al., 1996). While hatching date of the chicks themselves explained a large part of the variation in growth and guarding period, the breeding date of the parents raising the chicks had no significant effect (Moreno et al., 1997). One possible flaw in the study was that the first week of chick-raising was omitted for certain individuals (late breeders with early chicks) and repeated for others (early breeders with late chicks). This unavoidable problem derived from the experimental design is probably not serious, as constraints on parental performance seem to operate after the first two weeks of the chicks, given that there were no detectable effects of experimental treatments at 17 days of age of the chicks. This study offers the clearest evidence to date that parental quality may not be involved in seasonal trends in breeding success. As seasonal trends in food availability seem implausible and all pairs raised chicks during the peak period in the colony, when decreases in predation dilution are probably unimportant, the restraint hypothesis was advanced as the most strongly supported. The basic tenets of the restraint hypothesis apply in full force to this species as the breeding season in Antarctica is short, and moult in penguins (Adams & Brown, 1990) is both costly and time-consuming.

## Conclusions

There is ample evidence of seasonal declines in reproductive performance in seabirds. Age and/or breeding experience may be involved in these trends, as performance improves with age in many species. There is some evidence from descriptive studies of the importance of seasonal changes of food availability and of the benefits derived from predation avoidance through synchronization of breeding activities among neighbours. However, there is scant experimental evidence in favour of any hypothesis. Several experimental tests performed to date have incurred in serious errors of design and statistical analysis and their results are therefore flawed. The two field experiments which have avoided these pitfalls, have not supported the parental quality hypothesis. In the clearest experiment to date, the reproductive restraint hypothesis comes out as the most plausible. One has to consider that several selective factors may act jointly in certain cases, and that the different hypotheses are not mutally exclusive, which complicates experimental tests. There is an urgent need of further well designed field experiments excluding different selective factors like predation or food availability and randomly assigning breeding times to individuals without forcing them to relay.

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## Appendix: Sources of data

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