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# A model for the evolution of crèching behaviour in gulls.

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*Running headline* : Crèching behaviour in Gulls

## ABSTRACT

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Crèche is the aggregation of chicks outside the nesting territories in which chicks continue to be fed only by their own parents. Several adaptive functions of crèching have been proposed, the most frequent one being a reduction in predator pressure. Using an evolutionary stable strategy approach based on the computation of individuals' fecundity, we examined which regime of aerial and terrestrial predation is likely to favour the evolution and stability of the crèching strategy in gulls. Our results confirm the hypothesis that habitat instability associated with high levels of terrestrial predation favours the evolution and maintenance of the crèching behaviour. Moreover, our results suggest that a low aggressiveness against predators by offspring may be a pre-adaptation to the crèching strategy. In contrast, the high synchronisation often observed in crèching species does not favour the evolution of a crèching behaviour and is thus probably under selection pressures different from those modelled here.

## INTRODUCTION

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Coloniality, defined as aggregation on a breeding site that is dissociated from foraging sites (Wittenberger and Hunt, 1985; Siegel-Causey and Kharitonov, 1991) is a complex reproductive strategy that brings many individuals simultaneously to a relatively small breeding site. Although the evolution of coloniality has been intensively studied, the factors responsible for its evolution and maintenance are still subject of much discussion (see Danchin and Wagner, 1997 for a review). Coloniality is usually associated with several life history traits such as collective anti-predator behaviour (Wittenberger and Hunt, 1985; Siegel-Causey and Kharitonov, 1991), synchronisation of the breeding activities (Gochfeld 1980) and a high frequency of aggressive interactions (Tinbergen 1956, 1959).

The formation of large groups of chicks in or near the colony site is one of the most intriguing traits associated with coloniality. These groups are referred to as a crèche, the crèching strategy being defined as an aggregation of chicks outside the nesting territories in which the chicks continue to be fed only by their own parents. Crèching has been reported in seven of the 14 colonial waterbirds families (A. Besnard and C. Tourenq, unpubl. results). However, the proportion of crèching species within these families varies greatly, ranging from a single crèching species (e.g., the banded stilt, *Cladorhynchus leucocephalus*) in the Recurvirostridae (del Hoyo et al., 1996) to all members of the family (e.g. flamingos) in the Phoenicopteridae (del Hoyo et al., 1996).

Several functions of the crèching behaviour have been proposed, the most frequently mentioned being the reduction of predation (Pettingill, 1960; Schaller, 1964; Beer, 1966; Buckley and Buckley, 1972; Spurr, 1975; Evans, 1984; Carter and Hobson,

1 1988). In a previous study of the crèching behaviour in gulls (Laridae, Larini following  
2 Sibley and Ahlquist 1990), we demonstrated that crèching species all occupy unstable  
3 habitats such as lagoon or river islets (Besnard et al. submitted). Such unstable habitats  
4 are characterised by a high probability that colony sites become unsuitable following a  
5 drying of the lagoon or a flooding of the breeding site. This instability of the habitat  
6 could exert an important selective pressure on crèching behaviour and thus its evolution.

7         In non-crèching larids, the chicks usually remain on the nesting territories where  
8 they are fed and protected against conspecifics by their parents until they fledge (del  
9 Hoyo et al. 1996). In crèching species, the chicks leave the nesting territories only few  
10 days after hatching and roam in the colony for a short period before they congregate in a  
11 crèche at the periphery of the colony and possibly definitively leave the colony site  
12 (Beer, 1966; Isenmann, 1976; del Hoyo et al., 1996). To explain this behaviour we  
13 propose that crèching may allow for chicks to leave the colony site when it becomes  
14 unsuitable for rearing chicks (flooded or accessible to terrestrial predators following the  
15 drying of the water surrounding the colony) while maintaining the colony structure and  
16 its ability to defend against predation (Besnard et al. submitted).

17         In order to test this hypothesis, in this paper we study the effect of a high  
18 predation rate associated with a high probability for the colony site to become  
19 accessible to terrestrial predation over the course of a single breeding season. An  
20 Evolutionary Stable Strategy (ESS) approach is used. Individual fecundity was  
21 computed using a reproductive output model based on cumulative predation risks over  
22 time. We thus examined which characteristics of predation favour the evolution and the  
23 maintenance of the crèching strategy.



$$n(t) = mN[F(t) - F(t - t_b)] \quad (3)$$

Assuming that eggs and chicks have the same probability of being taken by a predator and let  $k$  be the instantaneous rate of predator attacks, the probability  $p$  for an egg or a chick to be preyed between time  $t$  and  $t + dt$  is given by:

$$p = \frac{k}{n(t)} dt \quad (4)$$

which reflects the dilution effect of the predation effort over  $n(t)$  items present at time  $t$  (cf. selfish herd effect Hamilton, 1971).

Our model considers two kinds of predation: aerial and terrestrial. The aerial predation rate,  $k_a$ , is assumed to be constant over the course of the breeding season. Gulls, usually breeding on sites surrounded by water, are protected against terrestrial predators. Terrestrial predation can only occur after the drying of colony periphery. The occurrence of such a drying during the breeding season is more or less probable according to the habitat characteristics occupied by a species (from highly probable in temporary marsh or lagoon to highly improbable in permanent marsh or lake). Let  $a$  be the date at which the colony becomes accessible to terrestrial predation. The terrestrial predation rate, denoted  $k_g$ , is null before  $a$  and constant after  $a$  until the end of the breeding season (*Model 1*).

Gulls often actively defend the colony site against predators using "mobbing" behaviour (Patterson, 1965; Kruuk, 1967; del Hoyo et al., 1996) which consists in collective flights directed towards the predator. While mobbing has been demonstrated to be an effective deterrent against aerial predators (reviewed in Wittenberger and Hunt,

1 1985), its impact on terrestrial predator is often described as null (Veen 1977,  
2 Wittenberger and Hunt 1985). In order to take the mobbing behaviour into account,  
3  $k_a$  is assumed to be a decreasing function of the number of breeding pairs still present at  
4 time  $t$  on the colony site (*Model 2*).

5 In order to retain the simplicity of the models, mortality is assumed not to affect  
6 the number of eggs or chicks present on the breeding sites. We do not expected  
7 qualitative results of the models to be changed by this assumption.

8

### 9 *Crèching versus Non-crèching strategy*

10 Chicks of non-crèching species stay on the colony site until they fledge  
11 (Tinbergen, 1956; del Hoyo et al., 1996) and are preyed on by aerial and terrestrial  
12 predators during the entire breeding season. In contrast, chicks of crèching species  
13 usually leave the site when it becomes accessible to terrestrial predators and move to a  
14 "safe" site (Beer, 1966; Isenmann, 1976; Zubakin and Flint, 1980; Besnard et al.,  
15 submitted). We thus considered that the chicks of the crèching species remain at their  
16 birth site as long as it remains protected against terrestrial predators. Contrary to the  
17 non-crèching chicks, they move to a site protected against the terrestrial predators in the  
18 immediate proximity of their birth site as soon as it becomes accessible. After having  
19 left their birth site, chicks escape terrestrial predators but remain exposed to aerial  
20 predators.

21 We examined the ecological conditions under which the Non-Crèching Strategy  
22 (hereafter NCS) or the Crèching Strategy (CS) are ESS. If adult survival is equal for  
23 two strategies A and B, strategy A is non-invasible by the strategy B when, in a  
24 population fixed for A, the fecundity of an A individual is greater than that of a B

1 individual (Maynard Smith 1982). If only two strategies, A and B, are possible, the  
2 study of invasibility of A is equivalent to the study of the evolutionary stability of A.  
3 Strategy A is ESS if, in a population fixed for the strategy A, the ratio of the fecundity  
4 of an individual exhibiting strategy A to that of an individual with strategy B is greater  
5 than one.

6         The number of surviving offspring at fledging, later called fecundity, for a pair  
7 laying at date  $l$  according to the biological rules stated above was derived. The four  
8 equations of fecundity were computed: (a) a NCS individual in a NCS population, (b) a  
9 CS individual in a NCS population, (c) a NCS individual in a CS population and (d) a  
10 CS individual in a CS population.

11         The fecundity of the four classes of individuals were derived for two cases: one  
12 with  $k_a$  constant (no active defence against predators: *Model 1*) and another one with  
13  $k_a$  a decreasing function of the breeding pairs on the colony site (active defence against  
14 predators: *Model 2*). When there is no active defence against predators, the non-  
15 crèching and crèching chicks suffer from the same aerial predation while only the non-  
16 crèching chicks suffer from terrestrial predation. Under these circumstances, CS always  
17 outperforms NCS. The predictions from *Model 1* are that crèching is an ESS as soon as  
18 terrestrial predation is not null. However, we chose to present the computation of this  
19 first model in order to progressively detail the different steps in our modelling approach.  
20 When adults present an active defence against predators, the pay-off of each strategy is  
21 affected by the number of chicks in the crèche or in the colony at all dates. Under these  
22 circumstances, the modelling becomes crucial. Fecundity for both models are  
23 respectively summarised in Tables 2 and 3 and more details are given in appendices A  
24 and B.

1 Table 1 approximately here

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3  
4 RESULTS

5  
6 *Model 1: without active defence*

7 Table 2 approximately here

8  
9 NCS is evolutionarily stable if the following inequality holds (Table 1 left part):

10 
$$\int_a^{l+tb} -\frac{k_g}{n(t)} dt > 0 \quad (5)$$

11  
12 Inequality (5) has obviously no solution in our ecological situations because  $k_g$  is  
13 positive or zero and  $n(t)$  is strictly positive whatever  $t$ . Hence, NCS is always invisable  
14 by CS.

15  
16 CS is evolutionarily stable if the following inequality holds (Table 2 right part):

17 
$$\int_a^{l+tb} \frac{k_g}{\omega(t)} dt > 0 \quad (6)$$

18  
19 Inequality (6) is satisfied in several ecological situations. However CS is invisable by  
20 NCS if the number of egg laid in the colony was infinite ( $\omega(t)$  infinite) but this situation  
21 is biologically uninteresting. CS is invisable by NCS if the rate of terrestrial attacks is

1 zero ( $k_g = 0$ ) or when the site becomes accessible to the terrestrial predators only when  
 2 or after the chick have fledged ( $a \geq l + t_b$ ).

3 To sum up, CS is evolutionarily stable if the actual terrestrial predation on the  
 4 chicks is not zero. On the contrary, NCS is always invasible by CS. As a consequence,  
 5 the CS is convergent as soon as the realised terrestrial predation on the chicks is not  
 6 zero. In contrast, if terrestrial predation is zero or if the colony site never dries up, none  
 7 of the strategies are evolutionarily stable. The evolutionary stability of the strategy does  
 8 not depend on the rate of aerial predation, the length of incubation or the laying date  
 9 distribution.

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11 *Model 2: with active defence*

12

Table 3 approximately here
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13

14 NCS is evolutionarily stable if the following inequality is fulfilled (table 3 left part).

15 
$$\int_a^{l+t_b} \frac{k_g + [k_a(N) - k_a(1)]}{n(t)} dt < 0 \quad (7a)$$

16 and relation (7a) holds if

17 
$$k_g + [k_a(N) - k_a(1)] < 0 \quad (7b)$$

18 In order to qualitatively explore conditions in which NCS is an ESS,  $k_a$  is assumed to

19 be N-dependent with the form:

20 
$$k_a(N) = k_{\max} \left[ \frac{\alpha}{N} + (1 - \alpha) \right] \quad (8)$$

21

1 where  $\alpha$  is the curvature of the function describing the protection efficiency with the  
 2 number of adult defending the site and  $k_{\max}$  is the avian predation rate when only one  
 3 pair breeds on the site. Hence, the overall predation rate decreased when  $\alpha$  increased.  
 4 Under these assumptions, the inequality (8) reduces to :

$$5 \quad k_g < \alpha k_{\max} \left( \frac{1}{N-1} \right) \quad (9)$$

6 Figure 1 shows the maximum rate of terrestrial predation  $k_g$  permitting the  
 7 evolutionary stability of NCS for different levels of  $\alpha$  and  $k_{\max}$ . Qualitatively, an  
 8 increase in active defence ( $\alpha$ ) or an increase in maximum rate of aerial predation ( $k_{\max}$ )  
 9 favours the evolutionary stability of NCS since it requires an increase in the rate of  
 10 terrestrial predation for CS to be invasive.

11 Fig. 1 approximately here

12  
 13 The CS is evolutionarily stable if the following inequality is satisfied (Table 3 right  
 14 part).

$$15 \quad - \int_a^{l+t_b} \frac{k_a [F(t-t_i) - F(t-t_b)] - k_a [F(t) - F(t-t_i)]}{n(t)} dt + \int_a^{l+t_b} \frac{k_g}{w(t)} dt > 0 \quad (10)$$

16  
 17  
 18 To qualitatively study the evolutionary stability of CS, we suppose the cumulative  
 19 distribution of the laying dates to be of the exponential form:

$$20 \quad f(t) = 1 - \beta \exp^{-\theta t} \quad (11)$$

21

1 where  $\theta$  describes the synchronisation of the laying. The active defence and its  
 2 efficiency are modelled as above.

3 The CS is thus evolutionarily stable if the following inequality is satisfied.

$$4 \quad \frac{k_g (\exp^{\alpha\theta} - \exp^{(t+t_b)\alpha})}{\theta N m \beta (\exp^{\theta t_i} - 1)} - \frac{k_{\max} \alpha (2 \exp^{\theta t_i} - \exp^{\theta t_b} - 1) (\exp^{(2\theta(t+t_b))} - \exp^{2\alpha\theta})}{2\theta N^2 m^2 \beta^2 (\exp^{\theta t_b} - 1) (\exp^{\theta t_i} - \exp^{\theta t_b}) (\exp^{\theta t_i} - 1)} > 0 \quad (12)$$

6  
 7 Figure 2 shows in which conditions CS is evolutionary stable for some usual population  
 8 parameters of larids. The main results are that the stability of CS depends on the relative  
 9 levels of terrestrial ( $k_g$ ) and aerial predation ( $k_{\max} \alpha$ ) and in a more complex way on the  
 10 synchronisation of laying dates ( $\theta$ ). In the range of biologically realistic parameters, CS  
 11 is frequently evolutionary stable. CS is invasible by NCS only if the population is  
 12 submitted to a high rate of realised aerial predation relatively to the terrestrial one and  
 13 shows at the same time a highly synchronised laying (figure 2).

14 Fig. 2 approximately here

15  
 16 We only developed here the equations of fecundity computed for individuals  
 17 whose chicks hatched before the site became accessible to the terrestrial predation.  
 18 When the chicks hatch after the site became accessible, they progressively reach the  
 19 "safe" site. Thus until they hatch, the late laid eggs experience exactly the same  
 20 predation as the non-crèching eggs. Thus, if the inequality satisfying the evolutionary  
 21 stability are slightly different, the qualitative results are of the same form and our  
 22 conclusions hold for the two different situations.

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## DISCUSSION

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Three main conclusions can be derived from our results: first the crèching strategy can simply evolve from a non-crèching strategy if the probability for the site to become accessible to terrestrial predation is high. Second, in a species with no anti-predator behaviour, the crèching strategy always invades and is stable in a large range of ecological situations. Third, when individuals actively defend their chicks against terrestrial predation, crèching and non-crèching strategy may both be ESS but remain invisable depending on the predation rates, the efficiency of the defence against predators and the synchronisation of laying.

In all cases, evolutionary stability is strongly influenced by the relative rates of aerial and terrestrial predation. The non-crèching strategy is favoured and generally the ESS if the aerial predation is high compared to terrestrial predation while crèching strategy is favoured and is the ESS when terrestrial predation is high relative to aerial predation. Since gulls generally occupy sites surrounded by water (del Hoyo et al. 1996), they are protected against the terrestrial predators and crèching strategy cannot evolve from a non-crèching strategy. However, in lagoons, where drying is frequent during the breeding season, terrestrial predation remains possible and is even highly probable over the course of the breeding season. This result confirms our original hypothesis that habitat instability associated with terrestrial predation could exert a strong selective pressure in favour of the crèching behaviour.

It has been shown that crèching species show little aggression against the predators of their eggs and chicks (Beer 1966, Isenmann 1976, Veen 1977, Zubakin 1985). We demonstrated in this paper that when no anti-predator behaviours exists, the

1 crèching strategy eventually converges. When a species has a reduced but not null  
2 aggressiveness against predators, the crèching strategy is no more convergent but is still  
3 invasive and evolutionary stable in many ecological contexts (in particular when  
4 terrestrial predation is not null). A little aggressive species could maintain the non-  
5 crèching strategy only under a very low rate of terrestrial predation. The non-crèching  
6 strategy could thus be maintained while being weakly aggressive only in highly stable  
7 habitats protected against terrestrial predation or species living in habitats where no  
8 terrestrial predation occurs. To our knowledge, this is the first demonstration that weak  
9 aggressiveness observed in crèching species could be a pre-adaptation to this strategy  
10 since it favours its evolution and its stability. Since a little aggressive non-crèching  
11 species is extremely likely to evolve to crèching and unlikely to then evolve back to the  
12 non-crèching strategy, it can explain why no intermediate stage seems to exist between  
13 non-crèching and crèching and why no reversion (evolution from crèching to non-  
14 crèching strategy) seems to have occurred in larids (A. Besnard, unpublished results).

15         Bearing in mind that the evolutionary stability of the non-crèching strategy is not  
16 conditional to the synchronisation of the laying date, we can reject the hypothesis that  
17 the high synchronisation of laying, observed in many crèching species (Beer, 1966;  
18 Isenmann, 1976; Zubakin, 1985; Mierauska and Buzun, 1991; Besnard et al., submitted)  
19 is a pre-adaptation to the crèching strategy. An extreme synchronisation of laying  
20 associated with a high rate of aerial predation favours the invasion of the crèching  
21 strategy and thus exerts a selective pressure against the maintenance of crèching  
22 behaviour. It can thus be suggested that the high synchronisation observed in several  
23 crèching species is a response to a selective pressure other than those studied here. We  
24 modelled the crèching strategy as a massive departure from the colony site when it

1 becomes accessible to terrestrial predation and by a progressive aggregation at the  
2 newly colonised site by late-hatched chicks. In the field, it seems that crèche formation  
3 is punctual and that late breeders who do not join the crèche often abandon their eggs  
4 (J.-D. Lebreton, pers. obs.). Such a constraint against a late laying should exert a strong  
5 selective pressure for the synchronisation of laying.

6 In summary, our results thus lead to three main conclusions concerning the  
7 evolution of the crèching behaviour in Larids. First they confirm our original hypothesis  
8 stipulating that crèching behaviour evolved in unstable habitats associated with a high  
9 terrestrial predation. Second, they demonstrate for the first time that a reduced  
10 aggressiveness against predators is a pre-adaptation to the evolution of crèching  
11 behaviour. Finally, high synchronisation of laying dates does not appear to represent a  
12 pre-adaptation to the evolution of the crèching and actually favours its invasibility in  
13 species actively defending their chicks.

14 The evolution of the crèching strategy under the selective pressure of two  
15 different predation rates (terrestrial and aerial) could have been modelled using simple  
16 models by comparing, for instance, the instantaneous rate of death for crèching or non-  
17 crèching chicks. However, our model allow for one to more easily incorporate  
18 parameters such as the synchronisation of laying and to later build up more complex  
19 behaviour of the crèching species than those examined here without changing the  
20 philosophy of the modelling. Such a flexibility in our way of modelling should favour  
21 its utilisation to examine the evolution of crèching strategy in other bird families  
22 submitted to different selective pressures.

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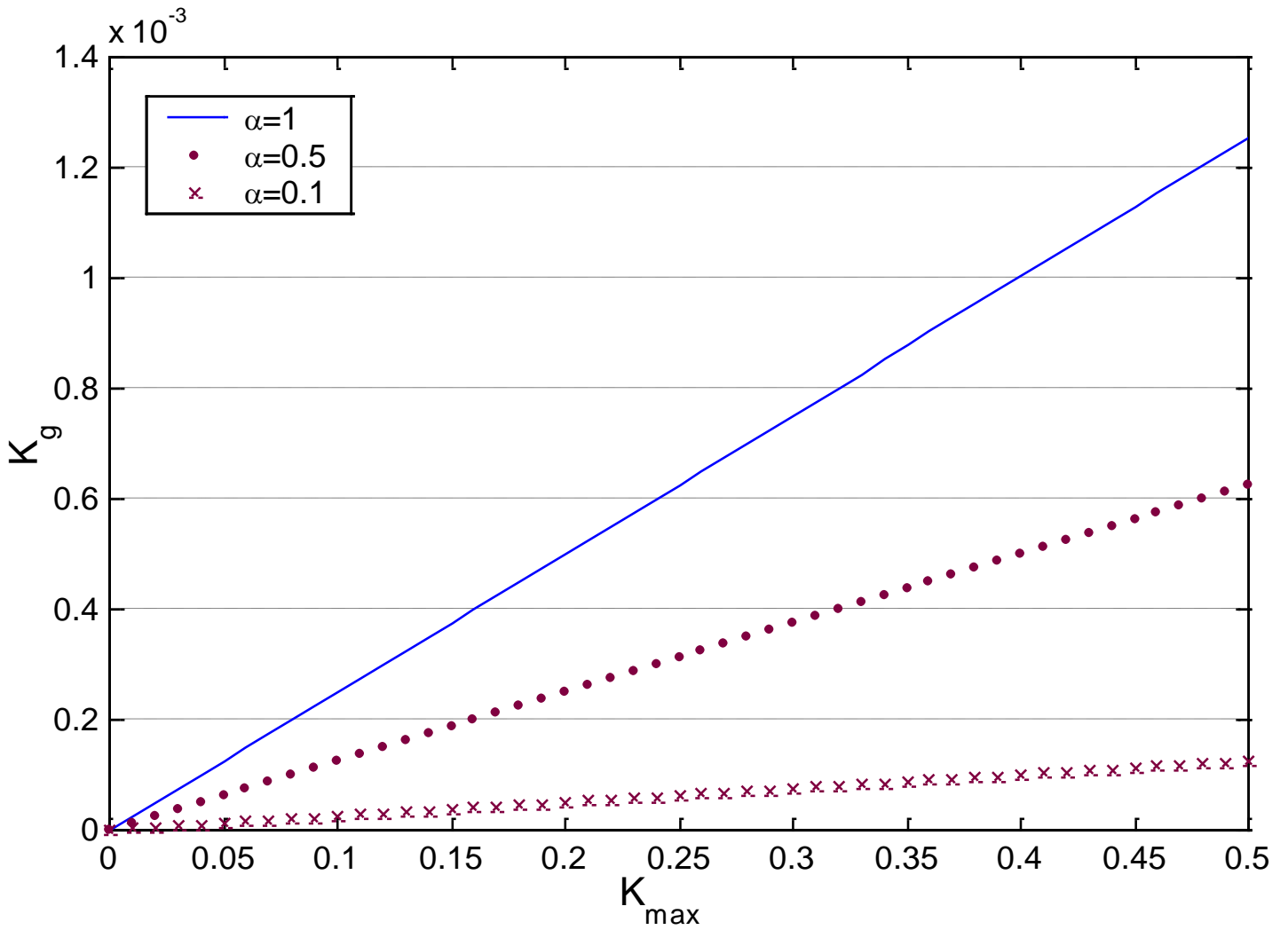
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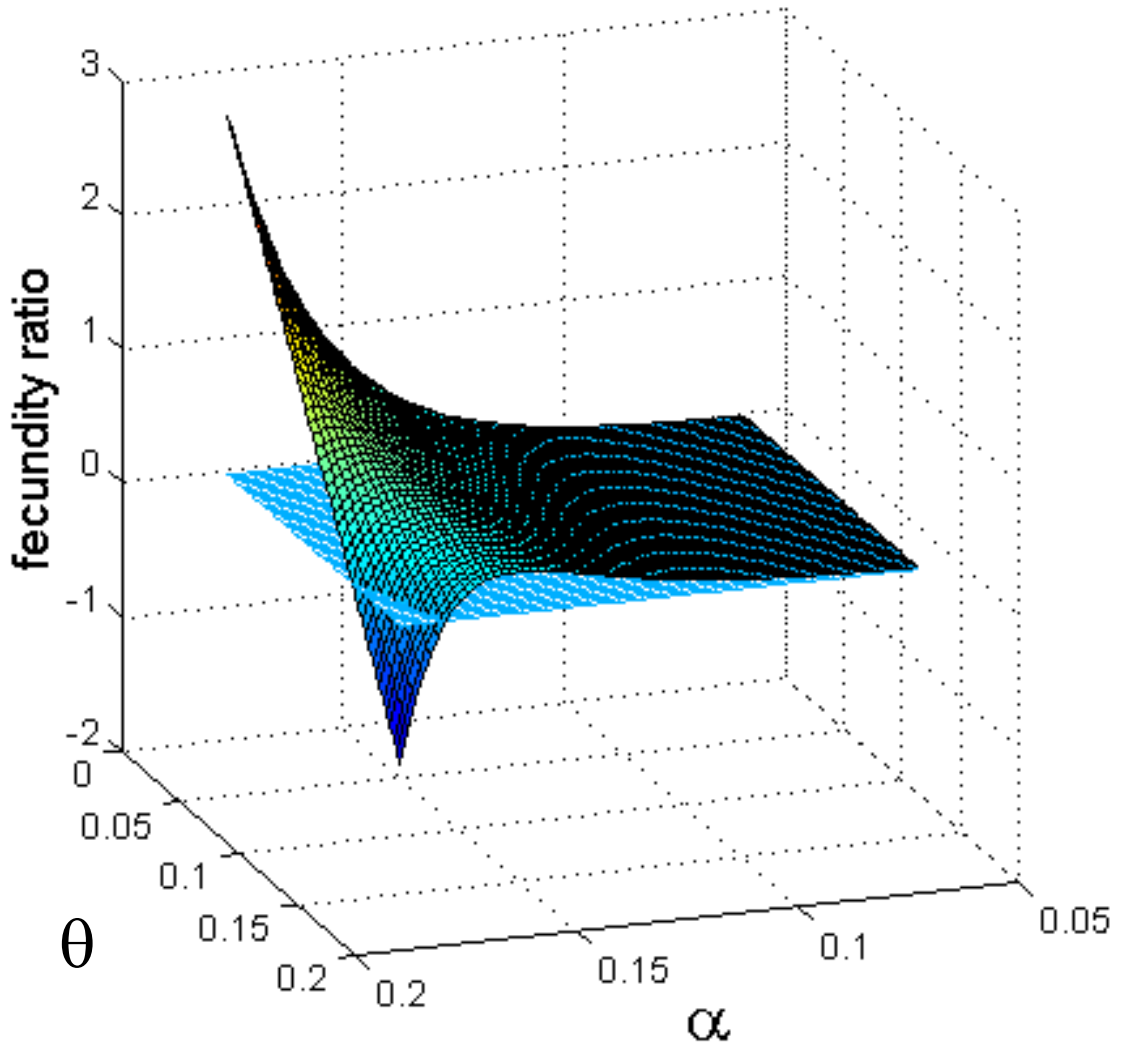
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**Figure 1** : Maximum rate of terrestrial predation  $k_g$  permitting the evolutionary stability of NCS for different levels of  $\alpha$  and  $k_{\max}$ . NCS is evolutionarily stable when  $k_g < \alpha k_{\max} \left( \frac{1}{N-1} \right)$ . An increase in active defence ( $\alpha$ ) or an increase in maximum rate of aerial predation ( $k_{\max}$ ) favours the evolutionary stability of NCS since it requires an increase in the rate of terrestrial predation for CS to be invasive.  $N$  was fixed to 400 pairs.



**Figure 2 :** Conditions in which CS is evolutionarily stable for different levels of synchronisation of laying ( $\theta$ ) and efficiency of the defence against aerial predators ( $\alpha$ ). CS is stable when the surface defined by the fecundity ratio is upper than the horizontal plan. The fecundity ratio is given by eq. (12). Parameters in eq. (12) where fixed in order to be biological realistic for gulls :  $N=400$ ,  $m=2$ ,  $t_i = 25$ ,  $t_b = 30$ ,  $l=32$ ,  $a=43$ ,  $K_g = 0.01$ ,  $K_{\max} = 0.5$ ,  $\beta=1$ .

**Table 1** : Definition of the different parameters used in the ESS modelling approach to model the individual fecundity of crèching or non-crèching birds in population fixed for crèching or non-crèching strategies.

$F(t)$	Cumulative distribution function of laying date at date $t$
$N$	Total number of breeding pairs in the area
$m$	Clutch size
$mNF(t)$	Cumulative number of eggs laid at date $t$
$t_i$	Length of incubation period
$t_r$	Length of the rearing period (from hatching to fledging)
$t_b$	Total time of rearing from laying to fledging, hence $t_b = t_i + t_r$
$\omega(t)$	Number of incubated eggs at date $t$
$\pi(t)$	Number of chicks (i.e. hatched but not yet fledged) at date $t$
$n(t)$	Total number of egg and chicks, i.e. number of items submitted to predation at date $t$
$k_a$	Rate of aerial predation
$k_g$	Rate of ground (terrestrial) predation
$l$	Laying date of an individual
$a$	Date at which the colony site becomes accessible to terrestrial predation

**Table 2** : Fecundity of the two possible strategies in function of the strategy fixed in the population when no active defence against the predators exists; the fecundity ratio gives the condition of ESS.

		<b>Population fixed for the strategy</b>	
		<b>Non-Crèching</b>	<b>Crèching</b>
<b>Rare Strategy</b>	<b>Non-Crèching</b>	$-\int_l^a \frac{k_a}{n(t)} dt - \int_a^{l+t_b} \frac{(k_g + k_a)}{n(t)} dt$	$-\int_l^a \frac{k_a}{n(t)} dt - \int_a^{l+t_b} \left[ \frac{k_a}{n(t)} + \frac{k_g}{\omega(t)} \right] dt$
	<b>Crèching</b>	$-\int_l^{l+t_b} \frac{k_a}{n(t)} dt$	$-\int_l^{l+t_b} \frac{k_a}{n(t)} dt$
<b>Condition satisfying the ESS</b>		$\int_a^{l+t_b} \frac{k_g}{n(t)} dt < 0$	$\int_a^{l+t_b} \frac{k_g}{\omega(t)} dt > 0$

**Table 3** : Fecundity of the two possible strategies in function of the strategy fixed in the population when an active defence against the predators exists; the fecundity ratio gives the condition of ESS

		<b>Population fixed for the strategy</b>	
		<b>Non-Crèching</b>	<b>Crèching</b>
<b>Rare Strategy</b>	<b>Non-Crèching</b>	$-\int_l^a \frac{k_a(N)}{n(t)} dt - \int_a^{l+t_b} \frac{[k_g + k_a(N)]}{n(t)} dt$	$-\int_l^a \frac{k_a}{n(t)} dt - \int_a^{l+t_b} \left[ \frac{k_a [F(t) - F(t-t_i)]}{n(t)} + \frac{k_g}{\omega(t)} \right] dt$
	<b>Crèching</b>	$-\int_l^a \frac{k_a(N)}{n(t)} dt - \int_a^{l+t} \frac{k_a(1)}{n(t)} dt$	$-\int_l^a \frac{k_a(N)}{n(t)} dt - \int_a^{l+t_b} \frac{k_a [F(t-t_i) - F(t-t_b)]}{n(t)} dt$
<b>Condition satisfying ESS</b>		$\int_a^{l+t_b} \frac{k_g + [k_a(N) - k_a(1)]}{n(t)} dt < 0$	$-\int_a^{l+t_b} \frac{k_a [2F(t-t_i) - F(t-t_b) - F(t)]}{n(t)} dt + \int_a^{l+t_b} \frac{k_g}{w(t)} dt > 0$

## Appendix A: Derivation of individual fecundity in a system where adults do not defend the colony site against the predators

(a) Derivation of the fecundity of an individual demonstrating CS in a population fixed for NCS

From (4), the number of offspring at date  $t + dt$  is given by :

$$f(t + dt) = \left[ 1 - \frac{k_a}{n(t)} dt \right] f(t) \quad (\text{A1})$$

so that

$$\frac{f(t + dt) - f(t)}{f(t)} = -\frac{k_a}{n(t)} dt \quad (\text{A2})$$

Which leads to

$$\frac{d \log[f(t)]}{dt} = -\frac{k_a}{n(t)} dt \quad (\text{A3})$$

Integrating between  $a$  and  $l$  both sides of equation (A3) and taking exponential, we obtain the number of offspring at date  $a$  of an individual laying at date  $l$  :

$$f(a)_{NC/NC} = f(l) e^{-\int_l^a \frac{k_a}{n(t)} dt} \quad (\text{A4})$$

where NC means Non-Crèching.

After the site became accessible to terrestrial predators, the offspring is submitted to the terrestrial predation  $k_g$  and the aerial predation  $k_a$ . Doing in the same way as above, we obtain :

$$f(l + t_b)_{NC/NC} = f(a)_{NC/NC} e^{-\int_a^{l+t_b} \frac{k_a + k_g}{n(t)} dt} \quad (\text{A5})$$

using (A4) in (A5), we obtain

$$f(l + t_b)_{NC/NC} = f(l) e^{-\left[ \int_l^a \frac{k_a}{n(t)} dt + \int_a^{l+t_b} \frac{k_a + k_g}{n(t)} dt \right]} \quad (\text{A6})$$

(b) Derivation of the fecundity of an individual demonstrating CS in a population fixed for NCS.

Here offspring are not submitted to terrestrial predation after  $a$  because they leave the site when it became accessible to terrestrial predation. The procedure described above remains valid.

The fecundity is thus given by

$$f(l + t_b)_{C/NC} = f(l)e^{-\int_l^{l+t_b} \frac{k_a}{n(t)} dt} \quad (\text{A7})$$

where C means Crèching and NC means Non-Crèching.

The ratio of the fecundity satisfying the ESS of NCS is given by

$$\frac{f(l + t_b)_{NC/NC}}{f(l + t_b)_{C/NC}} > 1 \quad (\text{A8})$$

Using (A6) and (A7), the inequality (A8) is reduced to:

$$\int_a^{l+t_b} -\frac{k_g}{n(t)} dt > 0 \quad (\text{A9})$$

(c) Derivation of the fecundity of an individual demonstrating NCS in a population fixed for CS.

Since many CS birds leave the site when it becomes accessible to terrestrial predators, the number of items on the colony sites submitted to terrestrial predation is given by the number of eggs still unhatched. The number of items submitted to aerial predation is still given by the total number of items on both sites.

We thus obtain :

$$f(l + t_b)_{NC/C} = f(l) e^{\int_l^a \frac{k_a}{n(t)} dt + \int_a^{l+t_b} \left[ \frac{k_a}{n(t)} + \frac{k_g}{\omega(t)} \right] dt} \quad (\text{A10})$$

(d) Derivation of the fecundity of an individual demonstrating CS in a population fixed for CS.

Chicks leave the site when it becomes accessible to terrestrial predators. Thus, they only experience the aerial predation diluted in the whole population of eggs and chicks.

Taking into account what it precedes,

$$f(l + t_b)_{C/C} = f(l) e^{-\int_l^{l+t_b} \frac{k_a}{n(t)} dt} \quad (\text{A10})$$

Then the fecundity satisfies the ESS of CS provided that

$$\int_a^{l+t_b} \frac{k_g}{\omega(t)} dt > 0 \quad (\text{A11})$$

## Appendix B: Derivation of individual fecundity in a system where adults actively defence the colony site against the predators

(a) Derivation of the fecundity of an individual demonstrating CS in a population fixed for NCS.

$$f(l + t_b)_{NC/NC} = f(l)e^{-\int_l^a \frac{k_a(N)}{n(t)} dt - \int_a^{l+t_b} \frac{k_g + k_a(N)}{n(t)} dt} \quad (\text{B1})$$

(b) Derivation of the fecundity of an individual demonstrating CS in a population fixed for NCS.

The chicks of the CS invader are defended only by their own parents on the site they reached after their birth site became accessible to terrestrial predators. The fecundity of an CS in a NCS is thus given by:

$$f(l + t_b)_{C/NC} = f(l)e^{-\int_l^a \frac{k_a(N)}{n(t)} dt - \int_a^{l+t_b} \frac{k_a(1)}{n(t)} dt} \quad (\text{B2})$$

Then the fecundity ratio satisfying the ESS of NCS is given by

$$\int_a^{l+t_b} \frac{k_g + k_a(N) - k_a(1)}{n(t)} dt < 0 \quad (\text{B3})$$

(c) Derivation of the fecundity of an individual demonstrating NCS in a population fixed for CS.

When the site becomes accessible to terrestrial predators, chicks already hatched leave the colony site. It remains on the colony sites all the eggs still unhatched and protected by their parents. The fecundity is thus given by:

$$f(l + t_b)_{NC/C} = f(l)e^{-\int_l^a \frac{k_a}{n(t)} dt - \int_a^{l+t_b} \left[ \frac{k_a [F(t) - F(t-t_i)]}{n(t)} + \frac{k_g}{\omega(t)} \right] dt} \quad (\text{B4})$$

(d) Derivation of the fecundity of an individual demonstrating CS in a population fixed for CS.

All the parents of the crèching chicks defend the new colonised site simultaneously protected against the terrestrial predation, the fecundity is thus given by:

$$f(l+t_b)_{C/C} = f(l)e^{-\int_l^a \frac{k_a(N)}{n(t)} dt - \int_a^{l+t_b} \frac{k_a[F(t-t_i)-F(t-t_b)]}{n(t)} dt} \quad (\text{B5})$$

Then the fecundity ratio satisfying the ESS of CS is given by:

$$-\int_a^{l+t_b} \frac{k_a[2F(t-t_i)-F(t-t_b)-F(t)]}{n(t)} dt + \int_a^{l+t_b} \frac{k_g}{w(t)} dt > 0 \quad (\text{B6})$$