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Research article

A model for the evolution of crèching behaviour in gulls

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Abstract. A crèche is an aggregation of chicks outside nesting territories, within chicks continue to be fed only by their own parents. Several adaptive functions of crèching have been proposed, the most frequent 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 (CS) in gulls. Our results confirm the hypothesis that habitat instability associated with high levels of terrestrial predation favours the evolution and maintenance of crèching behaviour. Moreover, our results suggest that a low aggressiveness against predators may be a pre-adaptation to a CS. 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.

Key words: crèching behaviour, ESS, gulls, habitat instability, predation

Introduction

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, unpublished 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

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

We test this hypothesis in this paper by studying the effect of a high predation rate associated with a high probability for the colony site to become accessible to terrestrial predation over the course of a single breeding season. An evolutionary stable strategy (ESS) approach is used. Individual fecundity was computed using a reproductive output model based on cumulative predation risks over time. We thus examined which characteristics of predation favour the evolution and maintenance of a CS.

Since all crèching larids demonstrate extreme synchronisation in laying date (Beer, 1966; Isenmann, 1976; Zubakin, 1985; Mierauska and Buzun, 1991), and are described as being poorly aggressive against the predators of their chicks (Beer, 1966; Isenmann, 1976; Veen, 1977; Zubakin, 1985), we focus on the effects of synchronisation of the laying and anti-predator behaviour on the evolutionary stability of the CS.

The models

All parameters used in the models are summarised in Table 1. We considered a colony of approximately constant size (i.e. N pairs) over the course of the breeding season. We were only interested in the predators of chicks. We distinguished two different phases of the breeding period, the incubation and the rearing period. Let $F(t)$ be the cumulative distribution of laying dates, i.e. the fraction of the N pairs which started to breed before time t and m the individual reproductive output, assumed to be constant. The number of eggs ω and chicks π on the colony site at time t are given by:

$$\omega(t) = mN[F(t) - F(t - t_\mathrm{i})] \tag{1}$$

$$\pi(t) = mN[F(t - t_\mathrm{i}) - F(t - t_\mathrm{b})] \tag{2}$$

where t_i denotes the duration of the incubation, t_r is the rearing period and t_b stands for the total time for which young were potential prey (from laying to fledging). The total number of items (eggs or chicks) in the colony at time t, denoted $n(t)$, is simply obtained as the sum of Equations (1) and (2):

$$n(t) = mN[F(t) - F(t - t_\mathrm{b})] \tag{3}$$

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

$$p = \frac{k}{n(t)}\mathrm{d}t \tag{4}$$

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 $t_\mathrm{b} = t_\mathrm{i} + t_\mathrm{r}$
$\omega(t)$	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

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 drying of the colony periphery. The occurrence of such drying during the breeding season varies in probability 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 zero 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 of collective flights directed towards the predator. While mobbing has been demonstrated to be an effective deterrent against aerial predators (reviewed in Wittenberger and Hunt, 1985), its impact on terrestrial predators is none (Veen, 1977; Wittenberger and Hunt, 1985). In order to account for the mobbing behaviour in the model, k_a is assumed to be a decreasing function of the number of breeding pairs still present at time t on the colony site (Model 2).

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

Crèching vs. non-crèching strategy (NCS)

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

We examined the ecological conditions under which the NCS or the CS are ESS. If adult survival is equal for two strategies A and B, strategy A is non-invasible by the strategy B when, in a population fixed for A, the fecundity of an A individual is greater than that of a B individual (Maynard Smith, 1982). If only two strategies, A and B, are possible, the study of invasibility of A is equivalent to the study of the evolutionary stability of A. Strategy A is an ESS if, in a population fixed for strategy A, the ratio of the fecundity of an individual exhibiting strategy A to that of an individual with strategy B is greater than one.

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

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

Model 1: without active defence

NCS is evolutionarily stable if the following inequality holds (Table 2 left part):

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

		Population fixed for the strategy	
		Non-crèching	Crèching
Rare strategy	Non-crèching	$-\int_l^a \frac{k_\mathrm{a}}{n(t)}\mathrm{d}t - \int_a^{l+t_\mathrm{b}} \frac{(k_\mathrm{g}+k_\mathrm{a})}{n(t)}\mathrm{d}t$	$-\int_l^a \frac{k_\mathrm{a}}{n(t)}\mathrm{d}t - \int_a^{l+t_\mathrm{b}} \left[\frac{k_\mathrm{a}}{n(t)} + \frac{k_\mathrm{g}}{\omega(t)}\right]\mathrm{d}t$
	Crèching	$-\int_l^{l+t_\mathrm{b}} \frac{k_\mathrm{a}}{n(t)}\mathrm{d}t$	$-\int_l^{l+t_\mathrm{b}} \frac{k_\mathrm{a}}{n(t)}\mathrm{d}t$
	Condition satisfying the ESS	$\int_a^{l+t_\mathrm{b}} \frac{k_\mathrm{g}}{n(t)}\mathrm{d}t < 0$	$\int_a^{l+t_\mathrm{b}} \frac{k_\mathrm{g}}{\omega(t)}\mathrm{d}t > 0$

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

		Population fixed for the strategy	
		Non-crèching	Crèching
Rare strategy	Non-crèching	$-\int_{l}^{a}\frac{k_a(N)}{n(t)}\mathrm{d}t-\int_{a}^{l+t_b}\frac{[k_g+k_a(N)]}{n(t)}\mathrm{d}t$	$-\int_{l}^{a}\frac{k_a}{n(t)}\mathrm{d}t-\int_{a}^{l+t_b}\left[\frac{k_a[F(t)-F(t-t_i)]}{n(t)}+\frac{k_g}{\omega(t)}\right]\mathrm{d}t$
	Crèching	$-\int_{l}^{a}\frac{k_a(N)}{n(t)}\mathrm{d}t-\int_{a}^{l+t}\frac{k_a(1)}{n(t)}\mathrm{d}t$	$-\int_{l}^{a}\frac{k_a(N)}{n(t)}\mathrm{d}t-\int_{a}^{l+t_b}\frac{k_a[F(t-t_i)-F(t-t_b)]}{n(t)}\mathrm{d}t$
	Condition satisfying ESS	$\int_{a}^{l+t_b}\frac{k_g+[k_a(N)-k_a(1)]}{n(t)}\mathrm{d}t<0$	$-\int_{a}^{l+t_b}\frac{k_a[2F(t-t_i)-F(t-t_b)-F(t)]}{n(t)}\mathrm{d}t$ $+\int_{a}^{l+t_b}\frac{k_g}{\omega(t)}\mathrm{d}t>0$

$$\int_{a}^{l+t_b} -\frac{k_g}{n(t)}\mathrm{d}t > 0 \tag{5}$$

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

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

$$\int_{a}^{l+t_b} \frac{k_g}{\omega(t)}\mathrm{d}t > 0 \tag{6}$$

Inequality (6) is satisfied in several ecological situations. However CS is invasible by NCS if the number of egg laid in the colony was infinite ($\omega(t)$ infinite) but this situation is biologically uninteresting. CS is invasible by NCS if the rate of terrestrial attacks is zero ($k_g = 0$) or when the site becomes accessible to terrestrial predators only when or after chicks have fledged ($a \geq l + t_b$).

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

Model 2: with active defence

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

$$\int_{a}^{l+t_{\mathrm{b}}} \frac{k_{\mathrm{g}} + [k_{\mathrm{a}}(N) - k_{\mathrm{a}}(1)]}{n(t)} \mathrm{d}t < 0 \tag{7a}$$

and relation (7a) holds if

$$k_{\mathrm{g}} + [k_{\mathrm{a}}(N) - k_{\mathrm{a}}(1)] < 0 \tag{7b}$$

In order to qualitatively explore conditions in which NCS is an ESS, k_{a} is assumed to be N-dependent with the form:

$$k_{\mathrm{a}}(N) = k_{\max}\left[\frac{\alpha}{N} + (1 - \alpha)\right] \tag{8}$$

where α is the curvature of the function describing the protection efficiency given the number of adults defending the site and $k_{\max}$ is the avian predation rate when only one pair breeds on the site. Hence, the overall predation rate decreased when α increased. Under these assumptions, the inequality (7b) reduces to:

$$K_{\mathrm{g}} < \alpha K_{\max}\left(1 - \frac{1}{N}\right) \tag{9}$$

Figure 1 shows the maximum rate of terrestrial predation k_{g} permitting the evolutionary stability of NCS for different levels of α and $k_{\max}$. Qualitatively, an increase in active defence (α) 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. The CS is evolutionarily stable if the following inequality is satisfied (Table 3 right part).

$$-\int_{a}^{l+t_{\mathrm{b}}} \frac{k_{\mathrm{a}}[F(t - t_{\mathrm{i}}) - F(t - t_{\mathrm{b}})] - k_{\mathrm{a}}[F(t) - F(t - t_{\mathrm{i}})]}{n(t)} \mathrm{d}t + \int_{a}^{l+t_{\mathrm{b}}} \frac{k_{\mathrm{g}}}{w(t)} \mathrm{d}t > 0 \tag{10}$$

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

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

where θ describes the synchronisation of the laying. The active defence and its efficiency are modelled as above. The CS is thus evolutionarily stable if the following inequality is satisfied.

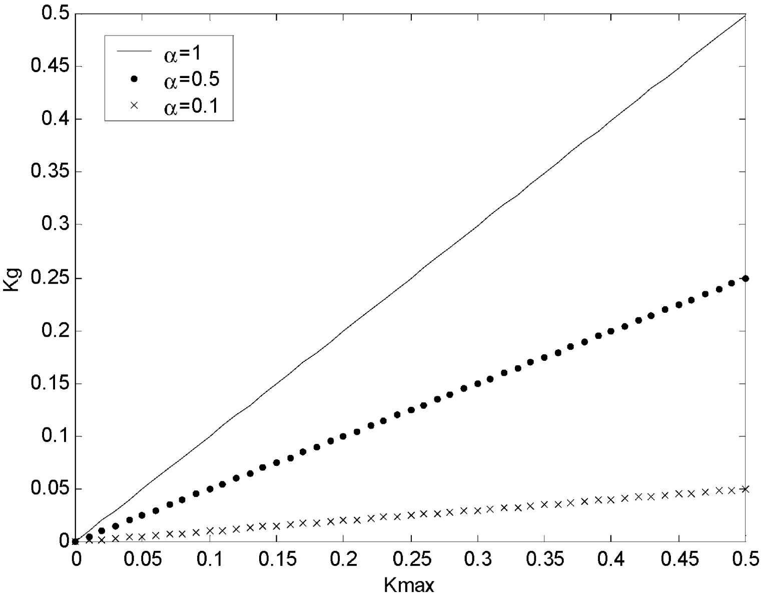

Figure 1. Maximum rate of terrestrial predation k_g permitting the evolutionary stability of NCS for different levels of α and $k_{\max}$. NCS is evolutionarily stable when $K_g < \alpha K_{\max}(1 - \frac{1}{N})$. An increase in active defence (α) or an increase in maximum rate of aerial predation ($k_{\max}$) 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.

$$\frac{k_g(\exp^{a\theta} - \exp^{(l+t_b)\theta l})}{\theta Nm\beta(\exp^{\theta t_i} - 1)} - \frac{k_{\max}\alpha(2\exp^{\theta t_i} - \exp^{\theta t_b} - 1)(\exp^{(2\theta(l+t_b))} - \exp^{2a\theta})}{2\theta N^2 m^2 \beta^2 (\exp^{\theta t_b} - 1)(\exp^{\theta t_i} - \exp^{\theta t_b})(\exp^{\theta t_i} - 1)} > 0 \qquad (12)$$

Figure 2 shows in which conditions CS is evolutionary stable for some usual population parameters of larids. The main results are that the stability of CS depends on the relative levels of terrestrial (k_g) and realised aerial predation ($k_{\max}\alpha$) and in a more complex way on the synchronisation of laying dates (θ). In the range of biologically realistic parameters, CS is frequently evolutionary stable. Figure 2 shows that CS is invasible by NCS when the active defence against predators is strong (high α value) and the synchronisation of laying high (Fig. 2). Since the evolutionary stability is dependent on the product $k_{\max}\alpha$, the same figure could be drawn using $K_{\max}$ instead of α. Thus CS is invasible by NCS when the maximum aerial predation is high and the synchronisation of laying is high as well. To summarise, CS is invasible by NCS only if the population is submitted to a high rate of realised aerial predation relative to terrestrial predation, with concurrent a highly synchronised laying.

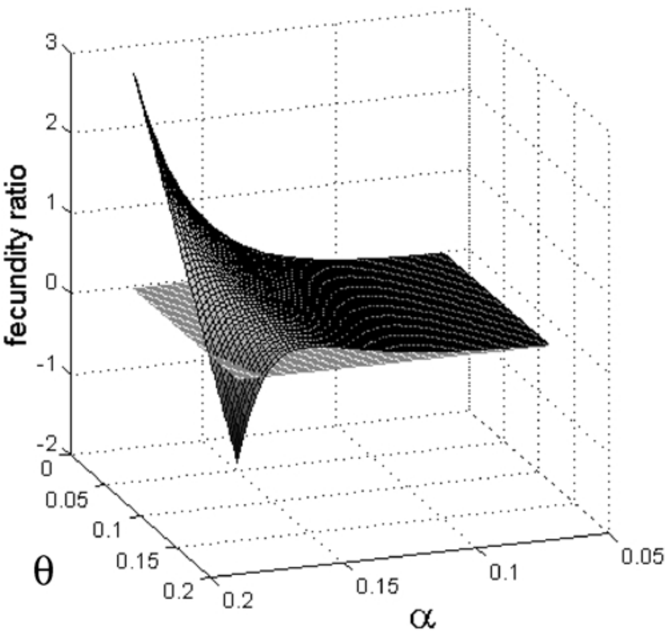

Figure 2. Conditions in which CS is evolutionarily stable for different levels of synchronisation of laying (θ) and efficiency of the defence against aerial predators (α). CS is stable when the surface defined by the fecundity ratio is upper than the horizontal plan. The fecundity ratio is given by Equation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

Here, we developed only equations of fecundity computed for individuals whose chicks hatched before the site became accessible to the terrestrial predation. When chicks hatch after the site becomes accessible, they progressively reach the 'safe' site. Hence until they hatch, late laid eggs experience exactly the same predation as non-crèching eggs. Thus, if the inequalities satisfying the evolutionary stability are slightly different, the qualitative results are of the same form and our conclusions hold for the two different situations.

Discussion

Three main conclusions can be derived from our results: first the CS can simply evolve from a NCS if the probability for the site to become accessible to terrestrial predation is high. Second, in a species with no anti-predator behaviour, the CS always invades and is stable in a large range of ecological situations. Third, when individuals actively defend their chicks against terrestrial predation, crèching and NCSs may both be ESS but remain invasible 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 NCS is favoured and is generally the ESS if aerial predation is high compared to terrestrial predation, while the CS 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 terrestrial predators and a CS cannot evolve from a NCS. 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 crèching behaviour. This result seems to result from the ability for crèching chicks to leave the colony site when it becomes accessible to terrestrial predators while non-crèching chicks stay on the colony site whatever the predation characteristics. Then the aerial predation suffered by chicks remains the same whatever the strategy, whilst the impact of terrestrial predation is only perceptible for non-crèching chicks.

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 CS eventually converges. When a species has a reduced but not non-existent aggressiveness against predators, the CS is no more convergent but is still invasive and evolutionary stable in many ecological contexts (in particular when terrestrial predation is not zero). A weakly aggressive species could maintain the NCS only under a very low rate of terrestrial predation. The NCS could thus be maintained while being weakly aggressive only in highly stable habitats protected against terrestrial predation, or by species living in habitats where no terrestrial predation occurs. To our knowledge, this is the first demonstration that weak aggressiveness observed in crèching species could be a pre-adaptation to this strategy since it favours its evolution and stability. A little-aggressive NCS is extremely likely to evolve crèching and then unlikely to evolve back to the NCS, explaining why no intermediate stage seems to exist between non-crèching and crèching and why no reversion (evolution from crèching to NCS) seems to have occurred in larids (A. Besnard, unpublished results). The relationship between weak aggressiveness against predators and a CS evolution appears to be the result of the relationship between the number of birds defending the colony and the efficiency of their defence. Indeed, if the crèche leave the colony site, they suffer from reduced defence since fewer parents defend the crèche. If defence is very efficient, the cost of crèching is high; conversely this cost is low when the active defence is weak or inefficient, favouring the evolution of the CS.

Bearing in mind that the evolutionary stability of a NCS is not conditional on the synchronisation of laying date, we can reject the hypothesis that the high synchronisation of laying, as observed in many crèching species (Beer, 1966; Isenmann, 1976; Zubakin, 1985; Mierauska and Buzun, 1991; Besnard *et al.*, submitted) is a pre-adaptation to the CS. An extreme synchronisation of laying associated with a high rate of aerial predation favours the invasion of the CS and thus exerts a selective pressure against the maintenance of crèching behaviour. We thus suggest that the high synchronisation observed in several crèching species is a response to selective pressures other than those studied here. We modelled the CS as a massive departure from the colony site when it becomes accessible to terrestrial predation and by a progressive aggregation at the newly colonised site by late-hatched chicks. In the field, it seems that crèche formation is punctual and that late breeders who do not join the crèche often abandon their eggs (J.-D. Lebreton, pers. obs.). Such a constraint against a late laying should exert a strong selective pressure for the synchronisation of laying.

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

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

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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 NCS in a population fixed for NCS From Equation (4), the number of offspring at date $t + \mathrm{d}t$ is given by:

$$f(t+\mathrm{d}t) = \left[1 - \frac{k_\mathrm{a}}{n(t)}\,\mathrm{d}t\right] f(t) \tag{A1}$$

so that

$$\frac{f(t+\mathrm{d}t) - f(t)}{f(t)} = -\frac{k_\mathrm{a}}{n(t)}\mathrm{d}t \tag{A2}$$

which leads to

$$\frac{\mathrm{d}\log[f(t)]}{\mathrm{d}t} = -\frac{k_\mathrm{a}}{n(t)}\,\mathrm{d}t \tag{A3}$$

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:

$$f(a)_{\mathrm{NC/NC}} = f(l)\mathrm{e}^{-\int_l^a \frac{k_\mathrm{a}}{n(t)}\mathrm{d}t} \tag{A4}$$

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. In the same way as above, we obtain:

$$f(l+t_\mathrm{b})_{\mathrm{NC/NC}} = f(a)_{\mathrm{NC/NC}}\mathrm{e}^{-\int_a^{l+t_\mathrm{b}} \frac{k_\mathrm{a}+k_\mathrm{g}}{n(t)}\mathrm{d}t} \tag{A5}$$

using Equation (A4) in (A5), we obtain

$$f(l+t_\mathrm{b})_{\mathrm{NC/NC}} = f(l)\mathrm{e}^{-\left[\int_l^a \frac{k_\mathrm{a}}{n(t)}\mathrm{d}t + \int_a^{l+t_\mathrm{b}} \frac{k_\mathrm{a}+k_\mathrm{g}}{n(t)}\right]\mathrm{d}t} \tag{A6}$$

(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

$$f(l+t_\mathrm{b})_{\mathrm{C/NC}} = f(l)\mathrm{e}^{-\int_l^{l+t_\mathrm{b}} \frac{k_\mathrm{a}}{n(t)}\mathrm{d}t} \tag{A7}$$

where C means crèching and NC means non-crèching.

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

$$\frac{f(l+t_\mathrm{b})_{\mathrm{NC/NC}}}{f(l+t_\mathrm{b})_{\mathrm{C/NC}}} > 1 \tag{A8}$$

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

$$\int_a^{l+t_\mathrm{b}} -\frac{k_\mathrm{g}}{n(t)}\,\mathrm{d}t > 0 \tag{A9}$$

(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:

$$f(l+t_{\mathrm{b}})_{\mathrm{NC/C}} = f(l)\mathrm{e}^{\int_{l}^{a}\frac{k_{\mathrm{a}}}{n(t)}\mathrm{d}t + \int_{a}^{l+t_{\mathrm{b}}} -\left[\frac{k_{\mathrm{a}}}{n(t)} + \frac{k_{\mathrm{g}}}{\omega(t)}\right]\mathrm{d}t} \tag{A10}$$

(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,

$$f(l+t_{\mathrm{b}})_{\mathrm{C/C}} = f(l)\mathrm{e}^{-\int_{l}^{l+t_{\mathrm{b}}}\frac{k_{\mathrm{a}}}{n(t)}\mathrm{d}t} \tag{A10}$$

Then the fecundity satisfies the ESS of CS provided that

$$\int_{a}^{l+t_{\mathrm{b}}} \frac{k_{\mathrm{g}}}{\omega(t)}\,\mathrm{d}t > 0 \tag{A11}$$

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 NCS in a population fixed for NCS.

$$f(l+t_{\mathrm{b}})_{\mathrm{NC/NC}} = f(l)\mathrm{e}^{-\int_{l}^{a}\frac{k_{\mathrm{a}}(N)}{n(t)}\mathrm{d}t - \int_{a}^{l+t_{\mathrm{b}}}\frac{k_{\mathrm{g}}+k_{\mathrm{a}}(N)}{n(t)}\mathrm{d}t} \tag{B1}$$

(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:

$$f(l+t_{\mathrm{b}})_{\mathrm{C/NC}} = f(l)\mathrm{e}^{-\int_{l}^{a}\frac{k_{\mathrm{a}}(N)}{n(t)}\mathrm{d}t - \int_{a}^{l+t_{\mathrm{b}}}\frac{k_{\mathrm{a}}(1)}{n(t)}\mathrm{d}t} \tag{B2}$$

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

$$\int_{a}^{l+t_{\mathrm{b}}} \frac{k_{\mathrm{g}} + k_{\mathrm{a}}(N) - k_{\mathrm{a}}(1)}{n(t)}\,\mathrm{d}t < 0 \tag{B3}$$

(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. All the eggs still unhatched and protected by their parents remain on the colony sites. The fecundity is thus given by:

$$f(l+t_{\mathrm{b}})_{\mathrm{NC/C}} = f(l)\mathrm{e}^{-\int_{l}^{a}\frac{k_{\mathrm{a}}}{n(t)}\mathrm{d}t - \int_{a}^{l+t_{\mathrm{b}}}\left[\frac{k_{\mathrm{a}}[F(t)-F(t-t_{\mathrm{i}})]}{n(t)} + \frac{k_{\mathrm{g}}}{\omega(t)}\right]\mathrm{d}t} \tag{B4}$$

(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 newly colonised site simultaneously, protecting against the terrestrial predation, the fecundity is thus given by:

$$f(l+t_{\mathrm{b}})_{\mathrm{C/C}} = f(l)\mathrm{e}^{-\int_{l}^{a}\frac{k_{\mathrm{a}}(N)}{n(t)}\mathrm{d}t - \int_{a}^{l+t_{\mathrm{b}}}\frac{k_{\mathrm{a}}[F(t-t_{\mathrm{i}})-F(t-t_{\mathrm{b}})]}{n(t)}\mathrm{d}t} \tag{B5}$$

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

$$-\int_{a}^{l+t_{\mathrm{b}}} \frac{k_{\mathrm{a}}[2F(t-t_{\mathrm{i}}) - F(t-t_{\mathrm{b}}) - F(t)]}{n(t)}\,\mathrm{d}t + \int_{a}^{l+t_{\mathrm{b}}} \frac{k_{\mathrm{g}}}{w(t)}\,\mathrm{d}t > 0 \tag{B6}$$

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