

hydrate BSR on the northwestern Mediterranean margin is shallow (0–100 m)²² and previous mass wasting may have resulted in gas release. Clathrate release has been implicated in the generation of some large submarine slides, such as the Storegga Slide, off Norway, where seismic activity may have initiated the slide, and gas escape, perhaps from clathrates, may have aided sediment mobilization^{6,23}. Seismic activity on the northern Mediterranean margin is limited, but repeated seismic activity is well documented in the Ligurian Sea, north of Corsica, throughout historical time²⁴. Many of these earthquakes have epicentres on, or close to, the continental margin and appear to be linked to rejuvenation of older distensive and strike-slip structures by compressive stress related to the convergence of the European and Africa plates²⁵.

The basal sand of the megabed thickens and coarsens in grain size towards the north, suggesting emplacement from that direction. Three major fan systems are present on the northwestern Mediterranean margin—the Var, Rhone and Ebro. All drain glaciated hinterlands, and would have had high rates of sediment supply during the last glacial. The entire northwestern Mediterranean margin is prone to gravity flow processes, however, reflecting its geological setting with a mountainous borderland and rapid deposition of undercompacted sediments²⁶. The underlying Messinian salt layer may contribute to general instability by lubricating slippage of overlying sediments²⁶. The exceptional size of the Balearic Abyssal Plain megabed, however, suggests that it is an

unusual event in terms of size and frequency in the recent history of this margin and therefore may have had an extraordinary trigger. Catastrophic destabilization of margin or fan sediments, possibly due to clathrate release and/or earthquake activity, after a long period of accumulation with an increased rate of sediment supply, seems likely. □

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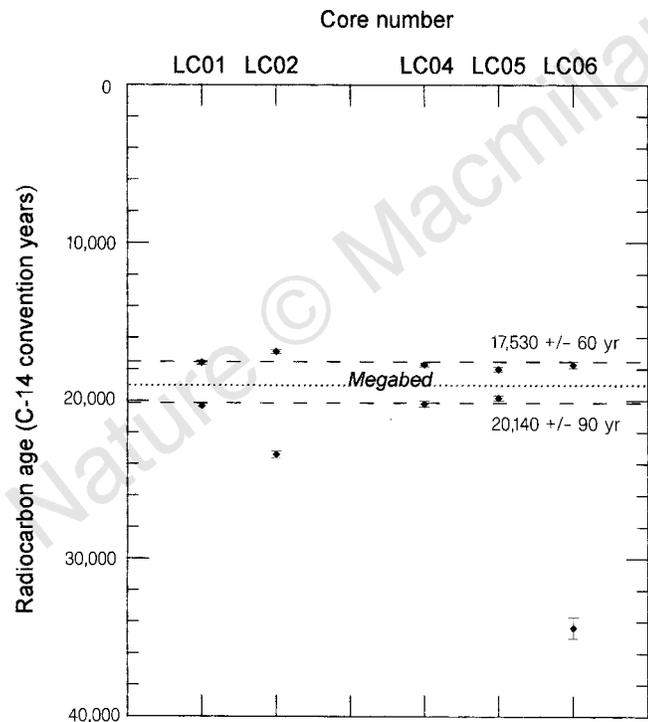


Figure 4 Radiocarbon ages derived from dating the pelagic intervals above and below the megabed in cores LC01, LC02, LC04, LC05 and LC06. The overlying pelagic samples from all five cores yield a cluster of ages between 16,900 and 18,010 radiocarbon years (Table 1), with a weighted mean age of 17,530 ± 60 radiocarbon years. There is a greater scatter in the underlying samples, with considerably older ages found for cores LC02 and LC06 than the other three. There may be unrecognized erosive effects from the megabed emplacement. The next pelagic unit down may have been selected for dating in the case of LC02. The LC06 sample was very thin (2 cm) and may have been misinterpreted as pelagic. The ages for the underlying samples in the remaining three cores are concordant, however, and yield a weighted mean age of 20,140 ± 90 radiocarbon years. The best estimate for the emplacement time of the megabed is the arithmetic mean of the weighted mean overlying and underlying ages, or 18,840 radiocarbon years.

Optimal clutch size and conspecific brood parasitism

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Egg-laying organisms should lay, in a reproductive bout, the number of eggs that maximizes fitness. Lack argued 50 years ago that clutch size for most birds is limited by the amount of food parents can provide for their offspring¹. Clutch sizes, however, are often smaller than this 'Lack clutch size', and this fact is the subject of much debate^{2–4}. Here I propose and test a new explanation for this pattern that is based on evidence that conspecific brood parasitism is widespread in birds^{5–7}, specifically when females

with their own nests also parasitize conspecific birds⁸⁻¹³. A graphical model of clutch size shows that the trade-offs a brood parasite faces when allocating eggs to her own nest or to nests of other conspecific females can favour a reduction in the parasite's own clutch size. This prediction is supported by a field study of American coots (*Fulica americana*). Moreover, the cost of receiving parasitic eggs also favours a reduction in clutch size for hosts, introducing a 'game'¹⁴ element to clutch size when parasitic females are themselves parasitized. These results indicate that conspecific brood parasitism should no longer be ignored as a force in clutch-size evolution.

Nesting females who also lay eggs parasitically in the nests of conspecific birds must allocate their eggs appropriately between the nests they parasitize and their own clutch. This trade-off could explain why some females lay smaller clutches in their own nests than the anticipated Lack clutch size, as illustrated by a simple optimal clutch-size model (Fig. 1). The model can be used to examine the 'fitness increment' resulting from adding each extra egg to a female's own clutch, under the assumption that increasing clutch size yields a diminishing return on parental fitness because of constraints such as the amount of parental care needed (Fig. 1). The fitness increment of an egg is the benefit resulting from the survival of offspring minus the cost to fitness both of producing the egg and of any negative impact the egg or chick has on the survival of siblings because of competition for limited parental care.

In the absence of brood parasitism, a female reaches her optimal clutch size (N_o^*) with the addition of the last egg to her clutch that yields a positive net fitness increment (Fig. 1). The female may be physiologically capable of laying more eggs than the optimal clutch size (for example, eggs below the zero net fitness line in Fig. 1), but the fitness costs of laying the eggs and raising the young would exceed the low expected benefits^{3,4}. If this same female now has the option of laying some of her eggs parasitically in the nests of other females, how should she allocate her eggs between other nests and her own clutch? The average fitness increment she gains from laying an egg parasitically (dashed line in Fig. 1) is the 'parasitism threshold', as it determines when she should switch allocation to parasitism and, consequently, determines the new optimal clutch size for her own nest (N_p^*) when parasitism is an option: beyond this new optimal clutch size, laying eggs parasitically yields higher fitness than laying the eggs in her own nest. The term 'switch' is used loosely and the order in which parasitic and parental laying occur is

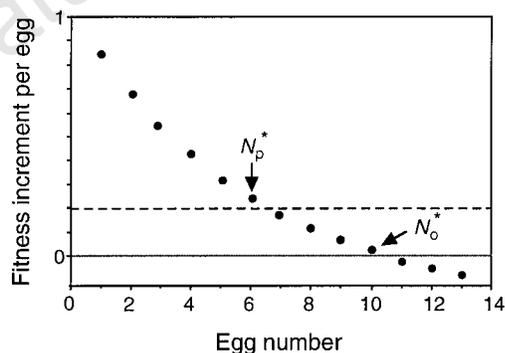


Figure 1 Model of optimal clutch size for females with, and without, the option of laying some of their eggs parasitically. The dashed line represents the average fitness per parasitic egg; eggs below this line fare better if laid parasitically rather than in the parental clutch. N_o^* is the optimal clutch size for non-parasitic females, whereas N_p^* is the optimal clutch size for brood parasites. For parasitic females, 'optimal' refers to the maximum total production of offspring in a reproductive bout (that is, parental plus parasitic young) whereas 'clutch size' is the number of eggs they lay in their own nests. Several factors can affect the average fitness of parasitic eggs relative to parental eggs^{15,21}; including when the eggs is laid in the host's breeding cycle, whether hosts reject eggs, and the number of parasitic eggs per host nest.

not important provided that females have some physiological mechanism for allocating the appropriate number of eggs to each of the two tactics.

Three main predictions for the fitness and behaviour of parasitic females derive from this model (Fig. 1). First, the fitness increment from the last egg laid to reach the optimal clutch size (egg number N_p) is greater than the average fitness gained from parasitic eggs (in rare cases, the last own egg could, by chance, yield equal fitness to parasitic eggs). Second, the average fitness gained from parasitic eggs should be greater than the fitness a female would gain from laying any additional eggs in her own nest (beyond N_p). Third, parasitism may favour a reduction in the parasite's own clutch size relative to the clutch size she would lay in the absence of parasitism (predicted reduction in Fig. 1 is $N_o^* - N_p^*$). The last prediction is particularly critical as it provides a new explanation for deviations from the Lack clutch size. A reduction in parental clutch size is predicted only when the total number of eggs a parasitic female lays is limited by her egg-laying capacity, not by her opportunities for parasitism; in other words, she has to make a trade-off.

I tested these predictions and assumptions with data from a study of parental care and brood parasitism in the American coot, a waterbird. This study took place from 1987 to 1990 near Riske Creek, British Columbia. Parasitism was very common in this population: 41% of nests were parasitized, mainly by nesting females who laid eggs parasitically immediately before starting their own nests^{12,15}. Brood parasites laid more total eggs (own plus parasitic) than did non-parasitic females¹². Moreover, the clutch sizes that parasites laid in their own nests correlated negatively with the number of eggs they laid parasitically (partial correlation, holding seasonal effects constant; $r = -0.31$, $N = 88$, $P = < 0.01$), supporting a trade-off between laying eggs parasitically and in the parental nest.

Egg survival shows a diminishing return with increasing egg position in the laying sequence (Fig. 2). This pattern results from the importance of parental feeding for chick survival, extreme hatching asynchrony and strong laying-order-dependent starvation within broods^{12,16}. Comparison of survival rates (Fig. 2) also indicates that parasites may switch between brood parasitism and laying eggs in their own nests at the appropriate clutch size, as predicted by the model; parasitic eggs (0.086 fledged chicks per egg) were less successful than last eggs laid in own nests (0.112 fledged chicks per egg), but more successful than predicted hypothetical 'next' eggs in own nests (0.063 fledged chicks per egg; survival of next eggs is predicted from a regression with the seven observed values). However, although these differences are consistent with the first two predictions of the model, they are not significant (both one-tailed $P = > 0.3$) and thus provide only qualitative support for the predictions. Given the extremely small expected (Fig. 1) and observed (Fig. 2) differences in survival among classes of marginal eggs, low statistical power makes definitive tests of the first two predictions difficult. Moreover, the observed fitness estimates do not include costs of reproduction for parental eggs or the costs associated with parasitic egg-laying, and may thus be imprecise. These two problems will probably exist in most studies. Comparisons of clutch size (the third prediction), however, should provide a more powerful and informative test of the model.

The pattern of egg survival leads to the prediction that parasitic egg-laying should be associated with a reduction in the parasite's own clutch size by one or two eggs (that is, the number of hypothetical 'next' eggs predicted to lie above the zero-fitness line but below the average fitness of parasitic eggs; Fig. 2, squares). I compared the clutch sizes of parasites with those of two different classes of non-parasitic females (Fig. 3a) that seemed to have been prevented from parasitism for different reasons. Some non-parasitic females lacked potential hosts to parasitize during their laying periods; many of these females were probably constrained by a lack of opportunity for parasitism. These females should have laid

their optimal clutch sizes (N_o^*) in their nests. In contrast, non-parasitic females who had potential hosts to parasitize were seemingly constrained by their limited fecundity. These females laid smaller clutches than the other non-parasites (Fig. 3a), supporting fecundity limitations and also suggesting that many failed to lay even their optimal clutch sizes. I therefore omitted data about these females when assessing whether brood parasites reduced their clutch sizes compared with non-parasites.

As predicted from the egg-survival data, parasites laid significantly smaller clutches than the non-parasites without hosts (Fig.

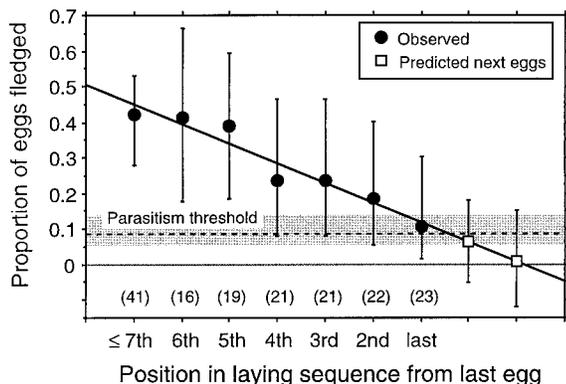


Figure 2 Observed reproductive success of eggs laid by 23 female American coots in their own nests (filled circles) as a function of position in the laying sequence, compared with the average success of 268 parasitic eggs laid by all nesting parasites (dashed line). Numbers of eggs are indicated in parenthesis. Linear regression through the seven observed data points ($F_{1,5} = 66.9$, $P = 0.0004$) predicts what females would gain by laying hypothetical 'next' eggs in the laying sequence (squares) in their own nests, rather than parasitically. Bars and shaded region denote 95% confidence intervals for parental and parasitic eggs, respectively.

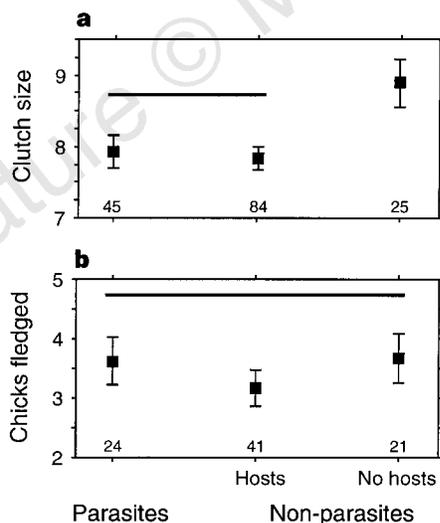


Figure 3 Comparison of clutch size and number of chicks fledged from parental nests for three classes of female American coots, namely, brood parasites, non-parasites with potential hosts to parasitize, and non-parasites that lacked potential hosts to parasitize. **a**, Mean (\pm s.e.m.) clutch size; **b**, number of chicks fledged. Sample size is number of females. Horizontal bars connect means not significantly different ($P = > 0.05$) according to Fisher's least significant difference posthoc tests. In theory, non-parasitic females should produce slightly more chicks than parasitic females in their own nests, because there are chicks that survive from the additional marginal eggs that non-parasites lay (Fig. 1). However, a huge sample size would be required to show whether such small differences are significant (ref. 24) (for example, a mere 2% increase in brood size is predicted on the basis of the summed survival probabilities of 'next' eggs in Fig. 2).

3a; means differ by 0.96 eggs, concurring with the predicted shift of one to two eggs). There was no difference between these two groups of females in the number of offspring fledged from their own nests (Fig. 3b), further indicating that this clutch-size difference may reflect the allocation trade-offs embodied by the model, and not simply general differences in quality between parasites and non-parasites. I believe this to be the first evidence that the competing demands of brood parasitism and own nesting for individual females can result in a shift in the optimal clutch size; these results provide a new explanation for deviations from the Lack clutch size.

The realization that brood parasitism might affect clutch size is not completely new, but the scant attention this has received previously has focused on how parasitism may affect the optimal clutch sizes of the recipients of parasitic eggs, or 'hosts'¹⁷⁻²⁰. My model of optimal clutch size also has implications for host clutch size. When parasitism is costly to hosts, it reduces the value of their eggs and should thus favour a reduction in their clutch size (Fig. 4a). In coots, parasitism is costly to hosts²¹, because of limited food and high starvation rates of chicks in general; hosts should therefore reduce their clutch sizes. Clutch-size comparisons confirm that hosts do adjust their clutch sizes in response to parasitism (Fig. 4b). Moreover, the amount of clutch-size reduction varied with two factors that affect the costs of parasitism²¹, namely, the number of parasitic eggs received and the timing of parasitism relative to the host's laying cycle (Fig. 4b). This is convincing evidence for adaptive clutch-size adjustment by hosts in response to parasitism¹⁷⁻²⁰.

An interesting consequence of adaptive clutch-size reductions for both parasites and hosts is that the optimal clutch size for parasites entails a 'game'¹⁴ element when parasitic females are themselves

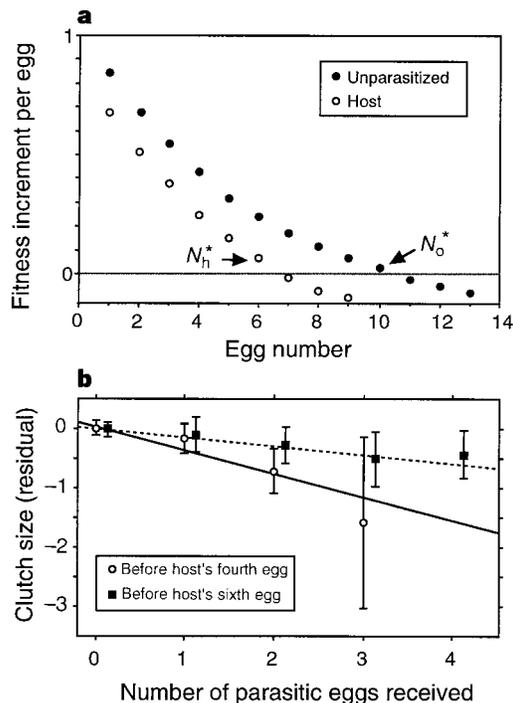


Figure 4 Adjustment of host clutch size in response to parasitism. **a**, Model of optimal clutch size for parasitized ('host') females (N_h^*) relative to unparasitized females (N_o^*). When parasitism is costly to hosts, the value of the host's eggs is reduced and a clutch-size reduction is favoured. **b**, Regressions of clutch sizes of host American coots as a function of the number of parasitic eggs they received before two different cutoff points in the laying cycle: before the host's fourth egg (solid line; $F_{1,135} = 7.36$, $P = 0.008$) and sixth egg (dashed line; $F_{1,135} = 2.15$, $P = 0.14$) were laid, respectively. Thus, host response increased with number of eggs and early parasitism: both of these factors affect the cost of parasitism and decrease the value of host eggs²¹. Regressions are based on individual nests but values shown are means and standard errors for each egg-number class.

parasitized by other females. At the population level, parasitic eggs decrease the average value of the parental eggs laid by parasites, in turn favouring even greater allocation to parasitism (trade-off in Fig. 1): optimal clutch size depends on the frequency of parasitism, and vice versa. The dynamic nature of the problem is further enhanced in species where the success of parasitic eggs is also frequency-dependent²². These various game aspects do not alter the qualitative assumptions or predictions of the graphical model. It will be important, however, to incorporate these assumptions and predictions into a more quantitative, theoretical study and into some empirical tests. For example, in populations in which parasites are also hosts, the fitness estimates for a parasite's own clutch must reflect her risks and costs of being parasitized. I have accounted for these fitness estimates; egg survival estimates (Fig. 2) included parasitic females who were themselves parasitized (6 of the 23 parasitic females). Some of these females raised parasitic chicks and, consequently, sacrificed some of their own chicks in the process.

Here I have shown that, for some species, clutch size cannot be understood without considering conspecific brood parasitism. The opposite is also true, and this clutch-size model provides a new framework for understanding brood parasitism. Most studies of parasitism do not examine clutch-size constraints and cannot explain why parasites lay eggs in the nests of others rather than in their own nests; in some cases, the hypothesis that parasitism yields a direct increase in mean fitness has been prematurely rejected²³. Earlier studies of brood parasitism now need to be reassessed. By integrating two fields of research that are generally considered in isolation of each other—study of clutch size and conspecific brood parasitism—this new clutch-size model provides a framework for enriching our understanding of both fields. □

Methods

Comparing survival of parental and parasitic eggs. Brood parasites were identified using standard techniques¹². Eggs were considered successful (fledged) if the chicks survived to 30 d after hatching¹². As it is the fitness of parental eggs relative to the fitness of parasitic eggs that is important, survival to independence is a good measure of relative fitness, assuming that post-fledging mortality is similar for both egg types. Survival rates for eggs in parasitic females' own nests were calculated for successful nests (some eggs hatched) but then adjusted by the proportion of parental eggs that were laid in successful nests (82.1% of 731 eggs). Only nests where the fates of more than half the chicks were known were included in these analyses. Confidence limits for proportion of eggs surviving (Fig. 2) were based on sample size²⁴ for observed eggs and on 1,000 bootstrapped regression equations for predicted next eggs. For statistical comparisons of egg survival, a G-test compared last parental eggs with parasitic eggs, whereas 1,000 bootstrapped predictions of 'next'-egg survival were used to compare 'next' eggs with parasitic eggs.

I examined egg success in relation to an egg's position in the laying sequence (backwards from the last egg laid in the clutch), rather than on the basis of clutch size, to enable pooling of results despite large variations in clutch size¹² and to predict what parasites would gain if they were to add 'hypothetical' next eggs in the laying sequence to their clutches (Fig. 2). The survival value of eggs from a specific position in the laying sequence would not indicate the fitness increments from those eggs if later-laid eggs survive at the expense of earlier-laid eggs, because the survival of the eggs would need to be discounted by the fitness reduction they caused through the death of siblings. However, the two measures (survival and fitness increment) will be equivalent where there is strict laying-order-dependent survival within broods; in this study, few later-laid eggs survived at the expense of earlier-laid ones^{12,16}.

Clutch- and brood-size comparisons. For analysis of sizes of clutches of parasitic and non-parasitic females, host availability was determined on the basis of the observed spatial and temporal patterns of host use¹⁵. To reduce variance due to strong seasonal decline in clutch size, the effects of date were controlled by analysis of covariance (ANCOVA) ($F = 9.04, P = 0.002$); clutch sizes (Fig. 3) are therefore adjusted means. For chicks, the assumptions of ANCOVA are violated, so analysis of variance was used ($F = 0.64, P = 0.53$)

but, to avoid bias due to differences among groups in timing of nesting, only birds who initiated laying within 20 d of the first egg laid in the population are included.

To avoid potential confounding effects of female quality in the analysis of host clutch-size responses, only host nests were included in these analyses. Residual clutch sizes from regressions of clutch size against laying data were used to control for strong seasonal declines in clutch size²¹.

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Exceptional soft-tissue preservation in a theropod dinosaur from Italy

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The Lower Cretaceous Pietraroia Plattenkalk (Benevento Province, southern Italy) has been known since the eighteenth century for its beautifully preserved fossil fishes. During Albian time (about 113 Myr ago¹), deposition of fine marly limestone in a shallow lagoonal environment, affected by cyclic periods of low oxygen levels², led to exceptional preservation of soft tissue in a