THE INFLUENCE OF NEIGHBOURS ON BREEDING SYNCHRONY IN CORY'S SHEARWATER *CALONECTRIS DIOMEDEA*

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SUMMARY

MOUGIN, J-L., JOUANIN, C., MOUGIN, M-C. & ROUX, F. 2001. The influence of neighbours on breeding synchrony in Cory's Shearwater *Calonectris diomedea*. *Marine Ornithology* 29: 51–56.

Among Cory's Shearwaters *Calonectris diomedea* of Selvagem Grande (30°09'N, 15°52'W), near neighbours are more synchronised in all the breeding activities (laying, incubation, chick growth and fledging) than birds breeding farther apart (>6 m). The existence of this local synchrony cannot be explained by the need to avoid predators because there is no predation on that species at that locality. The long duration of pair bonds and the faithfulness of pairs to their nest site means that near neighbours remain unchanged from year to year. Entrainment of synchrony over several years may explain the additional synchrony among near neighbours. New pairs of experienced breeders are formed mostly by birds coming from neighbouring nest sites. The familiarity of individuals with their near neighbours, built up with one another over several years by creating synchronisation within a radius of some metres during breeding, should facilitate the swift formation of new pairs at the beginning of a breeding season, allowing birds to avoid the loss of a breeding year.

Key words: Cory's Shearwater, *Calonectris diomedea*, breeding biology

INTRODUCTION

Among most colonial breeders, synchronisation during the breeding cycle is noteworthy at colony and population levels but, in some species, still higher between near neighbours. This is true in particular for Cory's Shearwaters *Calonectris diomedea* of Selvagem Grande (30°09'N, 15°52'W). Hamer & Read (1987) have shown a greater synchrony of adult visits in the closest nests, and Jones (1986a, 1986b), studying the tarsus of the chicks in August, has noted the closest similarity in length among birds settled on the closest nests.

The Cory's Shearwater is one of the five species of Procellariiformes breeding on Selvagem Grande, the largest of the Portuguese Selvagems Islands, situated between Madeira and the Canary Islands. Approximately 36 000 birds breed there at present; fewer than during past centuries, but the population is increasing after a decline caused by human exploitation (Mougin *et al*. 1996a). The birds visit the colony mainly at night but are partly diurnal at some stages of their breeding cycle, unlike their conspecifics at other Atlantic or Mediterranean breeding localities. In the colonies studied, many types of nests were observed. Nests with no roof and sheltered by one wall (4.2%) or with deep, individual cavities (6.5%) were rare. Nests in a simple niche constituted 41.3% of those found, while 29.4% were in a short, individual cavity. Some pairs (18.6%) nested in caves with one or several other pairs (n = 529). The distance to the nearest nest site varied between 0.2 and 6.3 m with 51% being less than 1 m.

However, the distribution of these distances was random and, *sensu stricto,* no high or low density zones could be identified in any colony. Similarly, the distribution of breeders was random with respect to age, breeding experience and 'quality' (J-L. Mougin in prep.). Faithfulness to mates (71.4%, Mougin *et al*. 2000) and to nest sites (81.3%, Mougin *et al*. 1999) in consecutive years was high; re-pairings and changes of site mostly followed breeding failure or temporary non-breeding.

During many years of work on Cory's Shearwater at Selvagem Grande, we have tried to find out whether the influence of near neighbours that was observed previously during chick rearing exists throughout the breeding period and, if so, what advantage resulted for the birds. Similar synchrony in other colonial birds has been linked to the avoidance of predators (Darling 1938), but some social advantage has also been postulated (Hamer & Read 1987).

MATERIAL AND METHODS

Data were collected at four colonies on Selvagem Grande, two of them studied since 1978 and two of them since 1980. A little fewer than 300 nest sites were involved at the beginning of the 1980s and a little more than 500 at the end of the 1990s. In these colonies, visited every year during incubation in June and July, all nests were marked and all breeding adults ringed or recaptured. This allowed us to identify mate changes and divorces. The turnover of mates on the egg during incubation was also checked during daily inspec-
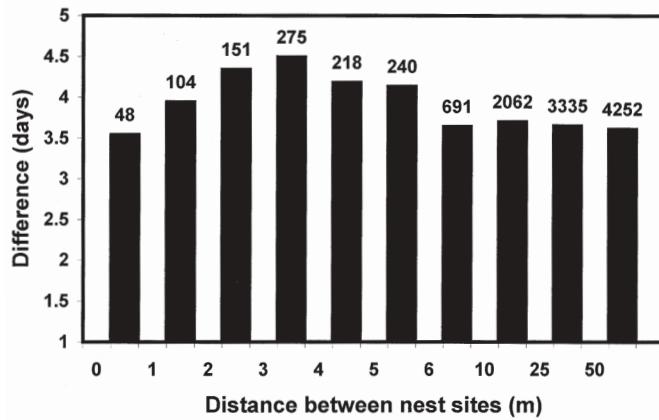
Fig. 1. *Differences between laying dates as a function of the distance between nest sites. Sample sizes are shown above bars.*
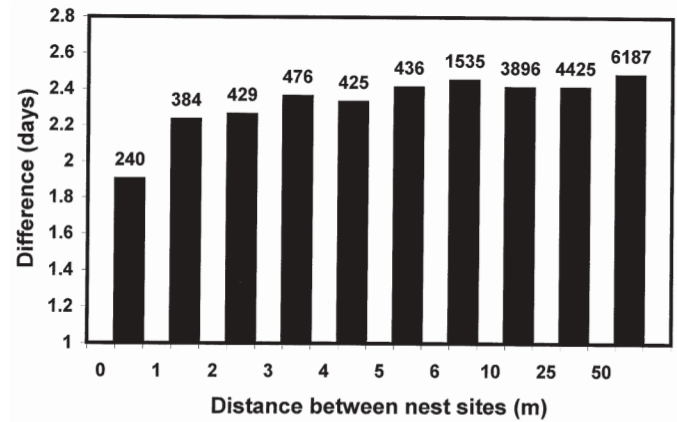

Fig. 2. *Differences between the dates of mate changeovers during incubation as a function of the distance between nest sites. Sample sizes are shown above bars.*

tions. The study of the chronology of laying, hatching and chick fledging permitted the estimation of the duration of incubation and chick rearing. Finally, 60 chicks were weighed daily between hatching and fledging (July to October 1993) to estimate the feeding frequency. The length of the flattened wing (between the carpal joint and the longest primary) was measured every five days on the same birds during the same period. To avoid an accumulation of data, only those collected at the end of July (shortly after hatching), in mid-August, in mid-September and in mid-October (shortly before fledging), were used in the present analyses. All colonies were mapped and all inter-nest distances were known. For all the parameters studied, every nest was compared with every other nest in the same colony.

As this investigation was retrospective, the samples used were somewhat heterogeneous. Not all information was collected for every site in every year (e.g. larger samples could be collected for laying dates than for the daily growth rates of chicks). Thus, in different years, data were collected in one, or the other, or in more than one of our colonies, the population of which increased regularly during the study. These variations account for the somewhat irregular sample sizes obtained for different statistical tests. In the case of data collected during more than one year, one of these years was selected at random. Overall, there was a low percentage of variation among years in the parameters measured.

For statistical calculations, we have made use of analysis of variance, Pearson's correlation, χ^2 and Student's *t*-test. Means are given ± S.D. and with sample size.

RESULTS

Laying dates

On Selvagem Grande the laying period lasted about three weeks, with the experienced, inexperienced and 'mixed' pairs (one experienced and one inexperienced mate) laying at similar average dates ($F_{2, 233} = 2.12$, n.s.), respectively 31.8 May ± 3.8 days (n = 177), 2.4 June ± 2.2 days (n = 10) and 1.7 June ± 3.7 days (n = 49). There was an average of 3.98 ± 3.13 days between the laying dates at different nests sites (0–21 days, n = 18 689). The

difference increased significantly with distance ($r_4 = 0.983$, $P < 0.05$; Fig. 1). Nests less than 1 m apart averaged 3.54 ± 2.37 days difference (range 0–9 days, n = 48), whereas those 3 to 4 m apart averaged 4.49 ± 3.48 days (range 0–15 days, n = 275, $t = 2.49$, $P < 0.05$). However, the effect did not continue at distances greater than 4 m. A slight difference existed between the nests 4 m or more and those less than 4 m apart; respectively, 3.97 ± 3.12 days (range 0–21 days, n = 18 111) and 4.27 ± 3.27 days (range 0–16 days, n = 578), $t = 2.17$, $P < 0.05$.

Turnover of mates during incubation

The average interval between changeovers observed on two nests during the whole incubation period was 2.42 ± 1.72 days (n = 18 433) with an average shift duration of 7.9 days (1–14 days). The greatest synchronisation occurred between nests less than 1 m apart (1.90 ± 1.37 days [range 0–6 days, n = 240]) and the least between those that were more than 50 m apart (2.48 ± 1.77 days [range 0–9 days, n = 6187, $t = 6.4$, $P < 0.01$]) (Fig. 2). The increase with distance was significant up to 6 m ($F_{5, 2384} = 4.02$, $P < 0.01$; $r_6 = 0.86$, $P < 0.05$), levelling off thereafter ($F_{4, 16474} = 4.38$, $P < 0.01$, $r_4 = 0.50$, n.s.).

Incubation and hatching dates

Incubation lasted 52–62 days with an average difference of 1.93 ± 1.36 days between nests (range 0–10 days, n = 2 906), independent of the distance between them ($F_{5, 2900} = 0.786$, n.s. , $r_6 = 0.328$, n.s.). Differences among hatching dates were also independent of the distance among nest sites ($F_{9, 767} = 0.287$, n.s.; $r_{10} = 0.517$, n.s.), presumably because variation in incubation periods among sites swamped the initial synchrony apparent at laying.

Chick rearing

During chick rearing, as the feeding visits of the adults became less and less frequent (Mougin *et al.* 1996b), there was a simultaneous decrease in synchrony among neighbours, presumably due to the increase in inter-feed intervals with chick age. The average difference among sites increased from 0.402 ± 0.567 days after hatching (range 0–3 days, n = 6693) to 0.677 ± 0.787 days

a

b

c

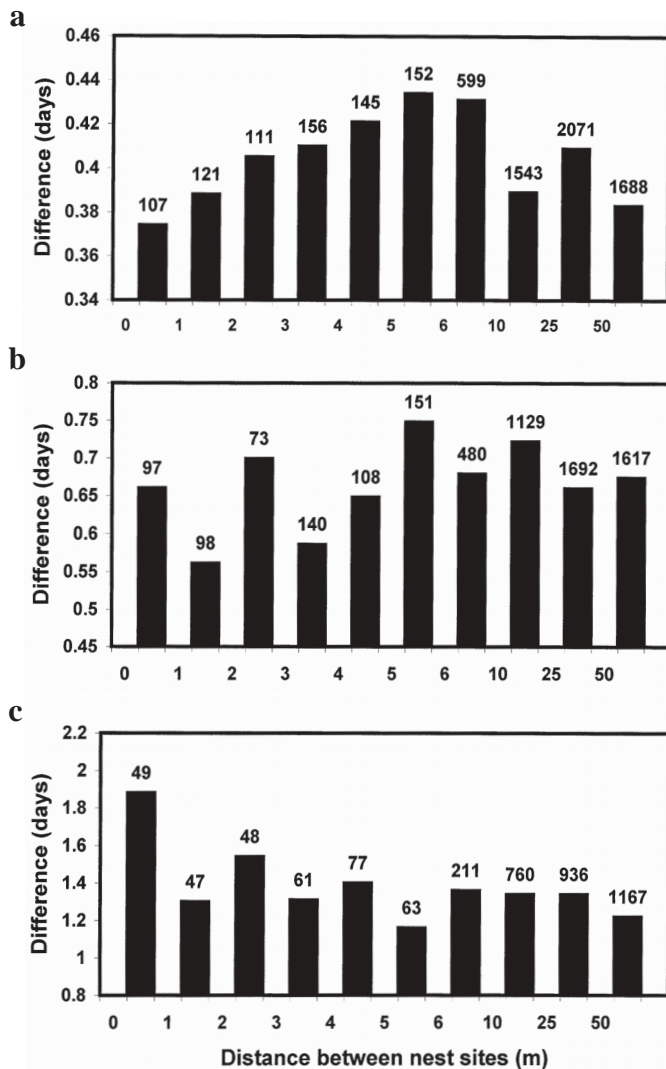
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Fig. 3. *Differences between the dates of the feeding visits of the parents during chick rearing as a function of the distance between nest sites during the days (a) following hatching, (b) preceding and (c) following the attainment of the maximum weight. Sample sizes are shown above bars.*

Fig. 4. *Differences in wing length of the chicks as a function of the distance between their nests. (a) end of July; (b) mid-August; (c) mid-September; (d) mid-October. Sample sizes are shown above bars.*

just before maximum mass was reached (range 0–5 days, n = 5585), and to 1.32 ± 1.28 days just afterwards (range 0–7 days, n = 3419) ($F_{2,\ 15\ 694} = 1\ 318$, $P < 0.01$). The ratio of the average difference to the mean trip duration increased from 0.182 to 0.264.

A significant correlation was found between synchrony and distance between nest sites for nests with young chicks, but only for those less than 6 m apart ($r_6 = 0.992$, $P < 0.01$; Fig. 3). The average values for nests less than and more than 6 m apart did not differ (0.408 ± 0.575 days, n = 792, and 0.401 ± 0.565 days, n = 5901, respectively) ($t = 0.322$, n.s.). For older chicks, no correlation was found between synchrony and distance between nest sites (respectively $r_6 = 0.452$, n.s. and $F_{5,\ 661} = 1.06$, n.s. before and $r_6 = -0.746$, n.s. and $F_{5,\ 339} = 1.77$, n.s. after maximum mass was reached).
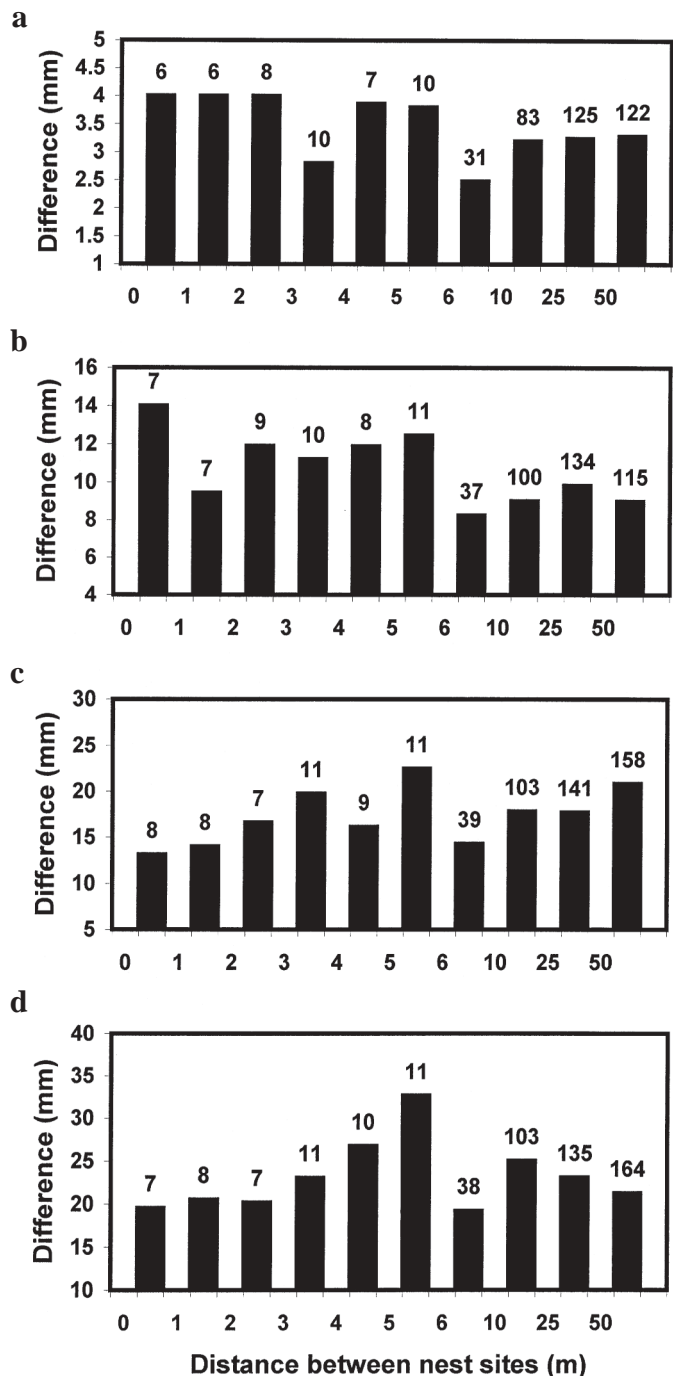
From September onwards, a significant correlation between the difference in wing length of two chicks and the distance between their nests was observed for distances shorter than 6 m (respectively $r_6 = 0.851$, $P < 0.05$ at mid-September and $r_6 = 0.913$, $P < 0.05$ at mid-October) but not for longer distances (respectively $\underline{r}_5 = 0.697$, n.s. and $r_5 = -0.156$, n.s.). Before September the differences among younger chicks was probably too slight to be apparent. Average
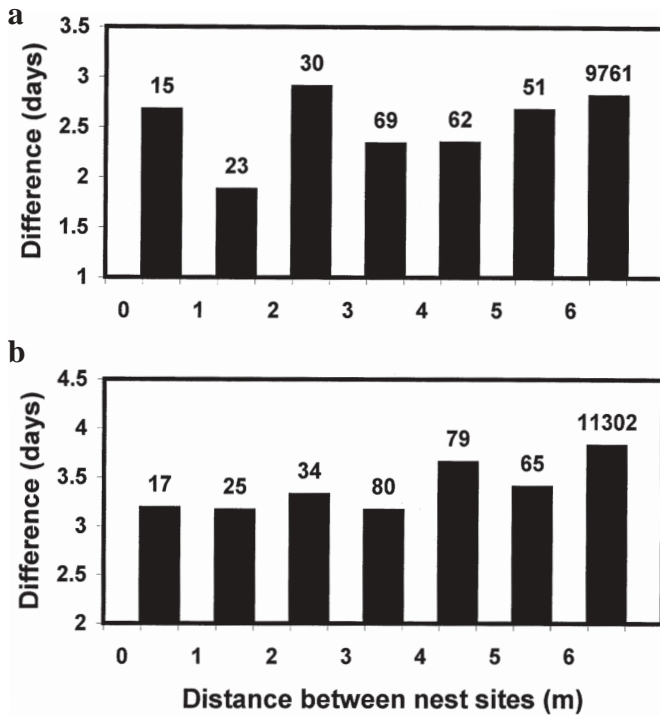
a

b

Fig. 5. Differences between neighbours as a function of the distance between their nest sites at the end of chick rearing. (a) duration of chick rearing ; (b) fledging dates. Sample sizes are shown above bars.

values for chicks less than and more than 6 m apart obtained in September (respectively 17.44 ± 15.87 mm, n = 54, and 18.53 ± 15.34 mm, n = 441) ($t = 0.48$, n.s.) and in October (respectively 24.46 ± 17.00 mm, n = 54, and 22.48 ± 16.81 mm, n = 441) ($t = 0.81$, n.s.) do not differ significantly.

In our sample, chick rearing lasted 91–105 days (n = 142), with an average difference of 2.80 ± 2.16 days (0–14 days, n = 10 011) between nest sites. Distance had no apparent influence on synchronisation ($F_{6, 10\,004} = 1.87$, n.s.; Fig. 5a).

Fledging occurred between 24 October and 12 November (n = 153) with an average difference of 3.81 ± 3.04 days (0–19 days, n = 11 602) between nest sites. There was a non-significant decrease of synchrony with the increase of distance, the difference varying between 3.18 ± 2.04 days (0–7 days, n = 17) for nests less than 1 m apart and 3.82 ± 3.05 days (0–19 days, n = 11 302) for nests 6 m or more apart ($F_{6, 11595} = 0.550$, n.s. , $r_7 = 0.809$, $P < 0.05$; Fig. 5b). The average values given by distances shorter (3.36 ± 2.61 days, n = 300) or longer than 6 m were significantly different ($t = 3.0$, $P < 0.01$).

Pairings

Although slight differences exist between colonies, new mates with previous breeding experience were in most cases very near neighbours during the year preceding their pairing (Fig. 6). An

Colony A
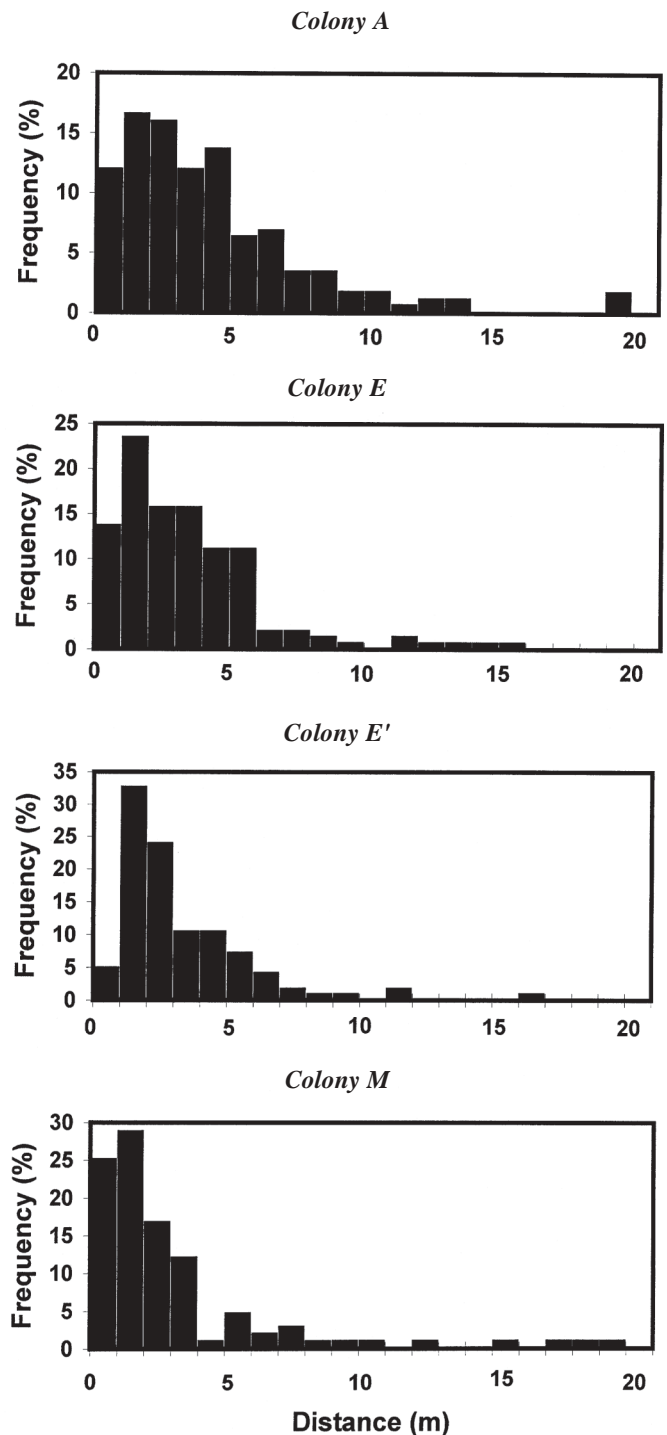

Colony E

Colony E'

Colony M

Fig. 6. The distance between the previous nest sites of the new mates during the breeding year before they paired together in four colonies on Selvagem Grande: A (n = 176), E (n = 154), E' (n = 126), M (n = 108). Six values lying outside the limits of the diagram have not been presented: four for colony A (22.1; 22.5; 30.6 and 60.6 m) and 2 for colony E (28.5 and 58.0 m).

average 13.3% of their nests (n = 564) were less than 1 m apart (4.8–25.0% according to the colony [χ^2_3 = 21.3, *P* < 0.01]) and 77.7% less than 5 m (69.8–83.3% [χ^2_3 = 9.6, *P* < 0.05]). Average values varied between 3.0 ± 3.7 m (n = 108) and 4.8 ± 6.1 m (n = 176) according to the colony ($F_{3,\,560}$ = 3.84, *P* < 0.01) for a general average of 3.8 ± 4.9 m (0.4–60.6 m, n = 564).

DISCUSSION

In the Cory's Shearwater at Selvagem Grande, synchrony is high at the population scale, with laying, hatching and fledging all taking place within 2–3 weeks. The highest synchrony was found among nearest neighbours, i.e. among birds nesting within not more than a few metres of each other. The effect of distance on synchrony disappeared at longer distances as would be expected considering the overall synchrony within the colony. Finally, the pairing of experienced breeders following the loss of former mates nearly always involves near neighbours.

The theory linking the synchrony observed among many species of seabirds to the avoidance of predators is not new (Darling 1938). Observations supporting the theory have been made for larids (Patterson 1965, Velarde 1992) and alcids (Birkhead 1977, Murray *et al.* 1983, Sealy 1976). This explanation also has been proposed for Cory's Shearwaters at Selvagem Grande (Hamer & Read 1987, Jones 1986b), but no predation exists for that species either there or elsewhere, either in the Mediterranean or Atlantic. It has been reported (Zino 1971, Den Hartog *et al.* 1984, Zino & Biscoito 1994) that the Yellow-legged Gull *Larus cachinnans* is a predator on Cory's Shearwaters, but our observations suggest that this is incorrect. Yellow-legged Gulls never attack adults. If they sometimes feed on eggs or chicks, the eggs were already deserted and the chicks dead. Moreover, even if predation can explain synchrony and nest density at the colony or population scale, it seems unable to take into account satisfactorily a higher synchrony among near neighbours.

Hamer & Read (1987) also postulated the existence of some social advantage resulting from synchrony between near neighbours. In fact, although the most striking feature of relations between neighbours is the frequency of fights during the pre-egg stage, these relations do not always involve conflicts. The long faithfulness of the birds to their mate and nest site (Mougin *et al.* 1993) creates a similar 'fidelity' to their neighbours, which may explain the reciprocal influence exerted.

Moreover, the effects on synchrony of distance between nests are not trivial, as they involve substantial numbers of birds: in our colonies, 1.09 ± 1.09 nests exist within a 1 m radius around a nest (0–4, n = 211) and 15.61 ± 7.02 within a radius of 6 m (2–31, n = 211). Thus, if the former mate fails to appear at the beginning of a new breeding season, pairing will be particularly easy with a long-acquainted neighbour similarly widowed. If familiarity with near neighbours creates improved synchrony during breeding, it also facilitates swift pairing at the beginning of a new breeding cycle if the former mate is absent. This could prevent the loss of a breeding year. Non-breeding seldom occurs in the Cory's Shearwater (Mougin *et al.* 1997).

Ring recoveries show that, as occurs in other petrels (Storey & Lien 1985), pre-breeders are present in the same colonies years before their first breeding, males being relatively faithful to their birth place. Thus, these young birds may also be familiar with their long acquainted neighbours.

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