FAITHFULNESS TO MATE AND NEST SITE OF BULWER'S PETREL *BULWERIA BULWERII* AT SELVAGEM GRANDE

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SUMMARY

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Relatively low on average – 79% of the birds are at the same nest site and 79% also pair with the same mate during two consecutive breeding years – the faithfulness to mate and nest site is not the same in all colonies, this depending on the stability of the substratum where the nest sites are located. High in colonies where they can be used during years, it is lower where their duration is shorter. Nevertheless, these differences have no effect on the breeding success which is the same in both types of colonies.

RÉSUMÉ

Relativement faible en moyenne – 79% des oiseaux occupent le même nid et 79% également sont appariés avec le même conjoint pendant deux années de reproduction consécutives – la fidélité au partenaire et au nid varie d'une colonie à l'autre en fonction de la stabilité des nids. Elevée dans les colonies stables, où les nids peuvent être occupés pendant des années, elle est beaucoup plus faible dans les colonies instables où leur durée est plus faible. Ces différences n'ont cependant aucun effet sur la réussite de la reproduction qui est la même dans les deux types de colonies.

INTRODUCTION

In a population of procellariids, faithfulness to mate and nest site are usually studied by marking all the nest sites and banding all the birds of a colony and, during an adequate number of following years, by controlling all the nest sites and all the birds.

However, it is not so easy for the Bulwer's Petrel *Bulweria bulwerii* of Selvagem Grande (30°09'N, 15°52'W). This very small petrel, the smallest of the procellariids (body mass *c.* 100 g), has access to breeding holes inaccessible, if not invisible to the observer who can never be sure to have taken into account all the nests of a colony. If banded birds move to a new nest site (which is quite frequent because the longevity of the nests is often much lower than that of the birds) the probability of further control is rather low. In fact, the recapture rate is far lower than the survival rate, which means that many birds escape observation, often definitively if they have moved to an inaccessible nest. So some calculations and adjustments, the details of which are given in the following pages, are necessary, permitting the estimation of the number of birds having left the nests under study and thus a better knowledge of the faithfulness to mate and nest site.

METHODS

Sources of data

The study has been carried out since 1982 in two colonies at Selvagem Grande and has involved 160 nests and 184 birds studied during 2–14 years. The first colony (colony A) is established in a wall made of big stones among which the birds breed. Owing to the general stability, very few nests disappear from year to year. The second group (colony B) has colonized unsteady scree and decaying walls where the longevity of nesting hollows is often very short. Nest density is variable but in favourable sites it can be as high as 2–3 nests/m^2. During visits paid every year to the colonies, mostly during incubation at the end of June and in July, all marked nests are examined, all the new accessible nests marked and all the adults recaptured or banded. To avoid unnecessary disturbance, the birds are handled only once each year, and one bird at each nest site is marked with white paint on the forehead and tail, to differentiate it from its mate. Sex is determined by bill measurements (Mougin 1989).

Preliminary computations

Nest changes

In the study colonies at Selvagem Grande, 19.7% of the banded birds surviving in a given year disappear during the following (n=734) – this figure including both dead birds and birds having moved to an unmarked inaccessible nest. The annual mortality rate of the adults being 4.1 % (unpubl. data), the rate of passage from marked to unmarked nests is thus 15.6%. Moreover, 5.6% of the birds back to marked nests (n=323) – 4.5% of the total numbers – have moved from a marked nest site to another marked nest site. So, 79.0% of the surviving birds are faithful to their nests.

TABLE 1

FAITHFULNESS TO NEST SITE, RATE OF REMATING AND CAUSES OF MATE CHANGES AMONG BULWER'S PETRELS AT SELVAGEM GRANDE. RESULTS ARE GIVEN IN PERCENTAGES. REMATING ALWAYS MEANS NEW MATING WITH THE FORMER PARTNER

	Birds breeding	Remating rate	Birds remated	Birds looking for a mate
At the same nest site	79.0	90.8	71.7	7.3
At a new nest site	21.0	35.7	7.5	13.5
Total	100		79.2	20.8
		Mate absent		
		– widowed		3.9
		– mate of sabbatical bird		6.1
		Mate present		
		– divorced		10.8

Rematings

90.8% of the birds (n=260) holding the same nest during two consecutive breeding years kept the same mate during the second year, against 35.7% only for the birds having moved to a new nest (n=28) – a very significant difference ($\chi^2_1 = 63.3$, $P<0.01$).

Causes of change of mate

The group of previous breeders looking for a mate at the beginning of a new breeding cycle is formed by divorced and widowed birds and by the mates of sabbatical birds – i.e. temporarily non-breeding breeders.

The annual adult mortality rate being 0.0411, widowed birds represent $0.0411 – (0.0411)^2$ or 3.9% of the total number of birds. In our sample, the sabbatical years represent 17% of the breeding years (unpubl. data). This being so, the absence of a bird often leading to the absence of its mate, only 51.4% of the previous mates look effectively for a partner (unpubl. data). So the number of birds looking for a mate is 35.7% of the number of sabbatical birds or 6.1% of the total number of birds. Finally, the number of divorced birds is procured by substracting from the number of lonesome previous breeders the cumulated total of widows and mates of sabbatical birds. It then amounts to 10.8%. The results of these preliminary computations are presented in Table 1.

RESULTS

General results

Table 2, derived from Table 1, allows us to draw some conclusions :

Faithfulness to nest site is low: nearly four-fifths only of the surviving birds hold the same nest site than during the previous breeding cycle. However, if the data given by the unstable nests are dismissed, the reoccupation rate is then 87.8% (n=189). Taking into account the annual adult mortality (4.1%), the rate of faithfulness to nest site is 91.6% – the longer the faithfulness from year to year the better it is ($r_{12} = 0.797$, $P<0.01$).

The nest changes of a few birds only (n=28) have been observed, the new and the former nest being then only a few metres apart. 42.9% of the new nest sites had never been attended previously and 57.1% had been – both previous mates (53.5%) or only one of them (3.6%) having then left it. 35.7% of the moving birds have remated with their former partner and 64.3% have taken a new mate – a new breeder (35.7%) or a lonesome former breeder (28.6%).

Nearly four-fifths of the birds remate with their former partner. The change of mate arises almost equally from its absence, following its death or its temporary non-breeding, or from a divorce. In fact, 11.8% of the birds pair with a new mate in the presence of the former, i.e. divorce *sensu stricto*, and the faithfulness to the former mate is thus high.

TABLE 2

FAITHFULNESS TO MATE AND NEST SITE AMONG BULWER'S PETRELS AT SELVAGEM GRANDE

Faithfulness to mate and nest site	
– birds breeding at the same nest site	260 (79.0%)
– remating with the same partner	266 (79.2 %)
– breeding at the same nest site with the same mate	236 (71.7%)
Birds breeding at the same nest site – with the same mate	266 (79.2%)
Birds moving to a new nest site – with the same mate	10 (35.7%)
Birds remated with their former partner – on the former nest site	236 (90.5%)
Birds mated with a new partner – on the former nest site	24 (35.1%)
Birds paired with a new mate – former mate present	46 (51.0%)
Birds whose former mate is present – remating with the former partner	266 (88.2%)
Birds breeding at a new nest site and/or with a new mate	
– new nest site	87 (74.2%)
– new mate	81 (73.5%)

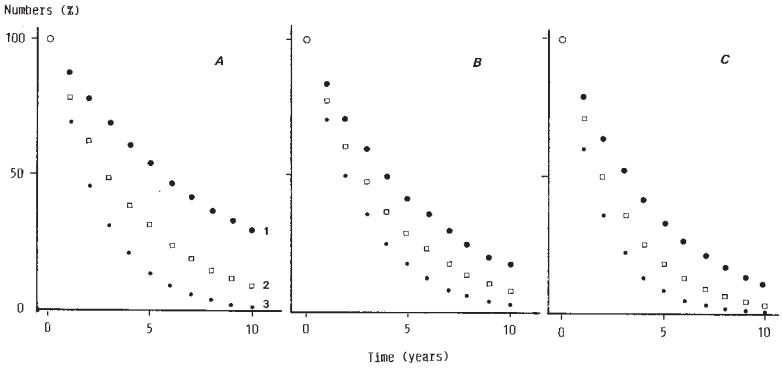

Fig. 1. *Evolution during the years of faithfulness to mate and nest site of Bulwer's Petrels at Selvagem Grande.* ***A****: faithfulness to nest site;* ***B****: faithfulness to mate;* ***C****: faithfulness to mate and nest site.* ***1****: colony A;* ***2****: both colonies;* ***3****: colony B.*

Faithfulness to the former mate and faithfulness to the former nest site are linked. A bird seldom breeds at a new nest site with its former mate and even more infrequently at its former nest site with a new mate. In fact, birds having taken a new mate breed mostly at a new nest site. Birds remated with their former partner breed even more frequently at the former nest site. In connection with this, the rate of divorce is low among birds faithful to their nest site (7.1%) and far higher among those which are not (40.3%).

In all, the joint fidelity to mate and nest site from year to year is only 72%. Among the birds which are not at the beginning of a new breeding year at the same nest site with the same mate as during the previous year, the same proportion – nearly three-fourths – have changed of nest site and/or of mate.

Mobility is not the prerogative of one sex, males as much as females being likely to change their nest site ($\chi^2_1 = 0.15$, N.S.). It is not either typical of the less experienced birds, the mean experience of the birds faithful to their nest site – 3.9 ± 2.2 years (2–13 years, n=288) in our sample – being the same (t = 0.08, N.S) as that of the birds which are not – 3.9 ± 1.6 years (2–8 years, n=21). Finally, birds moving in search of a new mate are, in the same proportions as those which take a new mate at their former nest site, liable to pair with birds which are less, equally or more experienced than them ($\chi^2_1 = 2.72$, N.S.).

With mean rates of 0.790 for faithfulness to the nest site, 0.792 for faithfulness to the mate and 0.717 for faithfulness both to mate and nest site, a considerable number of birds will have changed their mate and/or nest site after some years. In fact, after 10 years, about 10% of the surviving birds will theoretically be still settled on the same nest site, about 10% paired with the same mate and less than 4% settled with the same mate on the same nest site (Fig. 1) – the numbers of surviving birds amounting then to 65.7% of the initial numbers. With an annual mortality rate of 4.1% and a mean longevity of 23.8 years, the breeding life of Bulwer's Petrel at Selvagem Grande is a little less than 20 years long. This being so, very few birds will not change their mate or nest site during their life.

TABLE 3

FAITHFULNESS TO MATE AND NEST SITE IN TWO COLONIES OF BULWER'S PETRELS AT SELVAGEM GRANDE

Colony	A	B	χ^2
Faithfulness to mate and nest site			
– birds breeding at the same nest site	109 (88.3%)	151 (67.7%)	17.9 ***
– remating with the same partner	103 (83.2%)	163 (73.0%)	4.7 **
– breeding at the same nest site with the same mate	98 (79.3%)	138 (61.9%)	11.2 ***
Birds breeding at the same nest site			
– with the same mate	98 (89.8%)	138 (91.4%)	0.15 *
Birds moving to another nest site			
– with the same mate	2 (33.3%)	8 (36.4%)	0.01*
Birds remated with their former partner			
– on the former nest site	98 (95.3%)	138 (84.8%)	7.2 ***
Birds mated with a new partner			
– on the former nest site	11 (53.4%)	13 (21.6%)	7.4 ***
Birds paired with a new mate			
– former mate present	8 (39.5%)	38 (62.3%)	3.5 *
Birds the former mate of which is present			
– remating with the former partner	103 (92.6%)	163 (81.3%)	7.5 ***
Birds breeding at a new nest site and/or with a new mate			
– new nest site	15 (56.7%)	72 (84.7%)	9.1 ***
– new mate	21 (81.1%)	60 (70.8%)	1.1 *

*** P <0.01 ; ** P <0.05 ; * N.S.

Differences between colonies

The faithfulness of the birds to their mate and nest site being linked to the longevity of the nests, the results provided by the various colonies are likely to be different, in connection with their stability. The values of the various parameters provided by our A and B colonies are compared in Table 3.

As expected, differences exist, which are often significant. The birds breeding at the same nest site or with the same mate or both are more numerous in colony A, more stable than colony B, and the rate of divorce is lower. On the other hand, faithfulness to the mate with a change of nest site or without it is the same in both colonies but the second is far higher. So the important differences existing between the colonies are only caused by the instability of the second one and the resulting high frequency of nest site changes. The nests having a short life, the birds move frequently; their faithfulness to their mate being lower in case of nest change, they also often take a new mate.

So pair stability will be much higher in a stable than in an unstable colony (Fig. 1). After 10 breeding years, 29% of the surviving birds will still breed at the same nest site in the first one *v* 2% in the second; 16% will be paired with the same mate *v* 4% ; and 5% will hold the same nest site with the same mate *v* less than 1%.

This being so, the mobility of the birds breeding in unstable colonies does not seem to affect their hatching success which is the same as that of their congeners breeding at more stable sites – 0.668 (n=223) in colony B *v* 0.712 (n=132) in colony A ($\chi^2_1 = 0.71$, N.S.).

DISCUSSION

At the same locality, Selvagem Grande, faithfulness to mate and nest site of Bulwer's Petrel varies from colony to colony according to the available habitats; in the more unstable breeding sites the birds display a mobility they do not show in more stable places.

In fact, the Bulwer's Petrel is fundamentally faithful to its mate and nest site and it shows that clearly when possible – its faithfulness to the nest site is 91.6% and to the mate 92.6% at stable sites, not surprising for a bird belonging to a family, the Procellariidae, where such a behaviour is the rule, irrespective of body size or breeding habits – 0.86 ± 0.07 on average (0.72–0.96) for faithfulness to the mate (11 species) and 0.88 ± 0.05 (0.83–0.97) for faithfulness to the nest site (nine species, but not the giant petrels *Macronectes* spp., the colonies of which often move from year to year) (Mougin 1970, 1975, Macdonald 1977, Guillotin & Jouventin 1980, Hunter 1984, Ollason & Dunnet 1986, Voisin 1988, Brooke 1990, Marchant & Higgins 1990). But the sites available for breeding are not always optimal and the bird must breed in a variety of holes – interstices between the stones of walls and screes, but also rock cracks and burrows – and sometimes even in the open, which incidentally is surprising for a bird liable to predation by Yellowlegged Gulls *Larus cachinnans* (Mougin & Stahl 1981). However, the bird is opportunistic and it can change its behaviour and strategy to cope with all situations without affecting its breeding success – which is the same in all colonies whatever the breeding conditions may be, and very close to that displayed by other procellariids (Mougin 1970, 1975, Macdonald 1977, Guillotin & Jouventin 1980, Hunter 1984, Ollason & Dunnet 1986, Voisin 1988, Brooke 1990, Marchant & Higgins 1990).

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