Behaviour and patterns of attendance of non-breeding birds at the breeding colony in a Buller's albatross *Thalassarche bulleri* population at The Snares

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Abstract Colony attendance and behaviour of non-breeding Buller's albatrosses *Thalassarche bulleri* were studied at 2 Snares Is colonies in 2000-2004. Non-breeders comprised 31-32% of birds ashore in Mar-May (incubation to early chick-rearing), 44% in Jul (late chick-rearing), and 51% overall. Among non-breeders, the proportion of adults that had been recorded breeding in previous years decreased from 47% in Mar to 4% in Jul, with prebreeders (known-age birds that had not been observed breeding) dominating the composition overall (80%). The percentage of surviving birds seen ashore was 59% among prebreeders aged 6 years (modal age of first return), 88% among experienced prebreeders (birds that had been recorded ashore in >1 breeding season), 86% among remating (widowed or divorced) adults, and 63% among sabbatical (birds that had been recorded breeding in previous years, but were not breeding in the year of observation) adults. Colony attendance period was shortest among inexperienced prebreeders (latest birds to arrive), longest among 3rd year (i.e. known-age birds recorded ashore for the 3rd year) prebreeders (early arrival, late departure), and intermediate among last-time prebreeders and former breeders (early arrival, departure in mid-season). Failed breeders attended for up to 3 months, but departed after May irrespective of failure date. Birds stayed ashore for longer and at sea for shorter periods as they gained experience; the percentage of days ashore increased up to the 3rd prebreeding year, and was higher in males than females. Movements between colonies and subcolonies were most frequent during the first 3 prebreeding years. Prebreeders frequently joined display groups during their first 2 years (34% of observations in May), and associated with a nest site in May-Jul of their 3rd year. Among remating adults, displaying was most frequent in females and early in the season (Mar); their behaviour converged towards that of paired adults by May. Attendance patterns and behaviour were broadly similar to those of other albatrosses, except for earlier departure during the last prebreeding year not previously reported in an annually breeding species.

Keywords known-age; prebreeder; colony attendance; breeding season; albatrosses; *Thalassarche*

INTRODUCTION

In albatrosses, immature birds make their first landfall when on average 3-8 years old, and attend colonies as prebreeders for 2-6 seasons before their 1st breeding attempt (Fisher & Fisher 1969; Jouventin & Weimerskirch 1984; Pickering 1989; Weimerskirch 1992; Robertson 1993). Once adult, an average of 10-30% (annually breeding species) or 50-70% (biennial breeders) of paired birds skip breeding for typically 1-2 seasons between successive attempts (Harris 1973; Fisher 1976; Jouventin & Weimerskirch 1988;

Croxall 1991; Croxall *et al.* 1998; Sagar & Warham 1998), and most widowed birds also take 1-2 seasons to remate (Tickell 1968; Fisher 1976; Jouventin *et al.* 1999; Sagar *et al.* 2002). All such birds may attend and thus forage from the same colonies as breeding adults (Fisher & Fisher 1969), with the proportion coming ashore during non-breeding years ranging from 0-39% among sabbatical adults of biennial breeders (Tickell & Pinder 1967; Croxall 1991; Hector *et al.* 1986), to 67-82% among prebreeders (from modal age at first return) and former breeders of annually breeding species (Fisher & Fisher 1969; Anderson *et al.* 2002). As a result, non-breeders typically account for between a third and half of the birds associated with breeding colonies

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(black-footed albatross *Phoebastria nigripes*, sooty albatross *Phoebetria fusca*, and wandering albatross *Diomedea exulans*; Woodward 1972; Weimerskirch 1982; Pickering 1989), with up to 72% non-breeders reported in a Laysan albatross *Phoebastria immutabilis* population during a period of heavy disturbance (Woodward 1972). In addition to those birds, failed breeders, which on average account for 30-75% of annual breeding cohorts (Warham 1996), may also attend colonies for several weeks before dispersing.

Colony attendance by non-breeders has been extensively studied in wandering (Pickering 1989), royal *Diomedea epomophora* (Robertson & Richdale 1993), Laysan (Fisher & Fisher 1969) and sooty albatrosses (Jouventin & Weimerskirch 1984), with information also available for the waved *Phoebastria irrorata* (Harris 1973), black-browed *Thalassarche melanophrys* and grey-headed *Thalassarche chrysostoma* albatrosses (Tickell & Pinder 1975). Non-breeders of those species attend colonies from the pre-egg stage through to the early (wandering, royal, grey-headed), mid (Laysan, black-browed) or late part of chick-rearing (waved, sooty), with overall attendance periods ranging from 160-180 d (wandering, black-browed, grey-headed) to 260-280 d (waved, sooty). In all species, young and inexperienced prebreeders arrive latest, with a progression towards earlier returns and longer attendance periods in subsequent prebreeding years typical of long-lived seabirds (Harrington 1974; Nelson 1978; Ainley *et al.* 1983; Hudson 1985). In the last season before breeding, prebreeders return at about the same time as breeding birds, but, depending on species, depart either early (incubation period, biennially breeding wandering and sooty albatrosses) or late in the season (up to the end of fledging, annually breeding waved albatrosses). Former breeders tend to return at the same time as breeding birds; depending on species and status, they depart during the latter part of incubation (wandering, royal, sooty albatrosses; sabbatical Laysan albatrosses) or chick-rearing period (remating Laysan albatrosses). Colony attendance after breeding failure also varies according to species, with biennial breeders dispersing shortly after failure (Richdale 1952; Tickell & Pinder 1975), whereas annual breeders continue to visit their colonies for up to 1-4 months, less frequently so and for a shorter time as the season progresses (Fisher & Fisher 1969; Harris 1973; Tickell & Pinder 1975; Prince *et al.* 1998).

Least known is how non-breeders allocate their time between colony attendance and foraging. In the larger albatrosses (no data for other species), males spend more days ashore than females, and the percentage of days ashore increases from 11-27% in inexperienced prebreeders to 32-37% in experienced prebeeders and former breeders (wandering and royal albatross respectively;

Pickering 1989; Robertson & Richdale 1993). Documented attendance patterns of individual wandering and Laysan albatrosses suggest that non-breeders of these species alternate between spells ashore of up to 7 or 33 days, and spells at sea of up to 33 or 15 days respectively (Fisher & Fisher 1969; Tomkins 1985).

In this paper, we present the results of a study of attendance patterns and behaviour of non-breeders in an annually breeding albatross, the Buller's albatross. The main objective of this study was to determine colony attendance parameters for various categories of non-breeders and failed breeders; these parameters were used as inputs into an individual-based population model developed to simulate the distribution of central-place foraging birds (Broekhuizen *et al.* 2003). A detailed description of the attendance of non-breeders is also needed to provide information for a better understanding of the mechanisms underlying such behaviours.

METHODS
Study area and data collection
The study was carried out at North East I, The Snares (48°S 166°E), during the 2000-2004 breeding seasons. Attendance and behaviour of non-breeders was recorded in adjacent study plots (discrete subcolonies) established within the Punui Bay and Mollymawk Bay colonies (3 and 4 study plots respectively), both located on the east coast and about 650 m apart. In 2 study plots (hereafter main study plots) within each colony, all breeders and chicks had been banded and monitored annually since 1992; most cohorts of chicks raised in the additional plots were also banded during that period.

All study plots were monitored daily for 2-3 weeks during the incubation period (2000-04, extreme dates 16 Feb - 19 Mar), early part of the post guard stage (2001, 18 May - 4 Jun), and late part of chick-rearing (2000-03, 4 Jul - 5 Aug), hereafter referred to as Mar, May, and Jul. The only earlier records were made during a brief trip at the start of the 2002 breeding season (17-21 Dec 2001, pre-egg stage). During each field trip, banded non-breeders present in the study plots were caught during their first visit ashore, identified, and colour-coded with stock dyes for subsequent identification without further handling. In Mar 2000 and 2001, all unbanded non-breeders were also caught, banded, measured for sex determination (based on bill depth and tarsus width, Sagar *et al.* 1998), and colour-coded. Using this method the sex of an estimated 97% of adult birds (including prebreeders) could be classified correctly (Sagar *et al.* 1998). During other field trips, the number of unbanded non-breeders present in the study plots was recorded during each daily check. For banded birds, we recorded the location, behaviour, and identity of associated birds

during each visit ashore. Behaviour was categorized as alone, alone at nest site, displaying with another bird, displaying in a group, in pair (birds sitting side by side or preening each other), in pair at nest site.

Data analysis

Non-breeders were categorised using their recapture histories up to 2004 and the following definitions. *Prebreeder*: bird banded as chick and never recorded breeding, categorised according to experience (number of seasons ashore including season of observation). *Presumed prebreeder*: bird banded as a non-breeder of unknown status in the main study plots since 1998; such birds were not merely transients (80% of 160 banded in Mar and 90% of 40 banded in Jul were recaptured in the same plot in subsequent trips), and were unlikely to have been local or immigrant former breeders (pre-1992 cohorts of local breeders would have all bred again by 1998, and there are no documented instances of colony or subcolony shifts between breeding attempts, Sagar *et al.* 2002). *Remating adult*: former breeder which subsequently bred with a different partner, or (when subsequent partner unknown) whose previous partner was not recorded ashore during the season of observation. *Sabbatical adult*: former breeder which subsequently bred with the same partner, or (when subsequent partner unknown) whose previous partner was seen ashore during the season of observation. *Failed breeder*: breeding adult known to have lost its egg or chick by the time of observation.

Analyses of bird composition, proportions of non-breeders ashore and chronology of colony attendance are based on data from the 2001 breeding season, when recapture effort and seasonal coverage were most extensive. Bird composition was derived from the records of breeding pairs, breeding success and banded non-breeders, and estimates of the number of unbanded non-breeders associated with the main study plots in May-Jul (unbanded birds present in Mar were caught and banded). Those estimates were derived using daily counts of unbanded birds in May and Jul, and attendance patterns of banded prebreeders first seen in May or Jul; the latter group was used as reference because of similarity of arrival periods, and because prebreeders are the only category of non-breeders commonly arriving in mid or late season. For each colony, estimates of the May and Jul totals of unbanded birds were obtained by dividing the mean number of birds counted day^{-1} by the average proportion of reference non-breeders ashore during the same days (to correct for the fact that only a fraction of unbanded birds was ashore each day). Estimates of the May-Jul totals were obtained using the ratio between the May-Jul total and the sum of May and Jul totals among reference prebreeders (to correct for the fact that a proportion of unbanded birds attended the plots in both May and Jul).

For each category of non-breeders, the proportion of birds coming ashore refers to the number of birds recorded in the study plots among those known to be alive in 2001 (based on recaptures up to 2004). Chronology and extent of colony attendance were analysed using dates of first and last sightings of individual birds. Arrival and departure periods were categorized as Mar (first or last sighting 16 Feb – 19 Mar), May (18 May - 4 Jun) or Jul (4 Jul – 5 Aug). Differences in arrival and departure periods between bird categories were assessed by means of pairwise Fisher's exact tests of respective numbers first or last seen in a given period compared to other periods (cells were usually too sparse to test distributions across all periods or bird categories). Differences in minimum attendance periods (first to last sighting) between bird groups were assessed by means of nonparametric tests (Mann-Whitney and Kruskal-Wallis) because of significant deviation from normality (Kolomogorov-Smirnov 1 sample test, $P < 0.001$).

Daily attendance patterns, movements and behaviour were analysed using the pooled data from all years. The percentage of days ashore was calculated for the period associated with the longest field trips (Mar); because of unequal length of field trips, seasonal differences were analysed using attendance records from the first seven days of each field trip. Distributions of the duration of spells ashore and at sea were derived from the records of birds followed for at least 5 days from the 1st day of presence or absence respectively. Rates of movements between colonies (clusters of subcolonies on different coasts, or separated by a gap of at least 500 m) and subcolonies (discrete breeding patches within a colony) were assessed from the percentage of shifts among pairs of consecutive sightings cumulated for each bird category. Percentages of shifts between colonies were derived from the daily visits to the Mollymawk and Punui Bay study colonies, annual visits to other colonies on the south coast (Mar and Jul, all years) and north-east coast (Mar, all years), and survey of the entire North East Island in Mar 2001. Movements between subcolonies refer to shifts between the adjacent study plots in each colony. For behavioural categories, frequencies of occurrence by bird category and period were derived by pooling occurrences associated with each bird visit ashore. Behavioural differences among (seasonal differences) or between categories of birds were assessed by means of G-tests or pairwise Fisher's exact tests (when cells were too sparse). Statistical tests were performed with Systat version 10.2; all tests were 2-tailed with $\alpha = 0.05$. Means are reported ± *SD*.

Table 1 Overall and seasonal composition of Buller's albatrosses (*Thalassarche bulleri*) recorded in the main study plots during the 2001 breeding season.

Status of attending birds	Mollymawk Bay				Punui Bay				All months
	Mar	May	Jul	All months	Mar	May	Jul	All months	2001
Active breeders	218	176	166	166	224	176	172	172	338
Failed breeders	6	9	0	58	6	9	1	58	116
Prebreeders	11	13	32	44	12	12	28	41	85
Presumed prebreeders (banded)	38	15	12	44	47	13	32	60	104
Presumed prebreeders (unbanded)	0	27	77	93	0	26	74	90	183
Remating adults	25	11	6	29	12	6	3	15	44
Sabbatical adults	24	8	1	26	23	10	0	24	50
Total	322	259	294	460	324	252	310	460	920
% Active breeders	68	68	57	36	69	70	56	37	37
% Failed breeders	2	4	0	13	2	4	< 1	13	13
% Prebreeders (incl. presumed)	15	21	41	39	18	20	43	42	40
% Former breeders	15	7	2	12	11	6	1	9	10

RESULTS

Proportion and composition of non-breeders

Overall and seasonal composition of birds which attended the main study plots in 2001 are shown in Table 1. Of an estimated 920 birds present during that year, 49.3% were breeding adults (successful 36.7%, unsuccessful 12.6%), 10.2% were non-breeding adults (sabbatical 5.4%, remating 4.8%), and 40.4% were prebreeders (9.2%) or presumed prebreeders (banded as non-breeders 11.3%, unbanded birds estimated present in May-Jul 19.9%). The percentage of non-breeders (including failed breeders seen ashore) was significantly higher in Jul (late chick-rearing, 44%) than Mar (incubation, 32%) or May (early chick-rearing, 31%; $G_2 = 27.4$, $P < 0.001$). Among non-breeders, the percentage of adults declined from 47% in Mar to 33% in May and 4% in Jul ($G_2 = 126.5$, $P < 0.001$); this trend persists when excluding birds of uncertain status (81, 68, and 15% respectively, $P < 0.001$). Status composition did not differ significantly between the two study colonies (by period: $P > 0.82$; overall: $P > 0.28$).

Sex ratio was not significantly different from parity among sabbatical adults, remating adults or failed breeders (by status: Yates corrected χ^2, $P > 0.47$), but significantly male biased among prebreeders (79%, $n = 320$, $P < 0.001$). Sex ratio among those categories did not differ between colonies (Fisher's exact tests, $P > 0.70$) or periods (G tests, $P > 0.34$). Sex ratio among presumed prebreeders tended to be even at Punui Bay (43%, $n = 152$, $P > 0.24$), but male-biased (although not significantly different) at Mollymawk Bay (64%, $n = 91$, $P < 0.08$), with significant differences between the 2 colonies ($P < 0.01$), but not periods. Within areas and periods in which all non-breeders present were caught (main plots, Mar 2000 and

2001), sex ratio among prebreeders and presumed prebreeders combined was balanced at Punui Bay (51% males, $n = 142$, $P > 0.90$), and male biased at Mollymawk Bay (68%, $n = 103$, $P < 0.01$).

Proportion of non-breeders attending colonies

Of those known to be alive in 2001, 59% of prebreeders aged 6 years (modal age of 1st return, $n = 27$), 75% of prebreeders recorded in one previous season ($n = 48$), and 88% of prebreeders recorded in at least two previous seasons ($n = 30$) were seen ashore. Among former breeders, 86% of remating birds ($n = 36$) and 63% of sabbatical adults ($n = 48$) were seen. Attendance of sabbatical birds involved both partners of a pair (13 pairs), neither bird (7 pairs) or the male alone (4 pairs). There were no significant sexual differences in the proportions seen ashore (by status: Fisher's exact tests, $P > 0.37$).

Chronology and extent of colony attendance

Non-breeders were seen ashore over 230 d from 18 Dec (pre-egg stage) through 5 Aug (late part of chick-rearing), with no sign of an exodus in early Aug. Former breeders were the earliest, and inexperienced prebreeders the latest to arrive ashore (Table 2). Former breeders returned at broadly the same time as breeders, with the first seen on 18 Dec, and 89% present by Mar. Their arrival period showed no significant association with remating or sabbatical status, sex or breeding status in the following year; breeding in the previous year was associated with earlier arrival among remating females (Fisher's exact test, $P < 0.04$, Jul), but not remating males or sabbatical birds. Among prebreeders, the main period of arrival shifted from mid-Jun to early Jul in the 1st year ashore to Mar by the 3rd year (1st v. 3rd year, by sex: $P \leq 0.05$, Mar), with males in their 3rd year still arriving significantly later than
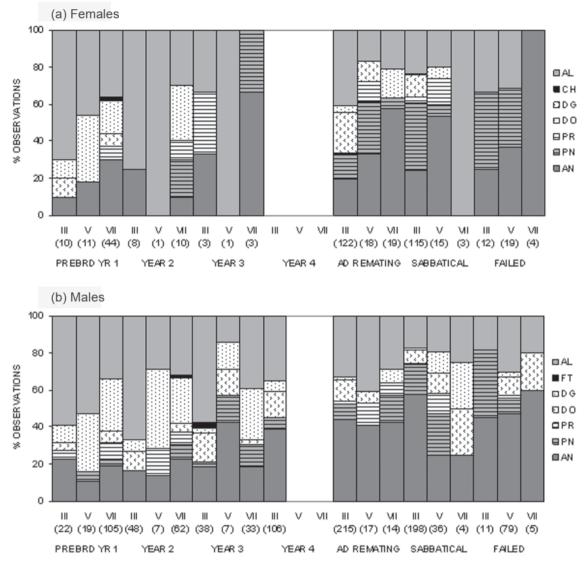
Fig. 1 Behaviour of non-breeding Buller's albatrosses (*Thalassarche bulleri*) in relation to status and period. AL: alone in colony; CH: attending chick; FT: fighting with another bird; DG: displaying among group; DO: displaying with another bird; PR: in pair; PN: in pair at nest site; AN: alone at nest site.

former breeding males ($P < 0.05$, Mar). Among males, breeding in the following year tended to be associated with return by Mar (83% v. 38%, $P < 0.08$) and arrival time similar to that of former breeders ($P > 0.37$). Females tended to return later than males during the first ($P < 0.08$, Jul), but not subsequent years ashore ($P > 0.40$).

Sabbatical adults and failed breeders were the earliest, and prebreeders the latest non-breeders to depart (Table 2). Sabbatical birds and breeders which failed early in the season (Feb to early May)

left mostly before mid-May, with failed breeders leaving significantly earlier than sabbatical birds among females ($P < 0.04$, Mar and May), but not males. Remating adults departed mostly before mid-May (males) or in mid-Jul (females), later than sabbatical birds or failed breeders among females ($P < 0.05$, Jul), but not males. Females tended to depart earlier than males among failed breeders and sabbatical adults, and later than males among remating birds, although none of the differences was significant. Departure period of former breeders was

Table 2 Chronology and extent of colony attendance by non-breeders and failed breeders of Buller's albatrosses (*Thalassarche bulleri*) at The Snares in 2001. Range and *n* in parentheses.

Sex	Status	*n*	% First seen			% Last seen			Mean and SD minimum attendance period (d)	
			Mar	May	Jul	Mar	May	Jul	All birds	Birds seen Mar
M	Prebreeder, 1st year	34	18	35	47	6	18	76	32 ± 53 (1-169, 34)	108 ± 83 (1-169, 6)
	Prebreeder, 2nd year	25	36	12	52	12	24	64	35 ± 58 (1-165, 25)	90 ± 70 (1-165, 9)
	Prebreeder, 3rd year	9	67	11	22	11	11	78	93 ± 74 (4-166, 9)	127 ± 64 (7-166, 6)
	Last-time prebreeder	6	83	17	0	67	17	17	30 ± 42 (1-98, 6)	22 ± 43 (1-98, 5)
	Remating adult	21	95	0	5	57	33	10	47 ± 53 (1-164, 21)	49 ± 54 (1-164, 20)
	Sabbatical adult	26	92	8	0	58	42	0	40 ± 46 (1-105, 26)	43 ± 47 (1-105, 24)
	Breeder, failed Mar	6				67	33	0	32 ± 49 (1-99, 6)	32 ± 49 (1-99, 6)
	Breeder, failed > Mar-May <	42				79	21	0		
	Breeder, failed ≥ May - Jul <	10				100	0			
F	Prebreeder, 1st year	16	6	19	75	6	6	88	6 ± 17 (1-68, 16)	1 (1)
	Prebreeder, 2nd year	7	29	14	57	29	14	57	4 ± 3 (1-10, 7)	6 ± 0 (6-6, 2)
	Prebreeder, 3rd year	3	67	33	0	33	0	67	78 ± 79 (8-164, 3)	86 ± 110 (8-164, 2)
	Remating adult	23	74	13	13	35	35	30	52 ± 66 (1-167, 23)	71 ± 68 (1-167, 17)
	Sabbatical adult	20	95	0	5	60	35	5	37 ± 49 (1-107, 20)	39 ± 49 (1-107, 19)
	Breeder, failed Mar	6				83	17	0	17 ± 39 (1-97, 6)	17 ± 39 (1-97, 6)
	Breeder, failed > Mar-May <	42				90	10	0		
	Breeder, failed ≥ May - Jul <	10				90	10			

Table 3 Patterns of colony attendance among non-breeding Buller's albatrosses (*Thalassarche bulleri*) at The Snares in Mar.

Sex	Status	% Days ashore	Consecutive days ashore (%)				Consecutive days at sea (%)			
			1-2	3-4	≥5	(*n*)	1-2	3-4	≥5	(*n*)
M	Prebreeder, 1st year	10 ± 6 (5-21, 12)	93	7	0	(14)	8	25	67	(12)
	Prebreeder, 2nd year	17 ± 16 (5-53, 17)	84	12	4	(25)	40	8	52	(25)
	Prebreeder, 3rd year	29 ± 11 (15-40, 6)	71	29		(14)	43	21	36	(14)
	Prebreeder, 4th-5th years	42 ± 18 (20-80, 13)	66	20	14	(35)	54	29	18	(28)
	Remating adult	36 ± 23 (5-85, 37)	75	15	9	(85)	53	20	27	(95)
	Sabbatical adult	39 ± 22 (10-80, 30)	69	15	16	(74)	51	26	23	(61)
	Failed breeder		65	35		(17)	55	0	45	(11)
F	Prebreeder, 1st year	5 ± 0 (5-5, 7)	100	0	0	(5)	0	0	100	(5)
	Prebreeder, 2nd year	8 ± 3 (5-11, 5)	100	0	0	(6)	0	20	80	(5)
	Remating adult	21 ± 15 (5-60, 27)	86	14	0	(56)	40	19	40	(57)
	Sabbatical adult	21 ± 15 (5-60, 34)	86	11	3	(65)	36	20	43	(69)
	Failed breeder		90	10	0	(10)	67	0	33	(9)

not related to their breeding status in the previous or following year. First to 3rd year prebreeders departed mostly after Jul, later than remating adults (by sex: $P < 0.001$, Jul); departure periods did not differ between those 3 years, nor between males and females. In males, breeding in the following year was associated with departure before mid-Jul (83% v.27%, $P < 0.02$), and time of departure similar to that of former breeders ($P > 0.30$).

Individual birds were seen ashore over periods of up to 169 d (Table 2). In both sexes, attendance period was shortest among inexperienced prebreeders, longest among 3rd year prebreeders, and intermediate among former breeders (males: Kruskal-Wallis $H_5 = 16.9$, $P < 0.01$; females: $H_4 = 9.6$, $P < 0.05$). Attendance of prebreeders showed no significant changes during the 1st 2 years ashore

(by sex: $P > 0.34$), but expanded significantly during the 3rd year (males: $U = 426$, $P < 0.01$; females: $U = 66$, $P < 0.01$). Early arrival during the 1st 2 years was associated with longer attendance in males but not females (Mar v. May-Jul, males: $U = 525$, $P < 0.001$; females: $P > 0.29$); attendance period of males present in Mar showed no significant changes between the 3 years (Kruskal-Wallis $H_2 = 1.4$, $P > 0.50$). Males tended to come ashore for a longer period than females during all 3 years, although the differences were not significant. In males, the attendance period tended to shorten again in the last year before breeding (last v. penultimate year: $U = 18.5$, $P = 0.07$), when similar to that of former breeders ($P > 0.19$). Attendance period of former breeders showed no significant association with status, sex, or breeding status in the following year;

Table 4 Percentage of shifts between colonies and subcolonies among consecutive recaptures of non-breeding Buller's albatrosses (*Thalassarche bulleri*) at The Snares.

Status	Mar			May-Jul		
	Colonies	Subcolonies	(*n*)	Colonies	Subcolonies	(*n*)
Prebreeder, 1st year	0	0	(5)	0	21	(42)
Prebreeder, 2nd year	1	6	(98)	3	12	(64)
Prebreeder, 3rd year	0	5	(56)	0	21	(23)
Prebreeder, 4th-5th years	0	2	(87)			
Remating adult	0	2	(174)	0	5	(41)
Sabbatical adult	0	7	(251)	0	0	(28)
Failed breeder				0	0	(6)

among sabbatical birds and remating females, birds which bred in the previous year tended to visit colonies over a longer period than those in their 2nd or subsequent non-breeding year (by status and sex: $P < 0.08$; remating males: $P > 0.51$).

Patterns of colony attendance
Individual birds spent up to 60% (females) or 80% (males) of days ashore in Mar, with the lowest mean values recorded among 1st year prebreeders, and highest among experienced prebreeders and former breeders (Table 3). In males, the percentage of days ashore was lowest during the 1st 2 prebreeding years (1st v. 2nd: $P > 0.66$), increased during the 3rd year (2nd v. 3rd: $U = 181.5$, $P < 0.05$), with no further significant changes recorded from the 3rd year onwards ($H_3 = 1.8$, $P > 0.61$; overall: $H_5 = 34.9$, $P < 0.001$); a similar pattern was apparent among females ($H_3 = 17.8$, $P < 0.001$). Attendance of failed breeders was similar to that of experienced prebreeders and former breeders (7 d average, by sex: Mann-Whitney test, $P > 0.38$). Males spent a greater proportion of days ashore than females in all categories, although differences were not significant among 2nd year prebreeders and failed breeders (Mann-Whitney test, $P > 0.32$; all other categories: $P < 0.03$). Attendance decreased between Mar and May-Jul among remating males (7 d average: 38 v. 22%, $U = 339$, $P < 0.01$), but not other categories ($P > 0.10$).

Spells ashore lasted up to 5 (females) or 15 (males) consecutive days, with the shortest spells recorded among 1st year prebreeders, and longest among experienced prebreeders and former breeders (Table 3). In males, the proportion of spells ≥3 d increased from 7 to 29% between the 1st and 3rd prebreeding year, with similar proportions (24-35%) recorded among more experienced prebreeders, former breeders, and failed breeders. A similar trend was apparent among females, although their spells ashore tended to be shorter than those of males in all categories (spells ≥3 d: 0-14%).

Non-breeders were absent for periods of up to 18 (males) or 20 (females) days between consecutive recorded visits, with the longest spells at sea recorded among 1st year prebreeders, and shortest among experienced prebreeders and former breeders (Table 3). In males, the proportion of absences ≥5 d decreased from 67% to 36% between the 1st and 3rd prebreeding years, and 18% in the 4th or 5th years, with comparable values recorded among former breeders (23-27%). Males switched from long to very short (1-2 d) rather than intermediate (3-4 d) absences as they gained experience. The same trend was apparent among females, although long absences tended to be more frequent than among males (all categories except failed breeders).

Movements between colonies and subcolonies
Only 3 non-breeders were recorded shifting colonies between consecutive recaptures. All were 2nd year prebreeders recaptured between the 1st and 2nd year ashore (2) or between May and Jul of the 2nd year (1). Shifts between subcolonies were infrequent during the incubation period (Mar), irrespective of non-breeding status (Table 4). The frequency of such shifts increased significantly during the chick-rearing period (May-Jul) among 1st to 3rd year prebreeders (6 to 17%, Fisher's exact test P < 0.01), but not among more experienced birds (4 - 3%, $P > 0.75$). Percentages of shifts did not differ between males and females (by status and period: $P > 0.30$).

Behaviour
Among adults with an established pair-bond (sabbatical birds and failed breeders, 501 records), 67% attended a nest site, 23% were seen paired with another bird, and 10% were displaying (Fig. 1); differences between the 2 groups were limited a lower incidence of pairings among failed compared to sabbatical males in May (Fisher's exact test $P < 0.01$), and lower nest attendance among sabbatical compared to failed females in Jul ($P < 0.03$). Nest attendance decreased between Mar and May among males ($P < 0.001$), but not females. Nest attendance also decreased between May and Jul among sabbatical birds and failed breeders, but the differences were not significant ($P = 0.10$ and $P > 0.30$, respectively). Nest attendance was more

frequent in males than females in Mar ($P < 0.04$), but not later in the season ($P > 0.27$). Pairing frequency was highest in Mar or May; none of the sabbatical birds or failed breeders seen in Jul was paired with another bird. Display frequency increased between Mar and Jul among males ($G_2 = 8.1$, $P < 0.02$), but not females ($P > 0.19$), and was higher in males than females in May-Jul ($P < 0.02$; Mar: $P > 0.24$).

Among remating adults (405 records), 51% attended a nest site, 17% were seen displaying, and 12% paired with another bird (Fig. 1). Early in the season (Mar), their behaviour differed from that of paired adults by their fewer associations with a nest site (by sex: $P < 0.001$) or another bird ($P < 0.001$), and more frequent displaying (females: $P < 0.02$; males: $P < 0.08$); their behaviour converged towards that of paired adults in all respects in May and Jul ($P > 0.25$). Remating females were seen displaying and away from nest sites more often than males during Mar ($P < 0.01$), but no longer so in May or Jul ($P > 0.31$). In females, pairing with another bird was more frequent in May than earlier or later in the season ($P < 0.02$); remating males showed no significant seasonal changes in nest attendance, displaying or pairing frequency.

Among prebreeders (551 records), 30% attended a nest site, 25% were seen displaying, and 9% paired with another bird; behavioural changes during their 1st 4 years are shown in Fig. 1. First and 2nd year prebreeders were mostly alone in colonies in Mar, but displaying accounted for 25-43% of observations in May-Jul, with no sexual differences in display frequency (by period: $P > 0.33$). In males, displaying frequency in May-Jul was higher than that of remating adults at the start of the season (by year: $P < 0.01$; females: $P > 0.85$). Group displays accounted for most display activities during the 1st 2 years (males: 78%; females 80%), and were proportionately more frequent than among non-breeding adults in Mar (years and sexes combined: $P < 0.01$) and May ($P < 0.001$), but not Jul ($P > 0.62$).

Nest attendance frequency was lower than that of remating or paired adults up to Mar of the 3rd year (periods combined, by sex: $P < 0.01$), but rose to comparable levels in May of the 3rd year among males (57% v. 23% in preceding periods, $P < 0.06$), and Jul of the 3rd year among females (100% v. 26% in preceding periods, $P < 0.03$). Sexual differences were limited to a higher nest attendance by females in Jul of the 3rd year ($P < 0.05$). Pairing frequency among females first increased in Jul of the 2nd year (30% v. 4% in preceding periods, $P < 0.04$), and from then onwards was similar to that of sabbatical females or failed breeders ($P > 0.59$); pairings at a nest site were only recorded in Jul of the 2nd and 3rd years (20-25% compared to 37% in paired adults in Mar, $P > 0.37$). In males, the frequency of pairings increased from 0-5% (Mar-May) to 12% in Jul of the 1st year, and 12-15% in May-Jul of the 2nd and 3rd years (Mar 0-3%), when not significantly different from that recorded among sabbatical males or failed breeders (17%, $P > 0.28$); paired males were mostly recorded away from nest sites during the 1st 2 years (96%, $n = 25$), but always at a nest site from the 3rd year onwards ($n = 15$).

DISCUSSION

Numerical importance and composition of non-breeders

Results of this and other studies highlight the numerical importance of non-breeders even among the land-bound (ie central-place foraging) component of albatross populations. Thus, about half the birds which attended our study plots were non-breeders, a proportion which comes closest to that reported for wandering albatross colonies at South Georgia (Pickering 1989). In waved albatrosses, the proportion of non-breeders (27%) was estimated from recaptures during the incubation period (May-Jun, Anderson *et al.* 2002), which is earlier than the main attendance period of young prebreeders (Aug-Jan, Harris 1973). A similar proportion (30%) would have been inferred for Buller's albatross using a comparable subset of recaptures (Mar, Table 1), suggesting that proportions of non-breeders are similar in both species.

An estimated 80% of non-breeders associated with the study plots were prebreeders, comparable to the 78% and 73-87% reported for sooty and black-footed albatrosses respectively (Woodward 1972; Weimerskirch 1982). Respective proportions of prebreeders and former breeders among colony attending birds are not expected to differ between annually and biennially breeding species, as lower attendance rates among sabbatical birds of biennial species (0-40% v. 63% in annually breeding Buller's albatrosses) are compensated by higher skipping rates (50-70% v. 10-30%), and hence higher proportion of sabbatical birds among adults of those species. The comparatively low proportion of prebreeders reported among wandering albatrosses at South Georgia (67%, Pickering 1989) may have been associated with reduced adult survival (hence higher number of remating birds), male biased adult survival, and difficulty for males to remate at the time of the study (Pickering 1989; Croxall *et al.* 1998).

Colony attendance and behaviour

A potential problem with our data on attendance collected over several discrete sampling occasions is that some individuals may have been present at a time when no observations were made. Such individuals may have been missed entirely from our records. Different capture-recapture approaches have been developed to account for the probability

of missing individual birds when studying the attendance of non-breeders (e.g., Cam *et al*. 1998). However, here we provide a more descriptive approach of how the observations fit hypotheses about the functional role of colony attendance of non-breeding birds.

With birds recorded ashore over a span of at least 230 d, and no sign of an exodus during our latest visits in early Aug (2 weeks before the onset of fledging), the overall period of colony attendance among non-breeding Buller's albatrosses falls within the upper half, and probably towards the upper end of the range recorded in albatrosses. Variations in attendance period do not seem to be related to phylogeny (*Thalassarche* 160 to >230 d, Tickell & Pinder 1975, this study; *Phoebastria* 200-280 d, Fisher & Fisher 1969; Harris 1973), age at 1st breeding (260-280 d in waved and sooty albatrosses), or breeding frequency (annual breeders 160-280 d, biennial breeders 160-260 d). However, all shortest attendance periods were reported from South Georgia (wandering, grey-headed and black-browed albatrosses 160-180 d, Tickell & Pinder 1975; Pickering 1989) suggesting that climate constrains colony attendance of non-breeders at the southern limit of the breeding range.

The progression of colony attendance chronology from inexperienced prebreeders to last-time prebreeders and former breeders is broadly similar to that in other albatross species. Buller's albatrosses typically return ashore for the 1st time at age 6 years, and attend colonies as prebreeders for 4 seasons before starting to breed (Sagar & Stahl unpubl). They return late in the season during their 1st year ashore, extend their spans of days ashore during their 2nd and 3rd years by returning progressively earlier while still departing late in the season, and spend the longest period ashore during their 3rd year. In the last season before breeding, their timetable converges towards that of adult non-breeders, with early arrival combined with departure in mid-season. Earlier departure in the last season before breeding has been reported in biennially breeding albatrosses (Jouventin & Weimerskirch 1984; Pickering 1989), but does not appear to be so in the annually breeding waved albatross. In the latter species, 22% of birds aged 4 years (minimum age at 1st breeding) recaptured at the end of the season bred in the following year (Harris 1973), compared to 7% among birds aged 9 years in Buller's albatross.

Late arrival of young, inexperienced prebreeders is the rule among long-lived seabirds (Danchin *et al*. 1991) and has been variously interpreted as a strategy to optimise information gathering on the quality of potential breeding patches (Boulinier *et al*. 1996) or ensure assortative mating (Fisher & Fisher 1969), although the latter has been shown to result from active mate selection by females rather than mere temporal segregation between age classes (Jouventin *et al.* 1999). There is experimental evidence that birds use conspecific breeding success as a cue for breeding habitat selection (Pärt & Doliguez 2003), and, under this assumption, the optimal time for assessing breeding patch quality is the period of highest correlation between overall and current breeding success at the time of prospecting. In kittiwakes *Rissa tridactyla*, this period coincides with the 2nd half of chick-rearing, and in turn period of highest attendance by prebreeders (Boulinier *et al.* 1996); in this species, prebreeders also preferentially attend and subsequently recruit in high quality breeding patches (Cadiou 1999), consistent with the performance-based conspecific attraction hypothesis.

In Buller's albatross, breeding habitat selection seems to proceed stepwise during the 1st 3 years ashore, starting with colony prospecting during the 1st 2 years (as observed in Laysan albatrosses, kittiwakes and alcids; Fisher & Fisher 1969; Harris 1983; Porter 1988; Halley *et al.* 1995) and breeding patch (subcolony) prospecting up to the 3rd year. This is followed by nest site selection during the 3rd year (as observed in wandering albatrosses, Pickering 1989). As predicted from the use of public information (breeding success) to assess patch quality, shifts between subcolonies were more frequent during the chick-rearing than incubation period, suggesting that prebreeders deliberately target this period for their prospecting activities. This may even apply to the selection of a nest site within a patch, as the 1st association with a nest site (in the 3rd year) was also recorded in May (males) or Jul (females).

Participation in display groups (gams) was the main social activity of prebreeders during their 1st 2 years ashore. As in wandering albatrosses (Pickering & Berrow 2001), display groups were mostly associated with prebreeders, with specific locations at the periphery of subcolonies, and composed of nuclei of males overflown and joined by prospective females which initiated most bouts of display. This suggests an analogy with the traditional display arenas of lekking species, and applicability of the female preference model (greater attraction to male groups; Bradbury 1981) to explain the evolution of such groups, albeit not for the purpose of instant mating. Participation in such group displays would allow simultaneous gathering of information on multiple partners (likely to be more efficient than sequential mate sampling, and increasingly so as the time needed to gather the relevant information increases), and possibly involving information on synchronicity of returns ashore among prospecting birds (which would explain the protracted involvement of prebreeders in such displays).

Early arrival of former breeders is consistent with the pattern recorded in other albatross species. In Buller's albatross, adult mortality occurs primarily during the non-breeding season (Sagar & Stahl, unpubl.), which implies that most widowed birds return at start of the following season unaware of the loss of their partner. Presumably because of the opportunity costs associated with each non-breeding year (6% of median reproductive period, Sagar *et al.* 2002), most remating birds were actively prospecting for a partner by mid-Feb (1.5 months after their probable return), wandering between nest sites (most pronounced in females, but also apparent in males) and displaying with single rather than groups of other birds. Most widowed/divorced birds appear to have formed a new pair bond by mid-May (4.5 months after probable return), when their behaviour was similar to that of paired non-breeding adults. Thus, as documented in wandering albatrosses (Pickering 1989), pair formation appears more rapid in former breeders than prebreeders, either because of greater experience in mate selection, or knowledge of a range of potential partners acquired during group displays during prebreeding years. Males may continue such information gathering in their adult years, as failed breeders, sabbatical adults and even chick-feeding birds were seen joining group displays towards the end of the season; it is not clear why females apparently do not do this. In Buller's and other albatrosses, remated birds may switch back to their former partner if the latter returns in a subsequent season (Fisher & Fisher 1969; Croxall 1991; Sagar & Stahl unpubl.), consistent with a bet-hedging strategy aimed at minimising the number of lost breeding attempts.

Later departure of females among remating adults together with the observation that females take longer to resume breeding with a new partner (Sagar *et al.* 2002) suggests that females have greater difficulty in remating than do males. This disparity is probably not caused by a lower availability of male partners, as sex ratio among non-breeders was either balanced or male-biased, and may indicate greater selectivity by or against remating females. Albeit increasing their chances of remating in a single season, longer attendance may be costly to females and possibly related to their later arrival in subsequent non-breeding seasons; if some of those birds were indeed remated but failed to return in time to breed, this would provide a plausible explanation for the longer time to remate taken by females.

In 2001, the arrival time of sabbatical birds was not significantly different from that of newly remating birds, suggesting that non-breeding in such birds was not related to a delayed arrival of their partner, or at least not beyond the time of our 1st field trip. This may not be the reason in years of poor food supply, as a late and major influx of sabbatical birds with low body mass has been documented in the Laysan albatross, coinciding with a year of low breeding rate (Fisher 1967; Fisher & Fisher 1969). Proposed functions of colony attendance by paired non-breeding adults (sabbatical birds and failed breeders) include assessment of the partner's survival, nest defence, and pair bond maintenance (Croxall 1991). The nest defence hypothesis is consistent with the general disappearance of sabbatical birds and failed breeders after May, coinciding with the end of the nest site selection period among prebreeding males, the most likely competitors for nest sites. However, neither of the proposed functions would have had a significant effect in 2001, since departure date showed no association with breeding status in the following year. Alternatively, colony attendance by paired birds may be a by-product of endogenous hormonal cycles, as suggested by the concentrations of prolactin (associated with parental care) among adult albatrosses and penguins being unaffected by breeding failure or experimental manipulation of incubation period (Hector 1988; Garcia *et al.* 1996; Vleck *et al.* 2000). Under this hypothesis, the marked decrease of prolactin concentrations at the end of the brood period (Hector *et al.* 1986) would explain the rapid dispersal of birds known to have failed after that time (May onwards).

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