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Speciation through temporal segregation of Madeiran storm petrel (*Oceanodroma castro*) populations in the Azores?

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Madeiran storm petrels *Oceanodroma castro* breed on three small islets in the Azores: Vila, off Santa Maria, and Praia and Baixo, off Graciosa. Analysis of data on brood patch, incubation periods, chick body size and recaptures of adults provides evidence of the existence of two distinct populations (hot- and cool-season) breeding annually on Baixo and Praia, out of phase by four to five months and overlapping in colony attendance during August and early September; on Vila only the cool-season population is present. Analyses of adult morphology indicate highly significant phenotypic differentiation between the sympatric hot- and cool-season breeders, whereas an almost complete phenotypic uniformity characterizes allopatric breeders within the same season. The hot-season birds are 10% smaller in egg and body mass but have longer wings and tails than cool-season birds. The two groups were readily separated by discriminant analysis. The preference to breed in the cooler season is interpreted as a consequence of greater food availability in that period. Morphological differentiation between seasonal populations is interpreted as an adaptative response to different environmental conditions in the two seasons. The hypothesis is given that the hot-season population has evolved from the cool-season population owing to density-dependent constraints on crowded colonies, forcing birds to time-share nest sites. These populations may represent a case of sympatric speciation through temporal partitioning of reproduction and may be better treated as sibling species.

Keywords: Madeiran storm petrel; Azores; breeding; sibling forms

1. INTRODUCTION

The Madeiran storm petrel, *Oceanodroma castro*, is widespread in subtropical areas of the Pacific and Atlantic oceans. The known breeding distribution comprises sites off the east coast of Japan, in Hawaii and the Galapagos, off the west coast of Portugal, in Madeira, Salvages, Canary Islands, Cape Verde, Ascension and St Helena Islands (Allan 1962; Bannerman & Bannerman 1965; Harris 1969; Teixeira & Moore 1981; Martin *et al.* 1984; Banko *et al.* 1991; Zino & Biscoito 1994). There may be a separate subspecies breeding on São Tomé, Gulf of Guinea (Harris 1969; Williams 1984). Although the species has long been known to occur in the Azores (Hartert & Ogilvie-Grant 1905), there was no proof of breeding (Bannerman & Bannerman 1966; Cramp 1977) until recently (Monteiro *et al.* 1996*a*,*b*). The species shows geographical variation, with several subspecies described based on differences in bill structure, wing length and amount of white on the rump. However, diagnostic characters and limits of variation of these subspecies are poorly known (Austin 1952) and the species has been treated as monotypic (Cramp 1977; Jouanin & Mougin 1979; Warham 1990).

The breeding cycle of the Madeiran storm petrel shows a noteworthy plasticity across its range, described as two seasons per year in the Galapagos (Snow & Snow 1966; Harris 1969), one season with some out-of-season nesting on Ascension Island (Allan 1962) and an extended season in the Salvages (Mougin *et al.* 1990). However, only the populations on Ascension Island and the Galapagos Islands have been studied in detail and phenologies in other areas are unclear. On the basis of significant differences in mercury concentrations in the plumage between hot-season (spring) and cool-season (autumn) breeders in the Azores, Monteiro *et al.* (1995) suggested that the Madeiran storm petrel found there may comprise two discrete populations. The hypothesis is supported by recent information on the phenology of the species there (Monteiro *et al.* 1996*a*).

In this paper we present an analysis of data on breeding phenology, moult, segregation of adults between populations and morphology of hot- and cool-season populations of Madeiran storm petrel in the Azores. We also discuss the possible ecological adaptations underlying the observed temporal partitioning of reproduction as well its evolutionary and taxonomic implications.

2. STUDY AREAS AND METHODS

The study areas comprised all known colonies of the species in the Azores (36–39° N, 25–31° W), situated on three small, rat-free islets (Monteiro *et al.* 1996*b*): Vila (off Santa Maria) and Baixo and Praia (off Graciosa and 4 km

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apart); Santa Maria and Graciosa are about 300 km apart. The data were obtained during monthly visits of 2–10 days to Vila during April–December 1993, March–October 1994, and January, March and October 1995; and to Praia and/or Baixo (when sea conditions permitted) during April–November 1993, March, June and August 1994, March and June 1995, and June and September 1996. Each islet was explored to determine the distribution, numbers and status of nest sites. The topography and geology of each islet dramatically affected the number of accessible active nest sites that we found, which totalled 131 at Vila, 20 at Baixo and five at Praia. The breeding populations were estimated as 200 pairs in the hot-season and 600 pairs (400 on Baixo–Praia and 200 on Vila) in the cool-season (Monteiro *et al.* 1996*b*).

Most adults were captured in mist-nets and a few were removed from burrows; playback was not used. Adults and chicks were ringed individually with numbered metal rings. Masses and up to nine mensural characters were taken by the first author: nape (head+bill), culmen (bill length), nostrils (bill depth at), gonys (bill depth at), tarsus, wing (flattened chord), tail maximum (dorsally from uropygial gland to tip of longest rectrix), tail minimum (dorsally from uropygial gland to tip of shortest rectrix) and body mass; tail fork was calculated (difference between tail maximum and tail minimum). Length, breadth and mass of eggs were measured. Linear measurements were taken with dial callipers (to 0.1 mm) or with a metal ruler (to 1 mm). Egg, chick and adult masses were taken with 50 g (eggs and small chicks) and 300 g Pesola scales (to 0.5 g and 2 g, respectively). The state of the brood patch was scored: 0 (no down was shed), 1 (only traces were lost), 2 (about half of the patch was coverd in down), 3 (traces of down remained), 4 (the entire brood patch was free of down) (Furness & Baillie 1981) and R (refeathering present). Moult of breast plumage was recorded as absent or in progress.

Means of two sets of measurements (nape, culmen, nostrils, gonys and tarsus) made by L. R. Monteiro on different occasions on the same 50 birds differed by less than 0.29% and not significantly (paired *t*-tests, $p > 0.05$), except for nostrils (relative difference = 1.78%, $t = 3.78$, $p < 0.001$), indicating an overall consistency of measuring. Brood patch scores of adults in each month did not differ significantly within colonies between years (Mann–Whitney *U*-tests, $p > 0.05$), and data were pooled for analysis. Measurements of adults and eggs did not differ significantly within colonies between years (*t*-tests, $p > 0.05$) and data were pooled for analysis.

Univariate and multivariate statistical analyses followed standard procedures (Zar 1984; Tabachnick & Fidell 1989) with casewise deletion of missing data. One-way analyses of variance (ANOVA) were followed by Tukey-tests for *a posteriori* pairwise comparison of means. Principal components analysis (PCA) was employed to reduce morphological information to a smaller number of mutually independent variables which account for most of the total phenotypic variation. Multivariate analysis of variance (MANOVA) was done to test differences in mean scores on the resultant principal components among populations. Finally, a stepwise discriminant analysis was used to examine differences between *a posteriori* groups indicated by PCA and MANOVA.

3. RESULTS

(a) *Breeding phenology*

(i) *Colony attendance*

Adults returned to Baixo and Praia by the end of March and numbers increased over the following weeks. Capture rates of birds in 12-m mist-nets were 0.3, 3.2 and 5.0 birds $h^{-1} net^{-1}$ on 29 March 1994, 16 April 1993, and 17 May 1993, respectively. Adults were recorded in these two colonies every month, from the end of March to mid-November (the latest visit).

In contrast, on Vila adults were absent until early August (with one exception, see next paragraph) and then numbers increased gradually during September. Capture rates of birds in 12-m mist-nets in 1993 were 0.8 and 3.6 birds $h^{-1} net^{-1}$ on 14 August and 14 September, respectively. During 44 nights spent on Vila between late March and late July 1993 and 1994, the Madeiran storm petrel was registered only once, on 18 June 1993. Then a single flying bird was calling repeatedly until an adult was caught and calling ceased, indicating that a single bird was involved. This individual was probably a non-breeder (brood patch, BP = 3) and it was caught again on Vila on 28 August 1994 (BP = 4).

(ii) *Brood patch*

Brood patch scores of mist-netted adults did not vary significantly between Baixo and Praia (Mann–Whitney tests, $p > 0.05$; June to September), and pooled data from these two colonies were compared with the state of brood patches of adults on Vila. In September, brood patches were less developed in Vila than in Baixo–Praia (mean, $n = 1.7$, 122 and 2.7, 366, respectively; Mann–Whitney test, $Z_{adj} = 6.40$, $p < 0.001$), but in October and November mean scores did not differ significantly between the two islands (Mann–Whitney tests, $p > 0.05$).

Presence of refeathering (score R), which is indicative of hatching (refeathering starts a week after hatching and in non-breeders at the same time; Harris 1969), occurs in two distinct periods on average about four months apart (table 1). The monthly frequency distribution of down-free brood patches (score 4) is bimodal, the two annual peaks (over 60%) being May–June and October–November, with an interval of about five months. Variably feathered brood patches (scores 0–3) showed rapid decreases across two main periods, coincident with increases in scores 4 and R, in April–July and September–December. The distribution of brood scores in August suggests an overlap of hot-season birds, represented by scores 4 and R (i.e. 70% of total) with the first returning cool-season birds, reflected in the reappearance of score 0 accounting for 20% of the total (table 1).

(iii) *Egg-stage*

A total of eight pre-laying females carrying eggs were captured during 1993: on Baixo–Praia, singles on 17 May, 24 June, 23 September and 25 September, and three on 25 October; on Vila, one on 22 October. In total, 67 eggs in incubation were found in 1993 and 1994 in the following months (three islets pooled): June (16), July (six), September (one, on the 23rd), October (23), November (seven), and December (14). Monitoring of laying on Vila during 12–29 October 1995 showed that 31 out of 46 eggs were laid before the 16th.

Table 1. *State of brood patches by month in adult Madeiran storm petrels mist-netted in Azores colonies*

(Data from Baixo–Praia (April–November 1993, 1994) were combined with data from Vila (December 1993, January 1995). For explanation of scores, see §2.)

	frequency (%) of birds with score						
month	0	1	2	3	4	R	*n*
April	27.3	18.2	54.5	—	—	—	11
May	—	4.8	9.5	21.4	64.3	—	42
June	7.9	2.6	4.8	14.8	69.8	—	189
July	—	—	1.3	3.9	23.4	71.4	77
August	20.1	2.4	2.4	5.3	20.7	49.1	169
September	10.1	8.2	19.7	25.4	36.6	—	366
October	—	2.4	7.3	19.5	70.7	—	41
November	—	—	—	5.0	77.5	17.5	40
December	—	—	1.3	—	46.1	52.6	76
January	41.7	—	4.2	8.3	—	45.8	24

Table 2. *Characteristics of eggs (mean±1 s.e. (n), range) from the two seasonal populations of Madeiran storm petrels breeding in the Azores*

character	hot-season	cool-season	t-test
length (mm)	32.0+0.2 (23) 29.9 − 33.2	33.6+0.1 (55) 31.5 − 35.5	6.77^{c}
breadth (mm)	24.2+0.1 (23) 23.7 − 25.3	24.4+0.1 (55) 22.7 − 25.7	1.37^{d}
mass (g)[a]	9.8+0.2 (20) 8.8 − 11.0	10.9+0.2 (22) 8.8 − 12.3	4.05^{c}
volume (cm^3)[b]	9.6+0.2 (23) 8.7 − 10.8	10.3+0.1 (55) 8.8 − 11.8	3.40^{c}

[a] Only values taken close to peak laying periods (hot-season: June; cool-season: October).

[b] External volume: $V = 0.512LB^2$, where L is length and B is breadth (Stonehouse 1966).

[c] $p < 0.001$.

[d] Not significant.

Egg measurements were classified into two groups: hot-season (laid in June–July) and cool-season (laid in October–December) (table 2). Lengths and breadths of cool-season eggs were pooled from Baixo–Praia ($n = 5$) and Vila ($n = 50$), as these did not differ significantly (t-tests, $p > 0.05$). Eggs from cool-season birds were significantly longer and heavier than those from hot-season birds, although egg breadth did not differ significantly between seasons (table 2).

(iv) *Chick-stage*

The earliest dates on which chicks were observed on Baixo–Praia were 5 July 1993 and 19 August 1993 ($n = 9$ chicks), and by 21 September 1993 eight had fledged, except one that had been abandoned and was starving to death (wing = 81 mm, weight = 24 g). Later, one chick of 51 g (of *ca.* 34-days-old) was found on 14 November. On Vila, no chicks were present on active nest sites inspected on 19 October 1994 ($n = 40$) and 29 October 1995 ($n = 46$), whereas on 4 December 1993, 33 out of 47 nest sites had chicks and 14 had eggs in incubation. Hatching eggs were observed on 5 July 1993 and 22 July 1993 on Praia and on 4 December 1993 on Vila. Pre-fledglings and fledglings were observed only in August (Baixo and Praia), January (Vila, 13 out of 22 young), and some out-of-season in March (Vila, two out of three young).

The stage of development of chicks from July and December 1993 is identical, and mean wing length, mass and age did not differ significantly between the two samples (table 3; t-tests, $p > 0.05$). Breeding is apparently less synchronous in the cool-season, as indicated by the overall wider range of body sizes of chicks measured in the cool-season compared with those from the hot-season. Chicks from the cool-season appear to be slightly heavier than chicks from the hot-season for the same wing length, as inferred from equations of growth curves fitted to mass (M) at given wing length (W) by season:

hot-season: $M = 13.40 + 1.22W - 0.0063W^2$ ($r = 0.84$, $n = 24$)

cool-season: $M = 16.55 + 1.37W - 0.0070W^2$ ($r = 0.88$, $n = 63$)

(v) *Breast plumage moult*

Adult breast plumage moult showed different patterns of breast feather moult between the two seasonal populations (table 4). More than 50% of hot-season breeders initiate breast plumage moult while in the colonies during July, i.e. shortly after hatching. In contrast, 50% of the cool-season breeders are in breast moult on arrival at the breeding grounds in August, the frequency decreasing to less than 6% in September. Breast moult reappears in December but only reaches a high frequency in January, i.e. about a month after the peak of hatching.

(vi) *Recaptures*

Recaptures of ringed adults on Baixo and Praia were classified by season (hot-season: March–July; cool-season: September–November). Data from August were treated separately because brood patches suggested that both hot- and cool-season birds were present in August.

Although 84 birds ringed in one season were recaptured in the same season in a subsequent year (table 5), there were only two possible interchanges between the hot- and

Table 3. *Mensural characters and estimated age (mean ± 1s.e., range) of Madeiran storm petrel chicks from the two seasonal populations breeding in the Azores*

population (colony)	period	*n*	wing (mm)	mass (g)	age[a] (days)
hot-season (Baixo/Praia)	19–22 July 1993	6	20.2 ± 3.7 12–32	33.5 ± 7.9 7–58	21 ± 14.9 1–41
	17–19 August 1993	9	90.1 ± 10.9 41–135	64.0 ± 1.5 56–71	—
	3–8 August 1994	11	67.9 ± 10.7 28–148	62.8 ± 3.6 38–80	—
cool-season (Vila)	2–4 December 1993	32	20.4 ± 1.8 10–51	41.1 ± 3.0 11–74	24 ± 14.5[b] 4–49
	10–17 January 1995	31	95.1 ± 7.5 16–160	71.6 ± 2.8 31–95	—
	11 March 1995	3	117.7 ± 20.4 77–140	66.0 ± 5.3 58–76	—

[a] Age estimated using the equation $\text{mass} = 132.6\ (1 - 0.964\ e^{-0.0131\ \text{age}})$, fitted with growth data (error *ca.* ± 2 days) of young (range 10–60 g) from the hot seasons in Galapagos (Harris 1969).

[b] $n = 29$; three chicks over the weight range of the former equation (weight–wing: 72 g–49 mm; 70 g–51 mm; 74 g–32 mm) were excluded.

Table 4. *Frequency by month (F_a—absolute; F_r—relative) of mist-netted adult Madeiran storm petrels with breast plumage moult on Baixo–Praia and Vila*

		Baixo–Praia			Vila		
month	seasonal population	*n*	F_a	F_r(%)	*n*	F_a	F_r(%)
April	hot	11	0	0	—	—	—
May	hot	41	0	0	—	—	—
June	hot	183	2	1.1	—	—	—
July	hot	78	41	52.6	—	—	—
August	hot	39	25	64.1	—	—	—
	cool	6	3	50.0	5	4	44.4
September	cool	252	7	2.8	138	8	5.8
October	cool	38	0	0	82	0	0
November	cool	40	0	0	45	0	0
December	cool	—	—	—	74	5	6.8
January	cool	—	—	—	24	11	45.8

cool-seasons. A bird ringed on Praia on 26 June 1993 (BP = 0) was recaptured in the same colony on 23 September 1993 (BP not recorded); a bird ringed on Baixo on 21 September 1993 (BP = 1) was recaptured in the same colony on 2 June 1996 (BP = 2). Data from August suggest that birds from the hot-season predominate in that month. Out of 18 birds ringed in August, 14 (78%) were recaptured in the hot-season, whereas only four (22%) were recaptured in the cool-season. Furthermore, out of 40 birds recaptured in August, 37 (93%) had been ringed in the hot-season and three (7%) in the cool-season.

Only one case of movement between colonies was recorded. An adult ringed on Praia on 24 September 1993 (BP = 3) was recaptured on Baixo in October 1993 (BP = 3). The birds recorded at more than one site or during different seasons are presumably non-breeders, as suggested by their brood patch scores.

A total of three birds ringed as chicks on Vila recruited into this colony during the study period. Ringing and recapture dates for these birds were, for one December 1993 and October 1996, and for two January 1995 and October 1996, indicating a minimum of 21 months for recruitment in this species.

(vii) *Overview*

Breeding and recapture data provide evidence of the existence on Baixo and Praia of two populations breeding annually, out of phase by four to five months and overlapping in colony attendance during August and early September. The periodicity of field trips did not allow precise determination of laying and hatching dates as well as incubation and fledging periods. However, these can be derived by coupling data on chick age (table 3) with mean incubation period (42 days) and mean fledging periods (70 days in hot-season and 78 days in cool-season) reported for the species by Harris (1969). These crude estimates of peak laying, hatching, and fledging dates are, respectively: 19 May, 30 June, 8 September for the hot-season population on Baixo–Praia; and 1 October, 11 November, 28 January for the cool-season population on Vila. Furthermore, the estimated age of chicks in July and December

Table 5. *Numbers of mist-netted Madeiran storm petrel adults ringed on Praia and Baixo in each season and numbers of subsequent retraps from one season to another, during* 1990–1996 *(hot-season: March–July; cool-season: late September–November)*

	birds retrapped in season						
	cool '91	hot '93	cool '93	hot '94	hot '95	hot '96	cool '96
(birds handled)	(40)	(225)	(417)	(103)	(60)	(78)	(89)
birds ringed in season:							
hot '90–'92 (58)	0	19	0	4	0	2	0
cool '91 (40)	—	0	4	0	0	0	1
hot '93 (166)	—	—	1	18	10	9	0
cool '93 (391)	—	—	—	0	0	1	7
hot '94 (83)	—	—	—	—	1	7	0
hot '95 (49)	—	—	—	—	—	2	0
hot '96 (57)	—	—	—	—	—	—	0

Table 6. *Mensural characters* (*mean*+1 *s.e.*, *n*) *from adult Madeiran storm petrels from different populations breeding in the Azores*

(All measurements made on live birds: mist-netted and known breeders pooled, except for body mass where only data from mist-netted birds are included. For units see § 2 and for population acronyms see § 3.)

character	GBH	GBC	GPH	GPC	SVC	ANOVA[a]
nape	40.36±0.08 (113)	41.89±0.07 (156)	40.59±0.14 (40)	41.99±0.05 (239)	41.82±0.05 (250)	107.21[c]
culmen	14.58±0.05 (153)	14.91±0.04 (156)	14.70±0.08 (68)	14.99±0.03 (239)	15.11±0.03 (250)	28.04[c]
nostrils	6.11±0.02 (154)	6.34±0.02 (156)	6.20±0.03 (68)	6.42±0.01 (239)	6.43±0.02 (250)	—[d]
gonys	4.94±0.02 (154)	5.19±0.01 (156)	4.96±0.02 (68)	5.20±0.01 (239)	5.22±0.01 (250)	74.14[c]
tarsus	23.54±0.06 (154)	24.06±0.06 (156)	23.54±0.10 (64)	24.03±0.04 (238)	24.18±0.04 (250)	25.11[c]
wing	157.4±0.3 (154)	157.5±0.2 (191)	158.3±0.4 (72)	157.2±0.2 (240)	158.1±0.2 (298)	2.94[b]
tail maximum	75.4±0.2 (153)	73.0±0.2 (156)	75.1±0.4 (64)	73.3±0.2 (239)	72.9±0.2 (252)	29.47[c]
tail minimum	67.4±0.4 (65)	—	67.8±0.4 (63)	—	67.6±0.2 (70)	0.46[a]
tail fork	8.4±0.4 (65)	—	7.6±0.3 (63)	—	5.6±0.2 (70)	24.11[c]
mass	44.0±0.4 (139)	49.2±0.4 (180)	44.0±0.5 (67)	48.5±0.2 (240)	49.3±0.3 (242)	55.33[c]

[a] Not significant.

[b] $p < 0.05$.

[c] $p < 0.0001$.

[d] Not tested owing to low consistency of measurements (see §2).

1993 (table 3) indicated an exact four-and-a-half-month interval between the hot-season breeding population on Baixo–Praia and the cool-season breeding population on Vila. Assuming that breeding is relatively well synchronized in the cool-season populations on Baixo–Praia and Vila (table 1), the seasonal populations on Baixo–Praia seem to be also out of phase by four-and-a-half months, which is supported by the monthly distribution of brood patches (table 1). Furthermore, estimated ages of chicks in the July and December 1993 samples lie in the range of 40–45 days, in close agreement with the spread of laying for the bulk of clutches known for the species (Harris 1969).

(b) *Adult morphology*

The reduced interchange of birds between colonies and seasons allowed the recognition of five populations: Graciosa–Baixo–Hot (GBH), Graciosa–Baixo–Cool (GBC), Graciosa–Praia–Hot (GPH), Graciosa–Praia–Cool (GPC) and Santa Maria–Vila–Cool (SVC). Adults from Baixo and Praia were assigned to one of the two seasonal populations according to the following criteria: hot-season, if ringed between March and July; cool-season, if ringed between September (the earliest visit in this month started on the 21st) and November; birds ringed in August were assigned to the hot- or cool-season populations if they were recaptured earlier than August or later than 21 September, respectively. For each population, all measurements except body mass did not differ significantly between mist-netted birds (unknown status) and incubating birds (t-tests, $p > 0.05$) and were pooled. Incubating birds were significantly heavier than birds of unknown status caught during the incubation period, both in hot-season (Baixo–Praia pooled: 48.4±0.9 s.e., $n = 27$ versus 43.7±0.4 s.e., $n = 161$, respectively; $t = 5.10$, $p < 0.0001$) and in the cool-season (Vila: 54.1±0.9 s.e., $n = 40$ versus 50.9±0.4 s.e., $n = 194$, respectively; $t = 3.39$, $p < 0.001$), and table 6 gives body masses of mist-netted birds.

Simultaneous comparisons by using ANOVA yielded significant differences among populations for all variables tested except tail minimum (table 6). Within the eight variables exhibiting significant differences, 38 significant ($p < 0.05$) pairwise comparisons were detected, with 37 (97%) representing differences between two dichotomous groups: hot-season (GBH–GPH) and cool-season

Table 7. *Principal component* (PC) *loadings on mensural characters of Madeiran storm petrel populations from the Azores*

character	PC1	PC2
nape	−0.865[a]	0.126
culmen	−0.704[a]	−0.062
gonys	−0.699[a]	0.184
tarsus	−0.618	−0.132
wing	−0.363	−0.826[a]
tail maximum	0.008	−0.907[a]
mass	−0.651	0.070
Eigenvalues	2.700	1.571
% variance	38.57	22.45

[a] Loadings equal or greater than 0.7.

Table 8. *Discriminant analysis between hot-season and cool-season breeders of Madeiran storm petrel in the Azores*

character	coefficient for canonical variable
nape	0.782
culmen	−0.230
gonys	0.349
tail maximum	−0.520
mass	0.302
Eigenvalue	0.950
centroid, hot-season	−2.033
centroid, cool-season	0.466

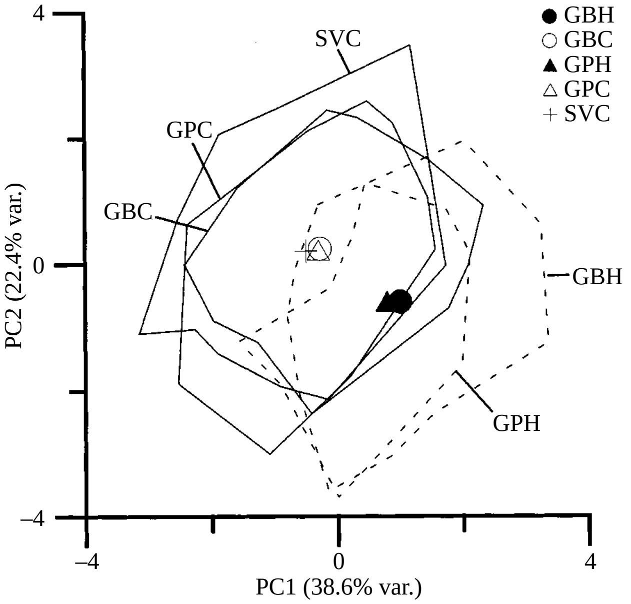

Figure 1. Plane 1–2 of principal component analysis done on seven characters of different hot- and cool-season populations of Madeiran storm petrels breeding in the Azores. Diagrams are group contours and symbols centroids. For acronyms see text.

(GBC–GPC–SVC) populations. Hot-season birds are smaller than cool-season birds in mensural characters expressing head and trunk, i.e. body size (nape, culmen, nostrils, gonys, tarsus and mass), but have longer and more forked tails (tail maximum and fork) and longer wings relative to body size.

In multivariate analyses tail minimum and tail fork were excluded owing to small sample sizes, and 'nostrils' was excluded because of low consistency in measurements. The first two principal components extracted accounted for 61% of the total variance in the data set (table 7) and all correlation coefficients between characters of each component are positive and highly significant. The first component (PC1) varies inversely with nape, gonys, culmen, tarsus and mass, representing a general body size character. The second component (PC2) varies inversely with tail maximum and wing, representing flight shape. The spatial diagram of PC1 against PC2 (figure 1) suggests a separation in two dichotomous groups; the hot-season populations having smaller body size and larger silhouette than the cool-season populations. Differences in adult morphology among populations are highly significant, as indicated by MANOVA on PC1 and PC2 scores of individual birds (Wilks' $\lambda=0.568$, Rao's $R_{8,1564}=63.81$, $p<0.0001$). All of the 12 significant ($p<0.005$) pairwise comparisons (six for PC1 and six for PC2) represented differences between the already mentioned dichotomous groups: hot-season (GBH–GPH) and cool-season (GBC–GPC–SVC).

The morphological difference between hot-season and cool-season birds indicated by ANOVA, PCA, and MANOVA was confirmed by stepwise discriminant analysis (canonical $R=0.698$, Wilks' $\lambda=0.513$, $\chi^2_5=523.21$, $p<0.0001$; table 8) and showed a good separation of the two groups. Associated classification functions correctly assigned 72.8% ($n=146$) of hot-season birds and 96.9% ($n=664$) of cool-season birds. Although the use of unequal sample sizes is considered not to influence discriminant analysis (Tabachnick & Fidell 1989), we found that a more even distribution of correctly classified cases between populations (87.8% in hot-season and 89.0% in cool-season) was achieved by using similar sample sizes ($n=146$ and $n=156$, respectively).

4. DISCUSSION

(a) *Breeding phenology*

The breeding phenology of the Madeiran storm petrel over its world distribution shows a continuum from pure synchrony (Japan, possibly Hawaii) to strict bimodality (Galapagos, Azores, possibly Madeira), through varying levels of asynchrony (Salvages, Canary Islands, Cape Verde, Ascension, St Helena) (Mougin *et al.* 1990; this study). This breeding plasticity may represent an ideal free-distribution conditional on four main factors: (i) availability of food resources; (ii) numbers of birds, both conspecific and heterospecific, exploiting those resources; (iii) availability of breeding habitat; and (iv) predation pressure.

The species shows a clear preference to breed in the cooler season, despite its pan(sub)tropical distribution. Winter breeding predominates in most places with a single population (Azores, Vila Islet: this study; Farilhões: J. P. Granadeiro, personal communication; Canary Islands: Martin *et al.* 1983; Concepcion 1992; Cape Verde: Hazevoet 1995; Ascension: Allan 1962), and in all known locations with two seasonal populations (Azores, Baixo and Praia Islets: this study; Galapagos, Plaza: Harris 1969). Hence, a primary question emerges: why is the cool-season widely preferred? The answer may be because of greater foraging efficiency compared with the hot-season. The Madeiran storm petrel and other *Oceanodroma* species feed mostly on mesopelagic lanternfish (e.g. myctophids) vertically migrating to the upper oceanic layers at night (see, for example, Prince & Morgan 1987; Croxall *et al.* 1988; Warham 1990). The pelagic distribution of the species indicates a preference for areas with surface turbulence associated with particular oceanographical features, such as localized upwellings (Haney 1985) and internal waves (Haney 1987). It has been shown that consistently high winds result in drift of surface waters (down to 10–20 m) and advection of mesopelagic prey over shelf or topographic irregularities (e.g. sea mounts) (Perissinotto & MacQuaid 1992). Therefore, enhanced food availability for the species might be predicted in the cooler season, together with a longer period of darkness to exploit their prey.

Greater interspecific competition for food and nest sites during the hot-season may also make breeding in the cool-season more advantageous. Nevertheless, this seems to be unimportant for the North Atlantic colonies, though a limited knowledge of the feeding ecology and nest site selection in local seabird assemblages prevents complete testing of this hypothesis. Circumstantial comparisons reveal that the presence–absence of hot-season populations of the Madeiran storm petrel does not correlate with the presence–absence of the most direct competitors for nest sites and/or food resources (Bulwer's petrel, *Bulweria bulwerii*; gadfly petrels, *Pterodroma* sp.; little shearwater, *Puffinus assimilis*; Cory's shearwater, *Calonectris dioemedea*; and white-faced storm petrel, *Pelagodroma marina*).

The apparent adaptation of the Madeiran storm petrel for the cool-season may be reflected in better breeding success in this season. In the Galapagos, Snow & Snow (1966) observed higher overall breeding success (hatching + fledging) in the cool-season compared with the hot-season, whereas Harris (1969) did not find differences in fledging success between seasons. However, in the more critical egg-stage, Harris (1969) found that the chances of an egg hatching decreased if left unattended, and that eggs laid in the hot-season were more frequently abandoned. Higher frequency and duration of egg neglect in petrels is known to arise from poor feeding conditions (Chaurand & Weimerskirsh 1994). The subsidiarity of the hot-season population might explain the lower numbers in the colonies where it coexists with the cool-season population (Galapagos: Snow & Snow 1966; Harris 1969; Azores–Baixo–Praia; Monteiro *et al.* 1996*b*) and its weak representation in other colonies with some out-of-season birds (Ascension and Cape Verde Islands: Allan 1962, Hazevoet 1995; Azores–Vila: this study). Subsidiarity suggests the prevalence of poorer niche conditions in the hot-season. This raises the question: why do some birds breed in the apparently less favourable season at certain colonies?

The strategy may be primarily a response to reduce intraspecific competition for nest sites during the cool-season in densely populated colonies, as seasonal populations do not differ in nest site selection and may use the same nest sites in consecutive seasons (Snow & Snow 1966; M. P. Harris, personal observation) and inter-specific competition for food and nest sites seems to be relatively unimportant (see previous paragraph). Intra-specific competition for nest sites is an important source of egg loss (Allan 1962; Harris 1969) with crowding affecting hatching success (Ramos *et al.* 1997), and it could be the cause for displacement of birds from being cool- to hot-season. Such a density-dependent constraint, forcing birds to share time because no further space was available for breeding, may have been strengthened recently because of an increased pressure to breed only on predator-free islets owing to the historical extinction or regression of colonies on main islands (Ashmole *et al.* 1994; Monteiro *et al.* 1996*b*). This rationale points towards a case of sympatric speciation (see last paragraph).

Varying predation pressure could be another factor affecting time of breeding, allied with varying lengths of darkness, as found for Leach's storm petrel, *Oceanodroma leucorhoa*, in Japan (J. Warham, personal communication). This appears of little importance at the Azores colonies, where the known predators are the yellow-legged gull, *Larus cachinnans*, on Baixo and the buzzard, *Buteo buteo*, on Vila (Monteiro *et al.* 1996*b*).

(b) *Morphological differentiation*

Both univariate and multivariate analyses of adult morphology indicate a significant amount of phenotypic differentiation between the sympatric hot- and cool-season breeders and simultaneously a great phenotypic uniformity of allopatric breeders within the same season. Adults in the hot-season are smaller and lay smaller eggs (average egg mass and body mass are 10% lower) and have longer wings and tails than cool-season birds. Chicks in the hot-season are 15% lighter than chicks in the cool-season.

The morphometric differences between the two segregated Azorean populations demonstrated in this study contrast with the uniformity of the two segregated populations in the Galapagos (Harris 1969). Local environmental influences may explain the fact that an apparently similar biological phenomenon (temporal segregation) led to different levels of phenotypic differentiation in the two archipelagos. The difference in marine climate (e.g. wind and temperature) to which the hot-(subsidiary) and cool-(main)season populations were subjected while breeding is far more pronounced in the Azores than in the Galapagos (Harris 1969; Monteiro *et al.* 1996*b*). Therefore, stronger selection pressure may exist in the Azores between the two seasons. For instance, it is advantageous for birds breeding in the cool-season to be larger, optimizing heat conservation. This seasonal variation in body size agrees with Bergmann's ecogeographic rule for body size in endotherms and correlates well with the temperatures during breeding (incubation presumed to be the most thermally stressing phase), although it is difficult to ascertain the possible influence of the temperatures in the non-breeding grounds because they are not well known (Cramp 1977). Conversely, the smaller wing and disc loading in hot-season birds (the 10% reduction in body mass implies an equivalent reduction for these two variables, assuming constant wing span and area between seasons; Pennycuick 1987) may have an important adaptative significance in the hot and less windy season, as storm petrels (in contrast to most larger procellariiforms) typically forage by flying near their maximum range speed (Pennycuick 1987). So, the apparent lack of specific phenotypic adaptations for the hot-season in the Galapagos may be merely a consequence of divergence in an environment with low seasonal contrasts.

The morphological differentiation observed between the two Azorean sympatric populations of the Madeiran storm petrel is more pronounced than that between the allopatric hot-season populations in the Azores and Madeira (L. R. Monteiro, unpublished data) or than that between two sympatric and seasonally segregated storm petrels classified as full species: Matsudaira's storm petrel, *Oceanodroma matsudaira* (hot-season), and Tristami's storm petrel, *O. tristami* (cool-season), breeding at Volcano Island (Harrison 1985; Warham 1990), and it is similar to differences between some subspecies of Leach's storm petrel in the Pacific (Power & Ainley 1986).

(c) *Evolutionary and taxonomic implications*

This study probes into the virtually unexplored dynamics of the population structure of storm petrels (and possibly other procellariiforms), with implications for speciation theory and process. Indeed, the occurrence of sympatric seasonal populations is an extremely rare situation among vertebrates and provides important case-testing for the disputed model of sympatric speciation, which postulates that populations may diverge and acquire reproductive isolation without geographic separation (Mayr 1963).

There are a number of precedent cases of sympatric 'seasonal races' among procellariiforms but the isolating mechanisms are poorly understood and are of unknown origin: (i) Madeiran storm petrels on the Galapagos—Harris (1969) stated that 'separation of birds present in the hot and cool-seasons, if associated with the young birds returning to breed at the same season of the year as they were raised, could potentially give rise to separate forms of the same species', and later three birds were found recruiting into the season they were reared (Harris 1979); (ii) Leach's storm petrels on Guadalupe Island—Power & Ainley (1986) proposed a subspecific taxonomic arrangement for the hot- and cool-season populations breeding there, based primarily on a canonical analysis where they formed independent clusters at the end of a well-defined clinal gradient; (iii) Matsudaira's (hot-season) and Tristami's (cool-season) storm petrels—seasonal segregation on sympatry at Bonin Island was the main rationale for discriminating at the species level among the four currently recognized all-dark *Oceanodroma* of the North Pacific (Warham 1990, p. 179); and (iv) dark-rumped petrels, *Pterodroma phaeopygia*, on San Cristobal, Galapagos—case limited by small sample sizes (Tomkins & Milne 1991).

The seasonal populations of Madeiran storm petrels in the Azores configure a case of sympatric speciation by seasonal isolation (Mayr 1963), but geographic speciation cannot be ruled out; indeed, observing populations–sibling species today in sympatry today does not necessarily mean that speciation took place in sympatry (see, for example, Hunter 1987). Under the sympatric speciation hypothesis, the cool-season population is the ancestral (see first paragraph of § 4) and the morphological differentiation between populations may be a result of reproductive isolation for many generations, maintained by ecological segregation in time (this study) and diet (as indicated by mercury burdens: Monteiro *et al.* 1995, 1998). Further investigations on populations' genetic drift and ecology (e.g. behaviour, diet, feeding and movements) will help to test the hypothesis for evolution in sympatry and to establish if they are in the process of, or have achieved, speciation.

A straightforward consideration of the morphologically differentiated seasonal populations of Madeiran storm petrels in the Azores shows that they have the biological characteristics of 'good' species (i.e. reproductive isolation in sympatry: Mayr 1963; Mayr & Ashlock 1991). Preliminary analysis of sequence variation in the mitochondrial control region suggests that storm-petrels breeding in the cool versus hot seasons are genetically isolated (V. Lodha, V. Friesen, L. R. Monteiro and R. W. Furness, unpublished data). We propose taxonomic recognition as sibling species to these populations, pending the extent of divergence indicated by further investigations on their genetics and vocalizations.

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