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The Call of Bulwer's Petrel (*Bulweria bulwerii*), and the Relationship Between Intersexual Call Divergence and Aerial Calling in the Nocturnal Procellariiformes

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Breeding colonies of nocturnal petrels are characteristically noisy places, with birds calling from below ground, on the surface, and in flight. The adaptive nature of this vocal activity has been investigated only recently (Brooke 1978; Simons 1981; James 1984a, 1985; James and Robertson 1985a, b). The majority of species exhibit aerial calling, but there are a few notable exceptions. One of these is Bulwer's Petrel (*Bulweria bulwerii*), a little-known species that occurs in the subtropical sectors of both the Pacific and Atlantic oceans (Cramp and Simmons 1977). That it is silent over the breeding colony is beyond doubt (Thibault and Holyoak 1978, Jouanin et al. 1979, James 1984b), despite a mistaken report to the contrary quoted in Cramp and Simmons (1977), which actually refers to the aerial calling of the Little Shearwater (*Puffinus assimilis*; Jouanin et al. 1979). For many of the species examined, a clear sexual dimorphism in voice has been detected (Brooke 1978; Ristow and Wink 1980; James 1984a; James and Robertson 1985a, b), a phenomenon considered to be an adaptation for sexual advertisement in the low light levels in which these birds nest (Brooke 1978). Research has been conducted on only a small proportion of the total

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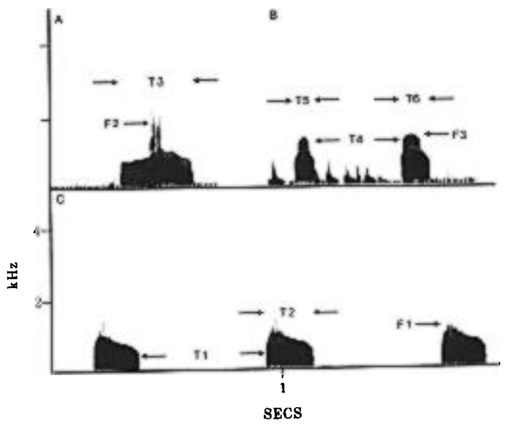

Fig. 1 Spectrograms of typical Bulwer's Petrel call variants: (A) Single Call, (B) Double Call, and (C) Repeat Call. The frequency (F) and temporal (T) variables measured on each call variant are shown. The maximum frequency of each was measured (F1, F2, and F3).

number of species involved. We recently had the opportunity to investigate the vocal behavior of Bulwer's Petrel on Great Salvage Island (30°09′N, 15°52′W) in the Atlantic Ocean from 17 June to 11 July 1983. Its one and only call has been described (Lockley 1952), but little else is known about it.

Breeding pairs of Bulwer's Petrels were located at night by their vocal activity. At the time of our visit, they were commencing egg-laying, so it was possible to sex all birds by cloacal inspection with absolute certainty (Serventy 1956) before banding them. The same nests were visited later, again at night, and the incubating birds (24 males and 18 females) stimulated to call by producing a human imitation of this species' call. This method was used because the birds were generally unresponsive to the playback of their own calls. Their vocal responses were recorded using a Uher-4000 Report IC tape recorder and spectrograms later produced on a Kay 6061-B Sound Sona-Graph using the wide-band filter.

To our ears, the calls of male and female Bulwer's Petrel were indistinguishable. This was in strong contrast to other species that we had investigated on Great Salvage Island (James 1984b; James and Robertson 1985a, b). A more quantitative analysis of their vocalizations therefore was performed to look for subtle differences. Bulwer's Petrel gives three variants of its basic call (Fig. 1), separable by their temporal patterning. Both males and females produced all three. For the purposes of this discussion, they are called the Repeat Call, the Single Call, and the Double Call. The Repeat Call was by far the commonest call heard at the colony, and birds within burrows gave it continuously for several minutes at a time. The Single Call was given either at the end of a long series of Repeat Calls or by itself. The Double Call always was given by itself and never in conjunction with the other call variants. Six temporal and three frequency variables were compared between males and females (Fig. 1). Only one of these, the time interval between successive repetitions in the Repeat Call, was significantly different between the sexes (Tables 1, 2). In other words, females called at a faster rate than males. The number of times that each call variant was used by males and females also was compared (Table 3), but there was no significant difference between the sexes.

Clearly, Bulwer's Petrel does not show the marked sexual dimorphism in voice that other nocturnal petrel species possess (Brooke 1978; Ristow and Wink 1980; Simons 1981; James 1984a; James and Robertson 1985a, b). While males and females may distinguish between each other on the basis of their Repeat Call rates (Table 1), further experimentation is necessary to demonstrate it. Even if they do, the degree of sex-

TABLE 1. Male and female Bulwer's Petrel temporal call characteristics (s, $\bar{x} \pm$ SD).

Call variant and variable	Male (*n*)	Female (*n*)	*t*	*P*
Repeat, T1	0.82 ± 0.17 (18)	0.68 ± 0.19 (24)	2.47	0.02
Repeat, T2	0.15 ± 0.04 (18)	0.14 ± 0.04 (24)	0.84	NS
Single, T3	0.28 ± 0.07 (7)	0.29 ± 0.07 (10)	0.29	NS
Double, T4	0.39 ± 0.11 (12)	0.37 ± 0.08 (11)	0.48	NS
Double, T5	0.10 ± 0.02 (12)	0.09 ± 0.03 (11)	1.09	NS
Double, T6	0.15 ± 0.04 (12)	0.14 ± 0.05 (11)	0.67	NS

TABLE 2. Male and female Bulwer's Petrel frequency call characteristics (Hz, $\bar{x} \pm$ SD).

Call variant and variable	Male (*n*)	Female (*n*)	*t*	*P*
Repeat, F1	2,147.5 ± 752 (18)	2,086.4 ± 743 (24)	0.26	NS
Single, F2	2,144.3 ± 557 (7)	2,566.5 ± 689 (10)	1.34	NS
Double, F3	3,386.7 ± 1,065 (12)	2,737.3 ± 839 (11)	2.01	NS

ual dimorphism in voice is still greatly reduced over that of other species. Because it has been suggested that such dimorphism is an adaptation to a nocturnal life-style (Brooke 1978), our results require further explanation.

Table 4 summarizes some of the vocal characteristics for nocturnal species in relation to sexual dimorphism in voice. The list covers part, but not all, of the taxonomic range within the Procellariiformes. One immediately apparent relationship is that species with sexually dimorphic calls also give aerial calls, whereas those species that do not show such dimorphism are silent in flight. There are two apparent exceptions to this general observation. The first is the British Storm-Petrel (*Hydrobates pelagicus*), which rarely gives calls in flight but which shows sexual dimorphism in voice (James 1984a). The dimorphism, however, is in the form of a call specific to the male only. The second exception is the Fork-tailed Storm-Petrel (*Oceanodroma furcata*), which calls in flight but also has a call that is given only by males on the ground or within burrows (Simons 1981). Both sexes produce the flight call, which appears to be similar. However, because the flight calls of other *Oceanodroma* species are sexually dimorphic (James and Robertson 1985b), the dimorphism simply may have been overlooked in *O. furcata*.

If it is assumed that aerial calling is mainly a form of sexual advertisement (James 1985), then why are some species silent in flight, particularly as calling in flight would seem to confer considerable signaling advantages? For example, the ground is a major cause of sound attenuation, and studies have shown that such attenuation is diminished significantly by moving just a few feet above the ground (Marten and Marler 1977). The presence of aerial calling, however, is not simply a function of taxonomy or bird size (see Table 4). For example, there are both shearwater and storm-petrel species with and without aerial calls. Predation pressure may be a reason for the absence of aerial calling in some species. In situations where avian predators are present, calling in flight may too readily attract their attention. However, this is difficult to reconcile because it is common for species both with and without aerial calls to breed in close proximity. At Great Salvage Island, for example, Bulwer's Petrel and the White-faced Storm-Petrel (*Pelagodroma marina*) give no aerial calls, whereas Cory's Shearwater (*Calonectris diomedea*), the Little Shearwater, and the Madeiran Storm-Petrel (*Oceanodroma castro*) do. All but Cory's Shearwater are subject to predation by the resident gulls.

Another explanation for the absence of aerial calling in some species may be male competition for nest sites. A study of the Manx Shearwater (*Puffinus puffinus*; James 1985) showed that immatures were responsible for the majority of aerial calling heard at the colony and that immature males were responsible for establishing and defending burrows. Immature males periodically would leave their burrows and engage in vocal display flights, presumably to attract potential mates. The cost of leaving a burrow to display in flight could be the loss of the burrow to another prospecting male if nest sites were in short supply. It is possible that in some species where burrow competition is acute, males are not able to leave their burrows to display in flight. To attract mates, they may remain in their burrows and call. Sexual dimorphism in calls may not be necessary in species without aerial calling, as males calling from burrows would be recognized as such by prospecting females. Female Manx Shearwaters that call in flight apparently are responding to the calls of flying males (James 1985), which suggests that in species where males do not call in flight, females also will remain silent. The entire population therefore would be silent in flight. In species where both males and females give aerial calls, sexual dimorphism in voice may evolve to facilitate pair formation in the darkness.

Burrow competition could arise through either an

TABLE 3. The number of times that male and female Bulwer's Petrels used the three call variants.

	Call variant used		
	Repeat	Double	Single
Males	18	19	11
Females	24	17	23
$\chi^2 = 3.03$, df = 2, NS			

TABLE 4. Summary of vocal parameters in certain nocturnal Procellariiformes.

Species	Aerial calls?	Dimorphic in aerial calls?	Dimorphic in ground calls?	Source
Calonectris diomedea	Yes	Yes	Yes	Ristow and Wink (1980)
Puffinus puffinus	Yes	Yes	Yes	Brooke (1978)
P. assimilis	Yes	Yes	Yes	James and Robertson (1985a)
Oceanodroma castro	Yes	Yes	Yes	James and Robertson (1985b)
O. furcata	Yes	?	Yes	Simons (1981)
P. pacificus	No	—	No	Shallenberger (1973)
Procellaria cinerea	No	—	No	Brooke (in prep.)
Pr. aequinoctialis	No	—	No	Brooke (in prep.)
Bulweria bulwerii	No	—	No	This study
Hydrobates pelagicus	No	—	Yes	James (1984a)
Pelagodroma marina	No	—	No	James (1984b)

excess of birds or a shortage of burrows. For example, it is possible that species breeding year-round in the tropics would experience relatively less burrow competition than the more synchronously breeding species in temperate areas, or that differences in the choice of microhabitat could affect the number of nest sites available. It has been suggested that species nesting in soil substrates have relatively less burrow competition than those nesting in rock substrates (Nelson 1980), presumably because soil-nesters theoretically have the choice of looking for existing burrows or digging their own, whereas rock-nesters do not. Neither breeding synchrony nor microhabitat entirely explains the observed calling patterns, however. Of the 5 species in Table 4 with aerial calling, only 1 (*O. castro*) has an extended breeding season (Cramp and Simmons 1977), although the other 4 nest mainly in soil substrates. Of the 6 species without aerial calling, all have a discrete breeding season, and only 2 (*Bulweria bulwerii* and *Hydrobates pelagicus*) are mainly rock-nesters (Cramp and Simmons 1977).

To summarize, species with aerial calls show sexual dimorphism in their calls, and species without aerial calling show no such dimorphism. The reasons for this striking dichotomy are unclear at present, although we suggest that male competition for burrows may have shaped the observed patterns. Clearly, further research is needed on sex-specific calls in other species, particularly in certain taxa such as *Pterodroma*, *Pachyptila*, and *Pelecanoides* where virtually nothing is known. In addition, it would be interesting to know whether similar patterns occur in the nocturnal alcids.

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Morphological Correlates of Synchronized Nesting in a Tricolored Blackbird Colony

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Our knowledge of the morphological and physiological changes associated with reproductive cycles in female birds has been derived largely from studies of the domestic fowl (Romanoff and Romanoff 1949), several species of domestic doves (Riddle 1916, Lehrman 1965), and the domestic canary (Hinde 1965). Few comparable data are available on seasonally breeding wild birds (but see Petersen 1955, Marshall and Coombs 1957).

The Tricolored Blackbird (*Agelaius tricolor*), because of extremely high nest densities in its huge breeding colonies (characteristically several nests per square meter) and, particularly, a remarkable breeding synchrony of colony members (all nests within a local colony unit of several hundred or thousand nests vary around a mean by only one or two days; Neff 1937, Lack and Emlen 1939), provides an unusual opportunity to collect specimen series for correlating reproductive condition with nesting stages.

While performing a study of the breeding behavior of this species (Emlen 1941), I shot 74 breeding females as they circled directly overhead or within 10 m of a typical, densely packed and closely synchronized cluster of Tricolored Blackbird nests in a colony near Davis, California. The specimens, collected at 2-day and later 3-day intervals, were measured and autopsied for data on the condition of reproductive tracts and brood patches. Data on body weights, brood patch condition, and oviduct lengths are summarized in Fig. 1, and data on ovum diameters are summarized in part in Table 1.

Body weights showed a significant downward trend ($P < 0.01$, $\chi^2 = 12.162$, 2×2 contingency test) from a mean of about 50 g at nest building and egg-laying to about 43 g at fledging. The main decline apparently occurred during the nestling stage.

Brood patch indices, based on 4 subjective classes of dermal edema, showed a steep drop from a high during egg-laying and incubation to a low during the nestling and fledgling stages. Defeathering of the brood patch was apparently nearly complete early in the nest-building stage.

The overall length of the oviduct (including infundibulum and vagina) dropped precipitously from a high during the nest-building and egg-laying stages to the incubation stage, then gradually dropped during the nestling stage to a low in the fledgling stage. I saw no evidence of a recrudescence at the end of the cycle indicative of an oncoming second breeding cycle.

The ovarian indicators of reproductive progress closely paralleled the patterns of reproductive behavior during nest building and egg-laying. In the late afternoon of 16 May, 1-3 days before nests in the colony section received their first egg [stages: NB1(1), NB2(3), NB3(9), NB4(3), E1(0); see Fig. 1], I collected 9 females, all of which were apparently within 1-4 days of laying their first egg (Table 1). Six held single ovulated ova in their oviducts (presumably ready to be laid the next day) and from 1 to 3 appreciably enlarged ova (diameter >5.0 mm) in their ovaries, numbers appropriate for predicting completion of the usual 3-4-egg clutch of the species (Emlen 1941). In the other 3 birds, the largest ovum diameters suggested that 2 probably would have laid their first egg on the succeeding day and the other on the following day. The slightly enlarged ova (2.5-5.0 mm; see Table 1) can be interpreted either as growing and potentially viable ova or as resorbing ova that had abortively initiated a terminal rapid-growth phase.

Because eggs are laid at 1-day intervals, the stepwise pattern of increasing ovum diameters in the 16 May specimens (Table 1) provides an indication of the growth curve of individual ova, and, combined with similar data from specimens collected before and after that date, a basis for tracing the daily progress of egg production in these birds. As in the domestic fowl (*Gallus gallus*) and the Ringed Turtle-Dove (*Streptopelia risoria*), ova apparently take 4-5 days to