

Dynamics of behavioural rhythms in a colonial, nocturnal, burrowing seabird: a comparison across different temporal scales

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Abstract There have been few studies on the temporal patterns of social behaviours and how they relate to timing of life history stages in nocturnal colonial bird species. This study focuses on the threatened Westland petrel (*Procellaria westlandica*; Procellariidae), to investigate temporal patterns in colonial interactions, including vocalisations and social behaviours, in the context of petrel sociality. We conducted extensive behavioural observations on the colony at different time-scales (throughout single nights, between seasons, and across years) to characterise the temporal dynamics of at-colony behaviours. These analyses show consistent temporal variation in several behavioural attributes (e.g., social interactions, vocalisations, eyes closed, body movements), with little or no temporal variation in others (e.g., self maintenance or stationary behaviours). These data provide the basis for specific predictions to test the role of social interactions between temporally varying vocalisations and social behaviours in nocturnal colonial birds.

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INTRODUCTION

Studies of the timing of behaviours, including the onset of reproduction, the nocturnal rhythm of vocalisations, or longer events, including annual migration, have been used to better understand the social and environmental mechanisms regulating life stage-specific behaviours (Takahashi *et al.* 2001; Dunlap *et al.* 2004). In a literature review of social effects on avian behavioural patterns across time,

Helm *et al.* (2006) drew attention to the relationship between avian seasonal activities and the social behaviours taking place at these times in what they termed “sociable schedules”. For example, some species become more vocal when they are ready to depart on migration which may affect departure times of conspecifics, from small communal reproductive units to large breeding colonies (Rees 1987; Piersma *et al.* 1990).

Most behavioural research in birds has focused on diurnal, terrestrial taxa, likely owing to the difficulty in studying other groups such as seabirds

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which typically also nest in remote locations (Brooke 2004). Yet many marine birds appear to have precisely timed events at circadian scales and are strongly social species living in colonies (Marchant & Higgins 1990). In particular, there is a dearth of ethological research on the petrels, or Procellariiformes, many of which are nocturnally-active colonially breeding taxa, even though their worldwide distribution, numbers, and biomass indicate that their social breeding strategies are evolutionarily successful (Warham 1990; Brooke 2004).

A major tool of ethology is the classification of behaviours in the form of an ethogram, which can be used as a template to address a wide range of hypotheses relating to specific behaviours (MacNulty *et al.* 2007). This vital component of behavioural studies provides a code both for each taxon of interest, and for interspecific comparisons, to drive the direction of future research (Scholes 2008). The lack of published literature on petrel sociality makes it no surprise that few examples of procellariiform ethograms are available, while behavioural repertoires are more commonly known in other, typically diurnal seabird groups, such as penguins (Seddon 1991), gannets (Matthews *et al.* 2008), and gulls (Tinbergen 1953).

This study focuses on the endemic New Zealand species, the Westland petrel (*Procellaria westlandica*; Procellariidae). It is listed as Vulnerable by the International Union for the Conservation of Nature (IUCN 2008) and is one of the largest (~1.2 kg) burrowing nocturnal seabirds in the world. Westland petrels are highly active at night at their colonies, vocalising and interacting with conspecifics (Warham 1990), suggesting an important role for sound and social behaviour in the bird's life cycle. The aims of this study were to produce the 1st ethogram of the species, as well as for the genus, and to test temporal patterns in vocalisations and social behaviours in general at the colony. We specifically asked what temporal patterns and what scales best predict the behavioural patterns and social dynamics at the breeding colonies of Westland petrels.

To explore the role of temporal dynamics we conducted behavioural observations of Westland petrels at night throughout their occupancy of the breeding colony at 2 different life history stages (territory/mate-pair, re-establishment and incubation) over 2 years, generating a record of activity levels over multiple temporal scales. By detailing all the colonial behaviours as essential but little known components of the natural history of this species, we aim to stimulate further behavioural investigations in this taxon as well as providing a template that may be applied to other nocturnal procellariiform taxa, particularly relevant

to 4 congeneric petrel species, 3 of which are IUCN ranked 'Vulnerable', needing urgent conservation attention (Sutherland 1998; IUCN 2008).

MATERIALS & METHODS

Study species and study site

Westland petrels are obligate biparental seabirds which tend to breed annually during the austral winter in a number of distinct colonies within the Paparoa National Park, Westland, New Zealand, mostly situated inside a 16 km² zone designated as a Special Conservation Area (Marchant & Higgins 1990; Waugh *et al.* 2006). Birds which skip breeding during the current year or which have not yet reached a breeding age are termed nonbreeders. After spending the austral summer at sea near coastal South America (Marchant & Higgins 1990), birds return in mid-Feb to late Mar (*i.e.*, austral autumn) to re-establish small nesting territories, followed by mating and the laying of a single egg in their burrow in late May to Jun (Jackson 1958; Bartle 1974; Baker & Coleman 1977). The birds, which are socially monogamous, incubate their egg in alternate shifts while the other parent forages at sea (Marchant & Higgins 1990). Hatching occurs between early Aug and mid-Sep after which parents take turns attending to their chicks for ~2 weeks (Jackson 1958; Baker & Coleman 1977). Later, chicks are left on their own and both parents provision larger nestlings (Marchant & Higgins 1990). Adults leave the colony in late Sep to Nov, migrate to South American coastal waters, and remain at sea until they return to the breeding colony in New Zealand the following year (Landers *et al.* 2011).

Recent work by Waugh *et al.* (2006) showed that individual variation exists in the return rates of breeding Westland petrels with some adults returning every year to breed, some returning but not breeding annually, and others not returning and instead returning the next year or two. Throughout the breeding season, surface colonial activity takes place between dusk and dawn when birds either return from sea (usually around dusk although some arrive later in the night) or emerge from their burrows. At dawn there is a mass exodus when birds either return to sea or their burrows (Warham 1990; T.J.L., *pers. obs.*).

Our study was conducted at the Scotchman's Creek colony located *c.* 140 m above sea-level and 3 km inland at 42° 08.8'S, 171° 20.5'E where ~4000 burrows are located in dense forest (Waugh *et al.* 2006). This population has been the subject of demographic studies since 1970, and so some birds are banded, however a large proportion are not (~30–40% not banded, G.C. Wood, *pers. obs.*). Birds used for data collection were captured when possible, and bands noted, while those without bands were

Table 1. The number of 10-minute observations collected in each season, with details on the subject pool (captured and previously banded birds).

Season	Number 10 min observations	Number nights observing colony	% observed birds captured	% captured birds banded	% captured birds previously recorded
Establishment (Mar-Apr 2007)	21	5	76	43	10
Incubation (Jul 2007)	22	4	73	32	5
Establishment (Mar-Apr 2008)	36	10	100	72	6
Incubation (Jul 2008)	36	6	100	47	17

newly banded under University of Auckland animal use and New Zealand Department of Conservation permits.

Behavioural observations

To compare behaviour across different temporal scales, observations were made over a 2-week period during late Mar-Apr (Establishment period) and Jul (Incubation) in each of 2007 and 2008, using a design whereby the single observer (always T.J.L.) walked haphazard tracks throughout the night on the study colony and observed each bird encountered for 10 minutes. Most birds (> 90%) were observed for the full 10 minutes; however, the few observation bouts that were < 10 min due to the bird moving away were still analysed as our statistical units were all proportional data. Observations were made either by viewing the bird through a night-scope and describing all behaviours witnessed into a Fostex FR-2 Field Recorder (for the 2007 trips) or by videoing the bird using a Sony HD HandyCam with IR 'night vision' lighting and noting the behaviours at a later time (for the 2008 trips). To test for consistency between the 2 observation methods (*i.e.*, audio recorder versus video camera), 10 observations in the Mar-Apr 2008 trip were subjected to both methods and analysed (described below). Due to the possibility of moonlight avoidance behaviour which has been documented in several petrel species (Watanuki 1986; Bretagnolle 1990; Mougeot & Bretagnolle 2000), and also the concern that the birds may see the observer during bright moonlight, all observations were made when the moon was at most half full or the night sky was overcast. Observations were only made when there was negligible wind and rain to assure consistency in both behavioural observations and data recording throughout the study.

A comprehensive description of all behaviours observed (*i.e.*, ethogram) was generated and individual behaviours and 1 non-behaviour (location at burrow) were grouped into categories which were used in analyses (described in Results).

The majority of the ethogram was created during several preliminary observations in the 1st season which were not analysed but only used to create a template for future data collection. Individual observations were analysed by creating 5-second time bins for the duration of the 10-minute observation (*i.e.*, a total of 120 bins per observation) and coding all categories that occurred in each bin. Next, the proportion of time bins observed including each category of interest was calculated and used as the data point in statistical analyses to test for temporal variation throughout single nights, between seasons, and across years (the data across the night by establishing 3-hour time intervals from sunset to sunrise; *i.e.*, 0-3, 3-6, 6-9, 9-12 hours after sunset). As we combined single nights when comparing data between seasons, we tested for potentially consistent variation between nights within each season using the most common behavioural category.

A total of 115, 10-minute observation periods were obtained, distributed across the temporal scales of interest (*i.e.*, over the night, seasons and years) (Table 1). The same procedure of calculating proportions for each category of interest was applied to the 10 observations from the Mar-Apr 2008 trip that were used to test for consistency between the 2 observation methods (*i.e.*, audio recorder versus video camera).

Statistical analyses

To test for any interactions between categories a Principal Component Analysis (PCA) was conducted using JMP 7 (Statistical Discovery Software; SAS Institute Inc., Cary, NC). However, as the percent contributions to explain the variance in the data of PC 1, PC 2 and PC 3 were similar at 26, 28 and 23%, respectively, with all of the data categories contributing similar extents to each of these components, the PCA indicated a lack of confounding covariance in the original variables and so we took a separate, behavioural category-based approach in our analysis. Also, due to the

Table 2. Ethogram of Westland petrel colonial activity divided into categories.

Behaviour/Location	Additional Description	Category
Body movement	Any non-specific movement	Body movement
Body turn	To right/left	Body movement
Climb	e.g., tree, stump	Body movement
Dig	With beak/foot	Body movement
Enter/exit burrow	-	Body movement
Move head into burrow	-	Body movement
Head movement forward	Both forward & to ground	Body movement
Head turn	To right/left	Body movement
Sit down/stand up	-	Body movement
Walk	-	Body movement
Wing movement	When climbing/walking	Body movement
Head tuck	Head resting on back	Stationary
Sit	-	Stationary
Stand	While not walking	Stationary
Head extension	Usually just before vocalisation	Head extension
Beak movement	All except yawning (see below)	Self maintenance
Beak prod	e.g., stick, ground	Self maintenance
Bite object	e.g., foot, stick, leaf	Self maintenance
Body adjustment	Movement while sitting	Self maintenance
Shake body	Head/tail shake	Self maintenance
Gulp	As if swallowing	Self maintenance
Head bobbing	Neck movement up & down	Self maintenance
Scratch	Head/body scratch	Self maintenance
Leg adjustment	From sitting position	Self maintenance
Leg/wing stretch	-	Self maintenance
Preen	Preening its own body	Self maintenance
Sneeze	Expulsion of air from nostrils	Self maintenance
Wing flap	When stationary	Self maintenance
Approach conspecific	<10 m distance between birds	Social interaction
Bite conspecific	In agonistic context	Social interaction
Turn towards conspecific	<10 m distance between birds	Social interaction
Preen conspecific	Both to or by a conspecific	Social interaction
Vocalize at conspecific	<10 m distance between birds	Social interaction
Aggressive wing pose	<10 m distance between birds	Social interaction
Quack call	See Warham (1988)	Vocalisation
Jackass call	See Warham (1988)	Vocalisation
Agonistic burrow call	Vocalise into burrow	Vocalisation
Eyes closed	Closed or half closed	Eyes closed
Yawn	Prolonged bill opening/closing	Yawn
At burrow	<1 m from any burrow	At burrow

independent variation of the categories, there was no need to adjust the alpha levels (see below). As data were proportional measures and not normally distributed, Kruskal-Wallis tests were used to assess for variation between 3-hour time intervals (*i.e.*, over the night) and Mann-Whitney *U*-tests for variation between observation method (*i.e.*, audio recorder versus video camera), seasons and years. Friedman's ANOVA by ranks was used to test for variation between nights within each season. All these statistical tests were done in STATISTICA 7.1 (StatSoft 2005) to assess significance ($\alpha < 0.05$).

RESULTS

Ethogram

A total of 40 individual behaviour traits plus a location trait were identified and grouped into 9 categories: body movement, stationary, head extension, self maintenance, social interaction, vocalisation, eyes closed, yawn, and location (Table 2). Note that birds which are stationary (*i.e.*, not walking) can still have body movements such as when a sitting bird moves its head.

Variation between observation methods

There were no significant differences between the 2 data collection methods (*i.e.*, audio recorder versus video camera) for any of the categories tested. This also supported our assumption that there were similar amounts of observer-caused disturbance, if any, in each of the 2 observation methods (Table 3).

Temporal variation in categories of behaviour

Table 4 shows the detailed statistical results of variation in the categories across different temporal scales (over nights, seasons and years) and these patterns are detailed below.

Nocturnal variation

Three categories varied significantly with time of night: social interactions, vocalisations, and eyes closed (Fig. 1). The mean proportions of social interactions were bimodal with significantly higher values ($H_3 = 18.52, P < 0.001$) during the 1st and last time intervals (*i.e.*, 3 hours after sunset and 12 hours after sunset, respectively). A similar bimodal pattern was found in vocalisation category with birds vocalising the least ($H_3 = 8.25, P = 0.041$) during the middle of the night in the 9 hours after sunset time interval. The mean proportion of time spent with eyes closed was significantly variable over the night ($H_3 = 9.34, P = 0.025$), with a higher mean proportion during the middle of the night (Fig. 1).

Seasonal variation

There was no variation between nights within any of the 4 seasons compared for the most common behavioural category of Stationary (Friedman's

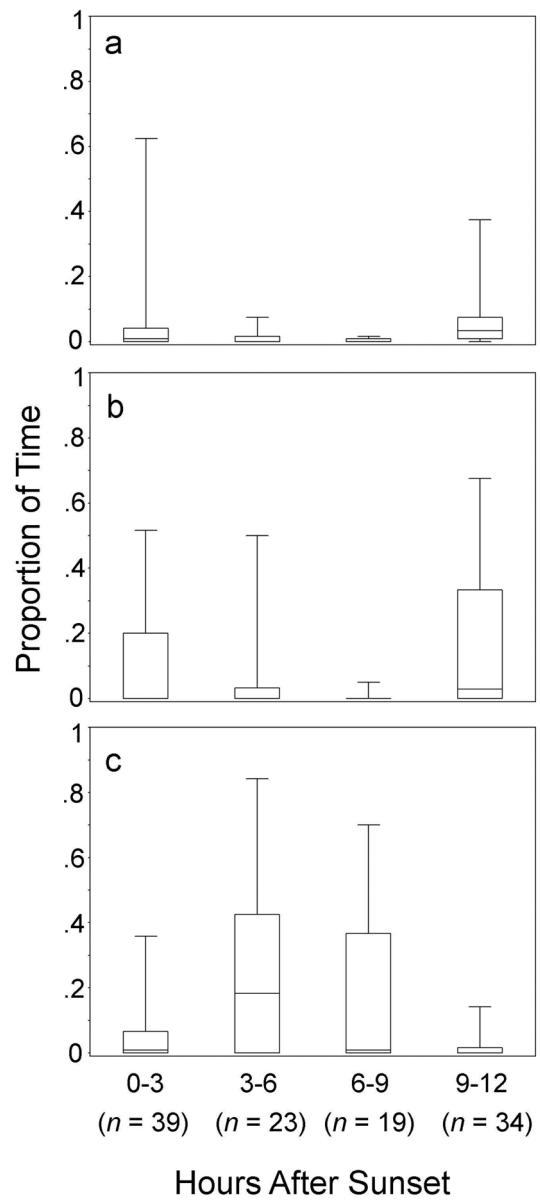


Fig. 1. The proportion of time Westland petrels spent during 10 min observations performing the categories (a) SOCIAL INTERACTION, (b) VOCALISATION and (c) EYES CLOSED separated by 3-hour time after sunset intervals. Box plots indicate 10th, 25th, 50th, 75th, and 90th percentiles.

ANOVA: Establishment 2007, $\chi^2 = 1.66, df = 3, P = 0.65$; Incubation 2007, $\chi^2 = 1.06, df = 2, P = 0.59$; Establishment 2008, $\chi^2 = 14.93, df = 8, P = 0.06$; Incubation 2008, $\chi^2 = 0.15, df = 2, P = 0.93$). There were no categories that varied significantly between the seasonal stages of establishment in late Mar to Apr and incubation in Jul (Table 4).

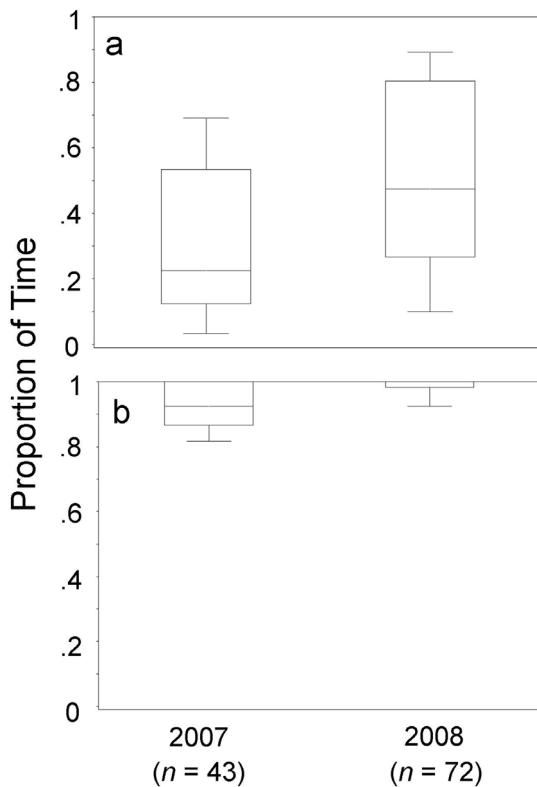


Fig. 2. The proportion of time Westland petrels spent during 10 min observations performing the categories (a) BODY MOVEMENT and (b) STATIONARY separated by year. Box plots indicate 10th, 25th, 50th, 75th, and 90th percentiles.

Annual variation

The average proportion of total time that birds performed body movements was significantly higher in 2008 versus 2007 ($Z = -3.17, P = 0.002$) (Fig. 2a). Likewise, birds spent significantly more time in a stationary position in 2008 than 2007 ($Z = -3.58, P < 0.001$) (Fig. 2b).

Seasonal & nocturnal variation within a year

As there was significant annual variation in the body movement and stationary categories (see Annual Variation above), we analysed these further by separating the data by year and re-running the Mann-Whitney and Kruskal-Wallis tests to assess for seasonal and nocturnal variation, respectively (Table 5). The 2007 data showed significant variability ($Z = -3.20, n = 43, P = 0.001$) in the body movement category between the 2 seasons, with Westland petrels performing overall more body movements during incubation than during establishment (Fig. 3a). Although body movement did not significantly vary between seasons for the 2008 data, there was a

Table 3. Results of non-parametric tests between the 2 observation methods used (audio recorder versus video camera) for each recorded category.

Category	Observation method (Mann-Whitney)		
	n	Z	P
Body movement	20	-0.04	0.97
Stationary	20	0.00	>0.99
Head extension	20	0.00	>0.99
Self maintenance	20	-0.04	0.97
Social interaction	20	0.00	>0.99
Vocalisation	20	0.00	>0.99
Eyes closed	20	-0.04	0.97
Yawn	20	0.00	>0.99
At burrow	20	0.00	>0.99

significant difference ($H_3 = 14.35, n = 72, P = 0.003$) in body movement over the time of night with birds on average moving more during the 0–3 hour and 9–12 hours after sunset intervals (Fig. 3b).

DISCUSSION

Ethogram

Our ethogram listing the 40 traits (Table 2), grouped into the 9 categories, is indicative of the large variety of activities, displays, interactions, and events taking place on the colony throughout the night. Understanding the activity patterns at the breeding sites is an important 1st step for studying a species and for providing a foundation for the quantitative study, experimental approaches (e.g., playback studies and/or olfactory cue presentations), and functional tests of its behavioural diversity (Lehner 1996; Bourgeois *et al.* 2008). The categories and the behaviours reported in our ethogram may be useful for designing other behavioural studies as well as for comparative work with the other 4 congeneric petrel species and other nocturnal, colonial, burrowing seabirds.

Temporal scales of variation in behaviour in Westland petrels

One of our major aims of this study was to test if temporal variation exists for particular behaviours in Westland petrels. We detected variation in some categories with annual and nocturnal variation yet no seasonal variation in any of the same categories. It was somewhat unexpected to find annual variation in the body movement and stationary categories, although it may be that colonial activity patterns do contain annual rhythms due to changes in the colony composition, for example, proportion of breeding

Table 4. Results of non-parametric tests for variation of the recorded categories across different temporal scales. Significant *P*-values are given in bold.

Category	Temporal scale (<i>n</i> = 115)							
	Time of night (Kruskal-Wallis)			Season (Mann-Whitney)		Year (Mann-Whitney)		
	<i>H</i>	df	<i>P</i>	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>	
Body movement	4.34	3	0.23	-1.12	0.26	-3.17	0.002	
Stationary	4.80	3	0.19	-0.47	0.64	-3.58	<0.001	
Head extension	6.18	3	0.10	-0.09	0.93	-1.19	0.24	
Self maintenance	2.73	3	0.44	-0.50	0.62	-0.97	0.33	
Social interaction	18.52	3	<0.001	-1.01	0.31	-0.56	0.58	
Vocalisation	8.25	3	0.041	-0.49	0.62	-1.50	0.13	
Eyes closed	9.34	3	0.025	-0.50	0.62	-0.90	0.37	
Yawn	1.82	3	0.61	-1.06	0.29	-0.99	0.32	
At burrow	3.24	3	0.36	-0.66	0.51	-0.35	0.72	

birds or sex ratio structure. However, even if our methodology to record data varied between years, we found no statistical differences when comparing data from those observation periods during which both methodologies were applied, and hence it is reasonable to assume the annual variation we detected is biologically relevant.

Waugh *et al.* (2006) showed in their 8 year demographic study that Westland petrels show variation in annual recapture rates depending upon their breeding status, with previously successful breeders returning to the colony each year whereas nonbreeders showed more fluctuating return rates. As we chose our observations of birds haphazardly, and because the sex or breeding status of most birds observed could not be determined by sight (with only a small subset of the colony burrows being monitored; also see Landers *et al.*, *in press*), it is plausible that the annual variation in movement may be due to variation in the proportional presence of the different sexes and/or non-breeders. The latest Westland petrel world population size is estimated at c. 20,000 birds of which c. 2,000 pairs are breeding annually (Brooke 2004), and so non-breeders are likely to make up a significant proportion of birds found on the colony at any time (Lawrence *et al.* 2008).

Although overall most of the behavioural categories did not vary between the 2 seasonal stages, there was significantly more body movement during the Jul incubation stage than the Mar-Apr establishment stage in 2007 (Fig. 3a). The presence of this trend in 2007 and not in 2008 may be due to the presence and activities of non-breeders in that particular year. Warham (1990) suggests that during the pre-egg and incubation stages non-breeders are

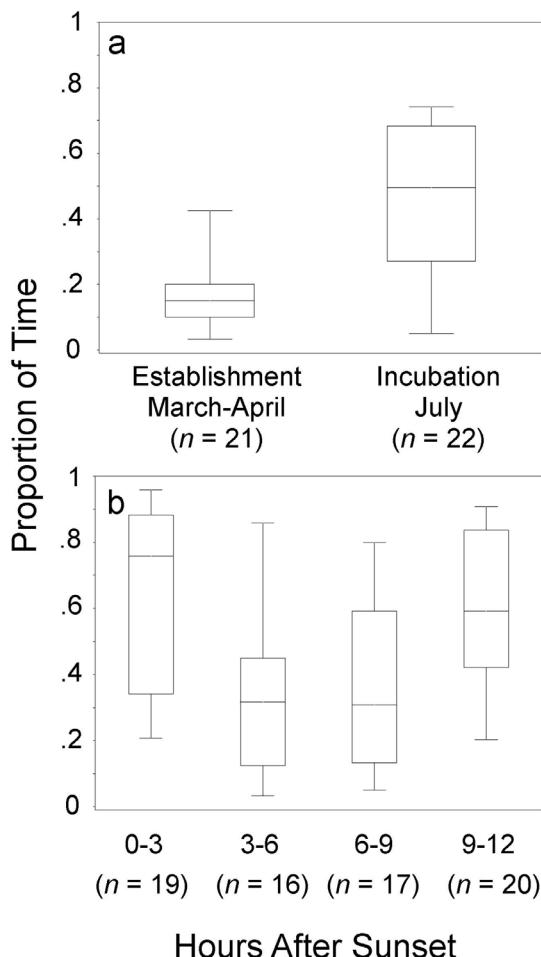
the most active birds on the colony when they are prospecting for a future nest site, whereas breeders tend to enter their burrows upon arrival. Hence, there may have been more non-breeders present in 2007, thus contributing to the increased body movement observed.

Our analysis of the variation in categories throughout the night revealed consistently bimodal distributions of both the social interaction and vocalisations categories (Fig. 1a & 1b), each being more common just after sunset and before sunrise. Roughly the inverse of these distributions was found for the eyes closed category with more occurrences taking place during the middle of the night (Fig. 1c). If eyes closed is indicative of a less mobile state then such an inverse pattern of behaviours is as expected. However, the lack of the applicability of the Principal Component approach in our data argues against a simple trade-off between different category behaviours. Therefore, other behaviours may thus be more likely to take place during these more active states of the night such as body movement or head extensions. Our results found body movement in 2008 but not in 2007 to fit this prediction (Fig. 3b).

The bimodal nocturnal pattern of vocalisations in nocturnal colonial seabirds has been briefly discussed in studies of Yelkouan shearwater (*Puffinus yelkouan*; Bourgeois *et al.* 2008), Barau's petrel (*Pterodroma baraui*; Brooke 1978a), fairy prion (*Pachyptila turtur*; Harper 1976), Manx shearwater (*Puffinus puffinus*; M. Brooke, *per comm.*) as well as Westland petrels (Marchant & Higgins 1990). Warham (1990) mentions this as a general pattern of petrels stating that noisy petrels peak in volume 1–2 hours after their arrival (usually after sunset)

Table 5. Results of non-parametric tests for variation of the body movement and stationary categories across different temporal scales. Significant *P*-values are given in bold.

Category	Year	<i>n</i>	Temporal scale				
			Time of night (Kruskal-Wallis)			Season (Mann-Whitney)	
			<i>H</i>	df	<i>P</i>	<i>Z</i>	<i>P</i>
Body movement	2007	43	3.65	3	0.30	-3.20	0.001
Stationary	2007	43	2.45	3	0.49	-0.34	0.73
Body movement	2008	72	14.35	3	0.003	-0.65	0.52
Stationary	2008	72	4.95	3	0.18	-0.85	0.40

**Fig. 3.** The proportion of time Westland petrels spent during 10 min observations performing the category BODY MOVEMENT in (a) 2007 separated by season (establishment and incubation) and (b) 2008 separated by 3-hour time after sunset intervals. Box plots indicate 10th, 25th, 50th, 75th, and 90th percentiles.

followed by a decline when the birds tend to sleep and then another peak of vocal activity in the half-light of dawn. This nocturnal vocalisation pattern appears to be common in the petrels, however, we suggest that quantitative analyses of more data be published on different species.

Our study describes the behaviour of a nocturnal seabird on its breeding colony throughout the entire night and how this varies at different temporal scales. Although the ethogram produced is descriptive we consider the results to be valuable in the context of the natural history and the behavioural ecological literature on colonial petrels that has focused on shorter nightly time frames and/or examined particular social behaviours and displays (Brooke 1978b; Warham 1988; Bretagnolle & Lequette 1990; Cure *et al.* 2009). We found little variation in categories at annual and seasonal scales, while consistent variations were detected at nightly time scales in body movement, vocalisations, and social interactions. It appears that temporal patterns in the variation of social behaviours are important in Westland petrels, and so we are left with ultimate questions such as when did these 'schedules' arise from (*i.e.*, regarding phylogeny) and how do they affect the reproductive success and survival of the species (*i.e.*, fitness function)? These questions can be explored by ascertaining more detail of the social correlates of the variation in these behavioural categories. Schedules of social behaviour events at the colony level, arising from the behavioural patterns of individual birds, may relate strongly to the colonial breeding system with which these nocturnal birds have evolved. For example, as activity levels change over time (*e.g.*, increased social interactions & vocalisations), birds may benefit from departing the colony in synchrony as Westland petrels do in massive numbers close to dawn, just after extensive periods of elevated levels of vocal and social activity (T.J.L., *pers. obs.*).

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