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At-sea activity patterns of breeding and nonbreeding white-chinned petrels *Procellaria aequinoctialis* from South Georgia

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Abstract Despite the recent burgeoning in predator tracking studies, few report on seabird activity patterns, despite the potential to provide important insights into foraging ecology and distribution. In the first year-round study for any small petrel, we examined the activity patterns of the white-chinned petrel *Procellaria aequinoctialis* based on data from combination geolocator-immersion loggers deployed on adults at South Georgia. The petrels were highly nocturnal, flying for greater proportions of darkness than any large procellarid studied so far, except the light-mantled albatross *Phoebetria palpebrata*. Flight bout durations were short compared with other species, suggesting a dominant foraging mode of small-scale searching within large prey patches. When migrating, birds reduced the proportion of time on the water and increased flight bout duration. Activity patterns changed seasonally: birds flew least during the nonbreeding period, and most frequently during chick-rearing in order to meet higher energy demands associated with provisioning offspring. The degree of their response to moonlight was also stage dependent (greatest in nonbreeding, and weakest in incubating birds), a trait potentially shared by other nocturnal petrels which will have repercussions for feeding success and prey selection. For the white-chinned petrel, which is commonly caught in longline fisheries, these results can be used to identify periods when birds are most susceptible to bycatch, and therefore when use of mitigation and checking for compliance is critical.

Introduction

Although seabirds are major consumers of marine resources, and often breed in large accessible colonies, until the last few years, detailed information on behaviour of known individuals at sea remained elusive. Recent data-logging studies have greatly increased knowledge of relationships between at-sea activity patterns and species, sex, breeding status, prey type, foraging strategy, and the timing and use of marine habitats (Phillips et al. 2008; Wakefield et al. 2009). Despite technological advances that have reduced the size, mass and cost of loggers, there have been relatively few studies of the at-sea activity of smaller procellariiform species (Catry et al. 2009; Guilford et al. 2009; Landers et al. in press; Rayner et al. 2008; Shaffer et al. 2009).

White-chinned petrels *Procellaria aequinoctialis* are medium-sized (1.3 kg) burrow-nesting procellariiforms that breed during the austral summer on sub-Antarctic islands throughout the Southern Ocean (Marchant and Higgins 1990). This wide-ranging and opportunistic species is capable of exploiting all marine environments if prey abundance is high (Catard et al. 2000; Phillips et al. 2006; Weimerskirch et al. 1999). White-chinned petrels travel by both gliding and flap-gliding flight, in contrast to albatrosses, which rely to a greater extent on the wind to sustain gliding flight; this may allow these petrels to travel more directly (Pennycuick 1987; Weimerskirch et al.

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1999). In addition, their smaller size and manoeuvrability results in relatively lower energetic costs of take-off, potentially enabling them to adopt a foraging mode involving frequent landings on the water (Weimerskirch et al. 2000a).

White-chinned petrels can reach depths up to 12 m (Huin 1994), and feed on euphausiids, fish and squid (Berrow et al. 2000a; Catard et al. 2000). Their diet and distribution overlap considerably with several of the smaller Southern Ocean albatrosses (Phillips et al. 2005). However, unlike albatrosses that actively seek and capture most prey during the day throughout the year (Mackley et al. 2010; Phalan et al. 2007), white-chinned petrels appear to show high nocturnal activity, e.g. 49% of feeding events observed at sea by Harper (1987) were during darkness. Ship-based observations of white-chinned petrels suggest that their nocturnal behaviour is not influenced in a consistent way by moon phase (Delord et al. 2005; Gandini and Frere 2006; Gómez Laich and Favero 2007; Moreno et al. 1996; Petersen et al. 2008a; Weimerskirch et al. 2000b). It might therefore be inferred that white-chinned petrels are well-adapted to nocturnal foraging and able to detect their prey, including Antarctic krill *Euphausia superba*, by sight or olfaction (Nevitt et al. 2004), independent of light levels. In contrast, Barnes et al. (1997) noted a diel cycle in their behaviour consisting of a midnight lull followed by increased activity peaking 2.5 h before dawn, which suggests a direct or prey-mediated response to ambient light levels.

During the nonbreeding period (austral winter), white-chinned petrels congregate in large numbers over productive continental shelves (Phillips et al. 2006; Weimerskirch et al. 1999). The South Georgia population utilises the Patagonian shelf during the nonbreeding, pre-laying exodus and incubation periods, but rarely during chick-rearing when they mainly forage over the South Georgia shelf and shelf-slope, and around the South Orkney Islands (Berrow et al. 2000a; Phillips et al. 2006). Over the Patagonian Shelf, white-chinned petrels are known to follow fishing vessels and to feed on discards in large numbers (Gandini and Frere 2006; Gómez Laich and Favero 2007; González-Zevallos and Yorio 2006; Moreno et al. 1996). Long-line fishing for Patagonian toothfish *Dissostichus eleginoides* is banned in the vicinity of South Georgia and the South Orkneys during the austral summer (Phillips et al. 2006), and discards will be rare in the diet of white-chinned petrels during chick-rearing.

Targeting of different types of prey, from fisheries or varying marine habitats, potentially requires different foraging techniques, which should be detectable by analysis of activity patterns. In addition, the few studies of activity in nonbreeding seabirds, which are without a central place constraint and therefore have lower energetic and nutritional demands, show that they generally rest on the water for longer during daylight than birds that are breeding (Mackley et al. 2010; Phillips et al. 2007). Whether activity patterns of white-chinned petrels vary in the same way is unknown. The aims of this study were therefore to: (1) test for stage-related differences in white-chinned petrel at-sea activity; (2) examine whether activity patterns vary with habitat; (3) compare the activity patterns of white-chinned petrels with those of other procellariiforms studied so far; and (4) test whether activity varies with moonlight. The white-chinned petrel population at South Georgia has shown a sustained long-term decline, attributable largely to fisheries bycatch (Berrow et al. 2000b; Martin et al. 2009; Phillips et al. 2006). We therefore discuss how our results can inform bycatch mitigation efforts for this threatened species.

Materials and methods

Combined geolocator-immersion data loggers attached to a plastic leg ring (total mass 10.5 g; <1% of adult body mass) were deployed on the tarsi of adult white-chinned petrels extracted from burrows on Bird Island, South Georgia (54°00′S, 38°03′W) (for details see Phillips et al. 2006). Thirty-five loggers were deployed from 5–7 February 2003, of which 12 were recovered over the three subsequent breeding seasons. Data were successfully downloaded from eleven loggers. Data from the 2003 nonbreeding period (February–October) and the following 2003/2004 breeding season (October–February) were used in the analysis. Birds were of unknown sex.

The data loggers measured visible light intensity every minute and tested for saltwater immersion every 3 s. The maximum (truncated) light level, and number of positive tests from 0 (continuously dry) to 200 (continuously wet) were stored at the end of each 10 min block. The light data were processed using MultiTrace (Jensen Software Systems) (see Phillips et al. 2004). Briefly, thresholds in the light curves, omitting those with obvious interruptions around dawn or dusk, were used to determine sunrise and sunset. Those with obvious interruptions around down or dusk were omitted when calculating distribution, whilst, for activity data, sunrise and sunset were inferred from adjacent days. Latitude was derived from day length and longitude from the timing of local midday with respect to Universal Time and Julian day. Latitudes were not available close to the equinoxes when day length is similar across the globe. Following the approach adopted by Mackley et al. (2010), a speed filter was used to highlight rapid easterly (20 kph) or westerly (12 kph) changes in location (min. 1 day duration) during the nonbreeding period, which were visually inspected for accuracy before designation as migrating (nonbreeding commuting) periods; otherwise, birds were considered to be resident.

The activity data were processed automatically using scripts written in R (R Development Core Team 2008) to give eight measures of activity: the proportion of time spent on the water, the length of flight bouts in minutes, and the number of flight bouts per hour, for both darkness and daylight, and; the proportion of the total time spent on the water, and time spent in flight in each day (consecutive light and dark period) that occurred during darkness. Each 10-min block was categorised as daylight or darkness, from the timing of nautical twilight (derived from the light curves in Multi-trace). Flight bouts were defined as a continuous sequence of dry (0) values (see Phalan et al. 2007).

The nonbreeding period started in February for all but one bird that departed in April, presumably following a successful breeding attempt. All birds began their pre-laying exodus between late October and early November, returning to the colony mid- to late November (Phillips et al. 2006). During the breeding period, activity data were visually inspected for extended dry periods ($\geq$1 day) that indicated birds were in burrows. For each foraging period, only data from the first to the last complete day of at-sea activity were used in the analysis. Birds spent longer periods in the burrow during incubation than chick-rearing (3–16 and 1–3 days, respectively) (Marchant and Higgins 1990). Chicks hatched in late December to late January, which was apparent in an immediate switch to a pattern of short visits. The first chick-rearing foraging trip followed the first short stay (1–3 days) in the burrow.

In order to improve statistical normality, flight bout durations were double log transformed and the numbers of bouts per hour were square root transformed. Proportion data were either arcsin transformed or treated using a GLM with binomial error structure with a logit link function. The effects of stage were modelled using mixed-effects Generalised Linear Models fitted by Penalised Quasi Likelihood (Venables and Ripley 2002) with individual identity treated as a random effect (Pinheiro and Bates 2000). In addition, a first-order autoregressive term (corAR1) was used to account for non-independence of errors due to temporal autocorrelation (however, due to insufficient computing power—R was limited to 2 Gb of memory with the windows operating system—this term was not used to model flight bout duration. Comparative *P*-values were extracted by refitting these models with different intercepts. A mixed-effects linear model was used to test the relationship between the visible proportion of the moon, and activity parameter during resident, pre-laying exodus and incubation stages. The illuminated proportions of the moon's visible disk at noon (universal time) were obtained from the Astronomical Applications Department of the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.html) following Phalan et al. (2007). For all other analyses using conventional tests, the activity measures were averaged for each individual bird to prevent pseudo-replication. The arithmetic observed mean ± SD are reported in the tables to facilitate comparisons with previous studies, and the estimated mean ± 95% confidence interval are shown in Fig. 1. Given the large number of comparisons, the threshold for statistical significance was set to $P < 0.01$.

Results

Immersion data were available from 11 birds during the nonbreeding phase, 10 during the pre-laying exodus, six during incubation (20 trips) and three during chick-rearing (8 trips). The distributions for 10 of the 11 birds in this study (the other logger was not retrieved until December 2005) are presented in Phillips et al. (2006). All eleven white-chinned petrels initially went to the Patagonian Shelf from South Georgia for the nonbreeding period. In mid-winter (May–June), three birds moved to the Humboldt Current west of South America, of which one returned directly to South Georgia and the other two via the Patagonian Shelf. These movements typically occurred as rapid and sustained periods of flight (mean: 1 day, range: 1–2 days), hereafter termed 'migration'. During their pre-laying exodus, all 10 birds travelled to the Patagonian Shelf to forage (mean: 18 days, range: 7–28 days). Similarly, most foraging trips during incubation (mean: 8 days, range: 2–16 days) were to the Patagonian Shelf, whereas chick-rearing birds feed in Antarctic waters south of the Polar Front, and in the southern Scotia Sea in particular (mean: 4.5 days, range: 2–8 days).

Individual variability

During the resident phase of the nonbreeding period, variation was consistently higher between than within individuals (One-way ANOVA for each activity measure: $F_{(10,2513–9595)} = 3.95–17.75$, $P < 0.001$) whereas behaviour was more fixed during migration (One-way ANOVA for each activity measure: $F_{(9–10,14–156)} = 0.97–2.32$, $P = 0.509–0.073$). Behaviour during the breeding period was generally invariant between individuals for all three stages (one-way ANOVA for each activity measure, pre-laying exodus: $F_{(9,168–629)} = 0.60–2.13$, $P = 0.797–0.025$; incubation: $F_{(5,156–159)} = 0.76–2.37$, $P = 0.437–0.042$; chick-rearing $F_{(2,31–313)} = 0.15–1.82$, $P = 0.858–0.178$). However, there were exceptions: during the pre-laying exodus both the number and length of flight bouts during daylight differed significantly between individuals

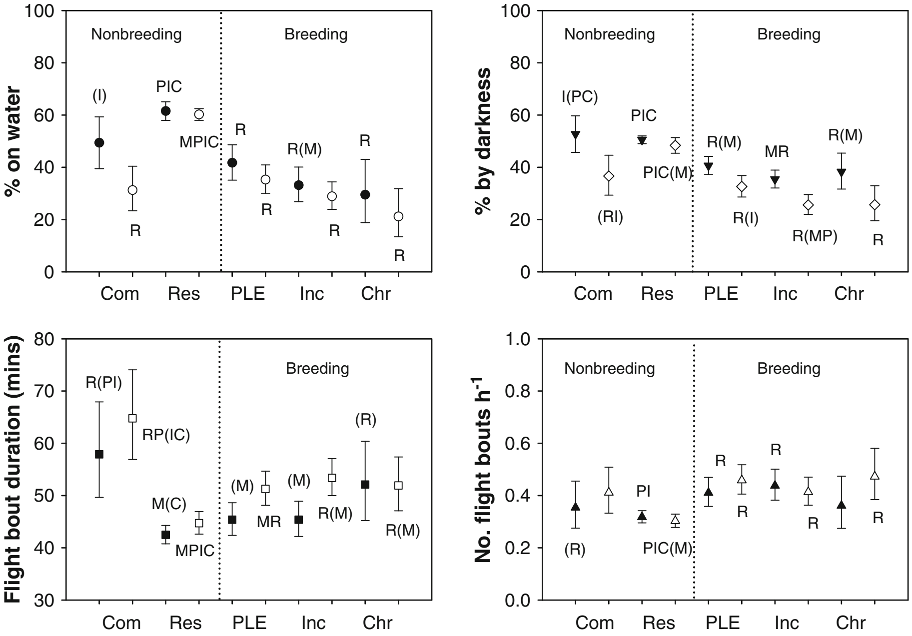

Fig. 1 Comparison of activity patterns (estimated mean ± 95% CI) of white-chinned petrels during different stages of the breeding and nonbreeding periods: migration (*Mig*), resident (*Res*), pre-laying exodus (*PLE*), incubation (*Inc*) and chick-rearing (*Chr*): **a** percentage of time spent on the water during darkness (*filled circle*) and daylight (*open circle*); **b** percentage of total time on the water (*filled inverted triangle*) or in flight (*open diamond*) per day that occurred in darkness; **c** flight bout durations (mins) during darkness (*filled square*) and daylight (*open square*); and, **d** number of flight bouts per hour during darkness (*filled triangle*) and daylight (*open triangle*). *Small letters* (*M*, *R*, *P*, *I* and *C*, respectively) indicate mean values that differ significantly (without brackets $P < 0.001$, with brackets $P \leq 0.01$)

($F_{(9,172)} = 2.69$, $P = 0.006$ and $F_{(9,1271)} = 4.50$, $P < 0.001$, respectively); during incubation flight bout length during darkness and daylight differed between individuals ($F_{(5,529)} = 3.86$, $P = 0.002$ and $F_{(5,1226)} = 8.96$, $P < 0.001$ respectively) as did the number of flight bouts per hour during daylight ($F_{(5,159)} = 16.98$, $P < 0.001$). Additionally, during chick-rearing, the proportion of flight that was at night showed a near significant difference between individuals ($F_{(2,34)} = 5.12$, $P = 0.011$).

Comparison of breeding stages and nonbreeding phases

During the resident phase of the nonbreeding period, birds spent significantly more time on the water than during any stage during daylight and, with the exception of migration, also darkness (Fig. 1a). The proportion of total time in flight that occurred during darkness was greatest for resident nonbreeders, and a similar trend was apparent in the proportion of total time on the water that occurred during darkness, for both nonbreeding phases, i.e. resident and migrating (Fig. 1b). This probably reflected the longer nights during winter, as the smallest values occurred during the incubation period, coinciding with the shortest midsummer nights. Flight bouts were longest when migrating, and shortest when resident, during both daylight and darkness (Fig. 1c). Resident birds showed the least frequent flight bouts during daylight, and there was a similar overall trend apparent during darkness (Fig. 1d). The proportions of time spent on the water decreased as the breeding season progressed; hence, chick-rearing birds rested for the shortest periods (Fig. 1a). The lack of statistical significance despite this clear trend is presumably related to the small sample size.

Ocean sector

For three birds that moved from the Patagonian Shelf to the Humboldt Current during the nonbreeding period, there were no significant differences in their resident activity patterns (Table 1).

Illuminated moon

There were no significant differences between stages in the range of values of the illuminated proportion of the moon's disc experienced (Fig. 2). However, as the migration and chick-rearing activity data did not include a complete lunar cycle, these were not included in the illuminated moon analysis. The influence of moon phase was greatest during the resident nonbreeding period. In contrast, fewer activity measures varied with illuminated moon during the pre-laying exodus and fewer still during incubation (Table 2). All nocturnal measures of activity were affected during the resident period: birds spent a lower proportion of time on

Table 1 Comparison of activity patterns (mean ± SD) for the three white-chinned petrels that divided their nonbreeding period (austral winter) between the Patagonian Shelf and Humboldt Current

	Patagonian Shelf	Humboldt Current	Test statistic
% Darkness wet	51.0 ± 11.2	50.7 ± 4.4	$t_2 = 0.04$, $P = 0.973$
% Daylight wet	54.5 ± 13.4	58.1 ± 5.7	$t_2 = 0.54$, $P = 0.644$
% Wet by darkness	43.0 ± 3.3	49.6 ± 3.8	$t_2 = 1.99$, $P = 0.185$
% Dry by darkness	45.8 ± 4.9	58.4 ± 1.8	$t_2 = 4.27$, $P = 0.051$
Flight bout duration in darkness (min)	65.0 ± 3.4	66.1 ± 7.2	$t_2 = 0.63$, $P = 0.595$
Flight bout duration in daylight (min)	72.7 ± 4.7	80.0 ± 2.2	$t_2 = 3.66$, $P = 0.067$
Number flight bouts/h darkness	0.34 ± 0.05	0.39 ± 0.04	$t_2 = 1.04$, $P = 0.407$
Number flight bouts/h daylight	0.29 ± 0.07	0.27 ± 0.01	$t_2 = 0.50$, $P = 0.669$

The remaining eight tracked birds stayed within the Patagonian Shelf

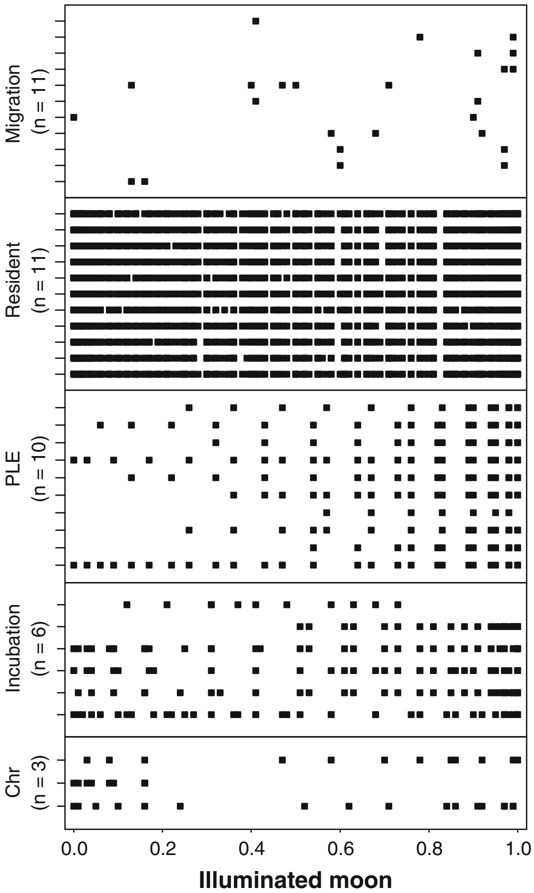

Fig. 2 The illuminated proportions of the moon experienced by individual white-chinned petrels during migration, resident, pre-laying exodus (*PLE*), incubation and chick-rearing (*Chr*) stages. Each datapoint represents a different day

the water and showed more frequent and longer bouts of flight as the illuminated moon increased. Furthermore, the duration of flight bouts during daylight increased. Flight bout durations and the proportion of time spent on the water during daylight increased with illuminated moon during the pre-laying exodus. During the pre-laying exodus the proportion of time on the water that occurred in darkness decreased, whereas the proportion of time spent in flight increased, with an increase in the illuminated moon. During incubation, only one measure of activity varied with illuminated moon: birds reduced the proportion of time spent on the water during darkness as the proportion of illuminated moon increased.

Discussion

Our study is unusual in that it is the first to provide comprehensive coverage of at-sea activity patterns throughout the annual cycle of any procellariid other than the large albatrosses. The relatively low logger recovery rate was attributed to the initial deployment on a high proportion of prospecting birds, consequent low burrow fidelity, and breeding deferral in subsequent seasons (Phillips et al. 2006). The logger load (<1% of body mass) was considerably less than that (ca. 3%) at which effects on bird behaviour generally become apparent (Phillips et al. 2003). It is unlikely therefore that the behaviour of these individuals was compromised by the loggers and presumably, the activity patterns are typical of the species.

Changes in white-chinned petrel activity patterns

Breeding stage and nonbreeding phase

Like Southern Ocean albatrosses, the at-sea activity of white-chinned petrels was highly influenced by the degree of central place constraint (Mackley et al. 2010; Phalan et al. 2007). During the resident phase of the nonbreeding period, when birds are unconstrained and energetic demand is lowest, the petrels spent the highest proportion of time on the water and exhibited the fewest and shortest flight bouts during daylight, with a similar trend apparent during darkness. Constraints increase across the breeding stages

Table 2 Relationships between the illuminated fraction of the moon's visible disk and white-chinned petrel activity patterns during the resident nonbreeding phase, pre-laying exodus and incubation stages

	Resident ($N = 11$, $T = 11$)		Pre-laying exodus ($N = 10$, $T = 10$)		Incubation ($N = 6$, $T = 20$)	
	t Value	*P* Value	*t* Value	*P* Value	*t* Value	*P* Value
% Darkness wet	−12.31	***	1.59	*0.114*	−0.09	*0.927*
% Daylight wet	−0.60	*0.550*	6.74	***	2.38	*0.019*
% Wet by darkness	−9.45	***	−4.22	***	−4.04	***
% Dry by darkness	9.72	***	4.24	***	1.39	*0.165*
Flight bout duration in darkness (min)	8.74	***	−0.31	*0.758*	−0.23	*0.818*
Flight bout duration in daylight (min)	2.52	***	−6.08	***	−1.12	*0.263*
Number flight bouts/h darkness	9.64	***	1.99	*0.048*	0.71	*0.480*
Number flight bouts/h daylight	0.08	*0.937*	0.29	*0.776*	0.05	*0.961*

N number of birds tracked; *T* number of trips

The significance of regressions are indicated by *** $P < 0.001$, *italics* $P > 0.01$

and are highest when provisioning chicks (Shaffer et al. 2003). That the proportion of time spent on the water decreased, and flight bout duration tended to increase as the breeding season progressed presumably reflects a significant ecological effect.

White-chinned petrels replace their primary feathers sequentially during the nonbreeding period (Marchant and Higgins 1990). This may alter their flight ability and thereby activity patterns, particularly if several primaries are shed simultaneously (Bridge 2006). However, because this species is highly dependent upon its aerial agility in order to capture prey it appears that, as in albatrosses (Mackley et al. 2010), their moult sequence may be adapted to have minimal impact on flight, certainly there was no evidence for a prolonged period of flightlessness. Furthermore, effects on activity may be minimal, because at this time of year energetic expenditure is in any case relatively low.

During the resident nonbreeding phase, white-chinned petrels exhibited similar levels of activity during darkness and daylight: the mean proportion of time spent on the water was 62 and 61%, flight bout durations were 63 and 67 min, and the numbers of flight bouts per hour were 0.32 and 0.30, respectively. This demonstrates the aptitude of this petrel for diurnal and nocturnal foraging. However, birds increased effort (expressed as flight) further during daylight in response to the increased energetic demands of migration or breeding. Similarly, Weimerskirch et al. (2000b) observed that attendance of petrels at fishing vessels increased with daylight during the breeding period. This tendency to increase diurnal activity mirrors that of Southern Ocean albatrosses, for which aerial detection and capture of prey is limited during darkness by low light levels (Mackley et al. 2010; Phalan et al. 2007). It seems therefore that there are periods of darkness during which even this nocturnal species is limited by ambient light levels (also see Barnes et al. 1997). Under such circumstances, white-chinned petrels may nevertheless continue to forage whilst resting on the water by surface-seizing crustaceans and squid (Harper 1987) utilising the sit-and-wait method described for albatrosses (Catry et al. 2004; Weimerskirch et al. 1997).

Mean flight bout lengths (excluding migration) were relatively short compared to other procellariiforms (Table 4), during both daylight (67–85 min) and darkness (62–77 min), which suggests white-chinned petrels consistently use confined searches in areas of high prey abundance (Weimerskirch et al. 1997). The longer mean flight bout durations recorded during breeding may result from increasing the search radius around prey patches, as well as the long commutes between the breeding colony and foraging areas (Berrow et al. 2000a; Phillips et al. 2006). In addition, high individual variability in measures of flight during breeding stages may reflect individual differences in distribution (Phillips et al. 2006).

During migration, the petrels reduced proportions of time spent on the water by 51–76%, and increased flight bout durations by 1.6–1.8 times relative to resident phases. This increased effort is in accordance with previous satellite tracks of their rapid long-distance movements (Catard et al. 2000; Weimerskirch et al. 1999). The gliding and flap-gliding flight of white-chinned petrels increases their metabolic rate (Pennycuick 1987). Therefore, the limited between-individual variation in behaviour during this phase would suggest that the petrels were working at or close to their energetic maxima.

Foraging location and environmental heterogeneity

White-chinned petrels forage widely across the Southern Ocean, opportunistically exploiting patches of high prey abundance (Catard et al. 2000). The apparent consistency in activity patterns of nonbreeding individuals utilising both the Patagonian Shelf (open shelf) and Humboldt Current (shelf-slope) suggests that either their prey were similar, or, perhaps more likely, that different prey types could be exploited with equal success in these two habitats using typical foraging behaviour.

Comparison with other procellariiforms

Nocturnal activity

Our results indicate that white-chinned petrels are more nocturnally active than Southern Ocean albatross species for which activity patterns are available (Tables 3 and 4), with the exception of nonbreeding light-mantled albatross (Mackley et al. 2010). This difference was greatest during the chick-rearing period, when white-chinned petrels spent only 28% of darkness on the water, and least during the resident nonbreeding phase (see Table 3).

Comparable studies of smaller procellariiform species are limited to a tropical shearwater and a gadfly petrel; both spent similar proportions of daylight on the water, but their nocturnal activity was notably different from white-chinned petrels (Table 3). Nonbreeding wedge-tailed shearwaters *Puffinus pacificus* spent a higher proportion of darkness on the water, probably preferring to maximise efficiency by foraging in association with tunas that pursue prey during daylight (Catry et al. 2009). Cook's petrels from two distant colonies in New Zealand generally forage far from their colonies in either sub-tropical (Little Barrier Island) or highly productive sub-tropical convergence waters (Codfish Island) (Rayner et al. 2008). Birds feeding chicks from these colonies spent a greater (40%), or lower proportion (20%) of time on the water at night, respectively, than white-chinned petrels (28%). These species are therefore similarly nocturnal, with the differences in activity most probably related to differences in the type and abundance of prey they exploit (Rayner et al. 2008).

For all stages (except migration), the proportions of time spent on the water by white-chinned petrels during daylight and darkness differed by only 1.3–7.4%. This lack of variability is in contrast to albatrosses, where the differences varied from 16.8% (resident phase light-mantled albatrosses) to 76.2% (post-brood grey-headed albatrosses *Thalassarche chrysostoma*), representing the nocturnal and diurnal extremes of the Southern Ocean species and stages (Table 3). Their greater flexibility in the timing of activity means that resident nonbreeding white-chinned petrels rest on the water, or at least do not actively pursue prey, for a greater proportion of daylight (61%) than any albatross (33–59%, (Mackley et al. 2010; this study). The closest value (59%) for the wandering albatross *Diomedea exulans* may not reflect rest per se but the longer time required for handling and digestion of larger prey (Mackley et al. 2010).

Flight

White-chinned petrels migrate for shorter distances between South Georgia and their wintering areas (the Patagonian Shelf and Humboldt Current) than sympatric albatrosses (Phillips et al. 2008). These transits are also more rapid, completed within 1–2 days (Phillips et al. 2006; this study) probably due to a combination of their direct flap-gliding flight and bouts that are longer, during both day and night (108 and 114 min), than all but wandering albatrosses (114 and 121 min (Mackley et al. 2010). This suggests that they are able to sustain long periods of fast, direct flight in order to minimise the time spent in areas of lower prey availability.

Mixed feeding flocks in the Southern Ocean are dominated by white-chinned petrels and black-browed albatrosses (Nevitt et al. 2004), which have comparably short durations of flight during daylight, indicative of prey searching over small spatial scales (Mackley et al. 2010; Phalan et al. 2007; Weimerskirch and Guionnet 2002). Differences between these species at night (Table 4) probably result from their nocturnal visual acuity, with black-browed albatrosses switching to prey searching predominantly by olfaction, with consequently longer flight bouts (Mackley et al. 2010). White-chinned petrels also have highly developed olfaction, important in the initial detection of prey patches (Nevitt et al. 2004) but are presumably not restricted to locating individual prey items by olfaction alone, given the consistency in flight bout durations between day and night.

Effect of illuminated moon on activity

In our study, we used the proportion of illuminated moon as a proxy for nocturnal light levels, although we were of course unable to account for the effects of variation in cloud cover. Nevertheless, changes in some measures of activity with this proxy were highly significant, suggesting that the confounding effect of cloud cover was slight. The effects on activity were stage dependent; all nocturnal activity measures were affected during the resident nonbreeding period, whereas effects were fewer, and more variable as the breeding period progressed. On moonlit nights, increased aerial activity indicated higher foraging effort, probably as prey became harder to detect or capture because they remained at depth. White-chinned petrels are constrained by their maximum dive depth (12 m; Huin 1994) and therefore lunar periodicity in the diel vertical migrations of their prey may alter foraging success, as recorded for immature Galápagos fur seals *Arctocephalus galapagoensis* (Horning

Table 3 Comparison of activity patterns of Procellariiformes by species and breeding stage, as measured by: the percentage of time spent on the water during darkness or daylight, and the percentage of total time on the water, or in flight per day (consecutive light and dark period) that occurred in darkness

Species and stage	Number of birds tracked	% Darkness on water	% Daylight on water	% Water by darkness	% Flight by darkness
Migration (nonbreeding commuting)					
White-chinned petrel	**11**	**30.5 ± 24.1**	**14.6 ± 10.4**	**48.4 ± 24.2**	**33.4 ± 12.4**
Wandering albatross[1]	15	58.6 ± 13.3	34.2 ± 12.6	54.5 ± 12.7	
Light-mantled albatross[1]	2	44.1 ± 26.2	24.6 ± 2.6	64.3 ± 21.3	
Black-browed albatross[1]	25	60.1 ± 7.8	17.9 ± 5.1	76.8 ± 6.1	
Grey-headed albatross[1]	7	72.9 ± 10.3	11.3 ± 5.0	82.8 ± 10.6	
Nonbreeding: resident					
White-chinned petrel	**11**	**61.8 ± 7.1**	**60.5 ± 4.2**	**50.5 ± 2.3**	**48.4 ± 5.6**
Wandering albatross[1]	18	77.5 ± 6.0	58.5 ± 9.4	54.1 ± 5.1	
Light-mantled albatross[1]	11	59.1 ± 9.0	42.3 ± 8.6	59.4 ± 11.0	
Black-browed albatross[1]	25	83.6 ± 5.6	50.8 ± 6.9	65.2 ± 3.5	
Grey-headed albatross[1]	8	74.2 ± 5.7	32.7 ± 5.5	70.5 ± 4.0	
Wedge-tailed shearwater[2]	9	85.5 ± 3.9	56.5 ± 6.0		
Pre-laying exodus					
White-chinned petrel	**10**	**42.6 ± 5.2**	**36.3 ± 9.4**	**40.7 ± 7.7**	**32.9 ± 5.3**
Wedge-tailed shearwater[2]	1	31.2 ± 18.2	56.6 ± 1.4		
Incubation					
White-chinned petrel	**6**	**36.2 ± 7.0**	**32.3 ± 5.8**	**33.5 ± 6.6**	**26.7 ± 3.9**
Wandering albatross[4]	14	80.2 ± 11.4	39.8 ± 11.1	57.2 ± 6.3	
Shy albatross[6]	4	79.8 ± 12.2	30.8 ± 11.1		
Grey-headed albatross[4]	19	78.0 ± 17.2	27.0 ± 12.0	50.3 ± 19.0	
Giant petrel: pelagic trip[7]	11	47	39		
Giant petrel: coastal trip[7]	4	3	18		
Chick-rearing (*post-brood*)					
White-chinned petrel	**3**	**28.2 ± 5.7**	**20.8 ± 5.2**	**36.7 ± 10.0**	**27.0 ± 5.9**
Wandering albatross[4]	17	71.1 ± 18.6	32.5 ± 12.7	73.3 ± 7.8	
Light-mantled albatross[4]	3	57.5 ± 9.3	21.6 ± 6.5	55.9 ± 8.6	
Black-browed albatross[4]	12	70.0 ± 6.2	21.1 ± 7.5	68.4 ± 6.3	
Black-browed albatross[5]	6	67.7	23.9	70.0	22.3
Grey-headed albatross[4]	4	90.5 ± 4.0	14.3 ± 6.2	81.4 ± 7.0	
Grey-headed albatross[5]	4	61.9	15.1	74.8	21.9
Indian yellow-nosed albatross[5]	4	83.3	30.0	58.6	9.8
Cook's petrel (LBI)[3]	7	40.0 ± 14.4	23.7 ± 10.7		
Cook's petrel (CDF)[3]	10	20.0 ± 11.3	18.4 ± 8.7		

Values taken or adapted from (1) Mackley et al. (2010), (2) Catry et al. (2009), (3) Rayner et al. (2008) (*LBI* Little Barrier Island, *CDF* Codfish Island), (4) Phalan et al. (2007), (5) Weimerskirch and Guionnet (2002), (6) Hedd et al. (2001), (7) González-Solís et al. (2002). All values are observed mean ± SD, with the exception of (7), which is the observed *median*. Values for white-chinned petrels are in bold

and Trillmich 1999). Possibly as a consequence of poorer nocturnal foraging success, the petrels increased aerial searches during daylight, particularly during the pre-laying exodus. This may reflect opportunistic exploitation of a seasonally available prey source, for example, juvenile squid *Martialia hyadesi* (Rodhouse et al. 1992), which may coincide with both the timing and dispersal pattern of the pre-laying exodus (Phillips et al. 2006). During incubation, nocturnal illumination had limited influence on activity, and it was not found to affect distance travelled by white-chinned petrels at night in a previous study (Weimerskirch et al. 1999). It is probable that increased energy demands as the breeding period progresses require consistent increases in effort regardless of moonlight.

This stage-dependent plasticity in activity may have caused the disparities in past studies that have examined

Table 4 Comparison of flight bout durations (means ± SD) between white-chinned petrels and Southern Ocean albatrosses during the nonbreeding period

Species and stage	Number of birds tracked	Flight bout duration darkness (min)	Flight bout duration daylight (min)
Migration (nonbreeding commuting)			
White-chinned petrel	**11**	**113.6 ± 66.5**	**107.4 ± 37.6**
Wandering albatross	15	120.6 ± 18.5	114.4 ± 18.4
Light-mantled albatross	2	89.6 ± 4.5	73.6 ± 4.5
Black-browed albatross	25	109.8 ± 20.6	100.9 ± 12.3
Grey-headed albatross	7	86.2 ± 13.9	97.7 ± 10.2
Nonbreeding: resident			
White-chinned petrel	**11**	**62.5 ± 7.0**	**66.8 ± 9.2**
Wandering albatross	18	87.6 ± 10.7	84.3 ± 11.0
Light-mantled Albatross	11	74.6 ± 5.2	76.1 ± 6.4
Black-browed Albatross	25	78.6 ± 8.7	63.7 ± 6.5
Grey-headed Albatross	8	72.4 ± 13.2	70.2 ± 7.6

Values for white-chinned petrels are in bold; the albatross data are taken from Mackley et al. (2010)

behavioural responses of white-chinned petrels to various measures of moonlight: those that were of nonbreeding or immature white-chinned petrels recorded significant effects (Moreno et al. 1996; Petersen et al. 2008a), whereas those that occurred during the breeding period (Delord et al. 2005; Weimerskirch et al. 2000b), or were based on long-term averages (Gandini and Frere 2006; Gómez Laich and Favero 2007) found no significant or consistent correlates. It is possible that artificial lighting is sufficient, regardless of moon phase, for breeding petrels to increase foraging effort around fishing vessels (Barnes et al. 1997), thereby masking any response to natural conditions. Stage-dependent responses to moonlight could be clarified by data on the activity patterns of grey petrels *Procellaria cinerea*, which share common attributes but breed during the austral winter, potentially explaining why in the austral summer, grey but not white-chinned petrels respond to illuminated moon (Delord et al. 2005).

Fisheries and conservation

Given the propensity of white-chinned petrels to forage in association with fisheries on the Patagonian Shelf (Gómez Laich and Favero 2007; Phillips et al. 2006), it cannot be assumed that the activity patterns observed during the nonbreeding, pre-laying exodus and incubation periods are entirely natural foraging (note that this is not the case during chick-rearing, when there is little overlap with fishing vessels). Nevertheless, tracking of individual black-browed albatrosses, which are similarly attracted to fisheries, found they spent surprisingly little time in association with fishing vessels (Petersen et al. 2008b), and the same may be true of many white-chinned petrels.

Incidental mortality of white-chinned petrels is disproportionately high, to a large extent related to their high levels of nocturnal activity (Delord et al. 2005). The success of night setting may be improved by avoiding moonlit nights during the nonbreeding period and by using additional mitigation measures during the breeding period. These are also the times when monitoring of compliance by fisheries observers is particularly important. During the chick-rearing period, when nocturnal activity is high, nights are short, and birds are actively foraging for their chicks as well as for self-maintenance, seasonal closures in petrel foraging areas will continue to be the most effective solution.

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