168 *Notornis, 2007, Vol. 54: 168-179*
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Assessing flight characteristics for the Chatham albatross (*Thalassarche eremita*) from satellite tracking

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Abstract From satellite tracking data, we recognised 5 major flight patterns in the annual cycles of 3 Chatham albatrosses (*Thalassarche eremita*) tracked in 1997 and 1998: foraging flights while the birds were breeding; eastward and westward migrations across the southern Pacific Ocean; northward migration along the South American coast; and localised foraging at low latitudes off the northwest coast of South America. We hypothesised that the 5 modes of flight indicated different biological activity. The associated speeds, point-to-point distances flown day^{-1}, and other indices of activity were inferred from distances and times between satellite location records. Mean minimum point-to-point flight speeds were up to 85 km h^{-1} and were a function of the time interval for the measurement. Daily rates of change for latitude and longitude and the minimum daily distances travelled were calculated. These are the 1st measurements for this species of the sustained speed of flight point-to-point over varied time periods, and for short and long distances throughout the year. These data and the analytical techniques developed show what information can be obtained from a few individuals, and the confounding variables that result from the satellites' orbits, and the transmitting characteristics of long-duration PTT experiments. The interrupted reception of transmitters through the intermittent satellite passes biases speed and other measurements and difficulties interpreting these data are discussed. The results provide a guide to the design of satellite transmitter experiments for long distance and duration studies with other oceanic species. They also contribute to an understanding of where this species obtains its food, and of its potential risk of interaction with fisheries.

Nicholls, D.G.; Robertson, C.J.R. 2007. Assessing flight characteristics for the Chatham albatross (*Thalassarche eremita*) from satellite tracking. *Notornis 54(3)*: 168-179.

Keywords Chatham albatross; *Thalassarche eremita*; satellite tracking; telemetry; CLS-Argos; albatross; migration; 'rest and recreation'; ground speed; air speed

INTRODUCTION

Despite many satellite tracking studies, the migration routes and foraging distribution of albatrosses, especially during the non-breeding stage of their life cycle, are little known for almost all taxa (BirdLife International 2004). Preliminary tracking studies during 1997-1998 to determine the distribution of the Chatham albatross (*Thalassarche eremita*: nomenclature based on Nunn *et al*. (1996); Robertson & Nunn (1998); Croxall & Gales (1998)) provided 1778 observations from 3 flight deployments. An appreciation of the at-sea distribution of this taxon, and of its flight parameters, particularly speed, is important, given its critically endangered status (Croxall & Gales 1998), because these data influence our understanding of the risks it faces from interaction with fishing enterprises. We investigated how the tracking data could be analysed to provide information on the speed and behaviour patterns of the species during flight away from the breeding island.

Received 2 August 2006; accepted 31 March 2007
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The estimated distance travelled, and the speed of flight calculated from CLS:Argos locations, depend on the accuracy of those locations and the time interval between the observations (Nicholls & Robertson 2007; Nicholls *et al*. 1994; Nicholls *et al*. 2005; Nicholls *et al*. 2007; Walker *et al.* 1995; Weimerskirch 1994). In turn, the accuracy of these factors are determined by the characteristics of the satellite's orbit, the transmission regimes of the satellite transmitter (platform transmitter terminals, PTTs) carried by the bird, its changes in latitude, and the change in longitude of the bird between time zones. Speeds have been measured from satellite-tracking data (Weimerskirch *et al.* 1993; Walker *et al.* 1995; Anderson *et al.* 1998; Stahl & Sagar 2000)the methods of measurement differ, however, between researchers. Additionally, procedures to extend the life of the satellite tracking deployment by intermittent duty cycles further affect the estimated speeds obtained.

From the tracking data, we recognised 5 stages of flight regime in the annual cycle of the Chatham albatross: (a) foraging flights while the birds were breeding at The Pyramid, Chatham Is (B); (b) rapid eastward migration across the Pacific Ocean (M1); (c) migration northward up the South American west coast (M2); (d) localised foraging at low latitudes off the coast of South America (R); and (e) westward migration to the breeding site at The Pyramid (M3).

We hypothesise that, these flight patterns were associated with different biological functions and their associated speeds and point-to-point distances flown day^{-1}, and that other indices of activity might be identified for each period of activity in its annual cycle. This information could contribute to our understanding of how this taxon obtains its food from the ocean, and to defining its foraging strategies. These flight data provide the 1st measurements of the sustained ground speed of point-to-point flight, over varied time periods, with short and long distances throughout the year for the Chatham albatross.

These tracking experiments were part of a group of joint exploratory experiments to determine the opportunities and limits of the satellite tracking of long-lived and mobile seabirds. They provide evidence of the extent of the patterns that can be explored by following a few individuals, while showing some of the confounding variables that result from the satellites' orbits and the chosen PTT transmitting characteristics and regimes. Difficulties in defining what is meant when reporting speed, and the interpretaction of these speed data in particular, are discussed. The results should assist in the design of the transmitters for experiments on long distance tracking of mobile organisms, and the scope for long-duration studies of other taxa.

METHODS

Three adult breeding Chatham albatrosses were tagged in 1997 and 1998 while incubating and rearing chicks at their nests on The Pyramid (44° 26´S, 176° 14´W) in the Chatham Is, 870 km east of the New Zealand mainland. The PTTs used were Telonics ST10 standard units (packaged by Sirtrack Ltd; 2 Ah power supply of 2 Li cells). The transmitting regimes are given in Table 1. The PTT was held in the middle of each bird's back by a flexible harness; together the PTT and harness were 3.1-3.6 % of the bird's body weight at the time of application. One PTT was recovered by CJRR from the tagged bird after 12.5 months. Neither of the other 2 birds was found at the breeding colony during the very limited opportunities available to visit this almost inaccessible island over the following 7 years.

The NOAA satellite with CLS:Argos location system was used, with the Location Service Plus and multiple-satellite options. CLS:Argos classifies the records on their defined positional accuracy and the reliability reported as a Location Class (LC) of (in descending order of reliability) 3, 2, 1, 0, A, B, Z, and a Quality Index (IQ) (Anon 1999; CLS:Argos FAQ). Records were selected from the CLS:Argos DIAG archive file, following the selection procedure defined in Nicholls & Robertson (2007). This selection process used the LC, IQ, and minimal data on the birds' probable behaviour (e.g., reluctance to fly over land except at the breeding site) in excluding poorer locations associated with excessive speeds. The selection procedure included criteria used by others when filtering satellite-tracking data (McConnell *et al*. 1992; Weimerskirch & Wilson 1992; Nicholls *et al*. 1994).

RESULTS

The statistics of the CLS:Argos observations are shown in Table 1. Some (*c*.11%, range 8.6-13.5%, for 4 duty cycle transmission regimes over 3 bird deployments) observations (LC = Z???) had no location data, and a further 5% were set aside by the selection method, leaving 1483 locations (83.4% of all records; 95% of records with locations) originally received from CLS:Argos. In comparison with other studies (e.g., Brothers *et al*. 1998; *c*.14% of records with locations rejected), this is the smallest proportion of records having location data set aside to be reported.

The repetition rate of transmissions (how regularly the PTT transmitted a signal) changed the number of messages received by the satellite. That factor, the transmission duty cycle (periods when transmissions on or off, e.g., 3 h on, 3 h off), and the latitude of the bird, interact to determine the quantity and the quality of the results. Longer transmission on-periods, shorter off-periods, higher latitudes, and a slow-moving or stationary bird increase the probability of a higher–precision location.

There were fewer messages for each location measurement for the 90-s than for lower repetition rates. Because ≥4 messages are required by the Argos system for a reliable location determination, longer repetition rate intervals increase the chance of receiving fewer and less accurate locations (Table 1). Location classes (LC) of poorer accuracy (LC = 0, A, B, Z) were more likely to be rejected in our selection procedure, thus increasing the time between the remaining locations, and therefore resulting in fewer calculated speeds and a higher proportion of slower speeds.

Flight deployments of up to 10 months were achieved, during which the birds covered many

Table 1 Number of CLS:Argos DIAG records for each Location Class during deployments of satellite-tracking Platform Transmitter Terminals on Chatham albatrosses (*Thalassarche eremita*), using the selection process described by Nicholls & Robertson (2007). Percentages are of total Argos records for each of the 4 deployments. PTT ID, ID (deployment)$^{-1}$; D, period of active deployment (days); Dates, period of deployment; Cycle, Duty cycle (h); Rate, signal repetition rate (s); Records, total Argos records received; Accepted/Rejected, records accepted or rejected during selection process.

						Accepted /Rejected	Records by Location Class (LC, %)							
PTT ID	D	Dates	Cycle	Rate	Records		3	2	1	0	A	B	Z	Z???
23081	110	21 Oct 1997 - 27 Aug 1998	3 on 3 off	77	480	404	1.0	4.0	17.9	41.9	9.8	8.3	1.3	
						76		0.2		1.7	0.6	1.5	1.3	10.6
23696	310	16 Feb 1997 - 7 Jul 1997	6 on 33 off	90	756	617	0.3	2.8	11.9	44.7	11.2	5.8	4.9	
						139			0.1	2.0	0.7	2.0	1.9	11.8
23594-1	150	19 Oct 1997 - 18 Mar 1998	6 on 66 off	78	245	208	0.4	4.9	17.1	41.2	13.1	6.5	1.6	
						37				3.3	0.8	2.0	0.4	8.6
23594-2	147	18 Mar 1998 - 12 Aug 1998	3 on 9 off	78	297	254	1.0	8.4	24.2	24.9	12.1	11.8	3.0	
						43					0.3		0.7	13.5

Percentage of messages received pass^{-1} for each PTT deployment, using all records received from CLS:Argos

	Accepted / Rejected	No. of messages											
PTT ID		1	2	3	4	5	6	7	8	9	10	11	12
23081	404		8.3	10.2	12.9	10.2	10.4	9.2	9.4	7.3	4.4	1.7	0.2
	76	9.4	1.5	1.9	0.6	0.4	0.6	0.6	0.8				
23696	617		5.8	12.3	15.9	14.3	13.0	11.9	6.1	2.4			
	139	9.0	2.2	1.5	1.6	1.5	1.2	0.7	0.4	0.4			
23594-1	208		6.5	13.5	19.2	14.7	10.6	5.7	7.3	4.9	0.8	1.6	
	37	6.1	2.0	0.8	1.6	0.8	0.4	0.8	1.6			0.8	
23594-2	254		11.8	12.5	9.1	13.5	14.8	11.8	6.4	4.0	0.7	0.7	
	43	11.8	0.7	0.3	0.7	0.3		0.3				0.3	

thousands of km. The resultant calculated speeds were influenced most strongly by the time interval over which the distance between locations was measured (Fig. 1). With 2 satellites, the time between satellite passes was typically 1-2 h. However, with the CLS:Argos multiple-satellite service, when up to 4 satellites were available, some locations were only minutes apart.

There were clusters of location observations at longer intervals, because the transmitters were on for 3 or 6 h and then off for 3, 9, 33, or 66 h during the tracking experiments. These intervals, and their combinations and multiples (which occurred when a location measurement was missed) can be detected in Fig. 1. Thus, the number of satellite passes and the duty cycles together determined the time interval between successive locations. Longer duty cycles biased the data by increasing the proportion of longer time intervals between records, and so yielded slower calculated speeds.

As satellite passes over a point on the Earth's surface were less frequent at lower latitudes (Anon, 1999), accordingly there were longer time intervals between observations when the birds were nearer the Equator. For example, the number of selected locations declined from 4 day^{-1} at 45°S to 1.5 day^{-1} at 10°S (Fig. 2). The decline was further exacerbated when an unfavourable duty cycle halved the potential data collected from the PTT, as for #23081, whose 3 h on 3 h off duty cycle doubled the time interval between many locations when the bird carrying it was between 16°S and 6°S, or *c*.1/2 the period of deployment on this bird.

The level of accuracy of the Argos locations is a potential source of error if flight activity over small areas (e.g., specific foraging locations) is the objective of the study. The accuracy is specified by CLS:Argos for LC = 3, 2, 1, but the accuracy is determined by the user for LC = 0, A, B, and occasionally Z (CLS:Argos FAQ), which constituted most of our locations. The accuracy had been measured before for stationary PTTs (Weimerskirch *et al*. 1989; Brothers *et al.* 1998; Anderson *et al*. 1998). However, Nicholls *et al*. (2007) explored the characteristics of both stationary and

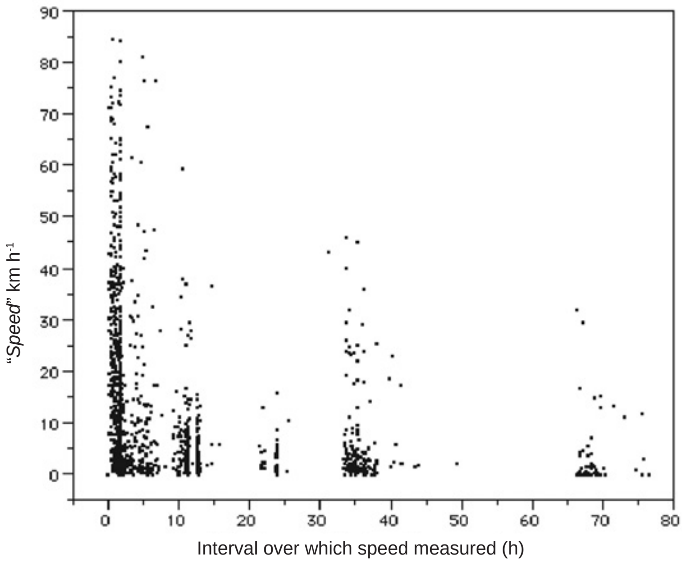


Fig. 1 Distribution of *'speeds'* for selected Argos locations of 3 Chatham albatrosses (*Thalassarche eremita*) satellite-tracked in 1997 and 1998, according to different time intervals. See Methods and Nicholls & Robertson (2007) for procedures used to select the records from the database provided by Argos.

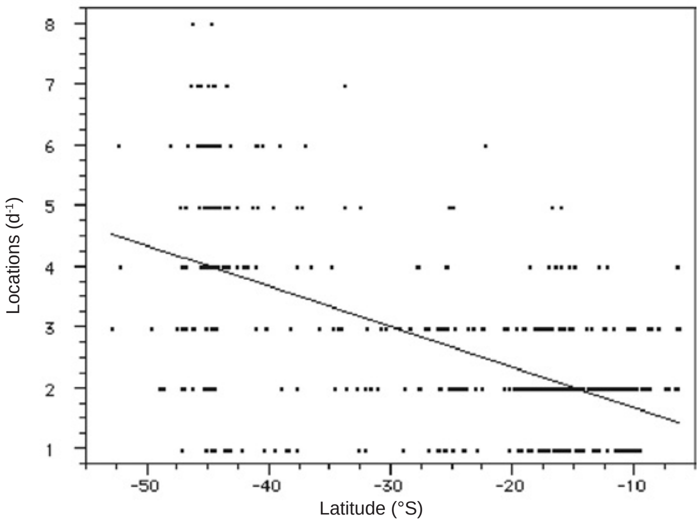


Fig. 2 Relationships between latitude of selected Argos locations of 3 Chatham albatrosses (*Thalassarche eremita*) satellite-tracked in 1997 and 1998, and the number of locations determined from the satellite telemetry, demonstrating the reduction in the number of positions available as a result of fewer satellite passes when the birds were near the equator during the deployments. See Methods and Nicholls & Robertson 2007 for procedures used to select the records from the database provided by Argos.

moving (especially fast i.e. 100 km h^{-1}) PTTs, and found that the average precision of the locations deteriorated and the number and quality of locations was lower, at higher target speeds and lower stability of the platform.

Calculated flight speeds

The calculated speed measured depended on the time interval over which it was measured, as noted above and shown in Fig. 1. For all the time intervals, the speeds calculated for the Chatham albatross were 0-84.9 km h^{-1}. For speeds calculated over 1-2 h (a common time interval between successive satellite passes), the range was almost the same, but the mean speeds calculated over all, and 1-2 h, intervals, differed (mean ± SE, SD] 11.8 km h^{-1} ±0.4, 15.4; n = 1480) and 15.2 ± 0.8 km h^{-1}, 16.3, n = 436, respectively). For the 1-2 h interval, 10% of the calculated speeds were between 38.9 and 84.5 km h^{-1}, but 1/2 were <9.25 km h^{-1}.

If the records associated with the breeding island (The Pyramid) are excluded, the at-sea records of speed for time intervals of 1-2 h (n = 366) were 17.2 ± 0.9 km h^{-1}, 16.9, (maximum 84.5 km h^{-1}, 90-percentile 41.4, median of 1.2 km h^{-1}. There was no significant difference between the calculated speeds of the 3 individuals over the 1-2 h intervals (ANOVA, df = 435, P = 0.45, ns) (Fig. 3) . Comparisons between individuals for other time intervals were confounded by differences between the duty cycles of their PTTs.

Other workers (Weimerskirch *et al*. 1994; Brothers *et al*. 1998) have measured flight speed by

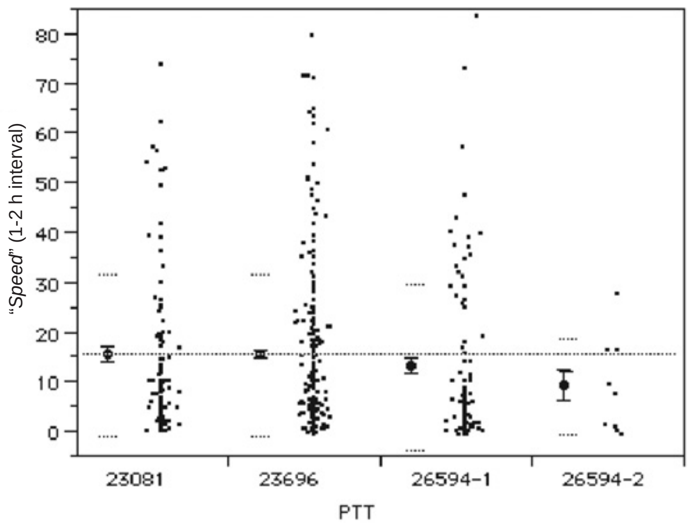


Fig. 3 Frequency distribution of the selected Argos location records (●) for 3 Chatham albatrosses (*Thalassarche eremita*) fitted with platform transmitter terminals (PTTs) in 1997 and 1998, showing mean for all observations (dotted line), and individual deployment means (●), SE (–), and SD (····) for the individuals. PTT 26594-2 changed duty cycle during the deployment. See Methods and Nicholls & Robertson (2007) for procedures used to select the records from the database provided by Argos.

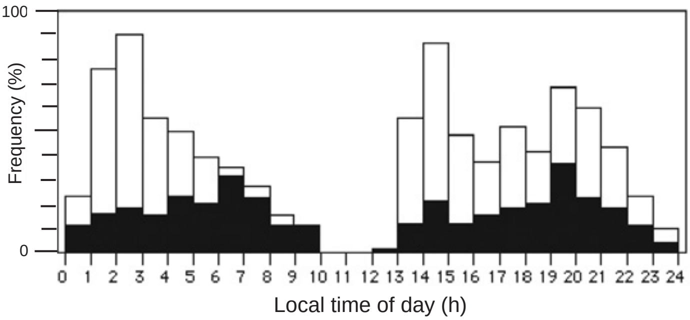


Fig. 4 Hourly frequency distribution (local time of day) of selected Argos locations combined for all deployments of platform transmitter terminals (PTTs) on 3 Chatham albatrosses (*Thalassarche eremita*) in 1997 and 1998. Unequal numbers of observations throughout local day result from variation in satellite orbits (0 near midday; fewer near midnight), and different duty cycle transmission regimes (e.g., PTT #23696-1, solid columns). See Methods and Nicholls & Robertson (2007) for procedures used to select the records from the database provided by Argos.

Table 2 Comparison of point-to-point *'speeds'* of Chatham albatrosses (*Thalassarche eremita*) for satellite-tracking records selected from the primary database using 2 different methods: (a) arbitrarily using only records of LC = 3, 2, and 1; and (b) using records selected according to protocol described in Methods and in Nicholls & Robertson (2007). The *'speeds'* (with means for both samples) tabulated here were measured over various, but comparable, time intervals in both methods of selection..

	Arbitrary LC =3, 2, 1 selection					
	Time intervals (h)					
	<1	≥1-4	≥4-24	≥24-72	≥72	All
Mean ± SE_{mean}	10.1 ± 4.0	3.8 ± 0.9	3.9 ±0.5	3.9 ±0.7	4.0 ±0.7	4.0 ±0.3
SD (*n*)	12.6 (10)	6.4 (48)	5.8 (136)	7.2 (104)	6.5 (77)	6.7 (375)
Max, Median, Min (90%-quantile)	37.4, 4.7, 0.7 (33.5)	28.6, 1.6, 0.1 (12.1)	34.8, 2.0, 0.1 (9.4)	46.5, 1.9, 0 (8.0)	32.5, 1.1, 0 (13.6)	46.5, 1.8, 0 (10.1)
	Authors' selection process: all LCs					
	<1	≥1-4	≥4-24	≥24-72	≥72	All
Mean ± SE_{mean}	26.3 ± 1.3	13.8 ± 0.7	6.4 ± 0.5	5.7 ± 0.6	4.7 ± 2.3	11.8 ± 0.4
SD (*n*)	19.4 (207)	15.6 (540)	10.4 (493)	8.9 (237)	5.6 (6)	15.4 (1483)
Max, Median, Min (90%-quantile)	84.9, 22.0, 0.7 (57.2)	86.5, 7.7, 0.1 (36.5)	81.3, 3.1, 0 (13.9)	46.3, 2.3, 0 (18.5)	11.9, 2.2, 0.1 (11.9)	84.9, 5.3, 0 (33.0)

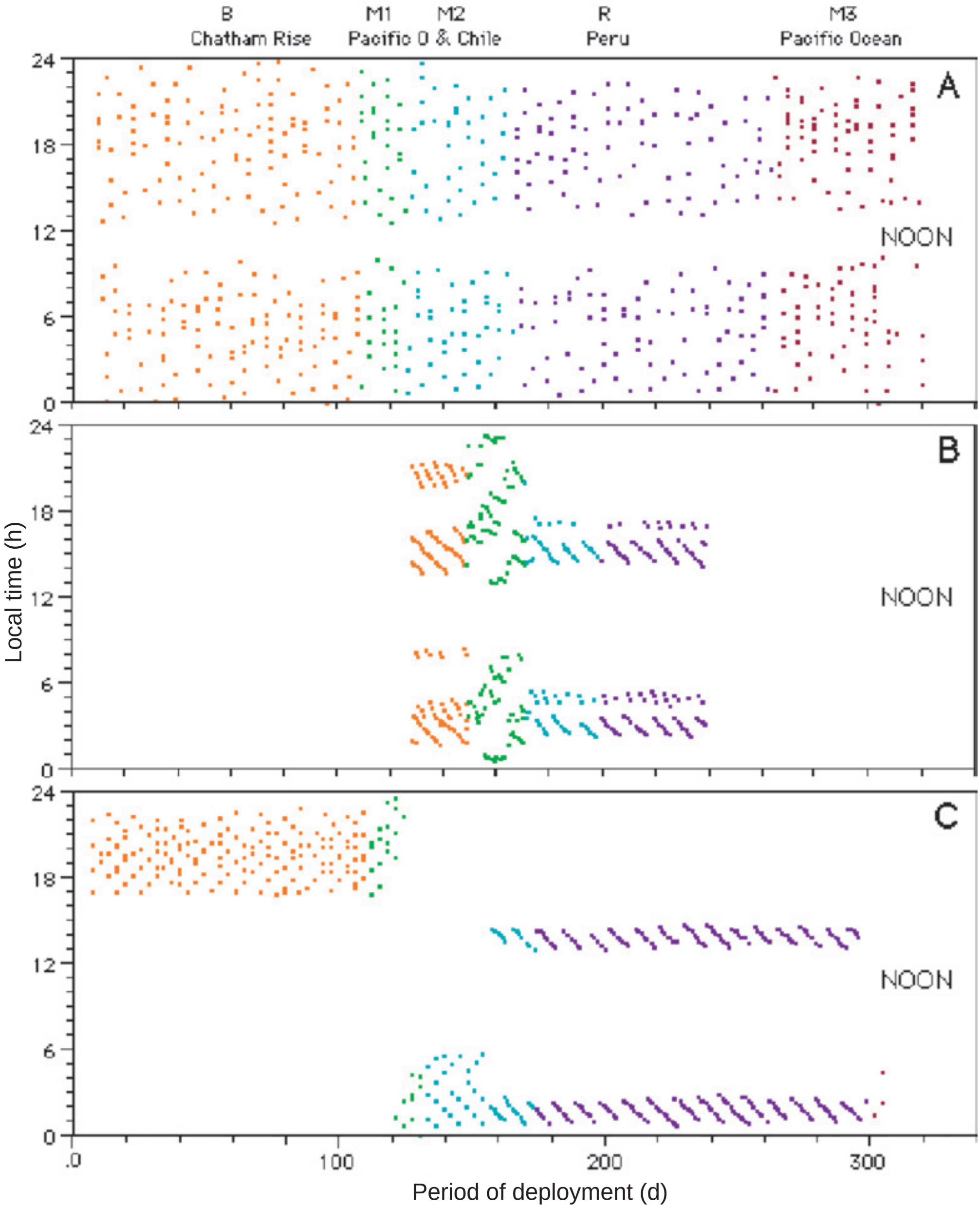
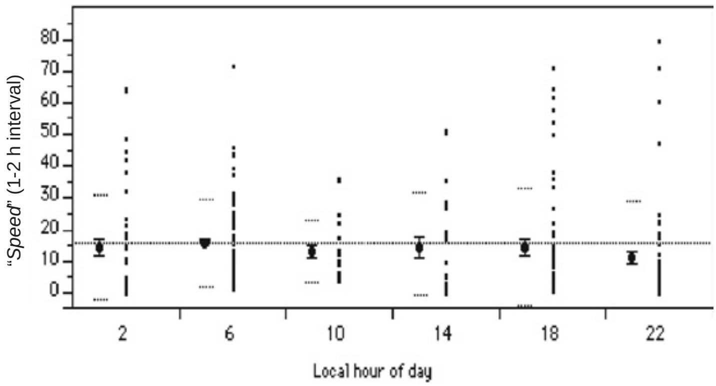


Fig. 5 Illustration of effects of timing of satellite passes and platform transmitter terminal (PTT) transmission regimes on patterns of reception during the local day for PTTs (A, #23696; B, #23081; C, 23594-1 (1997), #23594-2 (19981)) on 3 Chatham albatrosses (*Thalassarche eremita*). Locations for 3 PTTs (A, B, C) illustrated, of which C had 2 different duty cycle transmitter regimes. Each coloured point corresponds to a selected Argos location. Each colour represents the different location and flight pattern at each location point (see key and also Results): *y*-axis local time 24 h for a PTT, midnight to midnight; lower *x*-axis is time (days) from mid-Oct 1997, 0, to mid-Aug 1998, (320). See Table 1 for the transmission duty cycles and dates of deployments: Duty cycle for A (6 h on, 33 h off) gave rolling coverage throughout day; reception for PTTs B and C was confined to the same hours of the local day while the birds were nesting (orange) or at sea off Chile and Peru (blue & purple), and shifted (green & red) when the bird's track took it across different local time zones during migration. PTT#23594 (C) duty cycle changed at day = 155. See Methods and Nicholls & Robertson 2007 for procedures used to select the records from the database provided by Argos.

Fig. 6 comparison of '*speed'* (mean for all observations (dotted line), and individual time-period means (●), SE (–), and SD (····) for each time-period) calculated from selected Argos location records (•) for 3 Chatham albatrosses (*Thalassarche eremita*) satellite-tracked in 1997-1998, combined (calculated over a time interval 1-2 h) for 6 4-h periods during the local day. See Methods and Nicholls & Robertson (2007) for procedures used to select the records from the database provided by Argos.



using the locations of known accuracy (LC = 3, 2, 1) only. Applying their selection method to our data, the statistics of the calculated speeds were compared to a reduced set of the same data selected using the procedure described in Nicholls & Robertson (2007). The stringent criterion of selecting only LC = 3, 2, and 1 resulted in retention of only 25.3% of the records otherwise available and the maximum, mean, and median speeds measured were 0.5 to 0.67 of the larger selected dataset (Table 2).

Diurnal changes in calculated speed

Our Argos location data were not collected evenly throughout the day (Fig. 4 & 5), because of a combination of the satellite orbit pattern and the PTT duty cycles. Further, the combined effects of the satellite orbit pattern, the bird's trans-oceanic flights, and PTT transmission regimes produced complex patterns in the time data of the locations collected. These included the following varied patterns: (a) a random pattern throughout the day from a rolling transmission regime (except for 4 h about midday local time when there was no, or minimal, satellite coverage at the time of the deployments) (Fig. 5A); (b) when the PTT was on for the same 4 3-h periods day^{-1}, then switching to 2 periods every 12 h, coinciding with the bird's moving north of 16°S (Fig. 5B); and (c) a regular sampling at the same time interval twice each day, initially for 6 h every 3 days, then switching to a more intensive transmission rate (3 h every 12 h) (Fig. 5C). Travel in longitude (across time zones) caused different local times of the day to be sampled (Fig. 5B & 5C).

In addition to there being no satellite passes about noon local time (Fig. 4, 5), there were fewer passes about midnight. The absence of locations about noon reduced calculated speed observations immediately before and after local midday. The calculated speeds for 3 birds (over 4 transmitter duty cycle regimes) measured at intervals of 1-2 h were similar throughout the day, except for the 4 h at midday local time (Fig. 6), but there were no significant differences (ANOVA, $df = 234$, $P = 0.9$ ns, $n = 436$). Comparisons using all the speed data and for the PTTs with duty cycles that did not sample all times of the day, showed significant differences in speeds during the 24 h day, which was probably an artefact of the sampling regime. Failure to recognise the unequal sampling during the day caused by the satellite orbit patterns, and in this instance exacerbated by the transmission cycles, would lead to misunderstandings of the patterns of the birds' daily activity (Georges *et al.* 1997).

Annual changes in the rate of movement

The calculated speeds measured for time intervals of 1-2 h were compared for different periods of the annual cycle for the Chatham albatross. Five stages were identified using the location, rate of change of location, and the cumulative distance flown (Fig. 7). These stages were: (a) local flights from The Pyramid, within a very short range of 300 km while birds were incubating eggs and rearing the chick (B); (b) the rapid and consistent change in longitude eastwards from 170°W to east of 80°W while crossing the Pacific Ocean after probable successful breeding or failure during the late chick stage (M1); (c) a sustained flight northwards on the South American coast (M2); before (d) periods of sedentary behaviour where the longitude and latitude fluctuated over a range of 10º of longitude (80°W - 70°W) and 20º of latitude (26°S - 6°S) while the birds remained over the slope and shelf off the equatorial western coast of South America (R); and (e) where for 1 bird there was a return migration, which included 2 attempted flights across the southern Pacific Ocean (M3).

DISCUSSION

Factors affecting the use of information from PTTs in behavioural analysis

These data were collected originally for the 1st exploratory mapping of the at-sea distribution of the Chatham albatross, while we were investigating the practicality of using satellite tracking for year-long deployments that necessitated interrupted transmission duty cycles for the transmitters. Despite these limitations, it was possible to gain

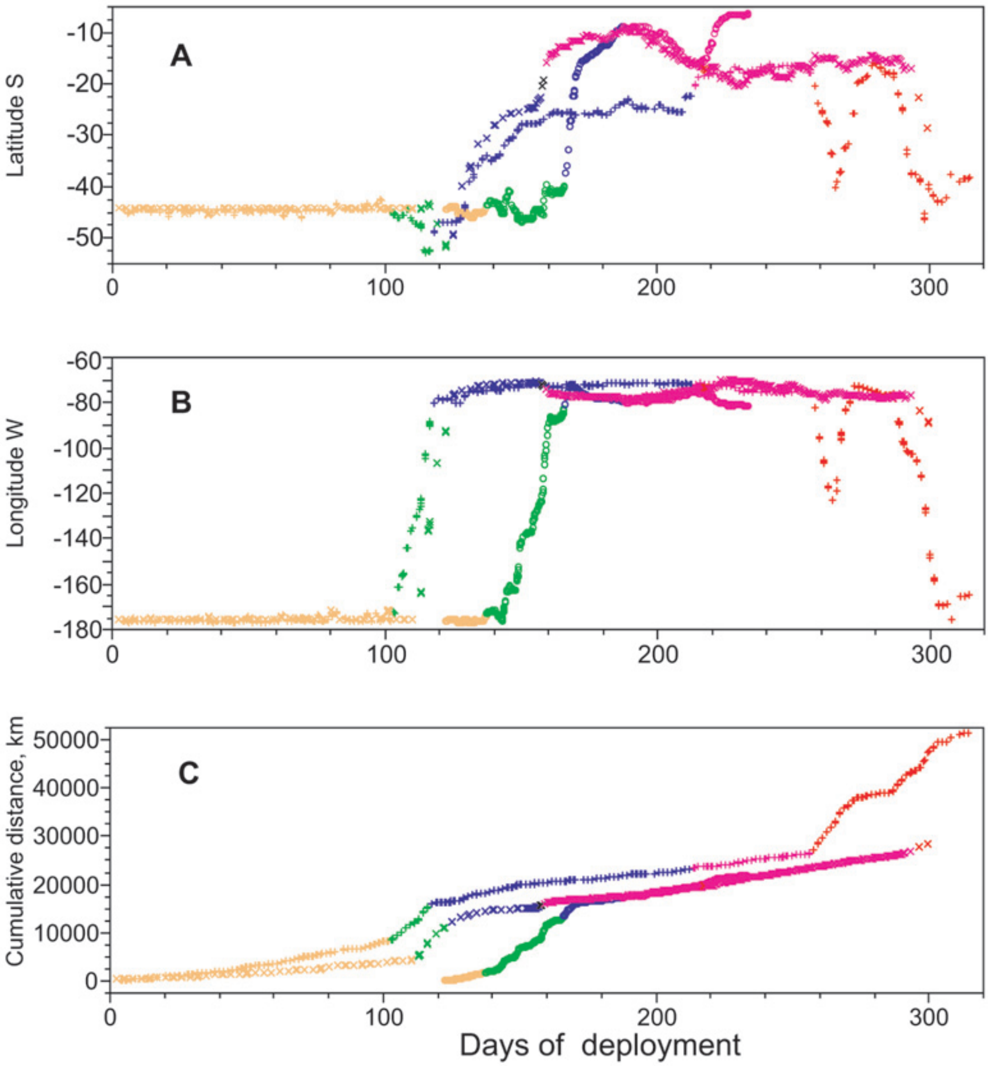


Fig. 7 Selected Argos locations according to latitude (A) and longitude (B) and cumulative distance (km) travelled (C) for 3 platform transmitter terminals (×, +, ○) deployed on Chatham albatrosses (*Thalassarche eremita*) from 20 Oct 1997 to 12 Aug 1998. Each point is a selected Argos location record and each colour represents the different location and flight pattern at each location point (see key, Results, and Fig. 5): lower *x*-axis is time (days) from mid-Oct 1997, 0, to mid-Aug 1998, (320). Timelines in days plotted for each bird in A, B, C: steep gradient represents rapid change. When they were foraging on the Chatham Rise near the breeding site at The Pyramid, Chatham Is, the birds (B, orange) remained at the same latitude and longitude while the cumulative distance increased slowly. Longitude changed rapidly and cumulative distance increased rapidly as the birds migrated across the Pacific Ocean (M1 green), followed by a rapid change in latitude during the northward migration (M2, blue). The 'rest-and-recreation' period (R, purple) yielded a similar amount of cumulative movement each day until steeper gradients indicated a change in behaviour as 2 birds moved west (M3, red). One of the birds moved west twice, returning once to Peru, but on the 2nd occasion it reached the Chatham Rise (A, B). Contact was lost with the other birds when the PTT batteries were exhausted. See Methods and Nicholls & Robertson (2007) for procedures used to select the records from the database provided by Argos.

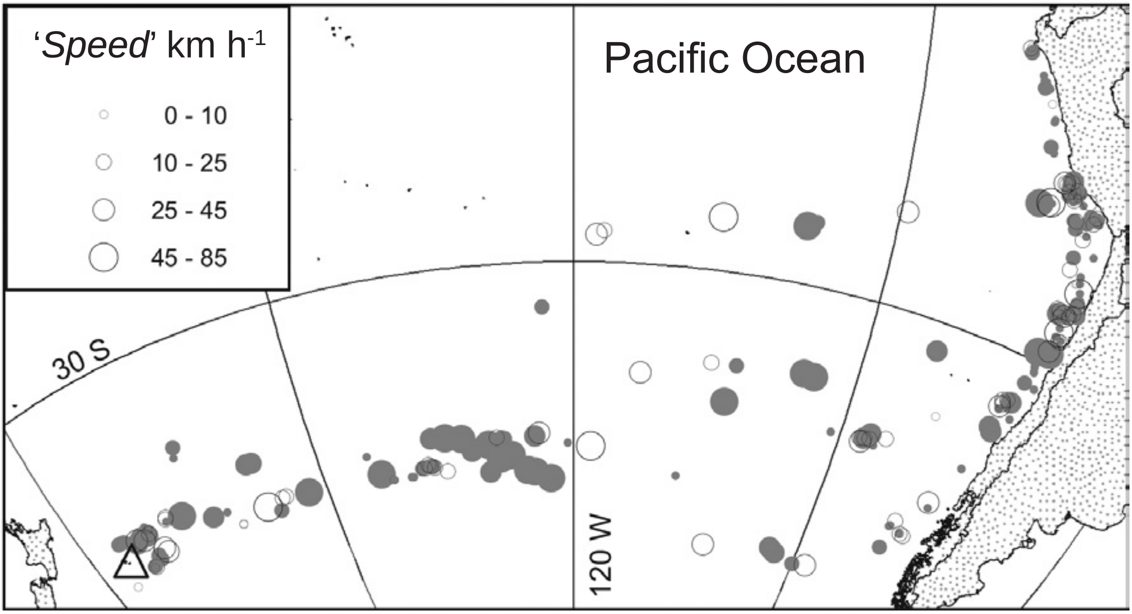


Fig. 8 Distribution of Chatham albatrosses (*Thalassarche eremita*) satellite-tracked from 20 Oct 1997 to 12 Aug 1998), excluding selected locations from 200 km surrounding the nesting colony at The Pyramid, Chatham Is, (△) to show range of '*speeds*' (from slowest, <5 km h^{-1}, to fastest, 23-84 km h^{-1}) recorded, according to local time, by day (open circles) and night (shaded circles).

a better understanding of the data's quality and information on the taxon's flight speeds relative to its annual activity cycle.

The speed measured was ground, not air, speed, and so was a point-to-point speed (mean speed for the distance travelled). In addition, it was a minimum mean speed, because albatrosses alternate flying with periods on the water (Viswanathan *et al.* 1996; Weimerskirch & Wilson 1992; BirdLife International 2004). They fly in a series of glides and pull-ups in the vertical plane and tacks (zig-zags) in the horizontal plane. The horizontal, zig-zagged, distance flown is greater (Pennycuick 1982; Alerstam *et al*. 1993) than the straight line point-to-point distance between start and finish, so the actual flying speed we estimated was correspondingly underestimated. In this paper we introduce the term 'point-to-point speed' ('speed') for this minimum mean speed and report mean, maxima, and other statistics for these 'speed's and for other factors that influence them.

There are various technical issues, however, that must be considered in interpreting the bird speeds measured in this way: i.e. the specifications under which the speed is measured will determine the 'speeds' obtained. Of the important variables, the accuracy of the measurement and the distance (or time interval) over which the measurement is made, are the most important. The accuracies of the distance and time measurement are fundamental, but the lack of information on the precision of the locations (Nicholls *et al*. 2007) makes it difficult to calculate the accuracy of the speed. The error of the time measurements was negligible, but the distance measurements had to be considered. Simple calculations of error, assuming 1 km and 20 km errors in 2 locations for a 1.5 h flight at 40 km h^{-1} indicated that there were errors of ±2% and ±20%, respectively, in the speed for typical individual measurements. Large samples with standard error measurements were the alternative solution used here, and we assumed that any distance measurement errors cancelled out.

The Argos satellite system does not allow predetermined distance measurements; calculated measurements made at the time intervals imposed by the satellite orbits must be accepted. The time interval over which the speed is measured is critical, being, as it were, the difference between a sprint and a marathon. The shortest time interval available is the time between successive orbits. Where there are 2 satellites involved, this is *c*.1.5 h. However, with additional satellites there may be simultaneous measurements, though usually only minutes separate the closest orbits. Measurements over such short periods have a potentially large error. The commonest time interval is 1-2 h; the time between successive passes of the standard 2 operational satellites. If a PTT is not on a continuous duty cycle, the proportion of 1-2 h time intervals is reduced. To maximise the chance of unambiguous locations, the 1-2 h time interval records must constitute a significant portion of the data set. As a PTT moves towards the equator, the time interval between locations increases.

The time of day of the satellite passes and therefore the timing of the speed measurements depends on the on-times of the PTTs and any longitudinal change of position. If the duty cycle (on-time plus off-time, e.g., 4 h on + 8 h off, or 8 h on + 40 h off) is a simple fraction or multiple of 24 h, the on-times occur at the same time of day. If the PTT is shifted longitudinally between records, the transmission is on at the same time of day relative to the Universal Time Constant (UTC) time, but the *local* on-time shifts. Presumably the behaviour of the animal may change with local time (e.g., in response to darkness). If the duty cycle is not a simple fraction or multiple of 24 h, the transmissions will come on at an earlier or later time of day relative to the UTC time. If the animal is moving longitudinally, this shift will be reduced or increased depending on the direction of the longitudinal shift. This will affect studies of day-night rhythms. These factors are illustrated in Fig. 5.

It is possible to set up duty cycle regimes so that nearly all times of the day are sampled randomly (although, in general there is a reduced reception about local noon in the Southern Hemisphere). The frequency of sampling can also be reduced to achieve a longer deployment. Alternatively, it is possible to sample at the same time of day, and by reducing this fraction of the day, again it is possible to increase the deployment duration. If the on-periods are moving through the day or the animal is moving longitudinally, or both, the local time of day of the period(s) sampled shifts each day. A valid comparison of speed, or other behaviour, may still be made, but the timing of the comparison must be considered.

Failure to include the characteristics of the satellite tracking systems and the consequences of intermittent transmission in analyses may result in the satellite system's behaviour being attributed, wrongly, to the animal's behaviour (George *et al*. 1997). Some of the inconsistencies are gross, but subtler biases may be introduced. For studies using PTTs transmitting throughout the day (continuous transmissions) these difficulties are minimised, but the introduction of intermittent transmissions means that each analysis must be done separately.

The *'speed'* measured is very sensitive to the time interval over which it is measured. Removal of records by more stringent filtering or selection criteria lowers the proportion of on-time in the duty cycles, reduces the number of records and their average quality, and so makes their removal from the data set more likely. PTTs operating on fast-moving organisms at lower latitudes, and which have unequal reception during a day with some duty cycles, will either directly or indirectly, increase the time interval and therefore decrease the *'speed'* measured. Fig. 8 illustrates a situation where there was a paucity of records close to the equator, as against the numbers in higher southern latitudes for all available records when only the *speed*s between 1-2 h separated locations are plotted.

Flight behaviour of Chatham albatrosses

The 3 adult Chatham albatrosses all exhibited similar behaviour patterns. Their flight *'speed'* did not change during the day. By restricting the measurements of *'speed'* to time intervals of 1-2 h only, and by assuming that large samples compensated for the inaccuracy of the distance measurements, we contend that a valid measurement of *'speed'* for the taxon was obtained. The similarity of the individuals' speed probably reflects the low level of sexual size dimorphism and that both sexes forage over the same areas of the ocean, unlike, for example, the wandering albatross (*Diomedea exulans*) in which the sexes differ in morphology and in their foraging distribution (Weimerskirch *et al*. 1993).

The maximum *'speeds'* were high, 2-3× higher than for measurements using only records of LC = 3, 2, or 1 (Weimerskirch *et al*. 1993; Brothers *et al*. 1998), and this held for speeds measured over the same time interval (Table 2), for at least 2 reasons. Firstly, precise locations were made when the PTT was slow-moving or stationary, which will bias the measured speed. Secondly, the imprecision of the locations leads to higher estimates of *'speed'*. We suspect that the 1st effect is the more important: in turn, using the lower speed from records of LC = 3, 2, 1 to select valid locations may bias the location data (Brothers *et al*. 1999). The *'speeds'* reported here for the Chatham albatross are comparable to maximum instantaneous speeds recorded for yellow-nosed albatross (*T. chlororhynchos*) (Alerstam *et al*. 1993) and short-tailed shearwaters (*Puffinus tenuirostris*) (Klomp & Schultz 1998). However, they are considerably higher than have been reported for a variety of other albatrosses, including the waved albatross (*Phoebastria irrorata*) (Anderson *et al*. 1998) and Buller's albatross (*T bulleri*) (Stahl & Sagar 2000), but the variety of methods used to measure the speed by other workers preclude more detailed comparison.

Studies of activity during the day, such as those of wandering albatross (Weimerskirch & Wilson 1992; Weimerskirch *et al*. 1994; Prince at al. 1992) produced different results for the periods during breeding and foraging. Our demonstration that flying speeds of Chatham albatrosses were not significantly different during day and night is different, to the extent that some breeding birds were observed at their nest for part of the day, while their mate was on the nest. However, many of our flight speeds were measured (Fig. 8) during migration, when the birds also flew during the night. We found consistent differences in flight '*speeds*' between the breeding season, trans-ocean migrations, and the 'rest and recreation' (when adults are not nesting or migrating) phases of the taxon's annual cycle.

There are few studies with which to compare our results because there have been few other studies of the movements of albatrosses outside the breeding season (BirdLife International 2004). Fast migratory travel, which is faster than foraging flights during the nesting period, has been measured for wandering, black-browed (*T. melanophrys*), and Buller's albatrosses (Nicholls *et al*. 1995; Prince *et al*. 1998; Stahl & Sagar 2000). Direct commuting flights have been studied by Prince *et al*. (1992), Walker *et al*. (1995), Anderson *et al*. (1998) , and Klomp & Schultz (1998). These observations are consistent with the higher flight speeds observed and predicted from the instantaneous flight speeds reported by Pennycuick (1982) and Alerstam *et al*. (1993).

The lower '*speeds*' reported here are likely to result from the longer time intervals between locations, and the underestimated distances while foraging and during non-flying time. The proportion of non-flying time may vary for direct flying migrating birds, commuting, and foraging nesting birds, and for birds off Peru that are just foraging locally and resting.

The similar flight speeds throughout the day suggests that the Chatham albatross could be equally vulnerable to interaction with fisheries throughout the day, unlike the wandering albatross in which Weimerskirch (1998) reported reduced flying activity and reduced bycatch at night. It is possible that its high-speed trans-oceanic flights (and long distances flown day^{-1}) may result in a lower risk for the Chatham albatross of adverse interaction with fishing operations during that time. In contrast, their seemingly relatively sedentary behaviour off the Peruvian coast in an area of high oceanic productivity and intense fisheries activity, could expose them to the risk of adverse interaction.

These results indicate that very long deployments of PTTs on large seabirds are possible using extended duty cycles for the PTTs. Such deployments introduce biases, but with judicious choice of transmission regimes it is practical to sample a bird's location within a day, and to device reliable point-to-point speeds from similar telemetry programmes.

ACKNOWLEDGMENTS

This work was funded in Australia by the Ian Potter Foundation, World Wide Fund for Nature, W.V. Scott Estate, and private donors, with additional support from La Trobe University, and in New Zealand by Department of Conservation and Wild Press. G.P. Elliott and M. Harger provided assistance with the great circle calculations. M.D. Murray provided critical advice throughout the study. Southlight farm through S. McGrouther, and Wild Press Laboratory, generously provided the facilities and accommodation where much of the analysis was refined. Chisholm Institute has generously supported the salary of D.G. Nicholls, while C.J.R. Robertson was employed by the New Zealand Department of Conservation until May 2000, and by Wild Press subsequently. David Bell and Hans Rook provided field assistance to CJRR at The Pyramid, with local logistical support in the Chatham Is from the Department of Conservation Area office. Permission to visit The Pyramid was generously provided by the Daymond Estate. Without the support and encouragement of these organisations this work would not have been completed.

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