Detecting population trends of Gibson's and Antipodean wandering albatrosses

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Abstract Counts, mark-recapture estimates of abundance, and simulations were used to assess the population trends of Antipodean wandering albatross (*Diomedea antipodensis*) and Gibson's wandering albatross (*D. gibsoni*). Estimates of population size based on mark-recapture analysis had much greater power to detect trends than did annual counts of nests. In fact, nest counts were so variable that significant trends would only be detected when populations had already changed by more than 25%. Population simulation models were constructed using survival and productivity data from the two species, and recruitment data from closely related species. The simulation models were sensitive to variation in recruitment data and suggested that the recruitment of Gibson's wandering albatrosses is significantly lower than to f Antipodean wandering albatrosses. The sensitivity of the models to variation in the surrogate data compromises the usefulness of such models as predictive tools. After large, probably fisheries-induced declines during the 1970s and 1980s, Antipodean wandering albatross populations are now increasing at about 3.1% per annum, while Gibson's wandering albatross populations are static.

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INTRODUCTION

Albatrosses are the most threatened group of all seabirds (Croxall & Gales 1998) and the five species of wandering albatrosses (previously all one species, *Diomedea exulans*) have been badly affected by oceanic, especially long-line, fisheries (Gales 1998). Of 10 wandering albatross populations that have been monitored well enough to assess population trajectories, nine have declined significantly in the last 40 years (Gales 1998). Fishing-induced mortality, mostly arising from the southern bluefin tuna (*Thunnus maccoyii*) long-line fishery, has been strongly implicated in the declines of at least three wandering albatross populations (de la Mare & Kerry 1994; Croxall *et al.* 1998; Weimerskirch *et al.* 1997; Tuck *et al.* 2001).

Wandering albatrosses are long-lived, slowbreeding birds. They first breed when between seven and 19 years old and, at best, raise one chick every two years (Tickell 2000). These features make them susceptible to even low levels of fisheries bycatch (Croxall *et al.* 1990). Wandering albatrosses can be counted reliably only when they come to land to breed, and their biennial breeding increases the variability of such counts. Most wandering albatrosses breed two years after a successful breeding attempt, but only one year after a failed attempt, and counts therefore vary not only with population change but with the previous two years breeding success. High variability of counts has meant that conclusions about wandering albatrosses population trajectories have most often been based on annual counts at nesting colonies undertaken for more than 20 years. In two cases detailed population studies have provided evidence of the mechanisms of wandering albatross population declines, but the inherent variability in the great albatross breeding system has meant that these conclusions have also only been possible after population data has been collected for more than 10 years (Croxall *et al.* 1990).

Antipodean (*Diomedea antipodensis*) and Gibson's (*D. gibsoni*) wandering albatrosses breed only in the New Zealand region on infrequently visited, uninhabited islands, but forage widely in the Tasman Sea, South Pacific and Southern Oceans. An estimated 5150 pairs of Antipodean wandering albatrosses breed each year on Antipodes Island (49° 41'S, 179° 48'E) (Walker & Elliott 2005), with less than six pairs breeding each year on Campbell

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Island (Gales 1998), and a single pair nesting on Pitt Island in the Chatham's group in 2005 (C. Miskelly pers. comm.). An estimated 5831 pairs of Gibson's wandering albatross breed in the Auckland Islands group each year, with > 95% breeding on Adams Island (50° 53'S, 166° 00'E) and the rest breeding on nearby Disappointment and Auckland Islands (Walker & Elliott 1999). Gibson's and Antipodean wandering albatrosses have only been counted and studied in detail since 1991 and 1994 respectively, and only recently has it been possible to determine whether these populations have suffered declines similar to those recorded in other wandering albatrosses. The numbers of both albatrosses appear to have declined during the last 40 years (Walker & Elliott 1999, 2005).

In this paper we assess the population trajectories of Gibson's and Antipodean wandering albatrosses, and compare methods of assessing population trends in biennially breeding albatrosses. In addition, we present the most recent population parameters for Gibson's wandering albatross, and compare the population dynamics of the two New Zealand species with those of other wandering albatrosses.

METHODS

Four methods of assessing population trajectory are compared: linear regression of counts of nests, randomization tests of counts of nests, mark-recapture estimates of population size and population models.

Linear regression of the counts of nests is the simplest and most obvious way of detecting population trends. Analysis of a simulated biennially breeding albatross population by Pascual and Edwards (1999) found that randomization tests of nest counts had higher power to detect trends than linear regression. Mark-recapture estimates of population size are likely to be more powerful at detecting population trends than methods involving nest counts because they incorporate the number of breeding birds seen, as well as an estimate of the number of breeding birds not seen but still alive, and are thus less variable than simple nest counts. Both nest counts and mark-recapture estimates can use only breeding birds seen on an island, and a decline caused by reduced productivity or recruitment would not be detectable in the number of breeding birds on land for about 10 years. Population models incorporating age-specific survival and productivity might predict otherwise undetectable declines amongst non-breeding birds at sea, but such models require data on recruitment which we have not yet collected.

Study areas and field methodology

The study areas and field methodology are described in detail elsewhere (Walker & Elliott

(1999, 2005). In brief, from 1991 on Adams Island (Auckland Islands) and from 1994 on Antipodes Island, annual visits were made during December -February when chicks of the previous season fledge and breeders of the new season lay. During repeated visits to a 61 ha study area on Adams Island and a 29 ha study area on Antipodes Island, the success of the previous year's nests was assessed and the chicks produced banded, new-season nesting birds were banded or had their existing bands recorded, and all active nests were mapped. To examine whether the albatrosses in each study area were representative of other albatrosses on the island, we also counted all the nests in three other blocks on Adams Island (25, 90 and 85 ha) and two blocks on Antipodes Island (97 and 21 ha) each year.

Estimating survival

Estimates of adult survival were calculated from banding and recovery data from the main study areas using the multi-strata formulation of Brownie et al. (1993) and Hestbeck et al. (1991) implemented in the program MARK (White & Burnham, 1999). We used the multi-strata formulation to overcome a potential bias caused by the unequal catchability of successful and failed breeders (Rothery & Prince, 1990). This bias has often been reduced in markrecapture models of biennially breeding albatrosses by regarding banded birds as having been re-sighted not only when they were actually re-sighted, but also when their previous years nesting attempt was successful (Croxall et al. 1990). The multi-strata method allows a more rigorous approach where the differing catchabilities of different groups of birds are explicitly estimated.

For the purposes of estimating survival using a multi-strata mark-recapture model, birds observed on the study area during our visits were divided into three categories: "successful breeders", "away birds", and "others".

Successful breeders were birds observed nesting and subsequently found to have successfully raised a chick. These birds do not return to breed for two years. Successful breeders invariably do not breed in two consecutive seasons because chick rearing takes a full year and they are still feeding last year's chick at the beginning of the next breeding season.

Away birds were those that had successfully raised a chick in the previous season and were having a sabbatical year. Away birds are most often not observed in the study area, though a few are seen feeding their chicks just before they fledge.

Others included birds that nested and failed, and non-nesting birds seen at the study area. These birds were usually seen in the study area during the next breeding season.

Multi-strata mark-recapture models estimate three groups of parameters: survivorships, recapture

probabilities, and transition probabilities between strata. Some of these parameters have to be fixed rather than estimated to provide an appropriate formulation for biennially breeding albatrosses. In particular, the transition probability between "successful breeders" and "away birds" was fixed at 1 because we never observed successful breeders attempting to breed two years in a row. The transition probabilities of "other birds" becoming "away birds" and "away birds" remaining "away birds" were fixed at 0 because birds can only enter the "away birds" category from the "successful breeders" category. The recapture probability of "successful breeders" was fixed at 1 because successful breeders in the study were almost never overlooked. Successful breeders spend a great deal of time at their nests, and we visited the study areas many times during each breeding season; the chance of a successful breeder escaping detection was almost zero. Survival estimates for the last year of our study were not included in our analysis as they had very large standard errors – a feature of the estimate of survival of bienniallybreeding birds.

Counts

Linear regression of counts

Growth rates of counts of breeding birds in the various blocks on the islands were estimated by least-squares linear regression of the logarithms of the counts against time.

Randomization tests

The randomization test used was devised by Pascual and Edwards (1999) and was similar to a moving block bootstrap (Efrond & Tibshirani 1993). It involved comparing the slopes of regressions with distributions of slopes generated by repeatedly re-sampling groups of three consecutive years of counts from the original data, and reconstructing time series of the same lengths as the original data. Because the data was re-sampled in groups, the randomized data sets will have kept some of the autocorrelation present in the original data, but because the groups were randomly re-ordered, the randomized data sets will be free of trend, i.e., will have an average growth rate of 0. The distribution of growth that arises from the generated data sets provides a distribution of growth rates where there is no growth against which the growth rate in the original data set is contrasted.

Representativeness of counts

We used ANOVA with mixed effects to determine whether there was significant variation in the growth rates between the blocks on each island. ANOVA models with random variation in growth rates between blocks were compared with models with a common growth rate for the blocks. A significant difference between these models implies that there is significant variation in growth rates between blocks and that the population trajectory of the whole population could only reliably be estimated from a sample of counted blocks. ANOVA was carried out on the logs of the counts of nests.

Mark-Recapture estimates of population size

Estimates of the number of breeding birds in our two study areas were derived from the multi-strata formulation of Brownie et al. (1993) and Hestbeck et al. (1991) implemented in the program MARK (White & Burnham 1999) that we used for estimating adult survival, except that we modified the data to account for permanent and temporary emigration.. Gibson's and Antipodean wandering albatrosses show strong nest site fidelity and consecutive nesting attempts are on average only 18 – 22 m apart (Walker & Elliott 1999, 2005) and there have been no recorded cases of breeding adults of these species (unpublished data) or Diomedea exulans (Inchausti & Weimerskirch 2002) moving to and breeding on another island. However, occasionally birds nesting near the edges of our study areas moved outside them, and even more rarely they moved back in again. We detected these movements because we not only searched our study areas for banded birds but we checked all birds nesting within about 500 m of the study areas. To account for a possible bias caused by the temporary emigration of birds, the sightings of birds that nested within our study areas then subsequently nested outside them were ignored once they moved outside, while birds that nested inside, then outside, then back inside the study area again were regarded as new birds when they moved back in. The multi-strata formulation does not explicitly estimate population size so we estimated the number of birds alive each year in each stratum by dividing the number of birds observed in each stratum each year by their recapture probability, which MARK estimated. Regressions of the logs of the estimated population size against year were used to assess whether the growth rates were >0 or <0.

Power of trend analysis

The power of linear regression of counts and markrecapture estimates was assessed by estimating the minimum number of counts required to detect 1% annual growth rates (alpha = 0.05, two tailed) with 80% confidence using a Monte Carlo simulation approach analogous to a bootstrap (Efron & Tibshirani, 1993); 1% was chosen as the threshold for power analyses because this was the rate of decline detected on South Georgian populations of wandering albatross between the 1960s and 1980s (Croxall *et al.* 1990).

Table 1 Annual survival, productivity (mean \pm *se* fledglings/pair/nesting attempt) and population trajectory (+ = increasing; 0 = static; - = declining; ? = unknown) of wandering albatrosses. * data from Croxall *et al.* (1990). ** Croxall *et al.* (1998). *** Weimerskirch *et al.* (1997).

Survival						
Species	Years	Male	Female	Productivity	Trajectory	
D. antipodensis	1994-2004	0.957 (0.007)		0.740 (0.016)	+	
D. gibsoni	1991-2004	0.961 (0.006)		0.631 (0.020)	?	
D. exulans (Bird I.)	1976-1986*	0.943 (0.010)	0.926 (0.008)	0.640 (0.002)	-	
	1988-1993**	0.920		0.68	-	
D. exulans (Possession I.)***	1966-1969	0.897	(0.006)	7	0	
	1970-1976	0.895	(0.002)		-	
	1977-1985	0.937	(0.001)	0.685 (0.021)	-	
	1986-1993	0.956	(0.001)		+	
D. amsterdamensis ***	1983-1994	0.957	(0.018)	0.716	+	



Figure 1 Annual survival of Gibson's and Antipodean wandering albatrosses measured in study areas on Adams and Antipodes Islands.



Figure 2 Nesting success of Gibson's and Antipodean wandering albatrosses.

Simulated data sets were created by generating deterministic declines of 1%. To simulate variability in these counts, residuals sampled with replacement from a fit of the original data were added to the deterministic counts. The "power" to detect a 1% trend was the proportion of simulated data sets for which the growth rate determined by regression was significantly (alpha = 0.05) >0 or <0. Power increases with the number of annual counts undertaken, so the power analysis was repeated with increasingly

large numbers of counts until the power exceeded 0.8. The simulations were written in the statistical program R (R development core team, 2005).

Population models

Population models were constructed using adult survival and productivity data from Gibson's and Antipodean wandering albatrosses and recruitment data from the better studied *D. exulans* on Possession Island (Weimerskirch *et al.* 1997). We used recruitment data from 1966 to 1973 when age at first breeding was high and juvenile survivorship was low (Weimerskirch *et al.* 1997) as a worst case scenario, and recruitment data from 1974 to 1982 when age at first breeding was lower and survivorship higher as a best case scenario. So that our model could estimate population growth rates and their confidence intervals we used Monte-Carlo simulation.

Rather than use estimates of survival in our models, we used the rates at which banded birds were re-sighted. Thus our models incorporated the proportion of successful breeders that returned to the islands after two, three and four years, the proportion of unsuccessful and non-breeders that returned after one, two and three years, and the proportion of fledged chicks that started breeding at 7, 8, 9...19 years of age. Using this approach we modelled the number of breeding birds, but not the total population size.

We constructed stage-structured matrices to describe the population structure. The classes in our matrix included 18 age classes of young prebreeding birds, breeding birds, successful breeders having two, three and four years away from the island, and failed breeders having one, two and three years away from the island. Birds more than seven years old have probabilities of joining the breeding class, and breeders have probabilities of

Table 2 Growth rates calculated by regression and significance tests for Antipodean and	Gibson's wandering albatross
nest counts in three areas on Antipodes Island and three areas on Adams Island.	
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				Regression		Randomization
Species	Area	Growth rate	F	df	p	p
Antipodean	Study area	1.042	10.168	1,10	0.010	0.005
	MCBA	1.031	6.804	1,10	0.026	0.028
	Block 32	1.035	4.184	1,7	0.080	0.124
Gibson's	SA-Astrolabe	0.994	0.033	1,6	0.862	0.823
	Fly Square	0.924	1.452	1,6	0.274	0.012
	Rhys's Ridge	0.983	0.154	1,6	0.708	0.458

Table 3 The number of years of annual nest counts or mark-recapture estimates required to detect declines of Antipodean and Gibson's wandering albatrosses of 1% per annum in two areas on Antipodes Island and three areas on Adams Island (alpha = 0.05 (two-tailed), 1 - beta = 0.8).

Species	Area	Counts	Mark- recapture estimates
Antipodean	Study area	27	15
	MCBA	25	
Gibson's	Study area - Astrolabe	34	17
	Fly Square	34	
	Rhys's Ridge	40	
	All areas	39	

successfully breeding and of subsequently spending one - four years away from the island. We modelled only females, but since we found no significant differences in male and female survival rates we pooled their observed return rates.

We started each simulation with a population structure comprising 5000 nesting pairs (about the same number as observed each year on both Adams and Antipodes Island), and numbers of birds in each of the other classes predicted by the eigenvector of an age-structured matrix with mean productivity and return values. We apportioned the variance of all the parameters used on our models amongst sampling and environmental variation using White's (2000) method. At the beginning of each 20-year simulation we randomly generated a set of productivity and return rate parameters from Beta distributions with variances equal to the sampling variances, and for each year in each simulation we randomly selected new parameter values from Beta distributions with variances equal to the environmental variances calculated above. Numbers of birds moving between stage classes



Figure 3 Counts of Antipodean wandering albatross nests in three areas on Antipodes Island 1994-2005.



Figure 4 Counts of Gibson's wandering albatross nests in three areas on Adams Island 1995-2005.

were treated as binomially distributed variables to simulate the effect of demographic stochasticity. After 20 years of simulation we calculated the average annual growth rate. We repeated this process 10,000 times to get median growth rates and upper and lower 95% percentiles (White 2000). The simulation was programmed in the statistical package R (R development core team, 2005).

RESULTS

Survival and productivity

The survival rates of the two species were very similar (*t* for difference = 0.09, *df* = 21, *p* = 0.93) and

		Growth Rate			
			Lower	Upper	% simulations
Species	Recruitment	Median	95% CI	95% CI	increasing
Antipodean	Low	1.0117	0.9889	1.0328	85
	High	1.0376	1.0183	1.0547	100
Gibson's	Low	1.0129	0.9891	1.0340	88
	High	1.0365	1.0178	1.0535	100

Table 4 Simulated population growth rates of Antipodean and Gibson's wandering albatrosses



Figure 5 The number of breeding Antipodean and Gibson's wandering albatrosses alive each year (\pm 95% confidence intervals) estimated by mark-recapture analysis of birds banded in the two study areas on Antipodes and Adams Islands and fitted regression lines of the log of the number of birds against time.

seemed to fluctuate in a similar manner during our study (Fig. 1). We detected no differences in survival between the sexes of either species. For Gibson's wandering albatross the mean annual survival of males was 0.966 (se = 0.005) and 0.952 (se = 0.008) for females. For Antipodean wandering albatrosses mean annual survival for males was 0.955 (se = 0.006) and 0.955 (se = 0.011) for females. The adult survival rates of both these albatrosses during the 1990's is more similar to those of the recently slow declining or recovering populations on Bird and Possession Islands than to the earlier, steep decline period on those islands (Table 1).

Mean nesting success of Antipodean wandering albatross at 0.74 (\pm se 0.016) fledglings/nesting pair was 11% higher than that of Gibson's wandering albatross (0.63 ± *se* 0.020) and the difference was significant (t = 4.188, df = 22, p < 0.001). While the pattern of variation in productivity was similar in the two species (Fig. 2), years of conspicuously low nesting success for Antipodean wandering albatrosses (1999 and 2002) occurred a year before those of Gibson's wandering albatross nesting success has decreased significantly over the last 11 years (F = 11.2, df = 1.9, p = 0.001) and is lower than that of most other wandering albatross species (Table 1).

Counts

Counts of nests in all blocks on Antipodes Island increased during our study (Fig. 3) but the increases were statistically significant in only two of the blocks (Table 2). Counts of Gibson's wandering albatross nests in all blocks on Adams Island decreased (Fig. 4), but the decrease was only significant in one block and only using the randomization test (Table 2). Mixed effects ANOVA showed there was no significant variation in growth rates of nest counts between blocks on either of the islands (Gibson's Likelihood Ratio = 0.000, df = 3, p = 1.000; Antipodean Likelihood Ratio = 0.001, df = 3, p = 1.000).

Population trend from mark-recapture analysis

The estimated number of both Antipodean and Gibson's wandering albatrosses alive in their study areas each year increased by 3.5 and 0.7% per annum respectively (Fig. 5), but only those of the former were statistically significant (Antipodean F = 34.51, df = 1.8, p < 0.001; Gibson's F = 1.45, df = 1.8, p = 0.263).

Power of trend detection techniques

Linear regression of mark-recapture estimates detect population change more powerfully than does linear regression of counts, and counts of large areas seemed no more powerful than small ones at detecting trends (Table 3).

Population trend from simulation

Table 4 shows the simulated population growth rates of the two albatrosses using the best and the

worst recruitment data from Weimerskirch *et al.*'s (1997) study of wandering albatrosses on Possession Island. All of the simulations gave median growth rates of more than one, with the simulations of Gibson's and Antipodean wandering albatrosses having very similar growth rates. The models were sensitive to recruitment rates, with models with high recruitment data taken from Weimerskirch *et al.*'s (1997) study producing growth rates about 2.5% higher than models with low recruitment data.

DISCUSSION

Comparison of population trend assessment methods

Counts

We found no significant variation in population trajectories based on counts from different blocks on the same island, and counts of nests in large areas had no more power to detect population trends than did counts in small areas (Table 3). In fact counting large areas might lead to a decrease in power. Although sampling variation decreases with population size (White, 2000), the large number of birds in even our smallest counting blocks means that sampling variation was already small. The existing counting blocks on Adams and Antipodes Islands are well defined by topographical features or white poles, are accessible and relatively easy to move around in, and nests easy to see. Thus, there is very little variation in our data attributable to mistakes made by field workers. However, further increases in the size of the counting blocks would necessitate counting nests in areas which are more difficult to count accurately. There were no significant differences between the trajectories in the different blocks counted for both species, suggesting that any one block provides a good indication of the population trajectory of the whole population, and there is limited value in counting more blocks, particularly if accuracy declines. Pascual and Edwards (1999) found that counts analysed using randomisation tests, such as we used, are more powerful at detecting trends than simple linear regression, but our study found that the increase in power they provided was not as great as that achieved by mark-recapture.

Mark-recapture

Mark-recapture estimates of population trends were derived from estimates of population size, not just from counts of the variable proportion of the birds that bred each year, so were better trend indicators than counts. Our power analysis suggests that linear regression of mark-recapture estimates is so superior to linear regression of counts that it will take about half the number of visits to a breeding colony to confidently detect trends (Table 3).

Simulation Models

A well formulated simulation model with good data has the potential to be an even more powerful tool for examining trends. By explicitly accounting for the processes underlying the population dynamics, a simulation model is resistant to the extreme values that plague empirical models. However, our models had an inherent weakness. Our study had not been running long enough to collect recruitment data, so we borrowed recruitment data from a study of *Diomedea exulans*. For this approach to be valid, we would have had to be confident, either, that the borrowed recruitment rates were similar to our population's, or, that the models were insensitive to recruitment rate, but neither assumption was found to be true.

However, although modelling in this instance proved of limited value in determining trends in the Antipodean and Gibson's wandering albatross populations, it did indicate likely causes for the different trajectories identified through count and mark-recapture studies. The fact that the simulated growth rates of both albatrosses were similar, despite the higher productivity of Antipodean wandering albatrosses, is consistent with studies of the elasticity of population growth rates of albatrosses which show that population growth rates are relatively insensitive to changes in fecundity (Lebreton & Clobert, 1991). The simulations of Gibson's wandering albatrosses with worst-case low recruitment rates have growth rates similar to that detected by mark-recapture analysis, whereas simulations of Antipodean wandering albatrosses with best-case high recruitment rates were most similar to the mark-recapture estimates of growth rates. This suggests that recruitment is better in Antipodean than in Gibson's wandering albatross.

What advice can this study provide to conservation managers wishing to monitor biennially breeding albatrosses? Simple counts of birds nesting in defined areas will require the least work in any one breeding season, but will take 25 - 40 years to confidently detect changes of about 1% per annum. To collect sufficient data to produce a good simulation model, data on recruitment, productivity and survival from the species under study is required; borrowed data will not suffice. Since most wandering albatrosses are 9 - 15 years old when they start breeding, a detailed population study lasting more than 20 years is required for simulation models. By contrast, population estimates based on mark recapture estimates will confidently detect changes of about 1% per annum after about 16 years. This will require the marking and recovery of all birds nesting in and around a study area, but does not require the banding of chicks or estimation of productivity. Markrecapture studies alone however, cannot identify key parameters affecting population trends.

Population trajectories of Gibson's and Antipodean wandering albatrosses

Both Antipodean and Gibson's wandering albatrosses probably suffered fisheries-induced declines of the order of 50% during the 1960s-1980s (Walker & Elliott 1999, 2005). Mark-recapture analysis suggests that Antipodean wandering albatrosses are now growing steadily at about 3.1% per annum, while Gibson's wandering albatrosses are static (Fig. 5). Even though their productivity is lower, the reason for the poorer performance of the latter seems to be poor recruitment.

Although Gibson's and Antipodean wandering albatrosses are closely related (Burg and Croxall 2004), and their breeding islands are only 1000 km apart, they mostly forage in different oceans: Gibson's wandering albatrosses in the Tasman Sea and Antipodean wandering albatrosses in the Pacific Ocean (unpublished data). Differences in fishing activity in their foraging areas, and in prey availability, are likely explanations for their differing trajectories. Continued monitoring of both species will not only provide information on any changes in their conservation status, but might also provide information about changes in the oceanographic conditions in the Tasman Sea and the south Pacific Ocean.

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