PAPERS

POPULATION SIZE AND TRENDS OF THE WAVED ALBATROSS *PHOEBASTRIA IRRORATA*

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SUMMARY

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Albatross populations world-wide face a variety of anthropogenic threats, including fishery bycatch and contaminant ingestion. Colony-based assessments of population size provide a necessary complement to studies of risks at sea to understand and minimize declines in albatross populations. We estimated the size of three components of the world population size of the Waved Albatross *Phoebastria irrorata* of the eastern Pacific Ocean in 2001. Adults that bred in 2000, but not in 2001, constituted 17.3% of the population present at the main breeding site, Isla Española in the Galápagos Islands, while breeders and non-breeders constituted 22.3% and 60.4%, respectively. The minimum estimate of the sum of these components ranged from 31 818 to 34 694 adults. An additional three adults were found on Isla de La Plata, and up to 11 adults were found as non-breeders on Isla Genovesa, Galápagos. In comparison with a 1970 count on Española the overall population has changed little, but the breeding distribution has changed, apparently due in part to regrowth of vegetation after the eradication of feral goats *Caprus hirca* in 1978.

RESUMEN

Las poblaciones de Albatros alrededor del mundo enfrentan una variedad de amenazas, que incluyen la pesca incidental y la ingestión de contaminantes. Estimados del tamaño poblacional en las colonias son complementarios a estudios de los riesgos en el ambiente marino para entender y minimizar las declinaciones poblacionales de los albatros. En el año 2001, estimamos el tamaño de los tres componentes de la población mundial del Albatros de Ondas *Phoebastria irrorata* del lado Este del Oceano Pacifíco. Los adultos que anidaron en el año 2000, pero que no anidaron en el año 2001, constituyeron el 17.3% de la población presente en el sitio principal de anidación, Isla Española en las Islas Galápagos, mientras que aves que anidaron y aves que no anidaron, constituyeron el 22.3% y el 60.4%, respectivamente. El estimado mínimo de la suma de estos componentes fue en un rango de 31 818 a 34 694 adultos. Adicionalmente, se encontraron tres adultos en Isla de la Plata, y hasta 11 aves no reproductoras fueron encontradas en Isla Genovesa, Galápagos. En comparación con los conteos de 1970 en Española, en general, el tamaño de la población ha cambiado poco, pero hay un cambio en la distribución, aparentemente debido en parte a la recuperación de la vegetación después de la erradicación de los cabras ferales *Caprus hirca* en 1978.

Keywords: Waved Albatross, *Phoebastria irrorata*, Galápagos, population size, population trends

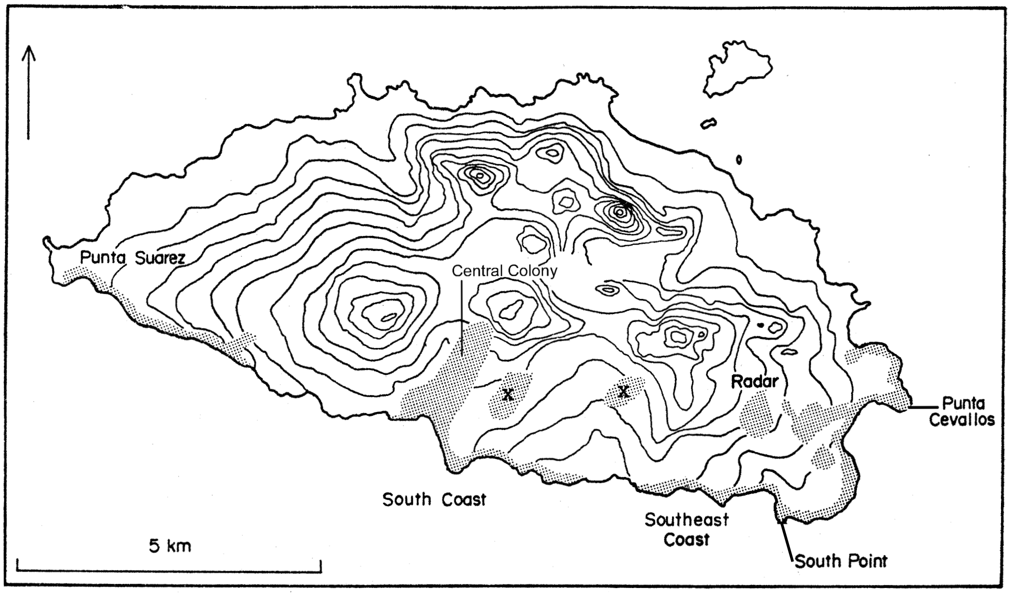

Fig. 1. Locations of Waved Albatross breeding colonies on Isla Española, Galápagos, redrawn from Harris (1973) with permission. Shaded areas are colonies identified by Harris (1973). **x** indicates two colonies that disappeared between 1971 and 1994 (Douglas 1998). The boundary between the Southeast Coast and Punta Cevallos areas is South Point (M.P. Harris pers. comm.).

INTRODUCTION

Many albatross populations worldwide have been affected in recent years by mortality caused by fisheries bycatch (Brothers 1991, Gales *et al.* 1998, Gould *et al.* 1998) and pollutant ingestion at sea (Sievert & Sileo 1993, Blight & Burger 1997, Ludwig *et al*. 1998). Both juvenile and adult mortality rates and reproduction have been affected. Several albatross species forage over continental shelves near concentrated human activity (Nicholls *et al.* 1995, Prince *et al*. 1998, Anderson *et al.* 1998, Fernández *et al*. 2000), making them particularly vulnerable to these threats. Waved Albatrosses *Phoebastria irrorata* exemplify these species, travelling from their oceanic nesting sites to the coastal Peruvian upwelling region to forage during the incubation and chick-rearing periods, and spending the non-breeding season in the same area (Anderson *et al*. 1998, Fernández *et al*. 2000, Tickell 2000). All nesting occurs within the protected Galápagos National Park (Isla Española, the primary site; Fig. 1) and Machalilla National Park (Isla de La Plata, <1% of the population) of Ecuador, so land-based threats are minimal (Anderson & Cruz 1998). The Galápagos population enjoys some protection from fishery bycatch within the Galápagos Marine Reserve (GMR), a Natural World Heritage Site created in 2001. However, the GMR encompasses only part of the foraging range of Waved Albatrosses. Given the potential at-sea threats outside the GMR, and until 2000 within the GMR, we focused on trends in population size of Waved Albatrosses in the present research.

The terrain and thick vegetation characteristic of Española complicate counts of albatrosses, and only two comprehensive efforts have been made. In 1970/71, a team led by Harris (1973) attempted to visit all nesting areas during the incubation period and counted the number of incubated and abandoned eggs encountered (or, in one area, chicks later in the season). Harris monitored egg laying and egg loss during the seasons of the counts, and used those data to adjust each day's counts for eggs that had been laid and already lost, and eggs that would be laid after the day's count. Harris (1973) concluded that 10 600 pairs bred on Española in 1970, and at least 12 000 pairs in 1971. At that time a substantial population of feral goats *Caprus hirca* roamed the island. The Galápagos National Park Service completed eradication of the goat population in 1978, and the vegetation across the island closed dramatically between Harris' count and the next one in 1994, by Douglas, two of us, and our associates (Douglas 1998). The second count was analyzed using four different methods; Method 2 was Harris' (1973) method, and indicated that 20 750 pairs laid eggs in 1994 (Douglas 1998), an increase of 73% over Harris' estimate of 12 000. In 1994, some areas were surveyed from a distance, and more restrictive assumptions regarding estimates for those areas yielded a lower number of breeding pairs, 15 581, still an increase of 30% over 1971 (Anderson 1995, Anderson & Cruz 1998). These apparent increases were observed despite the mounting difficulty of reaching nesting areas, and of detecting albatrosses present but perhaps hidden in vegetation.

The population on La Plata, just off the Ecuadorian continental coast, has been counted more frequently. Complete counts during the incubation period showed five adults in 1975 (Owre 1976), eight in 1981, one breeding pair in 1988 (Ortiz-Crespo & Agnew 1992), and four in 1991 (Curry 1993). Counts after hatching were more variable: two adults in 1985 (Nowak 1987), 30 in 1981 (Hurtado 1981, cited in Ortiz-Crespo & Agnew 1992), and 22 in 1990, plus six chicks (Ortiz-Crespo & Agnew 1992).

In 2001, we conducted a third count of the Española Waved Albatross population. We incorporated new methods to estimate the size of the non-breeding population present on Española in 2001, and the size of the breeding population alive but not breeding on Española in 2001. We also conducted counts at La Plata in 2000. We used these data to detect trends in the breeding population size on Española since Harris' 1971 count, and to estimate the overall population size.

METHODS

We counted the number of incubating albatrosses present on Isla Española (1°20'S, 89°40'W) between 26 May and 12 June 2001. Teams of two to four people made single visits to areas identified by Harris (1973) and Douglas (1994) as nesting sites (Fig. 1), checking all sitting birds to determine whether they were incubating an egg. In most areas, we conducted comprehensive counts, marking eggs where necessary to ensure each incubated egg was counted only once. In the inland strip linking the Punta Cevallos coastal area and the Radar site (Harris 1973), we searched and counted incubating birds that were seen, but we suspect that additional birds were not seen in the dense vegetation of that area. We attempted to reach the Central Colony/South Coast complex from the north, but thick vegetation prevented access. We did reach the Central and South Coast colonies from the east and verified the continued presence of albatrosses at both but we did not conduct counts at either. We did not attempt to visit the colonies that disappeared between 1970 and 1994 (Fig. 1). The search effort in each area is summarized in Table 1.

Throughout the incubation periods of 2000 and 2001, we monitored the breeding phenology of all albatrosses nesting in our Study Area at Punta Cevallos, the east point of the island. The Study Area is the north end of 'Subcolony 1' in Huyvaert & Anderson (in press). A total of 111 eggs was laid in the Study Area in 2001. For all areas except Punta Suárez, we assumed that the schedules of egg laying and egg loss in the Study Area represented those of all nesting areas. For each day of the 2001 counts, we retrospectively calculated two correction factors from the Study Area data: the number of eggs lost or abandoned before that day divided by the number of incubated eggs present on that day ('egg loss factor'), and the number of eggs laid after that day divided by the number of eggs present on that day ('egg gain factor'). The egg loss factor ranged from 0.143 on the first day of counts to 0.405 on the last day and the egg gain factor ranged from 0.067–0 over the same period. We multiplied each day's count of incubated eggs from other areas by those factors and added the resulting number of eggs to the raw counts, as in 1994 ('Method 3' of Douglas 1998). At Punta Suárez, it appeared that the rate of egg abandonment was dramatically higher than at Punta Cevallos, apparently due to high mosquito density (Anderson & Fortner 1988, unpubl. data), so we used the number of abandoned eggs among 163 incubated eggs in the western half of the Punta Suárez area to determine a separate egg loss factor (0.681) for this area. These 'corrected incubated egg counts' were directly comparable across the 1994 and 2001 efforts. The 1970 count used numbers of all eggs, including abandoned eggs, and so were not comparable. However, counts of all eggs reliably predict counts of incubated eggs; for the six areas for which Douglas (1998) provided both types of counts, they are related by the equation: # incubated eggs = # all eggs (0.994) – 209.7 (linear regression, $F_{1,4} = 328.3$, $P < 10^{-4}$, $r^2 = 0.99$). Since the regression's estimate for the y-intercept is not significantly different from 0 ($t = 1.07$, df = 4, $P = 0.35$), we simply multiplied the 1970 counts by 0.994 to make them comparable to the two later efforts. Harris (1973) did not report counts for individual colonies for 1971, so we compared our data to his 1970 counts only.

To estimate the proportion of the total breeding population present on the island in a given year, we marked all breeding adults nesting in the Study Area in 2000 with numbered plastic bands, and in 2001 documented which of these birds also bred (within or outside the Study Area) in 2001. Band retention across this one-year period was 100% (K.P. Huyvaert unpubl. data).

We used a 'removal by marking' method (White *et al*. 1982) to estimate the size of the non-breeding population. Since all breeders in 2000 and 2001 had already received plastic bands as part of another study, we assume that unbanded residents of the Study Area were non-breeders. On 26 May 2001, the first day of the whole island count, we 'captured' (i.e. counted, and marked or recorded the plastic band number from) all non-breeders in the Study Area at 07h00. At 12h00 and 17h00 we repeated this procedure for all unmarked non-breeders, and then summed the three counts to arrive at the total number of non-breeders present on that day. We repeated this procedure on each of the next 22 days for the unmarked non-breeders. Finally, we lumped the daily counts into six-day bins, because the date of capture of some birds from the first six days only was not explicit in our records. The last of the four bins actually represented a five-day period, due to our departure from the island. We used the program CAPTURE (Otis *et al.* 1978) to estimate the size of the study area's non-breeder population based on the four binned counts. CAPTURE uses a maximum likelihood technique to estimate the capture probabilities and allows heterogeneity in capture probabilities.

We visited Isla de La Plata (1°16'S, 81°04'W) on 27–28 July 2000 and searched the entire trail system and portions of the rest of the island, noting all albatrosses on land, in the air, and offshore. We suspect that all albatrosses present were counted, given the island's small size and open habitat. Two participants in the present study were involved in the 1994 count also, to ensure similarity of methods in the two efforts.

RESULTS

Isla Española breeding population

Estimates of incubated eggs, corrected for past egg loss and future laying, at Punta Suárez and coastal areas of Punta Cevallos in 2001 were 78% and 76%, respectively, of those in 1970; both were dramatically lower than counts in 1994 (Table 1).

In contrast, the breeding population of the Southeast Coast increased between 1970 and 2001 (Table 1). The Southeast Coast comprises a series of open headlands and long stretches of flat cliff-top nesting habitat. These areas regularly receive salt spray from the southeast sea swell; the partial plant cover includes primarily a salt-tolerant forb *Sesuvium edmonstonei* and grasses, and the woody vegetation closing interior parts of the island is essentially absent. The extent of nesting habitat has probably not changed in this coastal area in the past 31 years, in contrast to the changes in the interior areas.

In 2000, 208 banded adults bred in the Study Area. In 2001, 54 of those birds (26.0%) failed to breed anywhere on Española (36 were present but not breeding, and 18 were not seen at all in 2001). The annual adult survival probability of Waved Albatrosses averages 0.95 (Harris 1973; if survival has not been affected by

TABLE 1

Estimates of the breeding population size of Waved Albatrosss on Isla Española, Galápagos Islands*

	a 1970 Egg count	**b 1970 Egg count, corrected**	**c 1970 Incubated eggs, corrected**	**d 1994 Incubated eggs**	**e 1994 Incubated eggs, corrected**	**f 2001 Incubated eggs**	**g 2001 Incubated eggs, corrected**	**h 2001 Person/hrs of search effort**
Punta Suárez	1903	2789	**2772**	2392	**3330**	1225	**2167**	77.73**
Punta Cevallos,								
Coast	1916	2316	**2292**	4000	**5515**	2483	**3033**	15.01
Inland	602	743	**739**	224	**337**	111	**163**	8.75
Southeast Coast	514	642	**638**	803	**1200**	1232	**1494**	7.43
Subtotal			**6441**		**10 382**		**6857**	
South Coast	1026	1140	1133	*4027*	*6090*	No data	No data	
Central Colony,								
West Hill	*511*	*2000*	*1988*	*1149*	*1727*	No data	No data	
Other hills		*500*	*497*	*0*	*0*	No data	No data	

*__Column a__ includes all eggs, **column b** adjusts column **a** for lost and unlaid eggs (Harris 1973), and **column c** is **column b** multiplied by 0.994 (see Methods); **column d** includes only incubated eggs, and **column e** adjusts **column d** for lost and unlaid eggs (Douglas 1998); **columns f** and **g** are as columns **d** and **e**. Estimates including extrapolations are shown in *italics*. Directly comparable corrected egg counts with no extrapolations are shown in **bold**.

**Search efficiency at Punta Suárez was lower than in other areas because searching stopped for blood sampling in the case of many birds. The true search effort at Punta Suárez was approximately 25 person-hours.

long-line mortality) so 198 of the 208 breeders in 2000 and 52 of the subset of 54, were probably alive in 2001. In 2001, 154 of the year 2000 breeders bred, as did adults that did not breed in 2000, but the 2001 egg count would underestimate the size of the combined breeding population that was alive in 2001 by at least a factor of 1.286 (= 198/154).

Isla Española, non-breeding adults

The best fit model for the 'removal by marking' surveys indicated a constant capture probability of 0.433 (chi-square = 0.44, P = 0.80). Other models (of the removal surveys) that incorporated heterogeneity in capture rates also fit the data; however, the constant capture probability model was the most parsimonious. Additionally, because we binned the capture survey data, any heterogeneity in capture rates would be diminished; therefore, we had no *a priori* reason to expect appreciable variability in capture rates. Based on the constant capture probability model, the non-breeding population estimate for the Study Area was 88 (approximate 95% confidence interval 81–106). In 2001, 238 birds bred in the Study Area, so the adult population in the Study Area that year was at least 326 birds, 1.370 times that of the breeder population. This factor represents a minimum figure if some non-breeders attend the colony in some years but not others.

Isla Española, total population size

As we did not count eggs in the Central and South Coast colonies, we must make assumptions about their size to calculate total population size. If those two colonies decreased in number to 74–78% of 1970 levels, as the Punta Suárez and Punta Cevallos coast colonies did, then the breeder population on Española can be derived from the sum of the egg counts in Table 1 Column c for the Central and South Coast colonies (3618) multiplied by 0.76 (the average reduction in numbers from 1970 to 2001), plus the subtotal in Column g. This figure (9607 eggs) represents 19 214 breeders in 2001. The number of living year 2000 breeders not breeding in 2001 is estimated to be at least 28.6% of this figure, or 5495 birds. The number of non-breeders is estimated to be at least 37.0% of the number of breeders present, or 7109 birds. The total number of living adults, present and not present in 2001, would be at least than 31 818 under these assumptions. Three more birds were present on La Plata (see below). This estimate excludes an unknown number of non-breeding birds that were alive but not present on Española in 2001.

Assuming instead that the Central and South Coast colonies did not change in size between 1970 and 2001, and applying the same reasoning, the 2001 breeding population was 20 950 birds present, with an additional 5992 year-2000 breeders not breeding, and 7752 non-breeders present, for a total Española adult population of at least 34 694 birds.

Birds breeding in 2001 represented 60.4% of the adult population (solving for B, the breeding component of the population, in the equation B + 0.286B + 0.370B = 1). Birds that bred in 2000 but not in 2001, and non-breeders, constituted 17.3% and 22.3%, respectively, of the 2001 adult population.

Isla de La Plata

We found three non-breeding Waved Albatrosses on La Plata, two resting as a pair and one single bird. All were near the southern sea cliff. We saw no evidence of breeding.

DISCUSSION

Using IUCN criteria for assigning threat status (especially restricted breeding range), Croxall & Gales (1998) and BirdLife International (2000) considered the Waved Albatross population to be Vulnerable. In 1997 the species was added to Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals. Appendix II includes migratory species of unfavourable conservation status that would require, or benefit from, international agreement on their conservation and management. The Agreement on the Conservation of Albatrosses and Petrels (ACAP), drawn up in 2001 but not yet in force, includes the Waved Albatross. Ecuador has now signed and ratified the ACAP.

Our counts for La Plata continued to show a persistent presence of Waved Albatrosses, and in December 1998 we saw up to 11 non-breeders on the western point of Isla Genovesa in the Galápagos (D.J. Anderson & K.P. Huyvaert unpubl. data), but the Waved Albatross breeding population is effectively that of Española at present. The essentially single population's status is thus of significant conservation importance.

We have focused on the comparison of 1970 and 2001 counts, because the presence of breeders in 1994 was possibly inflated by the El Niño-Southern Oscillation (ENSO) conditions of the previous two years. Some adults fail to breed in the year after fledging an offspring (K.P. Huyvaert unpubl. data), so in a typical year part of the potential breeding population would not be represented in an egg count. Because the 1994 count occurred at the end of the 1992–94 ENSO event, the 1994 breeding population may have included most or all potential breeders (assuming that breeding was interrupted by the 1992–94 ENSO event as in 1982/83; Rechten 1985). Comparison of the 1970 and 2001 counts may thus provide the best indication of long-term population trends. Across that 31-year period, the estimates of numbers of breeders in the Punta Suárez, Punta Cevallos, and Southeast Coast colonies differed by only 6.5% (Table 1). However, within this apparent stability, the Punta Suárez population appeared to decrease somewhat and those of the Southeast Coast and Punta Cevallos increased. Although it is tempting to attribute this pattern to movements from Punta Suárez to the other areas, we have no evidence to support this position. In contrast, locations of banded birds argue against it. Virtually all banding of both adults and chicks on Española has occurred at Punta Suárez and Punta Cevallos, and almost all band resightings in the 2001 effort were in those two areas, and not at the Southeast Coast (Charles Darwin Research Station and D.J. Anderson unpubl data). This fact agrees with Harris' (1973) data indicating high natal philopatry and high nest site fidelity in this population.

Several other explanations for the different trends in different subcolonies remain possible. The proportion of a subcolony's total breeding population that in fact breeds in a given year may be poorly correlated across subcolonies, due to environmental, behavioural, or other differences across subcolonies. In that case the apparent trends that we detected would be misleading. Alternatively, reproductive success during the 31 years may have been above replacement level at the Southeast Coast and Punta Cevallos and below it at Punta Suárez; with high philopatry and nest site fidelity, the productive subcolonies would increase in size and Punta Suárez would decrease. We have little information to bring to bear on this possibility, except to note that the Punta Cevallos subcolony fledged young in most of the years between 1992 and 2000, and at least some of those banded young were recorded at Punta Cevallos in 2001. A final explanation implicates assumptions made in our methods, that rates of egg loss and egg laying in our Punta Cevallos study area differ from those elsewhere. We cannot evaluate this explanation at present, but even if correct it is not likely to be of sufficient magnitude to explain the large increase in the Southeast Coast breeding population.

Our observations at the Radar site indicate a continuing effect of increasing vegetative cover on Waved Albatross nesting habitat, following the removal of feral goats (Hamann 1984). The subcolony associated with the former airstrip appears to be shrinking, and with continued encroachment of woody vegetation this subcolony will disappear altogether. The same loss of habitat could be affecting the inland Central colony, which comprised approximately 28% of the 1970 count and approximately 43% of the 1994 count (although these figures were based partly on extrapolations; Harris 1973, Douglas 1998). A significant gap in our understanding of Waved Albatross population dynamics involves the ancestral habitat of the island, before the introduction of goats. If the open areas of the mid-20th century were maintained artificially by goats, as seems likely (Hamann 1984, Anderson & Cruz 1998) then the albatross population in inland areas may have been inflated in 1970 compared to that before the clearing action of the goats (Harris 1973). The re-growth of the woody vegetation, and exclusion of albatrosses from temporarily open areas, would represent a correction from an inflated albatross population size under this perspective (Anderson & Cruz 1998), and the coastal areas in which we worked, plus the South Coast, would contain the 'core' population. Although the 1970 and 2001 counts of most of this core population are similar (Table 1) and indicate numerical stability, the Waved Albatross continues to be one of the less abundant albatross species (Gales 1998).

The Española Waved Albatross population is difficult to count because the population is dispersed over wide areas of the island, with significant nesting in thick scrub vegetation. Reaching some subcolonies on foot is a logistical challenge, and detection of nesting birds, whose colouration blends with that of the habitat, is uncertain. Our data from the more open habitats in the Punta Suárez, Punta Cevallos, and Southeast Coast subcolonies indicate a redistribution of breeding attempts among subcolonies, but overall similarity in breeding attempts in 1970 and 2001. A more thorough assessment of the population's size will require counts of the Central and South Coast colonies, but the closed habitat in these areas imparts inherent error on counts of birds. Aerial surveys offer a possible solution to this problem, but at inland sites albatrosses nest under a canopy of woody scrub vegetation, impeding detection from the air. For the present, reliable trends in population size can be extracted only from the Punta Suárez, Punta Cevallos, and Southeast Coast subcolonies, and total numbers of breeding birds in these areas combined appear not to have decreased since 1970.

Counts in the inland areas of Punta Cevallos have declined in each of the two efforts since 1970, probably because regrowth of vegetation in these areas has closed formerly open spaces. The Radar site (Fig. 1) provided an example of this effect. During World War II, the U.S. Navy cleared a runway at the Radar site for combat aircraft. After it was abandoned, albatrosses used the runway and adjacent small clearings for nest sites with a nearby take-off area. Albatrosses can reach this inland area only from the air. In 2001, the runway was overgrown and the takeoff path largely obstructed. We saw two adults attempt to take flight, and both crashed into vegetation and fell to the ground. We saw a total of 29 albatross skeletons around the airstrip; four of these hung in woody vegetation, while the remainder indicated that the birds apparently rested under the bushes before dying of starvation. We suspect that the skeletons are those of full-grown juveniles which could not take flight to leave the area, assuming that juveniles on their first flight will have even greater difficulty than adults with becoming airborne. The decline in nesting in this area can thus be attributed to the failure of highly philopatric offspring (Harris 1973) to fledge and later recruit to the Radar site.

The failure of the population on La Plata to increase represents a conservation concern, because Waved Albatrosses breed in an essentially point population on Española (Croxall & Gales 1978). An expanded La Plata population could provide insurance against a disaster on Española. Satellite-tracking studies indicate that breeding Waved Albatrosses forage primarily in the Peruvian upwelling, and in the waters between Perú and Galápagos (Anderson *et al*. 1998, Fernández *et al*. 2000, Anderson *et al*. 2003). La Plata is closer to these areas than is Española, and some tracked birds breeding on Española pass by La Plata on foraging trips (Anderson *et al*. 1998). Our impression in 2000 was that abundant suitable nesting habitat was available on La Plata. We are not aware of any limiting factor required by Waved Albatrosses that is available in Galápagos and not on coastal islands on the continental shelf, although we note one possibility. Waved Albatrosses appear to be challenged by the high air temperatures of Galápagos: with the exception of Waved Albatrosses and three congeners of the North Pacific, albatrosses breed at high latitude in colder climates. On Española, breeders minimize the thermal challenge by nesting during the coolest part of the annual cycle, but incubating birds and chicks still thermoregulate laboriously by panting, and non-breeders leave the island from early morning to dusk, sitting offshore in large aggregations. A comparison of thermal environments on Española and La Plata could determine whether La Plata is even less suitable for nesting. An additional possibility is that La Plata is in fact suitable for nesting, and was occupied by Waved Albatrosses in the past, but the arrival of foraging humans on the islands of the South American continental shelf approximately 12 000 years ago led to the extirpation of that population. If so, the recent protection of the island as part of the Machalilla National Park may eventually permit immigration from the Española population, although high philopatry will retard this process.

The number of breeders present on Española in 2001 represented at most 60.4% of the total adult population that is ever present on the island, according to our assumptions and modelling. This large non-breeding population raises the question of habitat saturation. Surplus nesting habitat appears to exist in the areas that we view as the core population (Anderson & Cruz 1998). If so, then the number of breeding attempts per year could be limited by a number of other factors, including costs of reproduction of the previous year, for which we have presented some evidence; sex ratio bias limiting availability of mates; a long period of prebreeding adulthood; and food availability. We have summarized data on population size that indicate no overall decline over a 31-year period. However, the distribution of the breeding population appears to be in flux, due to habitat alteration. Future estimates of breeding population size are required, because the estimate from any particular year represents only the subset of breeders from the larger pool of potential breeders, and the size of this subset may vary dramatically between years (the 1994 count, following an ENSO event, may be an example of this effect). In addition, further research should focus on the processes that influence population dynamics, to complement the existing data on overall numbers.

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