ORIGINAL ARTICLE

Assessing the effect of satellite transmitters on the demography of the Wandering Albatross *Diomedea exulans*

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Abstract Satellite transmitters and other tracking devices are valuable tools for furthering our understanding of bird movements, and their use has been steadily increasing. Since the necessary handling of birds to deploy transmitters can have deleterious consequences and the transmitter itself can add substantial mass, particularly to small species, or bring discomfort to the individual birds to which they are attached, it is important to quantify the effect such devices on both the behavior and the fitness of equipped animals. Very few studies have focused on the demographic effects of equipping birds with a satellite transmitter, with the vast majority of such studies focusing on short-term behavioral effects. We have assessed the demographic effects of attaching a satellite transmitter to the back of adult breeding Wandering Albatross individuals using long-term demographic data (20 years) and recent developments in capture–recapture methodology. We found no evidence of any negative effects of the attached devices on the probability of survival, breeding, or breeding successfully in the current or following season in either males or females. We conclude that the current satellite transmitters and smaller devices used by researchers are valuable conservation and research tools that do not adversely affect the demographic traits of large albatrosses. Similar tests should be carried out on smaller species, which are more likely to be affected.

Zusammenfassung

Abschätzung des Effekts von Satellitensendern auf die Demographie des Wanderalbatrosses *Diomedea exulans*

Satellitensender und andere Routen-Kontrollgeräte sind wertvolle Hilfsmittel, um die Bewegungen von Vögeln zu verstehen, und werden zunehmend benutzt. Das Handling, das notwendig ist, um die Sender einzusetzen, kann jedoch schädliche Folgen haben, und die Sender können besonders bei kleinen Arten beträchtliches Gewicht hinzufügen oder für die Tiere, an denen sie befestigt werden, unangenehm sein. Daher ist es wichtig, ihren Effekt auf das Verhalten und insbesondere auf die Fitness der damit ausgestatteten Tiere zu quantifizieren. Nur sehr wenige Studien haben sich auf die demographischen Effekte von Satellitensendern auf Vögel konzentriert, und die überwiegende Mehrheit hat lediglich kurzzeitige Verhaltenseffekte untersucht. Wir haben die demographischen Effekte von Satellitensendern, die auf dem Rücken adulter brütender Wanderalbatrosse angebracht waren, abgeschätzt, unter Verwendung demographischer Langzeitdaten (20 Jahre) und neuer Entwicklungen in der Fang-Wiederfang- Methodik. Wir haben keine Belege für negative Effekte von angebrachten Geräten auf die Wahrscheinlichkeit, zu überleben, zu brüten oder in der aktuellen oder in zukünftigen Saisons erfolgreich zu brüten, bei Männchen und Weibchen gefunden. Wir folgern, dass die derzeit von Forschern verwendeten Satellitensender und kleineren Geräte nützliche Schutz- und Forschungshilfsmittel sind, welche die demographischen Eigenschaften großer Albatrosse nicht nachteilig beeinflussen. Ähnliche

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Tests sollten für kleinere Arten durchgeführt werden, die mit größerer Wahrscheinlichkeit beeinträchtigt sind.

Introduction

For the past 20 years the development of miniaturized tracking instruments, such as satellite transmitters and global positioning system (GPS) devices, have considerably advanced our knowledge on the at-sea ecology of seabirds (Weimerskirch 2007; Burger and Shaffer 2008). The majority of studies often make the implicit assumption that the tracking devices neither alter the normal behavior of the bird nor induce a bias in the parameters measured. However, several studies have detected behavioral effects of the tracking instruments, such as prolonged foraging trips (Phillips et al. 2003), decreased foraging efficiency (Passos et al. 2010), or reduced breeding success (Phillips et al. 2003). In long-lived animals it is important not only to take into account the short-term behavioral or demographic impact of the tracking device, but also the longer term effects. To the best of our knowledge, no study has investigated the effects of satellite transmitters on the vital rates of seabirds, such as the probabilities of adult survival, breeding, or success in the following season. The lack of such studies is likely partly due to the lack of both long-term individual capture–recapture data for transmitter-equipped and control birds of sufficient sample sizes and adequate modeling tools for estimating unbiased survival and breeding probability parameters in seabirds. Measuring transmitter effects on breeding probabilities is particularly difficult in several species of seabirds that are known to skip breeding and stay at sea for a number of years (Chastel et al. 1995) and therefore remain unobservable for identification. If these unobservable states are ignored, heterogeneity in capture probabilities can bias vital rate estimates (Kendall and Bjorkland 2001). As such, the effect of tracking devices on vital rates can not be properly tested.

Capture–recapture models that explicitly incorporate observable and unobservable states have recently been developed (Fujiwara and Caswell 2002; Kendall and Nichols 2002); these appear to be a powerful approach for estimating demographic parameters while explicitly accounting for temporary emigration due to individuals that skip breeding (Schaub et al. 2004, Converse et al. 2009). These models have been successfully developed and used for studying albatrosses, enabling survival, breeding, and success probabilities to be estimated (Hunter and Caswell 2009). Observable birds are those that attempt to breed (successfully or not), while unobservable birds are nonbreeders that remain at sea, but potentially will return the next year to breed in the colony.

In the study reported here, we have examined the effects of deploying satellite tags (platform terminal transmitters, PTTs) on the probabilities of adult survival, breeding, and breeding success of the Wandering Albatross *Diomedea exulans*, which breeds on the Crozet Islands. Since 1989, 138 individual albatrosses have been tracked using PTTs (Jouventin and Weimerskirch 1990), with all individuals being part of a long term capture–mark–recapture (CMR) study (Weimerskirch et al. 2005). We estimated vital rates using multistate CMR models and individual long-term CMR data and then compared the vital rates of individuals during the season of equipment (for breeding success) and following their equipment with PTTs with the vital rates compiled during other seasons (i.e., not following equipment with a PTT). Since no effect of PTTs was detected on foraging trip duration during incubation or brooding in this population of Wandering Albatross (Weimerskirch et al. 1992), we expected no effect on breeding success probability for the current or subsequent breeding season. Because the Wandering Albatross is a long-lived species in which individuals are commonly thought to abandon offspring rather than jeopardize their own survival (Williams 1966; Goodman 1974), it follows that by predicting no effect on breeding success, we predict no effect on the probability of breeding the following season, or survival.

Methods

Study area and field study

Monitoring of the Wandering Albatross population was carried out at Possession Island (46°S, 52°E), Crozet, south-western Indian Ocean. The entire breeding population consists of approximately 580 breeding pairs (Delord et al. 2008), with approximately 320 pairs breeding annually. Since 1960, the population has been counted annually. All breeding adults were ringed with a stainless steel band which allowed individual identification of both members of each pair at the time of the visits (three to four from December to April) to the colony during the breeding season (see Weimerskirch and Jouventin 1987 for details). At the fledging period, breeding performance was determined and chicks were ringed. Each year, new individuals found in the colony were ringed. Although CMR data are available each year since 1966, sufficient detailed individual breeding success data are only available since 1985. Therefore, demographic analyses were conducted for the 1986–2006 period on 1,446 males and 1,420 females. Adults were sexed on the basis of plumage characteristics, size, and previous capture history, and there was no uncertainty when sexing individuals (Weimerskirch et al. 2005).

Since 1989, 138 breeding adults (73 males, 65 females) have been equipped and tracked using PTTs. Among these, 12 males and ten females were equipped twice. From 1989 to 1992, the transmitters were fitted on the birds using a harness made of fine goat leather with elastic sections (Weimerskirch et al. 1992). Since 1993, the transmitters have been taped on the back feathers. Incubating or brooding adults were caught and PTTs attached to between five and ten mid-dorsal feathers of the mantle using three strips of Tesa tape (Weimerskirch et al. 1994). The weights of the PTTs varied from a maximum of 180 g (approx. 1.8–2.2% of the bird mass) during the early 1990s to a minimum of 30 g (approx. 0.3–0.4% of the bird mass) since the late 1990s. All birds were recaptured after one or several foraging trips [mean 12.0 days, standard deviation (SD) 8.1 days, minimum 2 days, maximum 53 days] when they returned to their nest and the PTTs removed. Upon recovery, the harness or tape strips were completely removed.

Capture–recapture analysis

Adult survival, breeding, and success probabilities in the following season were estimated using multistate models (Pradel 2005; Hunter and Caswell 2009; Barbraud and Weimerskirch 2011). Since the Wandering Albatross is a quasi-biennial breeder, with a few birds able to breed immediately 1 year after a successful breeding season (Barbraud and Weimerskirch 2011), our starting point was the model developed by Hunter and Caswell (2009) for biennial breeders. This model distinguishes four states: two observable states consisting of the failed breeder (FB) and successful breeder (SB), and two unobservable states consisting of nonbreeders whose previous breeding attempt failed (PFB) and nonbreeders whose previous breeding attempt was successful (PSB). The unobservable states account for a temporary absence, corresponding to birds that skip breeding after breeding unsuccessfully or successfully. To model the effects of PTTs on demographic parameters, and since PTTs were only deployed on breeding individuals, we included two additional states consisting of failed breeders which were equipped with a PTT (FBp), and successful breeders which were equipped with a PTT (SBp). Although never observed, the state "dead" was explicitly included in the model (Pradel 2005); this state is an absorbing state representing death or permanent emigration from the study area. We thus considered seven states (FB, SB, FBp, SBp, PFB, PSB, and dead). States occupied were directly observed and we thus considered four states to construct capture histories: 1 = "seen as a failed breeder;" 2 = "seen as a successful breeder;" 3 = "seen as a failed breeder with a PTT;" 4 = "seen as a successful breeder with a PTT". States were considered to

Table 1 Definition of parameters used in the multistate mark–recapture model

Parameter	Definition
π_s	Probability that an individual is in state s when first encountered
s_s^t	Probability that an individual in state s at time t survives to time $t + 1$ and does not permanently emigrate from the study area
β_s^t	Probability that an individual in state s at time t breeds at time $t + 1$ given that it survives to $t + 1$
γ_s^t	Probability that an individual in state s at time t breeds successfully at time $t + 1$ given that it survives to and breeds at time $t + 1$
α_s^t	Probability that an individual in state s at time t is not equipped with a PTT given that it survives to and breeds at time $t + 1$
p_s^t	Probability that an individual in state s at time t is encountered at time t

be random variables, and successive states were assumed to obey a Markov chain. Models were parameterized in terms of the probability of survival, the probability of breeding given survival, the probability of success given breeding, and the probability of being equipped with a PTT. Transition probabilities between states were thus modelled with a four-step procedure where survival, breeding, success, and equipment are considered as four successive steps in transition matrices. Parameters of the model are defined in Table 1.

Several constraints were made to ensure that the model reflected the life cycle of the Wandering Albatross and did not contain redundant parameters. The state dead was explicitly included in the model, but as it was never encountered, several constraints were implied (initial encounter probability was fixed to 0, transition probabilities from the state dead to the other states were fixed to 0, and capture probability was fixed to 0; see Pradel 2005; Choquet et al. 2009a). The probability of seeing individuals in unobservable states and transitions between unobservable states were constrained to zero. To limit redundancy in the parameters and given the relatively small number of events concerning individuals equipped with PTTs, we only considered models for which survival, breeding, and success probabilities were constant. Given that individuals equipped with PTTs were captured, their detection probability was fixed to 1. Finally, since Hunter and Caswell (2009) found strong evidence for state-dependent breeding and success probabilities for the Wandering Albatross population breeding at South Georgia (their Table 7), we started with models for which breeding and success probabilities were entirely state-dependent. This initial multistate model is parameterized by the initial state probabilities vector:

$$\Pi = \begin{pmatrix} \pi_{FB} & \pi_{SB} & \pi_{FBp} & \pi_{SBp} & 0 \\ (1 - \pi_{FB} - \pi_{SB} - \pi_{FBp} - \pi_{SBp}) & 0 \end{pmatrix},$$

where π_{FB}, π_{SB}, π_{FBp}, π_{SBp}, are, respectively, the initial proportions of failed, successful, post-failed and post-successful breeders; the first 0 indicates that the initial proportion of failed breeders with a transmitter is null, $1 - \pi_{FB} - \pi_{SB} - \pi_{FBp} - \pi_{SBp}$ indicates that the initial proportion of successful breeders with a transmitter is null, and the last 0 indicates that the initial proportion of dead individuals is null since only resighting data are used. Initial state probabilities need not to be estimated since there was no state uncertainty and the model includes conditions on capture; these were therefore fixed to 1.

The survival–transition probabilities matrix of the initial model was (see Table 1 for parameter definitions):

	FB	SB	FBp	SBp	PFB	PSB	Dead	
	$s_{FB}\beta_{FB}(1-\gamma_{FB})\alpha_{FB}$	$s_{FB}\beta_{FB}\gamma_{FB}\alpha_{FB}$	$s_{FB}\beta_{FB}(1-\gamma_{FB})(1-\alpha_{FB})$	$s_{FB}\beta_{FB}\gamma_{FB}(1-\alpha_{FB})$	$s_{FB}(1-\beta_{FB})$	0	$1-s_{FB}$	FB
	$s_{SB}\beta_{SB}(1-\gamma_{SB})\alpha_{SB}$	$s_{SB}\beta_{SB}\gamma_{SB}\alpha_{SB}$	$s_{SB}\beta_{SB}(1-\gamma_{SB})(1-\alpha_{SB})$	$s_{SB}\beta_{SB}\gamma_{SB}(1-\alpha_{SB})$	0	$s_{SB}(1-\beta_{SB})$	$1-s_{SB}$	SB
$\Phi =$	$s_{FBp}\beta_{FBp}(1-\gamma_{FBp})\alpha_{FBp}$	$s_{FBp}\beta_{FBp}\gamma_{FBp}\alpha_{FBp}$	$s_{FBp}\beta_{FBp}(1-\gamma_{FBp})(1-\alpha_{FBp})$	$s_{FBp}\beta_{FBp}\gamma_{FBp}(1-\alpha_{FBp})$	$s_{FBp}(1-\beta_{FBp})$	0	$1-s_{FBp}$	FBp
	$s_{SBp}\beta_{SBp}(1-\gamma_{SBp})\alpha_{SBp}$	$s_{SBp}\beta_{SBp}\gamma_{SBp}\alpha_{SBp}$	$s_{SBp}\beta_{SBp}(1-\gamma_{SBp})(1-\alpha_{SBp})$	$s_{SBp}\beta_{SBp}\gamma_{SBp}(1-\alpha_{SBp})$	0	$s_{SBp}(1-\beta_{SBp})$	$1-s_{FBp}$	SBp ,
	$s_{PFB}\beta_{PFB}(1-\gamma_{PFB})\alpha_{PFB}$	$s_{PFB}\beta_{PFB}\gamma_{PFB}\alpha_{PFB}$	$s_{PFB}\beta_{PFB}(1-\gamma_{PFB})(1-\alpha_{PFB})$	$s_{PFB}\beta_{PFB}\gamma_{PFB}(1-\alpha_{PFB})$	$s_{PFB}(1-\beta_{PFB})$	0	$1-s_{PFB}$	PFB
	$s_{PSB}\beta_{PSB}(1-\gamma_{PSB})\alpha_{PSB}$	$s_{PSB}\beta_{PSB}\gamma_{PSB}\alpha_{PSB}$	$s_{PSB}\beta_{PSB}(1-\gamma_{PSB})(1-\alpha_{PSB})$	$s_{PSB}\beta_{PSB}\gamma_{PSB}(1-\alpha_{PSB})$	0	$s_{PSB}(1-\beta_{PSB})$	$1-s_{PSB}$	PSB
	0	0	0	0	0	0	1	Dead

As indicated in Table 1, s is defined as a survival parameter, and because the states are defined as reproductive states, the combinations of breeding attempt (β) and breeding success (γ) define the transition to the states. For example, the cell in row one column two of the matrix indicates that for individuals in the FB state to transition into the SB state, they have to survive with probability s_{FB}, attempt to reproduce with probability β_{FB}, successfully fledge young with probability γ_{FB}, and not be tagged with probability α_{FB}. Individuals in the FBp or SBp state that transited to the SB, FB, PFB, or PSB states were those who survived with the PTT and then had the PTT removed.

Finally, the encounter probabilities matrix of the initial model was

$$B^t = \begin{array}{c} \\ \\ \\ \\ \\ \\ \\ \end{array} \begin{pmatrix} 1-p^t_{FB} & p^t_{FB} & 0 \\ 1-p^t_{SB} & 0 & p^t_{SB} \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \end{pmatrix} \begin{array}{l} FB \\ SB \\ FBp \\ SBp , \\ PFB \\ PSB \\ Dead \end{array}$$

with column headers: not seen, seen FB, seen SB.

The encounter probability p is thus the probability of detection given that individuals attempted to breed (i.e., they were in the observable state).

Therefore, our initial model had constant and state-dependent state probabilities, constant and state-dependent survival, breeding, and success probabilities, and time- and state-dependent encounter probabilities. We tested several hypotheses by considering constrained models for each parameter type. First, we tested whether encounter probabilities were time- or state-dependent. We then tested whether success, breeding, and survival probabilities differed between individual birds equipped with a PTT and those not equipped with a PTT. At each modeling step we retained the favored model, which was then used as a reference model for the following modeling step. Males and females were analyzed separately to respect the hypothesis of independence of fate since breeding and success probabilities are determined by both members of the pairs.

The assessment of goodness-of-fit (GOF) remains an open question with multistate models with unobservable states (Pradel et al. 2003). We therefore performed approximate GOF tests following Viallefont et al. (1995) and Rivalan et al. (2005) by discounting the change of deviance (Δdev) between models that accounted for reproductive skipping (i.e., models with two observable and two unobservable states) and models that did not account for reproductive skipping (models with two observable states). In this case the GOF tests were approximated as:

$$GOF = testWBWA + test3G.Sr + test3G.Sm + testM.ITEC + testM.LTEC - \Delta dev$$

with

$$df = df_{testWBWA} + df_{test3G.Sr} + df_{test3G.Sm} + df_{testM.ITEC} + df_{testL.ITEC} - 1$$

Briefly, testWBWA tests the null hypothesis of no difference in the expected state of the next encounter among the individuals previously encountered in the different states; test3G.Sr tests the null hypothesis of no difference in the probability of being later reencountered between "new" and "old" individuals encountered at occasion t in state I; testM.ITEC tests the null hypothesis of no difference in the

probabilities of being re-encountered in the different states at $t + 1$ between individuals in the same state at occasion t whether encountered or not encountered at this date, conditional on presence at both occasions; *testM.LTEC* tests the null hypothesis of no difference in the expected time and state of next encounter between the individuals in the same state at occasion t that were not encountered at occasion $t + 1$ whether encountered or not encountered at occasion t conditional on presence at both occasions t and $t + 2$; *test3G.Sm* gathers what remains of the GOF test after the other components have been isolated. GOF tests were performed with the program U-CARE 2.5 (Choquet et al. 2009b) and were run for males and females separately.

We based inference on information–theoretic model selection, using the AICc (Burnham and Anderson 2002) for model selection. Data analyses were completed in program E-SURGE 1.4.6 (Choquet et al. 2009a). Because multistate models are prone to local minima during the likelihood maximization routine, we ran each model 20 times from different initial values to ensure that they converged to the lowest deviance. Estimates are given ±1 standard error (SE).

The capture–recapture analysis permitted us to estimate the effect of satellite transmitters on the probabilities of survival, breeding, or breeding successfully in the following season. However, we were also interested in the effect of transmitters on breeding success during the current season. We therefore compared the breeding success in year t of individuals equipped or not with satellite transmitters in year t using a generalized mixed linear model using function lme in the lme4 package in R (R Development Core Team 2009). Breeding success of individuals in year t was modeled as year and whether or not individuals were equipped with a satellite transmitter for each sex. Individual identity was included in the model as a random effect.

Results

Goodness of fit

The approximate GOF tests indicated that the multistate models fitted the data for both males ($\chi^2 = 251.9$, $df = 400$, $P = 1.0$) and females ($\chi^2 = 270.6$, $df = 372$, $P = 1.0$). Accounting for reproductive skipping considerably improved the fit of the models since models without unobservable states had a poor fit (males: $\chi^2 = 595.4$, $df = 401$, $P < 0.001$; females: $\chi^2 = 651.8$, $df = 373$, $P < 0.001$).

Survival, breeding, and success probabilities

The detection probabilities were time and state dependent for both male and female albatrosses (Table 2 model M1

Table 2 Modeling detection probabilities and testing for an effect of platform terminal transmitters on the probabilities of adult survival, breeding, and success in the male Wandering Albatross on Possession Island, Crozet between 1986 and 2006

Model	Hypothesis tested	Parameters[a]	ΔAICc	Deviance	Rank[b]
M1	Time- and state-dependent detection	$s_s, \beta_s, \gamma_s, \alpha_{ss}, p_s^t$	4.2	21,716.3	62
M2	Constant and state-dependent detection	$s_s, \beta_s, \gamma_s, \alpha_{ss}, p_s$	82.5	21,871.6	24
M3	Time-dependent detection	$s_s, \beta_s, \gamma_s, \alpha_{ss}, p^t$	115.6	21,868.4	42
M4	Constant detection	$s_s, \beta_s, \gamma_s, \alpha_{ss}, p$	148.2	21,939.3	23
M5	No effect of PTT on success	$s_s, \beta_s, \gamma_{noPTT}, \alpha_{ss}, p_s^t$	0.9	21,717.0	60
M6	No effect of PTT on breeding	$s_s, \beta_{noPTT}, \gamma_s, \alpha_{ss}, p_s^t$	4.7	21,720.9	60
M7	No effect of PTT on survival	$s_{noPTT}, \beta_s, \gamma_s, \alpha_{ss}, p_s^t$	2.3	21,718.5	60
M8	No effect of PTT on success and survival	$s_{noPTT}, \beta_s, \gamma_{noPTT}, \alpha_{ss}, p_s^t$	2.8	21,723.1	58
M9	No effect of PTT on breeding and survival	$s_{noPTT}, \beta_{noPTT}, \gamma_s, \alpha_{ss}, p_s^t$	2.1	21,722.3	58
M10	No effect of PTT on success and breeding	$s_s, \beta_{noPTT}, \gamma_{noPTT}, \alpha_{ss}, p_s^t$	2.8	21,723.1	58
M11	No effect of PTT on success, breeding, and survival	$s_{noPTT}, \beta_{noPTT}, \gamma_{noPTT}, \alpha_{ss}, p_s^t$	0	21,724.3	56

AIC, Akaike information criterion; PTT, platform terminal transmitter

[a] Parameters indicate the form of the parameters, for example, *noPTT* indicates that $\theta_{FB} = \theta_{FBp}$ and $\theta_{SB} = \theta_{SBp}$ with $\theta = (s, \beta, \gamma)$. See Capture–recapture analysis section in text

[b] Rank indicates the number of estimated parameters

Table 3 Modeling detection probabilities and testing for an effect of PTTs on the probabilities of adult survival, breeding, and success in the female Wandering Albatross on Possession Island, Crozet between 1986 and 2006

| Model	Hypothesis tested	Parameters	ΔAICc	Deviance	Rank
M1	Time-and state-dependent detection	$s_s, \beta_s, \gamma_s, \alpha_s, p_s^t$	9.4	20,203.9	61
M2	Constant and state-dependent detection	$s_s, \beta_s, \gamma_s, \alpha_s, p_s$	105.0	20,376.6	23
M3	Time-dependent detection	$s_s, \beta_s, \gamma_s, \alpha_s, p^t$	99.0	20,334.2	41
M4	Constant detection	$s_s, \beta_s, \gamma_s, \alpha_s, p$	130.6	20,404.3	22
M5	No effect of PTT on success	$s_s, \beta_s, \gamma_{noPTT}, \alpha_s, p_s^t$	8.0	20,208.7	58
M6	No effect of PTT on breeding	$s_s, \beta_{noPTT}, \gamma_s, \alpha_s, p_s^t$	5.9	20,204.6	59
M7	No effect of PTT on survival	$s_{noPTT}, \beta_s, \gamma_s, \alpha_s, p_s^t$	8.2	20,204.0	61
M8	No effect of PTT on success and survival	$s_{noPTT}, \beta_s, \gamma_{noPTT}, \alpha_s, p_s^t$	8.3	20,207.0	59
M9	No effect of PTT on breeding and survival	$s_{noPTT}, \beta_{noPTT}, \gamma_s, \alpha_s, p_s^t$	1.9	20,204.6	57
M10	No effect of PTT on success and breeding	$s_s, \beta_{noPTT}, \gamma_{noPTT}, \alpha_s, p_s^t$	4.1	20,208.8	56
M11	No effect of PTT on success, breeding, and survival	$s_{noPTT}, \beta_{noPTT}, \gamma_{noPTT}, \alpha_s, p_s^t$	0	20,208.9	54

All parameters as in Table 1
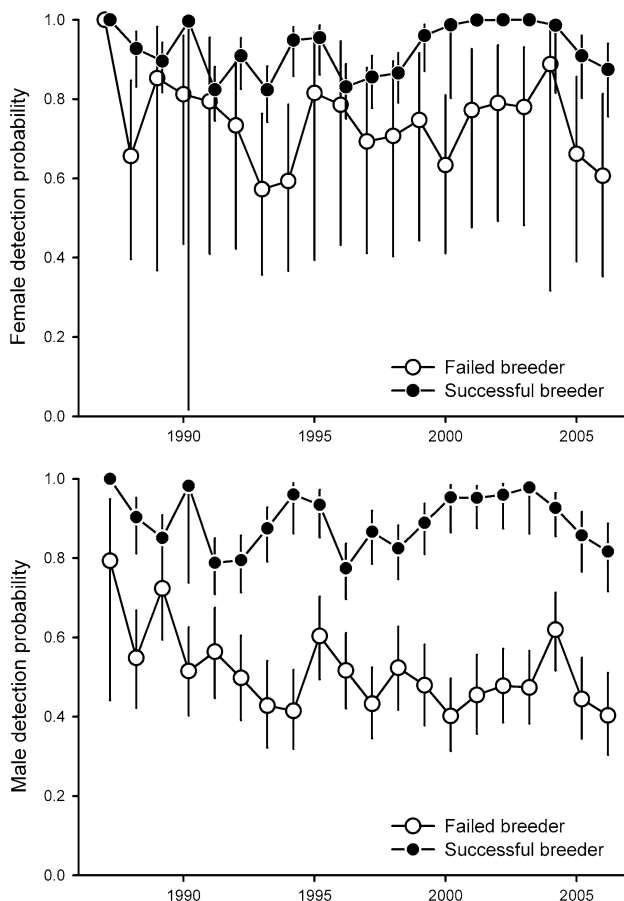
Fig. 1 Detection probabilities for female and male Wandering Albatrosses breeding on Possession Island, Crozet, 1986–2006. Estimates (from model M11) are means. *Errors bars* 95% confidence intervals

vs. models M2, M3 and M4; Table 3 model M1 vs. models M2, M3 and M4, respectively). Detection probabilities are shown in Fig. 1 and indicate that failed breeders had lower detection probabilities than successful breeders; this was particularly evident for males.

For both male and female birds, models in which the probabilities of survival, breeding, and success did not differ between individuals with and without a PTT were preferred to those models where vital rates differed between individuals with and without a PTT (Tables 2, 3: model M11 vs. models M5–M10).

Estimates of survival, breeding, and success probabilities for males and females are shown in Tables 4 and 5, respectively. Survival estimates can be seen to be remarkably close, except for males that failed in their previous breeding attempt for which those equipped with a PTT tended to have a lower survival probability than those not equipped with a PTT, although the difference was not significant ($\chi^2 = 0.98$, $df = 1$, $P = 0.32$; program; contrast, Hines and Sauer 1989).

Annual breeding and success probabilities for individuals equipped with a PTT were not lower than for those not equipped with a PTT (Tables 4, 5). Although females that failed in their previous breeding attempt and were equipped with a PTT tended to have a lower success probability than those not equipped with a PTT, the difference was not significant ($\chi^2 = 1.42$, $df = 1$, $P = 0.23$). The average probability that a PTT was deployed on a male or female 0.011 (0.001) and 0.012 (0.001), respectively.

There was no effect of transmitters on breeding success of the current year for both males and females (Table 5).

Discussion

Coherent with the earlier finding that PTT deployment has no effect on foraging trip duration of the Wandering Albatross (Weimerskirch et al. 1992), we found no negative effect of PTTs on breeding success during the year of

Table 4 Probabilities of adult survival, breeding, and success for male and female Wandering Albatrosses according to their breeding status the previous year on Possession Island, Crozet, 1986–2006

Parameter	Failed, no PTT	Failed with PTT	Success, no PTT	Success with PTT
Males				
Survival probability	0.893 (0.013)	0.786 (0.105)	0.924 (0.071)	0.928 (0.086)
Breeding probability	0.868 (0.022)	0.999 (0.001)	0.047 (0.005)	0.000 (0.000)
Success probability	0.629 (0.020)	0.689 (0.126)	0.510 (0.042)	0.949 (0.000)
Females				
Survival probability	0.900 (0.009)	0.904 (0.093)	0.990 (0.034)	0.995 (0.039)
Breeding probability	0.877 (0.074)	0.931 (0.192)	0.055 (0.009)	0.062 (0.035)
Success probability	0.607 (0.055)	0.403 (0.162)	0.346 (0.067)	0.592 (0.299)

Estimates are means $\pm$ SE

Table 5 Testing for the effect of the satellite transmitter on breeding success in the current year for male and female Wandering Albatrosses on Possession Island, Crozet, 1986–2006

Effect	t	df	P	Estimate[a]	Standard error
Males					
Transmitter	1.291	3,689	0.197	0.813 (+)	0.016
				0.752 (−)	0.003
Individual				0.123	
Residual				0.416	
Females					
Transmitter	0.962	3,934	0.336	0.800 (+)	0.018
				0.751 (−)	0.003
Individual				0.129	
Residual				0.415	

Variance components are shown for random effects

[a] (+) and (−) indicate estimates for individuals equipped or not with transmitters, respectively

PTT deployment and the year immediately following deployment. Similar results have been reported in several other seabird studies (Phillips et al. 2003). As predicted, negative effects of PTT deployment were also not detected on the survival or the breeding probabilities of male and female Wandering Albatrosses the season after they were equipped with a PTT. To the best of our knowledge, this study is the first to evaluate the effect of PTT deployment on the probabilities of breeding and adult survival. Several other studies have examined the effect of PTT deployment on return rates (Green et al. 2004; Hamel et al. 2004; Paredes et al. 2005; Robert et al. 2006). However, return rates are the product of three probabilities, namely, the probability to survive, to breed at the colony conditional on survival, and to be detected conditional on breeding and survival, respectively. Therefore, any variation in the return rates may reflect a variation in any one or more of these three probabilities; it may also only reflect a variation in detection probability. In the Wandering Albatross, the detection probability estimates shown in Fig. 1 indicate relatively important between-year variations that are

associated with previous breeding status and sex, suggesting that evaluating the effects of devices using only return rates would likely be biased. CMR methods, such as the one used here, explicitly take into account detection probabilities and enable survival, breeding, and success probabilities to be estimated, which in turn enables the effect of PTT deployment on these probabilities to be estimated. Similarly, McMahon et al. (2008), using a CMR approach, found no evidence that tracking devices deployed on the Elephant Seal (*Mirounga leonina*) had any effect on survival.

Taken together, our results provide evidence that PTTs attached with tape or with harnesses (although this concerns only a few individuals) to an adult Wandering Albatross do not compromise fitness. This is an important result for this species and likely applicable to studies focusing on species of a similar size. All *Diomedea* species of albatrosses have a critical conservation status (IUCN 2009), with some being critically endangered with only a few tens of individuals. Consequently, an understanding of their at-sea distribution and foraging ecology is of primary

importance for developing conservation strategies. Within this context, it is essential to establish that there are no negative effects due to the presence of tracking devices. However, similar studies should be carried out on smaller species, for which the ratio of the mass of the device to the mass of the individual is less favorable, and where negative short-term (Phillips et al. 2003) and long-term effects are more likely.

In some studies, a satellite transmitter is attached to an individual and never removed. In contrast, in our study, the satellite transmitter was only attached to the bird for a short time. Therefore, one can not exclude the possibility of negative fitness consequences were a satellite transmitter to be attached to the bird for a much longer time. This possibility could be tested using an approach similar to the one used here.

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