

Dispersal and survival rates of adult and juvenile Red-tailed tropicbirds (*Phaethon rubricauda*) exposed to potential contaminants

E. A. Schreiber, P. F. Doherty Jr. & G. A. Schenk

Schreiber, E. A., Doherty, P. F. Jr. & Schenk, G. A., 2004. Dispersal and survival rates of adult and juvenile Red-tailed tropicbirds (*Phaethon rubricauda*) exposed to potential contaminants. *Animal Biodiversity and Conservation*, 27.1:

Abstract

Dispersal and survival rates of adult and juvenile Red-tailed tropicbirds (Phaethon rubricauda) exposed to potential contaminants.— Annual survival and dispersal rates of adult and juvenile red-tailed tropicbirds were examined in connection with exposure to heavy metals. From 1990–2000 the incineration of a U.S. stockpile of chemical weapons stored at Johnston Atoll exposed nesting tropicbirds to increased levels of human disturbance, smoke stack emissions and potential leaks. Using a multi-state mark-recapture modeling approach, birds nesting in this site (downwind of the plant) were compared to those nesting in a reference site (upwind of the plant) with less human disturbance, no exposure to smoke stack emissions or other potential incineration emissions. We did not find any difference in survival of adults or juveniles when comparing the two sites. Adult breeding dispersal rates did not differ between the sites but we did find differences in the age-specific natal dispersal rates. Birds fledged from downwind areas were less likely to return to their natal area to nest and more likely to immigrate to the upwind area than vice-versa. This asymmetry in emigration rates is believed to be due to differing vegetation densities and has implications for vegetation management in relation to tropicbird nest success and population size.

Key words: *Phaethon rubricauda*, JACADS, Johnston Atoll, Age-specific breeding and dispersal, Survival, Chemical munitions.

Resumen

Tasas de dispersión y supervivencia de adultos y juveniles del ave del trópico de cola roja (Phaethon rubricauda) expuestas a contaminantes potenciales.— Se examinaron las tasas de dispersión y de supervivencia anual de adultos y jóvenes de las aves del trópico de cola roja en relación a la exposición a metales pesados. Entre los años 1990 y 2000, la incineración de un arsenal de armas químicas del ejército de Estados Unidos almacenadas en Johnston Atoll expuso a las aves del trópico que anidaban en la zona a niveles más elevados de perturbaciones antrópicas/contaminación humana), emisiones procedentes de chimeneas y fugas potenciales. Se empleó un enfoque de modelación de marcaje-recaptura de fases múltiples para comparar las aves que anidaban en este emplazamiento (la planta quedaba situada a favor del viento) con las que anidaban en un emplazamiento de referencia (en cuyo caso la planta quedaba situada en contra del viento), caracterizado por menos perturbaciones antrópicas y ninguna exposición a emisiones procedentes de chimeneas ni a ningún otro tipo de emisiones potenciales de incineración. Al comparar ambos emplazamientos, no se halló ninguna diferencia en cuanto a la supervivencia de las aves adultas o jóvenes. Las tasas de dispersión reproductiva de los adultos no difirieron entre los emplazamientos; en cambio, sí que se observaron diferencias en las tasas de dispersión natal por edades. Las aves jóvenes que abandonaron las áreas situadas a favor del viento era menos probable que regresaran a su área natal para anidar y más probable que inmigraran al área situada en contra del viento. Se considera que esta asimetría en las tasas de emigración obedece a las diferentes densidades de vegetación, repercutiendo en la gestión de la vegetación con respecto al éxito de los nidos de las aves del trópico y el tamaño poblacional.

Palabras clave: *Phaethon rubricauda*, JACADS, Johnston Atoll, Dispersión y reproducción por edades, Supervivencia, Munición química.

E. A. Schreiber, National Museum of Natural History, Smithsonian Institution, E607 MRC 116, Washington D.C. 20560, U.S.A.– P. F. Doherty, Jr., Dept. of Fishery and Wildlife Biology, Colorado State Univ., Fort Collins, CO 80523–1474, U.S.A.– G. A. Schenk, 4109 Komes Court, Alexandria, VA 22306, U.S.A.

Corresponding author: P. F. Doherty, Jr. E-mail: Doherty@cnr.colostate.edu

Introduction

The Johnston Atoll Chemical Agent Disposal system (JACADS) is located on Johnston Atoll and was the first operational facility in which parts of the U.S. stockpile of chemical weapons were destroyed (Schreiber et al., 2001; U.S. Army, 1994). Seven states in the mainland United States also have stockpiles of chemical weapons that are slated to be incinerated and the lessons learned at the Johnston Atoll site are important for judging the safety of incinerating these chemical weapons. Johnston Atoll is also a U.S. Fish and Wildlife National Wildlife Refuge and a breeding location for approximately a half-million seabirds of 13 species. Further details on the incineration process and the site can be found in Schreiber et al. (2001) and Schreiber (2002). Our previous work (Schreiber et al., 2001) examined survival and movement rates of adult Red-tailed tropicbirds (*Phaethon rubricauda*) during eight years of the burning of chemical munitions and found no effect on the tropicbirds. This study follows the adults through an additional four years, including three years post-burning, and additionally analyzes juvenile survival and natal dispersal rates.

At the time of our previous analysis we did not have enough years of data to estimate juvenile survival due to the fact that tropicbirds have delayed breeding (young birds stay at sea approximately for up to six years before returning to breed; Schreiber & Schreiber, 1993). This delayed breeding and the fact that tropicbirds first return to breed at varying ages (age-specific first breeding probabilities) further complicates the estimation of juvenile survival (Clobert et al., 1994; Pradel & Lebreton, 1999; Schwarz & Arnason, 2000; Spendelov et al., 2002; Williams et al., 2002; Lebreton et al., 2003). Juvenile survival and age-

specific breeding probabilities are of particular interest on Johnston Atoll because of the potential for negative effects on these metrics from the JACADS operation. For instance, inhalation of heavy metals emissions from the smoke-stack of the JACADS plant could affect juvenile survival (see table 7 in Schreiber et al., 2001, for list of these emissions).

With the additional data collected in the past four years, we now have 12 years of data. The recent developments in model structures to estimate juvenile and adult survival, as well as breeding and age-specific natal dispersal probabilities while taking detection probabilities into account, allow us to test the predictions that these population dynamic parameters are negatively affected in the area adjoining the JACADS plant when compared to a reference area.

Materials and methods

Study area, study species, and data collection

Details on the study area, study species and data collection were presented elsewhere (Schreiber, 2002; Schreiber & Schreiber, 1993; Schreiber et al., 2001). In brief, Johnston Atoll (fig. 1) is located in the central Pacific approximately 1150 km southeast of Hawaii and is home to the Johnston Atoll National Wildlife Refuge and JACADS. The JACADS plant incinerated chemical weapons from 1990 through 2000. Johnston Atoll is in the easterly trade wind belt and winds are from the east, except during El Niño–Southern Oscillation (ENSO) events and on a few still days during the year. The incinerator was situated on the downwind side of Johnston Island (fig. 1). Birds nesting in the smokestack outfall plume (fig. 1) were consid-

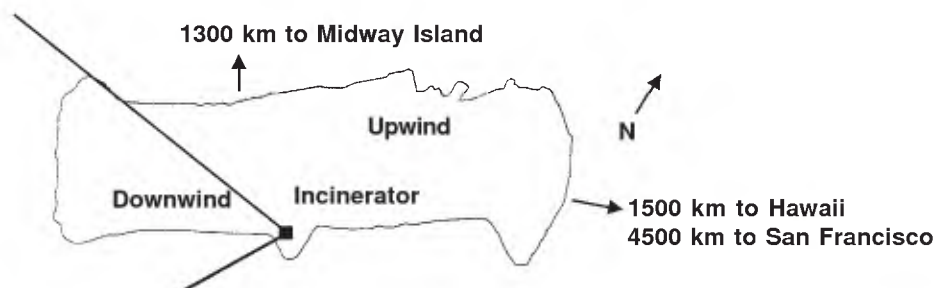


Fig. 1. Johnston Island with the location of the incinerator, downwind and upwind breeding areas designated.

Fig. 1. Isla Johnston, con la situación del incinerador y las áreas de reproducción designadas a favor del viento y en contra del viento.

ered to be in the "downwind" area, where there was potential for contamination from the smoke-stack emissions (see table 7 in Schreiber et al., 2001) or from chemical spills and leaks (material to be incinerated was stored in the downwind area). The 3 smokestacks were each 30.48 meters high. Emissions fell on land around the stacks and out towards the wind direction. In days of particularly high winds, there may have been times when no emissions fell on the land, but high winds were rare. The great majority of the time winds on the atoll blow between 18.5–30 km/h, when outfall from the stacks was determined to fall on land where birds were nesting (Anonymous, 1996). Birds nesting outside this plume were considered to be in "upwind" areas with no potential for contamination from the incineration process. No incineration was carried out during days of westerly winds. Tropicbirds invariably lay one egg (Schreiber, 1999). Tropicbirds are strongly nest-site philopatric, nesting in the same spot each year once they have successfully nested (Schreiber, 1999; Schreiber et al., 2001). Tropicbirds exhibit deferred maturity, with most birds returning to their natal colony to breed between ages two and six years of age (Schreiber & Schreiber, 1993). A few birds are caught for the first time at 7–12 years of age, but since only 40–50% of the breeding adults are recaptured each year, these birds could have bred earlier and not been caught. In previous analyses (Doherty et al., 2004) age-specific breeding probability could be reliably estimated up to age five. After this time, so few birds had not returned that estimating a first-time breeding probability for age 6+ could not be done. Thus, we feel comfortable with assuming in our modeling that any bird that has not bred by age six will attempt to do so in later years with probability equal to one. If adult breeders do not breed with probability equal to one, then age-specific first-time breeding probabilities are in relation to what this probability is.

In each year most adult birds were generally caught by hand during a February or March field visit. A second field visit was made during sometime during the period from May–July to band chicks, as well as additional adults not caught on the first visit. Bands showing wear were replaced each year and band loss is assumed to be negligible. Movement of adult birds between breeding seasons (breeding dispersal), both between islands and within islands (Schreiber et al., 2002) is at very low rates and generally owing to loss of the nest site or mate. However, natal dispersal rates were not previously known. Our analysis used only data from birds nesting on Johnston Island since 1992. Whereas in our previous analysis we were only able to analyze demographic parameters associated with adult birds, in this current analysis (with four more years of data) we are also able to analyze pre-breeding survival and age-specific natal dispersal rates.

Statistical analysis

We used a multi-state capture–mark–recapture approach (Arnason, 1972; 1973; Nichols & Kendall, 1995; Nichols, 1996; Williams et al., 2002; Lebreton et al., 2003) as available in program MARK (White & Burnham, 1999). In Schreiber et al. (2002) we used this approach to estimate recapture probabilities (probability that a bird is caught and band read in any one year, given that it is available for capture), adult survival probabilities and breeding dispersal probabilities between upwind and downwind areas of Johnston Island.

Modeling age-specific breeding probabilities (or the transition from pre-breeding to breeding status) in a seabird (Roseate tern; *Sterna dougallii*) has recently received attention (Spendelov et al., 2002; Lebreton et al., 2003) and the modeling of transition (movement) rates between spatially different areas or transition rates between status (i.e. non-breeding and breeding) can be done in an analytically similar way using a multi-state model. The combining of recruitment and dispersal over several sites can also be accomplished using a multi-state model as has recently been outlined by Lebreton et al. (2003). We used this latter approach.

For our data, we considered a bird to be in one of four states; downwind pre-breeding, upwind pre-breeding, downwind breeding, or upwind breeding. A limited number of possible transitions exist from one survey period (or breeding season) to the next. For instance, a pre-breeder can become breeder or stay a pre-breeder. We assume that a breeder cannot become a pre-breeder, a fledged bird can first breed at the upwind or downwind site and that once a bird has attempted to breed, it will always attempt to breed in subsequent years (but may change sites). All birds that are going to breed are assumed to attempt to do so by age six.

Other general assumptions required by this model are similar to those required by Cormack–Jolly–Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965); (1) recapture and transition probabilities are the same for all marked birds found in a particular state and sampling period; (2) birds behave independently with respect to survival, recapture and transition probabilities; (3) bands are not lost; (4) all samples are instantaneous; and (5) state transition probabilities reflect a first order Markov process in the sense that the state of an animal at time $t + 1$ is stochastically determined as a function of its state at time t only. (Williams et al., 2002). We believe that our study and the study species are an ideal candidate for this type of modeling because we meet these assumptions well.

Red-tailed tropicbirds do not flock and are thought to behave independently except during the breeding season. We restricted our sampling to the breeding season, while not instantaneous, it is a period in which high mortality is unlikely to

occur (i.e. a dead adult is rarely found). We performed a goodness of fit test on our most general model and, to help correct for any over dispersion in our data, we also estimated an over dispersion factor (\hat{c}) to adjust estimates and other statistics (Burnham & Anderson 2002). Our goodness of fit test and \hat{c} were based on a Pearson χ^2 goodness-of-fit test.

Model set

We constructed models including adult survival (ϕ^A), juvenile survival (defined as survival from fledging until age one; ϕ^J), recapture probability (p), and adult movement (or breeding dispersal) probabilities ($\psi^{breeder}$). Each of these parameters was modeled as a function of time (t) and site (upwind or downwind of the JACADS site). The age-specific natal dispersal probabilities (age = 1 to 5; ψ^{age}) were modeled as a function of site only due to the data requirements associated with temporal estimates. Due to the tropicbirds propensity to stay out at sea for up to six years after fledging, with our 12 years of data we were only able to estimate juvenile survival rates meaningfully for the first five years of our data set. Since, in this case, some individuals do attempt to breed at age one, our juvenile survival rates (or pre-breeding rates) are for the time from banding to the next breeding season. All birds are assumed to survive at the same rate after this first year. By definition, there is no recapture rate for juveniles (when a bird is recaptured for the first time it is a breeding adult). Thus our most general model was designated as $\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site^t}^{age} \psi_{site^t}^{breeder}$. Our predictions of interest focused on the effects of site. We thus constructed a set of reduced models in which the effect of site was removed for each parameter independently, as well as for both of the survival rates together. These models were designated as $\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site^t}^{age} \psi_{site^t}^{breeder}$ for adult survival being constant over site, $\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site^t}^{age} \psi_{site^t}^{breeder}$ for juvenile survival being constant over site, $\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site^t}^{age} \psi_{site^t}^{breeder}$ for both adult and juvenile survival being constant over site, $\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site^t}^{age} \psi_{site^t}^{breeder}$ for recapture probabilities to be constant over site, $\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site^t}^{age} \psi_{site^t}^{breeder}$ for age-specific natal dispersal probabilities being constant over site, and $\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site^t}^{age} \psi_{site^t}^{breeder}$ for breeding dispersal rates being constant over site. We also, *a posteriori*, constructed a model with an additive effect of site for all parameters ($\phi_{site^t+site}^A \phi_{site^t+site}^J p_{site^t+site} \psi_{site^t+site}^{age} \psi_{site^t+site}^{breeder}$) and report the associate beta estimates from this model.

We used Akaike's Information Criteria (AIC; Burnham & Anderson, 2002) to compare the fit of these models. We specifically used the small sample approximation and \hat{c} adjusted form of AIC denoted as $QAIC_c$ (Burnham & Anderson, 2002) and considered models with $QAIC_c$ values differing by less than 2 to be equally suitable models. We also calculated AIC weights for each model to help us interpret the relative strengths of each model

(Burnham & Anderson, 2002). This also allowed us to calculate model-averaged estimates. A model-averaged estimate is essentially a weighted average over a set of models based on each individual model's weight. This allows inference to the entire model set. Such a model-averaging approach is preferable to relying on parameter estimates from a single model (Burnham & Anderson, 2002). All results present in the figures are model-averaged estimates with their associated 95% confidence intervals unless otherwise noted.

Results

We followed 31,527 birds banded as juveniles and adults over 12 years of data collection (1992–2003). Our goodness of fit test failed ($P < 0.01$), which indicated that our data were over dispersed. To help correct for this over dispersion we incorporated a $\hat{c} = 2.55$. This was more conservative than the correction we used in our previous analysis ($\hat{c} = 1.6$; Schreiber et al., 2002).

Overall the model that ranked highest by $QAIC_c$ coded for temporal variation in adult survival, juvenile survival, probability of recapture and breeding dispersal rates and variation across sites for detection probability and both age-specific natal dispersal as well as breeding rates (table 1). None of the other models described the data well with $QAIC_c > 19$. Below we examine the parameter estimates associated with recapture, adult and juvenile survival, as well as age-specific natal dispersal and breeding dispersal rates.

Recapture probability

The probability of recapture differed between the upwind and downwind sites through time and ranged from 0.32 to 0.59 in the upwind area and from 0.39 to 0.63 in the downwind area. Generally the downwind site ($\bar{x} = 0.48$, $SE = 0.09$) had a higher probability of recapture than the upwind site ($\bar{x} = 0.38$, $SE = 0.08$; fig. 2). The beta estimate from a model with site as an additive effect was 0.50 with a 95% confidence interval of [0.41, 0.60] also indicating an effect of site.

Adult survival rate

The most supported model indicated only temporal variation in adult survival with little variation associated with site (downwind $\bar{x} = 0.86$, $SE = 0.04$; upwind $\bar{x} = 0.86$, $SE = 0.04$; fig 3). We found no consistent effect of site for adult survival with the beta estimate being 0.02 with a 95% confidence interval of [−0.06, 0.11].

Juvenile survival rate

Since juvenile tropicbirds can take six years (and in a few cases longer) to return to the island to breed, we do not present estimates of juvenile survival for

Table 1. The relative likelihood, number of parameters, and AIC rankings of each model. We used the small sample approximation and adjusted AIC using \hat{c} as denoted by the $QAIC_c$ term. $\Delta QAIC_c$ is the relative difference of each model from the best fit model (lowest $QAIC_c$). The $\Delta QAIC_c$ weight is the relative weight of evidence for each model. Adult survival (ϕ^A), juvenile survival (defined as survival from banding until age 1; ϕ^J), recapture probability (p), age-specific natal dispersal probabilities (age = 1 to 5; ψ^{age}), and breeding dispersal rates ($\psi^{breeder}$) were modeled as functions of time (t) and site (upwind or downwind of the JACADS plant).

Tabla 1. Probabilidad relativa, número de parámetros y clasificaciones de cada modelo según el criterio de Información de Akaike (AIC). Utilizamos la aproximación de muestras pequeñas y ajustamos el AIC utilizando \hat{c} según lo indicado por el término $QAIC_c$. $\Delta QAIC_c$ es la diferencia relativa de cada modelo con respecto al modelo mejor ajustado ($QAIC_c$ más bajo). El peso de $\Delta QAIC_c$ es el peso relativo de la evidencia para cada modelo. La supervivencia adulta (ϕ^A), la supervivencia juvenil (definida como la supervivencia desde el anillamiento hasta alcanzar 1 año de edad; ϕ^J), la probabilidad de recaptura (p), las probabilidades de dispersión natal por edades (edad = de 1 a 5; ψ^{age}), y las tasas de dispersión reproductora ($\psi^{breeder}$) se modelaron como funciones del tiempo (t) y del emplazamiento (en contra del viento o a favor del viento con respecto a la planta JACADS).

Model	$QAIC_c$	$\Delta QAIC_c$	$\Delta QAIC_c$ weight	Number of parameters
$\phi_t^A \phi_t^J p_{site^t} \psi_{site}^{age} \psi_{site^t}^{breeder}$	43397.49	0.00	1.00	85
$\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site}^{age} \psi_{site^t}^{breeder}$	43417.13	19.64	0.00	96
$\phi_{site^t}^A \phi_t^J p_{site^t} \psi_{site}^{age} \psi_{site^t}^{breeder}$	43417.48	19.99	0.00	97
$\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site}^{age} \psi_{site^t}^{breeder}$	43433.45	35.96	0.00	107
$\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site}^{age} \psi_t^{breeder}$	43447.74	50.26	0.00	96
$\phi_{site^t}^A \phi_{site^t}^J p_t \psi_{site}^{age} \psi_{site^t}^{breeder}$	43574.46	176.97	0.00	96
$\phi_{site^t}^A \phi_{site^t}^J p_{site^t} \psi_{site}^{age} \psi_{site^t}^{breeder}$	43816.14	418.66	0.00	97
$\phi_{site^t+site} \rho_{site+1} \psi_{+site}^{age} \psi_{site+t}^{breeder}$	43848.34	450.85	0.00	52

the last 5 years (many birds from those cohorts would not have returned to breed yet). Over the first five years we did not find any differences in juvenile survival rate for tropicbirds upwind ($\bar{x} = 0.77$, $SE = 0.09$) as compared to downwind ($\bar{x} = 0.77$, $SE = 0.09$) of the JACADS (fig 4). However, there was variation associated with time with juvenile survival rates being lower in 1994 and 1995 and higher in the other years. The 1994–1995 time period was at the end of an extended El Niño period. The beta estimate associated with site was 0.02 with a 95% confidence interval of [−0.06, 0.11].

Breeding dispersal rates

Although there was much variation associated with the breeding dispersal rate estimates, overall the breeding dispersal rates were low; $\bar{x} = 0.012$, $SE = 0.008$ for birds dispersing upwind to downwind and $\bar{x} = 0.022$; $SE = 0.018$ for birds dispersing downwind to upwind (fig. 5).

Age-specific first-time breeding probabilities and natal dispersal

We found differences in the philopatry and emigration rates of tropicbirds that fledged upwind and downwind of the JACADS plant. For all ages at which birds recruited to breeding status, birds that fledged from upwind sites showed greater philopatry and were less likely to first breed elsewhere than were birds that fledged downwind (fig. 6). For both sites the rate at which birds recruited into the breeding population increased with age (fig. 6).

Discussion

As previously discussed (Schreiber et al., 2002), the main concerns for survival of birds nesting downwind of the JACADS plant were inhalation of heavy metals from the smoke stack and direct

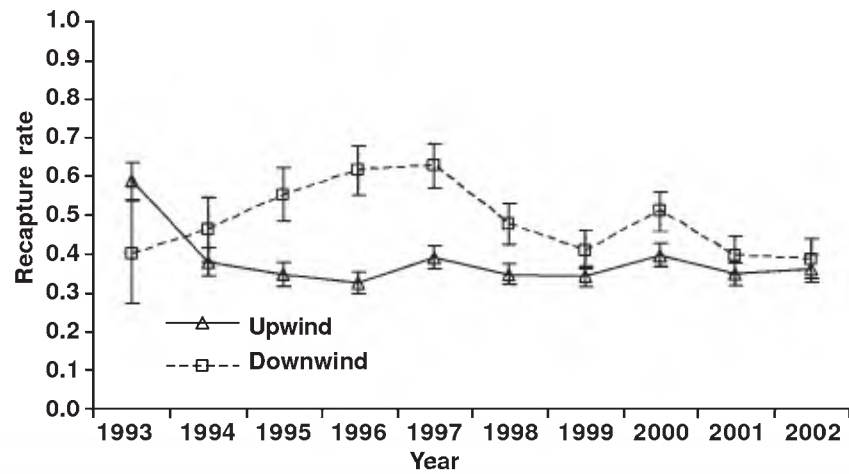


Fig. 2. Probability of recapture for birds at upwind (squares and solid line) and downwind (triangles and dotted line) sites of the JACADS plant from 1993 to 2002. Model-averaged means and 95% confidence intervals are shown.

Fig. 2. Probabilidad de recaptura de las aves en áreas situadas en contra del viento (cuadrados y línea continua) y a favor del viento (triángulos y línea discontinua) con respecto a la planta JACADS, desde 1993 hasta 2002. Se indican los promedios de las medias de los modelos y los intervalos de confianza del 95%.

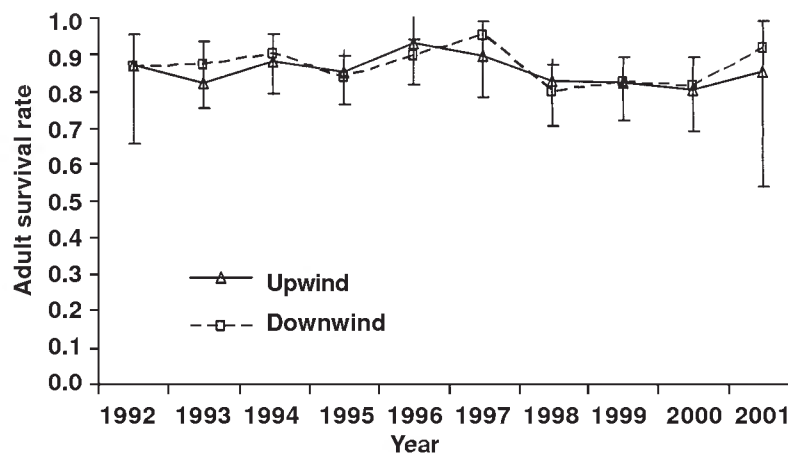


Fig. 3. Adult survival rates for birds upwind (triangle and solid line) and downwind (squares and dotted line) of the JACADS plant from 1992 to 2001 (Year t to $t+1$). Results are estimates and 95% confidence intervals from model $\varphi_{site^t}^A \cdot \varphi_t^J \cdot \rho_{site^t} \cdot \psi_{site}^{age} \cdot \psi_{site^t}^{breeder}$.

Fig. 3. Tasas de supervivencia de las aves adultas en áreas situadas en contra del viento (triángulos y línea continua) y a favor del viento (cuadrados y línea discontinua) con respecto a la planta JACADS, desde 1992 hasta 2001 (del año t al $t+1$). Los resultados son estimaciones e intervalos de confianza del 95% del modelo $\varphi_{site^t}^A \cdot \varphi_t^J \cdot \rho_{site^t} \cdot \psi_{site}^{age} \cdot \psi_{site^t}^{breeder}$.

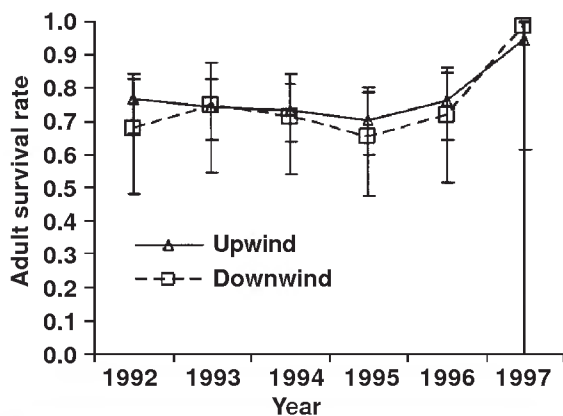


Fig. 4. Juvenile survival rate for birds upwind (triangle and solid line) and downwind (square and dotted line) of the JACADS plant from 1992 to 1997 (year t to $t+1$). Results are estimates and 95% confidence intervals from model $\varphi_t^A \varphi_{site^t}^J \rho_{site^t} \psi_{site}^{age} \psi_{site^t}^{breeder}$.

Fig. 4. Tasas de supervivencia de las aves jóvenes en áreas situadas en contra del viento (triángulos y línea continua) y a favor del viento (cuadrados y línea discontinua) con respecto a la planta JACADS, desde 1992 hasta 1997 (del año t al $t+1$). Los resultados son estimaciones e intervalos de confianza del 95% del modelo $\varphi_t^A \varphi_{site^t}^J \rho_{site^t} \psi_{site}^{age} \psi_{site^t}^{breeder}$.

mortality from leaks of chemical agents. Ingestion of heavy metals from soil was not considered to be a problem since tropicbirds do not feed on land and do not tend to pick objects with their bill while on land (Schreiber & Schreiber, 1993). In our previous work (Schreiber et al., 2002), we did not find any evidence of negative effects of the JACADS plant on tropicbird fledging success or adult survival. Nor did we find any evidence that adult tropicbirds were moving out of the downwind area as if avoiding nesting there for some reason. We did find a higher recapture probability downwind as compared to upwind, and this was attributed to greater effort made to monitor birds in the downwind area. Our current analysis supports these past results concerning adult survival, recapture and dispersal rates (figs. 2, 3, 5). The lack of any difference between the two areas now, two years after burning of munitions has ceased, may indicate that there was no build-up of heavy metals in the birds.

We could not estimate a juvenile survival rate or associated age-specific natal dispersal rates in our previous analysis (Schreiber et al., 2001). This was due to the fact that the time series of data

was not long enough, as well as the fact that models that allowed these parameters to be estimated were still under development (Clobert et al., 1994; Pradel & Lebreton, 1999; Schwarz & Arnason, 2000; Spendelov et al., 2002; Williams et al., 2002; Lebreton et al., 2003).

We did not find any effects associated with the JACADS plant on juvenile survival (fig. 4). We also did not find any negative effects associated with JACADS on age-specific breeding probabilities: birds in both areas returned to breed at similar ages. However we did find an effect that birds fledging downwind were more likely to first return to breed upwind than were birds fledged upwind to first breed downwind (lower natal philopatry rates downwind than upwind; fig. 6).

This result was unexpected given that we have no differences in adult movement rates. Several possibilities must be considered as a reason for this difference. We believe the higher emigration rate from the downwind area is due to the fact that this area has no large patches of growing vegetation to attract new nesters. Most vegetation downwind consists of narrow strips bordering roads, or small patches next to buildings. All of the large courting/nesting areas (also associated with vegetation) occur in the upwind section of Johnston Island. This causes two events that can affect natal philopatry. The larger groups of aerially courting birds that form over large vegetation patches may be particularly attractive to first time breeders, thus attracting more of them to breed upwind, rather than downwind. This idea could be tested through the planting and manipulation of nesting vegetation over a period of years.

Secondly, the downwind area (with all the operations associated with weapons incineration) has a greater density of buildings and roads. Here, human activity and development restrict the amount of habitat available and also restrict growth of new habitat. Since birds return to their historic nesting sites, areas with no new, growing vegetation offer little opportunity for first time nesters to claim a site: most sites are taken. Areas of growing and spreading vegetation, that have not had previous nesters, are the best opportunities for new nesters. Experienced nesters are aggressive about defending their nest site from interlopers, and site owners historically are known to win in battles over nest sites (Schreiber & Schreiber, 1993). Thus, the downwind area presents less opportunity for a new nester, even if attracted to the area, causing a returning downwind first-time breeder to consider other parts of the island.

We believe that an indirect effect of the JACADS plant (vegetation control) has caused a difference in nesting philopatry in the downwind as compared to the upwind area. We predict that once the JACADS plant is dismantled and the area deserted of heavy human activities, the differences in natal philopatry rates between the two areas will disappear as the vegetation grows normally. Possibilities exist to test these ideas in the years subse-

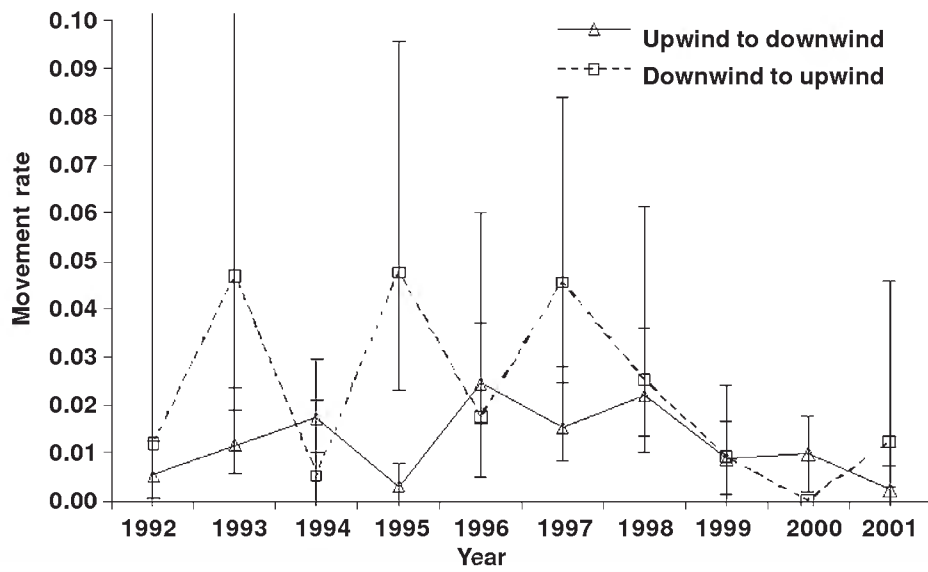


Fig. 5. Adult movement (breeding dispersal) rates of red-tailed tropicbirds nesting upwind and downwind of the JACADS. Model-averaged means and 95% confidence intervals are shown.

Fig. 5. Tasas de movimiento (dispersión reproductiva) de las aves del trópico de cola roja adultas que anidaban en áreas situadas en contra del viento y a favor del viento con respecto a la planta JACADS. Se indican los promedios de las medias de los modelos y los intervalos de confianza del 95%.

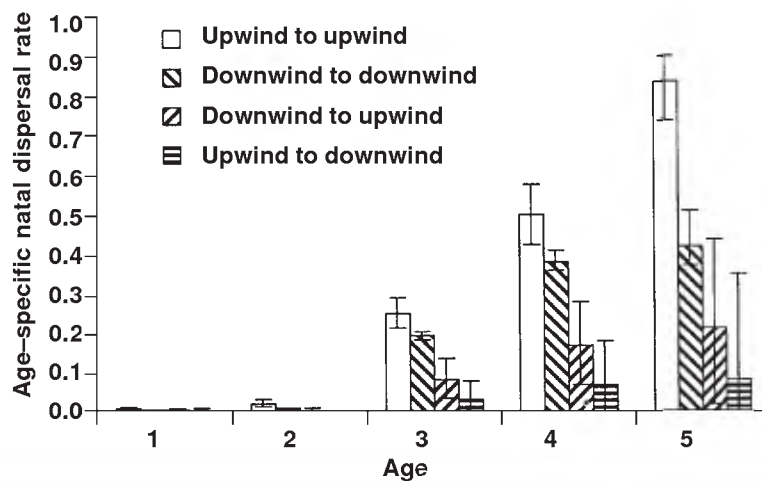


Fig. 6. Age-specific breeding probabilities for tropicbirds of age 1 to 5 for sites upwind (clear bars) and downwind (hatched bars) of the JACADS. Model-averaged means and 95% confidence intervals are shown.

Fig. 6. Probabilidades de reproducción por edades de las aves del trópico, de entre 1 y 5 años de edad, en emplazamientos situados en contra del viento (barras transparentes) y a favor del viento (barras sombreadas) con respecto a la planta JACADS. Se indican los promedios de las medias de los modelos y los intervalos de confianza del 95%.

quent to the dismantling of the incinerator and the abandonment of the atoll by the military.

Another reason for the differences in natal philopatry might be a negative effect associated with emissions from the JACADS plant. We feel this is unlikely due to no effects being detected in the adult movement rates or in any other parameters measured (reproductive success, chicks growth rates, adult mass, adult survival, adult movement rates; see Schreiber, 2002; Schreiber et al., 2001). It is also possible that the degree of human activity downwind caused returning first-breeders to look elsewhere for a nest site. However, there are other areas on Johnston Island that have the same degree of human activity, and where vegetation growth is not restricted, yet the nesting population continues to increase.

Management implications

Over the 10 years of operation of the chemical agent disposal system on Johnston Atoll we could document no effect of the operation on breeding red-tailed tropicbirds in adult survival, juvenile survival (this paper), reproductive success, egg mass, adult mass or chick growth (Schreiber, 2002). Although there was a difference in natal dispersal rates that could be attributed to the plant, we think that this result is most likely tied to differences in vegetation and activity differences downwind of the plant as compared to upwind. If this is so, then this suggests that stack emissions of trace amounts of heavy metals and nesting close to human activities was not harmful to nesting tropicbirds. Since incineration plants will be built in seven mainland states of the United States, our results may have important implications for those sites. Careful monitoring of those sites and the wildlife associated with those sites is warranted. *A priori* consideration of possible confounding factors and incorporating these into the data collection design may help tease apart direct and indirect effects associated with these plants. The results of this study and the interpretation of those results point out the need to understand the ecology of a species when (1) making management decisions to maintain healthy, viable populations, and (2) making permitting decisions on issues that will expose birds to unusual levels of contaminants. Additional experiments associated with management include altering human disturbance and planting of vegetation in a controlled way to further test what makes good courting and nesting habitat.

This analysis also points out the importance of jointly modeling survival, dispersal and capture rates in a way that can account for heterogeneity in such rates. If site heterogeneity in the recapture rates was not modeled correctly, differences in adult survival associated with site may have been erroneously reported due to an overoptimistic assessment of the statistical power

of our modeling exercise. If age-specific breeding and dispersal probabilities were not included in the modeling effort, then juvenile survival may have been thought to be lower, especially in the downwind area, owing to emigration to other nesting sites.

Acknowledgements

We thank the Defense Nuclear Agency, Project Manager for Chemical Demilitarization, G. McClosky, R. Moll, and P. O'Connell for many years of grant and logistical support for our work on Johnston Atoll. The U.S. Fish and Wildlife Service, Dept. of Interior, permitted access to the refuge. We thank B. D. Smith and C. M. Francis for comments on a previous draft of the manuscript. Many people have assisted us over the years in catching and banding the birds (and in all our others studies on the atoll), and we are extremely grateful for their help and the great company while in the field. We are deeply indebted to R. W. Schreiber for having the idea to return here and begin work again in 1984 after having spent part of the Pacific Ocean Biological Survey Project working here.

References

- Anonymous, 1996. *Johnston Atoll Chemical Agent Disposal System, Human Health and Ecological Risk Assessment*. Raytheon Engineers and Constructors, Inc., Philadelphia, PA.
- Arnason, N., 1972. Parameter estimation from mark-recapture experiments on two populations subject to migration and death. *Res. in Pop. Ecol.* 13: 97-113.
- 1973. The estimation of population size, migration rates and survival in a stratified population. *Res. in Pop. Ecol.*, 15: 1-8.
- Burnham, K. P. & Anderson, D. R., 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York, USA.
- Cormack, R. M., 1964. Estimates of survival from the sighting of marked animals. *Biometrika*, 51: 429-438.
- Clobert, J., Lebreton, J.-D., Allaine, D. & Gaillard, J.-M., 1994. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations. II. Longitudinal models. *Biometrics*, 50: 375-387.
- Doherty, P. F., Jr, Schreiber, E. A., Nichols, J. D., Hines, J. E., Link, W. A., Schenk, G. A. & Schreiber, R. W. Testing life history predictions in a long-lived seabird: a population matrix approach with improved parameter estimation. *Oikos*, 105: 606-618.
- Jolly, G. M., 1965. Explicit estimates from capture-recapture data with both death and immigration - stochastic model. *Biometrika*, 52: 225-247.
- Lebreton, J.-D., Hines, J. E., Pradel, R. Nichols, J.

- D. & Spendelow, J. A., 2003. Estimation by capture–recapture of recruitment and dispersal over several sites. *Oikos*, 101: 253–264.
- Nichols, J. D., 1996. Source of variation in migratory movement of animal populations: statistical inference and a selective review of empirical results for birds. In: *Population dynamics in ecological space and time*: 147–197 (O. E. Rhodes, Jr., R. K. Chesser & M. H. Smith, Eds.). University of Chicago Press. Chicago, Illinois, USA.
- Nichols, J. D. & Kendall, W. L., 1995. The use of multi–state capture–recapture models to address questions in evolutionary ecology. *J. of Appl. Stat.*, 22: 835–846.
- Pradel, R. & Lebreton, J. D., 1999. Comparison of different approaches to the study of local recruitment of breeders. *Bird Study*, 46: 74–81.
- Schreiber, E. A., 2002. Breeding biology and ecology of the seabirds of Johnston Atoll, central Pacific Ocean, 1998: long–term monitoring for effect of Johnston Atoll Chemical Demilitarization Project 1984–1998. Report to the Department of Defense, Aberdeen Proving Ground, Maryland, USA.
- Schreiber, E. A., Doherty, Jr., P. F. & Schenk, G. A., 2001. Effects of a chemical weapons incineration plant on red–tailed tropicbirds. *J. Wildl. Manage.*, 65: 685–695.
- Schreiber, E. A. & Schreiber, R. W., 1993. Red–tailed tropicbird (*Phaethon rubricauda*). The birds of North America, number 43. The American Ornithologists’ Union, Washington, D.C., USA, and The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
- Schreiber, R. W. & Schreiber, E. A., 1984. Central Pacific Seabirds and the El–Nino Southern Oscillation – 1982 to 1983 Perspectives. *Science*, 225: 713–716.
- Schwarz, C. J. & Arnason, A. N., 2000. Estimation of age–specific breeding probabilities from capture– recapture data. *Biometrics*, 56: 59–64.
- Seber, G. A. F., 1965. A note on the multiple recapture census. *Biometrika*, 52: 249–259.
- Spendelow, J. A., Nichols, J. D., Hines, J. E., Lebreton, J.–D. & Pradel, R., 2002. Modelling postfledging survival and age–specific breeding probabilities in species with delayed maturity: a case study of roseate terns at Falkner Island, Connecticut. *J. Appl. Stat.*, 29: 385–405.
- U. S. Army, 1994. U.S. Army’s alternative demilitarization technology. Executive Summary Report for Congress, Washington, DC, USA.
- White, G. C. & Burnham, K. P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study 46 suppl.*, 120:138.
- Williams, B. K., Nichols, J. D. & Conroy, M. J., 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego, USA.
-