At-sea distributions and abundance of tropicbirds in the eastern Pacific

LARRY B. SPEAR* & DAVID G. AINLEY

H.T. Harvey and Associates, 3150 Almaden Expressway, Suite 145, San Jose, CA 95118, USA

During spring and autumn 1980–95, we surveyed Red-tailed *Phaethon rubricauda*, White-tailed *P. lepturus* and Red-billed Tropicbirds *P. aethereus* at sea in the Pacific between the coast of the Americas and 176°W. For the Pacific, we had complete coverage of the range of *aethereus*, but only partial coverage of that of *rubricauda* and *lepturus*. Six areas of higher density were indicated: three of *rubricauda*, two of *lepturus* and one of *aethereus*. After pooling data across years, the 'abundance' (total number including subadults and adults) estimate for *rubricauda* was 81 700 (boreal spring) and 86 500 (boreal autumn) birds. Abundance of each of the three *rubricauda* subpopulations differed between seasons by about 50% despite seasonal consistency when populations were grouped. Furthermore, high densities of *rubricauda* occurred at the edge of our study area, indicating that neither of the seasonal estimates for this species could be considered as total numbers. Abundance estimates of *lepturus* during the non-breeding season (when these birds had dispersed from colonies) were 11 000 and 41 500 birds for northern and southern populations, respectively. Estimated abundance of *aethereus* during the boreal spring was 26 700 birds, and 33 400 during the boreal autumn. Because tropicbirds are attracted to survey vessels, we also estimated the abundance after excluding those recorded as flying in a steady direction, or having been attracted to the ship. Considering only stationary birds (i.e. those that could not have been attracted), our minimum estimates were 41 000 *rubricauda*, 15 750 *aethereus*, 28 000 southern *lepturus* and 6400 northern *lepturus*.

Each of the three species of tropicbird (Family: Phaethontidae) occurs over the tropical and subtropical waters of the eastern and central Pacific (ECP). These include the Pacific race of Red-billed Tropicbird *Phaethon aethereus mesonauta*, hereafter '*aethereus*', Pacific race of White-tailed Tropicbird *P. lepturus dorothea*, hereafter '*lepturus*', and the Red-tailed Tropicbird *P. rubricauda*, several races (not distinguished in this study), hereafter '*rubricauda*'.

The at-sea ranges of these species in the ECP have been well described (King 1970, Gould *et al.* 1974, Harrison 1983, Pitman 1986). However, estimates of tropicbird abundance in the ECP have been rough. Gould *et al.* (1974) estimated densities of *rubricauda* for 10° latitudinal bands for all months of the year from data collected during 1963–68 by the Pacific Ocean Biological Survey Program (POBSP) primarily in the central Pacific. Pitman (1986) also presented abundances (birds sighted per hour) for each of the

three species plotted for 2° × 2° cells for much of the ECP.

'Abundance' (hereafter defined as the total number of birds, including subadults and adults) estimates of *aethereus* and *lepturus* in the Pacific are non-existent because of: (1) censusing difficulties – these species nest on cliffs and trees, and (2) the lack of information on the number of subadults. The only estimate known to us for any colony of *aethereus* is that of a 'few thousand breeding pairs' nesting on the Galápagos Islands (Harris 1977). For *lepturus*, Harrison (1990) estimated that a maximum of 2400 pairs bred on the main Hawaiian Islands.

Estimates for numbers of breeding *rubricauda*, which nest on flat terrain, especially on tropical atolls, are largely incomplete because they breed throughout the year at many locations (thus not all birds are breeding at any given time). A census by the POBSP of breeding *rubricauda* on ECP islands from the equator northward indicated that at least 31 000 birds nested there (Gould *et al.* 1974). Harrison (1990) estimated total abundance (i.e. adults and subadults) for the

*Corresponding author.
Email: spearlarry@yahoo.com

same area exceeding 75 000 birds, including 50 000 birds (of which a maximum of 24 130 were breeders) from the Hawaiian Islands. However, this author gave no description of the method he used to estimate total abundance for the east Pacific or Hawaiian population. Population estimates are rough and incomplete for *rubricauda* breeding locations in the South Pacific (Garnett 1984, Marchant & Higgins 1990).

The aim of this study was to determine more precisely the tropicbirds' distributions and at-sea abundance in the ECP.

BACKGROUND

Harrison (1983) summarized the breeding range of *rubricauda* in the world's oceans. In the Pacific, it breeds on most islands that offer flat, open terrain, including locations in the South Pacific extending from the most southern breeding locations on Norfolk and Lord Howe islands off western Australia (van Tets & Fullagar 1984), west to the South China Sea, east across the Polynesian Islands to the Pitcairn Islands (130°W; Garnett 1984) and, perhaps, Easter Island (Garnett 1984); thence north to the Leeward Chain of the Hawaiian archipelago (Harrison 1990, see figure 1 in Spear & Ainley 2005). Thus, within and adjacent to our study area, this species breeds on most central Pacific archipelagos (reviewed in Garnett 1984, Harrison *et al*. 1984).

In the Pacific, *rubricauda* have been recorded northwest to Japan (39°N; Austin & Kuroda 1953); east to the coast of Mexico (20°N, 106°45′W, 113 km from shore; this study), and northeast to 300 km off California, USA (40°N, California Rare Birds Committee in press); southeast to 780 km off Chile (28°S; this study), and southwest to waters off Asia (Harrison 1983) and to about 42°S off Australia (Harper; in Gould *et al*. 1974). Analysis of recoveries of banded *rubricauda* indicated that birds originating from colonies in the North and South Pacific remain in those hemispheres (Gould *et al*. 1974).

In the Pacific, *aethereus* breeds on rocky islands along the coast of the Americas from the Gulf of California and Revillagigedo Islands, Mexico (Howell & Webb 1995), south to the Galápagos Islands (Harris 1969, figure 1 in Spear & Ainley 2005), and possibly Isla Plata, Ecuador (Murphy 1936, Duffy & Hurtado 1984), and San Lorenzo Island, Peru (Harrison 1983). This species has been known to occur offshore to 3000 km west of the Galápagos islands (117°W, 3°N; Spear *et al*. 2001), north to Washington state (45°N; Harrison 1983), and south to 32°S off Chile (Murphy 1936).

Harrison (1983) summarized the breeding range of *lepturus*, which breeds on steep, forested islands of many archipelagos in the study area (figure 1 in Spear & Ainley 2005). Within and immediately adjacent to the study area, they breed on islands between the Gambiers (135°W) and Fijis (180°W), and between 22°S (Gambiers) and 22°N (main Hawaiian Islands; Garnett 1984, Harrison *et al*. 1984). At sea, this species has been recorded mostly between latitudes of 30°N and 30°S, west of 110°W in the South Pacific, and mostly west of 130°W in the North Pacific (this study, King 1970, Pitman 1986).

Breeding chronology of tropicbirds is important for interpreting patterns in seasonal abundance. On the Leeward Hawaiian Islands, *rubricauda* begin nesting in the boreal spring, with fledging in mid autumn (Table 1). *Rubricauda* nesting near the Equator (e.g. Line Islands) lay eggs between June and November (average = August–September; Table 1). With an average incubation period of 45 days, and an average chick-rearing period of 100 days (Schreiber & Schreiber 1993), peak fledging should occur from January to February and be completed by April. The available information on the timing of breeding of *rubricauda* south of the Equator is sparse, although information from the Pitcairn Islands (Brooke 1995) indicates that they breed throughout the year, possibly with peak laying in the austral autumn. Assuming that they have a similar incubation and chick-rearing period as Line Island birds, fledging should peak in the austral winter and spring.

The only information on the breeding chronology of *aethereus* is from the Galápagos Islands, which shows egg-laying throughout the year on some islands (Table 1).

Lepturus breed during the boreal spring and summer on the main Hawaiian Islands with fledging probably occurring mostly in the boreal autumn (Table 1). We are not aware of information on breeding chronology of *lepturus* in the South Pacific.

METHODS

Study area

Our data are from 26 cruises in 1980–95, mostly between 20°N and 20°S, and between 176°W and the Americas (hereafter termed 'study area', Fig. 1), primarily during the months of April–July (hereafter termed the boreal spring and austral autumn) and September–December (hereafter termed the boreal autumn and austral spring). Our surveys were

Table 1. Breeding chronology of the three species of tropicbirds in various regions of the ECP.

Species: location	Chronology	Source
Red-tailed Tropicbird		
Leeward Hawaiian Islands		
Egg laying	March	Gould *et al.* (1974)
Fledging	November	King (1970)
Equatorial islands		
Peak egg laying	Aug/Sept	Schreiber and Ashmole (1970)
Peak fledging*	Jan/Feb	Schreiber and Schreiber (1993)
South Pacific; Polynesian Islands	unknown	
South Pacific; Pitcairn Islands	probably throughout year	Brooke (1995)
Red-billed Tropicbird		
Galapagos Islands	throughout year	Harris (1969)
White-tailed Tropicbird		
Hawaiian Islands	boreal spring and summer	Harrison (1990)
South Pacific	unknown	

*See Methods; Background.
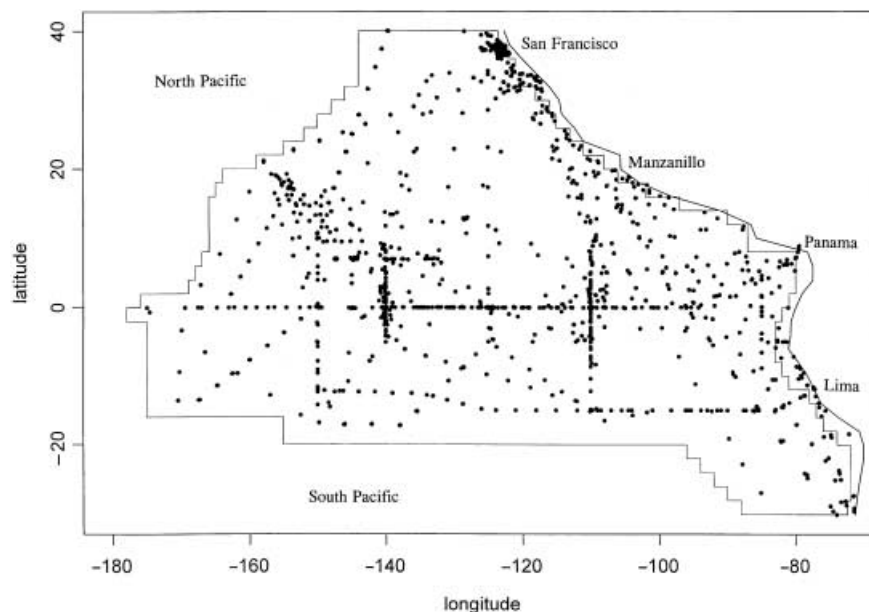
Figure 1. Noon-positions (*n* = 1186, each denoted with a dot) of ships on which we conducted tropicbird surveys in the eastern Pacific (1980–95).

conducted only in part of the at-sea ranges of *rubricauda* and *lepturus* in the Pacific (see Background for complete ranges), but throughout the at-sea range of Pacific *aethereus* in both the boreal spring and the boreal autumn.

Our study area included waters representing three equatorial current systems (South Equatorial Current (SEC), Northern Equatorial Current (NEC) and Equatorial Countercurrent (ECC)) and three boundary current systems (California, Peru and Costa Rica currents; see Spear & Ainley 2005 for location and details on characteristics of current systems).

Survey protocol

With two or three people observing simultaneously, we conducted continuous strip-surveys from the ship's flying bridge (top) while the ship was underway.

Tropicbirds seen within a 90° quadrant strip of known width were counted. Strip-width was 400–600 m depending on height of the flying bridge (12–15 m asl; width determined following Heinemann 1981). By noting ship speed (range 18–28 km/h), we calculated the surface area of ocean surveyed. Surveys were divided into 30-min segments. Within the study area, we surveyed seabirds during 1186 days in which at least 10 km^2 of ocean was surveyed, over an area of 105 546 km^2; 57 346 km^2 in spring and 48 200 km^2 in autumn. Data also recorded for each survey-day were noon position, ship speed and course, ocean depth, and distance to nearest point on the mainland and nearest colony.

For each sighting we noted behaviour: resting on the water, feeding or circling over a potential food source, attracted to the ship, or flying in a steady direction. For the last of these behaviours, we noted flight direction to the nearest 10°. We recorded as 'attractees' only those birds that approached the ship from the direction included within the 90° strip quadrant extended towards the horizon. Thus, birds that appeared from behind or from the opposite side of the ship were not recorded at all. Use of this method allowed Clarke *et al.* (2003) to correct abundance estimates for another ship-attracted species – a large Larid (Western Gull *Larus occidentalis*). However, we do not believe that we were able entirely to eliminate the attractee problem in this study (see Results and Discussion for other adjustments).

Using plumage and bill characteristics, we noted age as adult, subadult or young-of-the-year (hereafter 'fledglings') for all birds when possible. Specifically, all birds with the two central retrices extending ≥ 10 cm beyond the ten outer retrices were considered to be adults. Birds with shorter central retrices were considered to be subadults (most subadult *rubricauda* also have easily seen dusky mottling on breast belly). Birds were considered to be fledglings if they had short rectrices and bills that were grey (*rubricauda* and *lepturus*) or yellow (*aethereus*; see also Howell & Webb 1995 for bill colour); many fledglings also have black-tipped bills and tails. Because often we could not distinguish fledgling from subadult *lepturus*, we only noted adult vs. subadult when recording that species. Our reason for recording age was to determine or confirm the timing of breeding for different populations, assuming that fledglings appear in the boreal autumn if the breeding season began in the boreal spring, and the reverse for populations breeding in boreal autumn.

We also compared distance from the nearest colony for adults vs. subadults/fledglings; here we grouped colony distances into three categories: a 'near' zone, a 'mid' zone and a 'far' zone (see Spear & Ainley 2005 for location of colonies).

Statistical analyses

Unless noted otherwise, we used vector analysis (Spear *et al.* 1992) to adjust observed counts for the effect of bird movement relative to that of the ship; flight speeds as related to wind speed were from Spear and Ainley (1997). This adjustment is required when estimating abundance from at-sea surveys because the use of observed counts generally results in density overestimation, particularly for fast fliers such as tropicbirds.

Birds attracted to the ship were recorded as 0.3 birds per individual (details given in Spear *et al.* in press). Hereafter, tropicbird counts are given as the values adjusted for bird movement and attraction to the ship, unless noted otherwise.

For each of the species' ranges (see below), means ± 1 sd for ocean area per survey-day were 103 ± 51 km^2 ($n = 878$ days) for *rubricauda*, 75 ± 51 km^2 ($n = 888$) for *aethereus* and 108 ± 53 km^2 ($n = 428$) for *lepturus*. None of the samples included days with less than 10 km^2 of survey effort.

In addition to estimating abundance, we used these data to estimate and compare within-season densities among populations as well as between seasons for each population. Sidak multiple comparisons tests (an improved version of the Bonferroni test; SAS Institute 1985) were used to compare within-season means and *t*-tests were used to compare between-season means. Log-likelihood G-tests were used to compare numerical proportions among age classes. Significance was assumed at $P < 0.05$.

Estimation of population size and temporal trend

In S-Plus (1997), generalized additive models (GAMs, Hastie & Tibshirani 1990) were used to estimate seasonal abundance, including 95% confidence intervals (Efron & Tibshirani 1993), of each tropicbird population (see Clarke *et al.* 2003) in our study area. The principal strength of additive models is their ability to fit complex smooth functions in the predictor rather than being constrained by the linearity implicit in generalized linear models (GLMs). A GAM is expressed as:

$$g(E[y]) = \beta_0 + \sum_k S_k(x_k).$$

The right-hand side of the equation is the additive predictor. β_0 is an intercept term and S_k is a one-dimensional smoothing function for the kth spatial covariate, x_k. The degree of smoothing is determined by the degrees of freedom (df) associated with the smoothing function. The larger the degrees of freedom, the less the smoothing performed and the more flexible the function obtained. A GAM in which all the smoothing functions have 1df is equivalent to a GLM. An offset (a linear covariate whose coefficient is one) can also be included in the predictor. This is useful when a transformation of the response variable can be modelled using a standard distribution. For example, rather than modelling density, we could model numbers, with area surveyed as an offset.

GAMs were fitted using the observed tropicbird counts during each survey day as the response variable. Survey days outside the study area(s) were excluded. The explanatory variables considered for each model were latitude, longitude, shortest distance to mainland, ocean depth and distance to the primary breeding colony within the area being modelled. Ocean depth and distance to mainland were calculated for each transect using the position of the transect along with coastline and bathymetry data obtained from http://rimmer.ngdc.noaa.gov/coast/ and http://ingrid.ldgo.columbia.edu/SOURCES/WORLDBATH/, respectively. For analyses to estimate abundance of northern, southwestern and southeastern *rubricauda* (see Tropicbird population delineations below) colony locations used for each GAM were Midway (Leeward Hawaiian Chain), Phoenix and Pitcairn Isles, respectively; for northern and southern *lepturus*, colony locations used were Kauai and Line Isles, respectively; and for *aethereus*, colony location was the Galápagos Isles (figure 1 in Spear & Ainley 2005). Each GAM is constrained to use a single colony position. However, the fact that several major colonies exist within the range of each tropicbird population was not a problem because the density relationship with colony location could be modelled as non-linear ('smooth'; see Results), i.e. high densities in association with other distant colonies are readily modelled with GAMs even with multiple colony locations.

Count data were modelled using a Poisson variance function and estimating a dispersion parameter (e.g. Venables & Ripley 1997, Clarke *et al.* 2003). Because observed counts must be adjusted for bird movement and depend on the area surveyed within the survey-day, we used the logarithm of the area surveyed multiplied by the bird-movement adjustment factor (which varies for each data point) as an offset. The logarithm was used because we used a log-link function.

Being model-based rather than sample-based, inference from GAMs is not dependent on a random survey design. Substantial improvements in precision over sample-based methods also are possible with GAMs because they capture non-linear trends in density while using few parameters. Once fitted, a GAM provides a smoothed density surface over the area of interest, including unsampled areas. Abundance is estimated by integrating numerically under this surface. This was achieved by first creating a fine grid across the study area. The fitted surface was then used to predict densities of birds in each grid-square. Finally, abundance was estimated as the sum of the predicted numbers over all grid-squares within the study area.

Bootstrap variance estimation

Confidence intervals for abundance estimates were obtained using bootstrapping, which involves creating many new data sets from the original sample, and analysing these new samples in the same way as the original. The distribution of the statistic of interest is then estimated from its empirical distribution among the bootstrap samples.

To control for the correlation between counts from survey transects that were close in space and time, we used an adaptation of a moving-blocks bootstrap (Efron & Tibshirani 1993). In a moving-blocks bootstrap, the data are resampled with replacement from all possible contiguous blocks of some specified length. The block lengths were chosen by taking into account the strength of the autocorrelation between 0.5-h survey transects; the block must be long enough that observations further than one block length apart are independent.

Because counts from 0.5-h transects within a day could be correlated, day was used as the sampling unit. The 'length' of each day was measured as the number of transects surveyed. The resampling algorithm works through the data set, recreating each day's data in turn. Generating data for a day involved randomly selecting a day from the survey data and randomly selecting a 0.5-h transect to start from within that day. Counts for the survey transects in the original day were then recreated in turn from the survey transects in the new day using the semi-parametric

bootstrap procedure of Davidson and Hinkley (1997) described below. If the end of a survey-day was reached before enough 0.5-h transects had been resampled, the resampling was continued at the start of the next day.

A bootstrap count b_i for transect i was generated from transect j as follows:

$$b_i = \hat{f}_i + \hat{s}_i \varepsilon_j,$$

where $\hat{f}_i = E[y_i]$ is the fitted value for count i, $\hat{s}_i$ is the estimated standard deviation for count i and ε_j is the deviance residual of count j. For overdispersed Poisson errors, such as those encountered in most seabird survey data (Clarke *et al.* 2003), $\hat{s}_i$ is defined by:

$$\hat{s}_i^2 = \hat{\phi} \hat{f}_i (1 - h_i)$$

(Davidson & Hinkley 1997), where h_i is the leverage of count i (McCullagh & Nelder 1989), and $\hat{\phi}$ is the estimate of the dispersion parameter ϕ.

In total, 199 bootstrap resamples were generated for each data set modelled. Models were refitted to each bootstrap and a new abundance estimate obtained. The coefficient of variation (CV) of the estimate was calculated by dividing the sample standard deviation of the scaled bootstrap estimate by the original abundance estimate. The 95% confidence intervals (CIs) were estimated with the percentile method of Davidson and Hinkley (1997).

Clarke *et al.* (2003) validated the strip-survey method we used for estimating abundance of three species of seabirds by comparing abundance estimates derived from data collected at sea, with those estimated from colony counts. They found a high level of consistency between the at-sea and colony-based abundance estimates. Their data were collected by us using identical survey methods and many of the same observers.

A problem inherent in the estimation of tropicbird abundance from surveys conducted at sea results from their being strongly attracted to ships, the result being inflated abundance estimates unless measures are taken in the analyses to account for attracted birds. This constraint limited our abundance estimates to what we believe are minimum and maximum numbers (details in Results: Abundance estimates).

Tropicbird population delineations

For reasons explained in the Results (see Tropicbird distributions) we defined six tropicbird 'populations',

including three of *rubricauda*, one of *aethereus* and two of *lepturus*; these populations were delineated by visual examination of the GAM distribution plots of each species. Hereafter we term the population of *rubricauda* that occupied waters north of the Equator as 'northern *rubricauda*'. The two other populations of *rubricauda* occupied waters to the south of the Equator. We term one as 'southeastern *rubricauda*', occupying waters south of the Equator and east of 130°W, and the second as 'southwestern *rubricauda*', occupying waters south of the Equator and west of 130°W. Hereafter, we collectively termed the latter two populations south of the Equator also as 'southern *rubricauda*'.

The two populations of *lepturus* included birds occurring south of the Equator (hereafter termed 'southern *lepturus*'), and north of it (hereafter termed 'northern *lepturus*').

RESULTS

Tropicbird distributions

The adjusted count of *rubricauda* (see Spear & Ainley 2005, Behaviour at sea, for number of attractees of each tropicbird species) was 170.0 birds (original number = 213). Only five *rubricauda* were recorded north of 30°N, all during autumn, and all during El Niños in 1983 (three birds), 1986 (one) and 1991 (one).
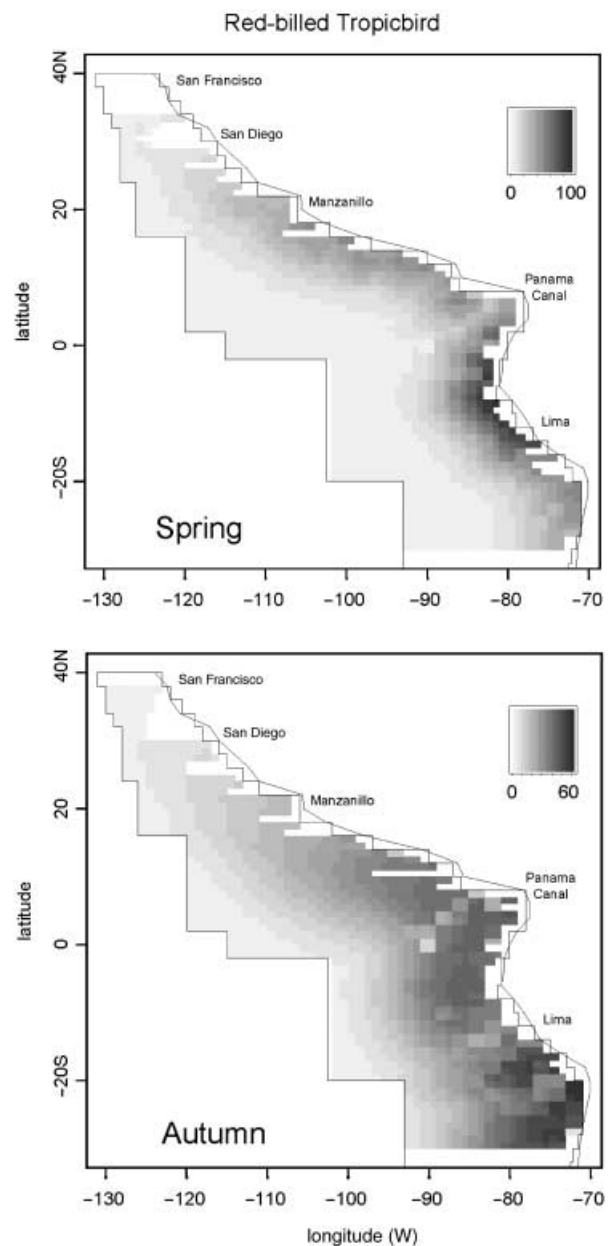
During the boreal autumn, three areas had distinctly higher densities of *rubricauda* (Fig. 2). One occurred northwest of about 6°N (near the southern boundary of the ECC; see Gould *et al.* 1974 for similar results), and southeast of large colonies on the Leeward Hawaiian Islands (hereafter termed the 'northern *rubricauda*'; but see qualifications in Discussion). This population was more concentrated in the boreal autumn than spring. The other two areas with high densities occurred south of 6°N. One was found west of 130°W in association with the central Pacific Polynesian islands (hereafter termed the 'southwestern *rubricauda*'), and was more concentrated during the boreal spring than autumn. The other southern high-density area occurred east of 130°W, immediately north of the Pitcairn Islands (hereafter the 'southeastern *rubricauda*'; see Pitman 1986 for similar observations). That population was most concentrated during the boreal autumn, when its distribution also was skewed further to the west and north (mostly between 100°W and 120°W and north to about 5°N). During autumn, there was also

Red-tailed Tropicbird

Red-billed Tropicbird
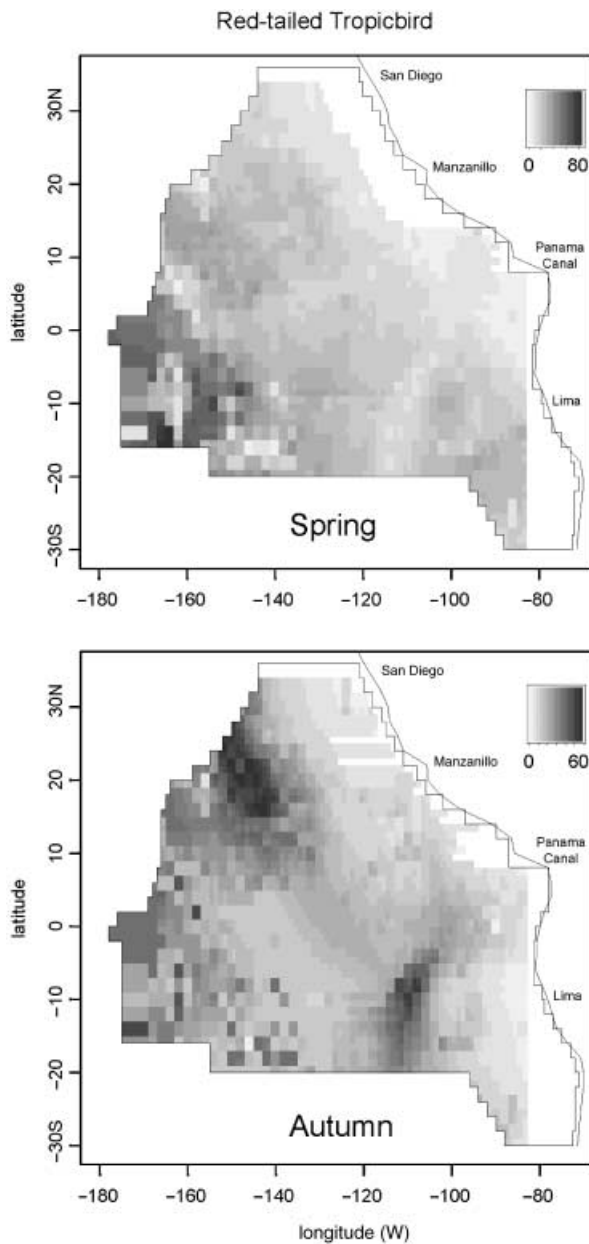
Figure 2. Predicted distributions (birds per 2° latitude × 2° longitude cell) of *rubricauda* during the boreal spring and autumn as determined from at-sea surveys (1980–95). Number of birds per cell are smoothed values predicted and plotted using a GAM. Abundance estimates are given in Table 4.

Figure 3. Predicted distributions (birds per 2° latitude × 2° longitude cell) of *aethereus* during boreal spring and autumn as determined from at-sea surveys (1980–95). Number of birds per cell are smoothed values. Abundance estimates are given in Table 4.

an area of moderate density bridging between the southeastern and northern populations.

The adjusted count of *aethereus* was 118.2 birds (original = 171). All were recorded within 1684 km of the Galápagos Islands and the Americas (Fig. 3). During the boreal spring, there was an area of high

densities from 200 to 800 km east of the Galápagos Islands, with moderate densities distributed along the coasts of North and South America. In autumn, there was also an area of high density east of the Galápagos Islands, although densities were skewed towards the south in waters offshore of southern

White-tailed Tropicbird
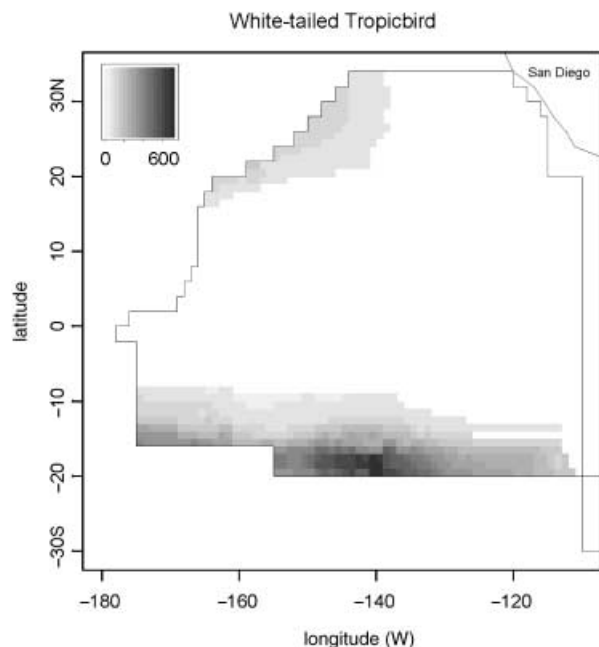
Figure 4. Predicted distribution (birds per 2° latitude × 2° longitude cell) of *lepturus* as determined from at-sea surveys (1980–95); number of birds per cell are smoothed values. The GAM was performed on survey data from boreal autumn for waters north of the Equator, combined with data from austral autumn for waters south of it (see Results, Abundance estimates, for rationale). Abundance estimates are given in Table 4.

Peru and northern Chile. *Aethereus* were more concentrated in the boreal spring than autumn.

The adjusted number of *lepturus* was 41.5 birds (original = 55). *Lepturus* formed two very distinct at-sea populations (Fig. 4), one in the South Pacific (hereafter 'southern *lepturus*') in association with the lower SEC, and the other mostly north of 15°N (hereafter 'northern *lepturus*') in association with the NEC. Only four of the *lepturus* recorded were over waters between 15°N and 5°S. Thus, there was essentially a 2000-km hiatus between the northern and southern populations.

Age-classes

Of the 353 birds for which age-class was noted (179 *rubricauda*, 126 *aethereus*, 48 *lepturus*), 272 (77%) were adults and 81 (23%) were subadult/fledglings. For these three species, the proportion that were adults was 73, 86 and 69%, respectively, a difference that was significant (ratios of adults to subadults were compared; $G_2 = 8.7$, $P < 0.02$), due primarily to the higher proportion of adults among *aethereus* and lower proportion among *lepturus*.

For each species, the proportion of adults vs. subadults seen at various distances from the nearest colony differed little (G_2 tests, *rubricauda*; $P > 0.3$, *aethereus*; $P > 0.1$, and *lepturus*; $P > 0.1$; Fig. 5). After grouping species, however, the subadult distribution was significantly further from the nearest colony than that of adults ($G_2 = 8.3$, $P < 0.02$).

A significantly greater proportion of fledgling *aethereus* and northern *rubricauda* were recorded during the boreal autumn than in the spring ($\chi_1^2 = 7.0$, $P < 0.01$ and $\chi_1^2 = 5.5$, $P < 0.05$, respectively; comparisons were of the original number of fledglings vs. the combined original number of subadults and adults; Fig. 6). We recorded no fledgling *rubricauda* in the southwest part of the study area. Although we observed fledgling *rubricauda* only in the boreal spring in the southeast area, the proportion of fledgling birds compared between seasons was insignificant ($\chi_1^2 = 3.1$, $P = 0.08$).
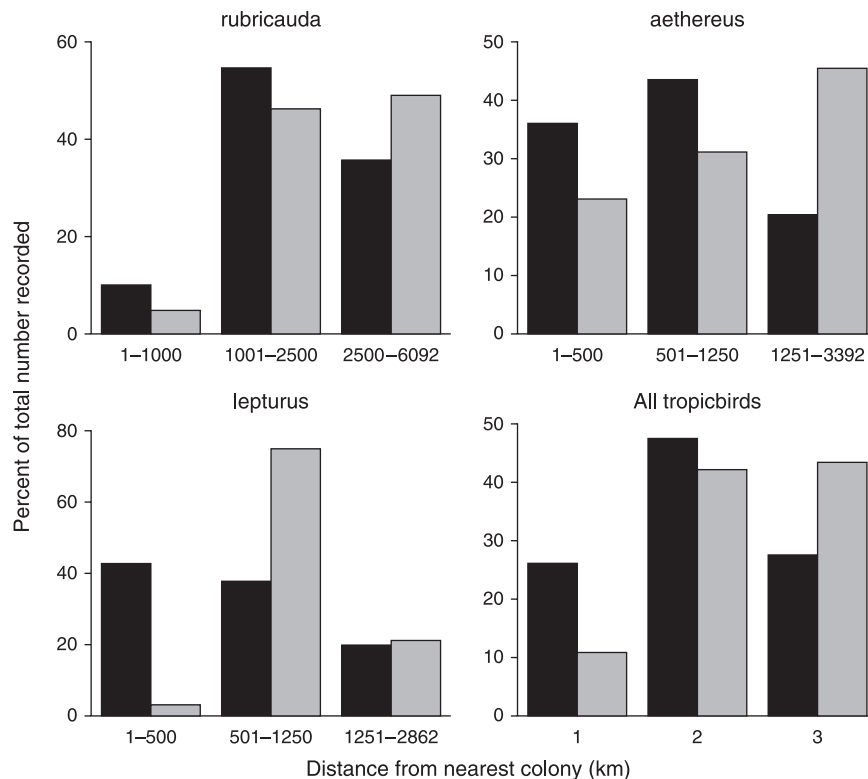
Tropicbird densities

During the boreal spring, densities of southern *lepturus*, and southern and northern *rubricauda* differed insignificantly (data log-transformed – details in Spear & Ainley 2005; Sidak tests, all $P > 0.3$, Fig. 7), but were significantly greater (all $P < 0.05$) than densities of *aethereus*, south-east *rubricauda* and northern *lepturus*, among which densities were similar (all $P > 0.2$). During the boreal autumn, northern *rubricauda* density was significantly greater than that of each of the other populations (all $P < 0.01$, Fig. 7). Densities of southeast and southwest *rubricauda*, *aethereus* and southern *lepturus* were similar (all $P > 0.5$), while the density of northern *lepturus* was significantly lower than all other populations (all $P < 0.05$) except southern *lepturus*.

Within-population comparisons of density between seasons showed no significant differences between any except that of southern *lepturus*, which was greater in the austral autumn than austral spring (Table 2, Fig. 7).

Abundance estimates

Selected models for the distribution of different populations of tropicbirds during the boreal spring and autumn usually included most of the variables, although ocean depth and distance from the mainland were selected less often than latitude and distance to colony (Table 3). The latter two variables were modelled as 'smoothes' except twice in each of the 13 GAMs.

Figure 5. Proportion of adult (■) and subadult (▨) tropicbirds observed at different distances from the nearest colony, given as the percentage of the total seen for each age-class (note that proportions are not necessarily consistent with densities). See Results, Age-classes, for sample sizes.

Abundance estimates of *rubricauda* were 81 700 birds in the boreal spring and 86 500 in the boreal autumn (Table 4). However, the estimate for northern *rubricauda* was higher during the boreal autumn than the boreal spring, which was also true of the southeast *rubricauda* (higher abundance in austral spring than austral autumn), but opposite the seasonal pattern in southwest *rubricauda* (higher numbers during austral autumn than spring). CVs for total abundance estimates were low (9–10), indicating high precision of the estimates. However, CVs of the three subpopulations ranged considerably. CVs for southwest *rubricauda* were especially high as there were few survey data for that area.

Abundance estimates for north, southeast and southwest *rubricauda*, when summed across respective areas for boreal spring and autumn, respectively, deviated from the total *rubricauda* estimates for respective seasons by several thousand birds in each case (Table 4; also true for the summed northern and southern *lepturus* estimates compared with the total *lepturus* estimate). This is explainable by the fact that the models and 'smoothes' chosen by GAMs for

different areas/seasons differed among populations, and also with those of the GAMs chosen for the total abundance estimates (Table 3). Thus, some divergence is expected when abundance estimates for area subsamples are compared with an estimate for the total area. Specifically, design-based methods of estimation would be self-consistent in this situation, but model-based methods, such as GAMs, are not. In fact, abundance estimates summed among the three *rubricauda* populations (and two *lepturus* populations) agree well, given that the CIs around the total estimates are substantially wider than the differences when compared with the pooled estimates (Table 4).

The abundance estimates for *aethereus* were 26 700 birds in the boreal spring and 33 400 in the boreal autumn (Table 4). The CVs for that species were also low, indicating high precision for each estimate.

Preliminary GAMs indicated that southern *lepturus* were highly clumped during the austral spring (when these birds occurred primarily adjacent to Polynesian archipelagos) and that northern *lepturus* were highly clumped during the boreal spring (when these birds occurred primarily adjacent to the breeding area on
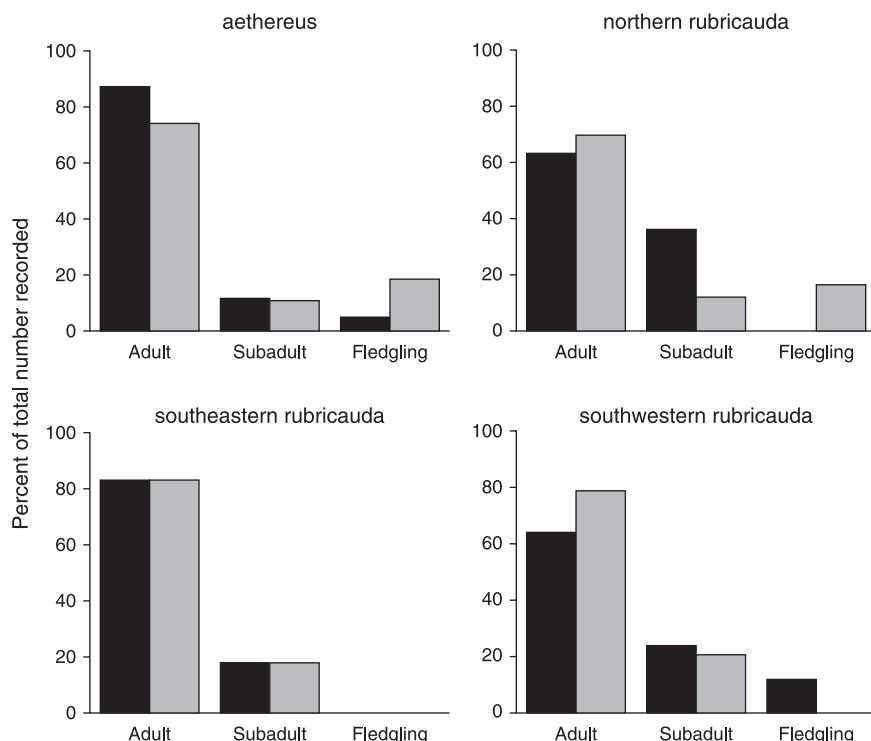
Figure 6. Proportion of adults, subadults and fledglings observed during at-sea surveys in spring (■) and autumn (▨) for *aethereus* and three populations of *rubricauda*. Sample sizes (i.e. the original counts as opposed to adjusted counts as χ^2 analyses will not allow decimal values characteristic to the latter) for spring and autumn were: *aethereus*, 75 and 51; northern *rubricauda*, 29 and 56; southwestern *rubricauda*, 12 and 12; southeastern *rubricauda*, 25 and 24; for definition of populations see Results, Tropicbird population delineations.

the Hawaiian Islands), resulting in relatively meaningless abundance estimates for the *lepturus* populations, as indicated by very large CVs for the estimate obtained when analysing these data in a GAM.

Therefore, to estimate abundance of this species, we grouped the northern data collected during the boreal autumn, when this population was most dispersed, with the southern data collected during the austral autumn, when that population was most dispersed.

The non-breeding estimate for northern *lepturus* and southern *lepturus* combined was 49 000 birds (Table 4, Fig. 4). Using separate GAMs, the estimated abundance of southern *lepturus* during austral autumn and northern *lepturus* during the boreal autumn were 11 000 and 41 500 birds, respectively. The very large CVs for this species were primarily due to the low number of birds recorded.

As noted earlier, the fact that tropicbirds are strongly attracted to ships can result in inflated abundance estimates unless some adjustments are made. Indeed,

it is likely that some birds whose behaviour we recorded as 'directional flight' had, in fact, deviated course to inspect our vessel. As a result we consider the abundance estimates reported above as the 'maximum'. 'Minimum' estimates were calculated after removing all counts of attracted individuals (i.e. birds whose counts were set at 0.3 birds per bird recorded), and all individuals recorded in directional flight. Thus, these analyses included only birds that were recorded as sitting on the water or foraging/ feeding (i.e. stationary), and that could not have been recorded as a result of being attracted to our vessels.

Counts of stationary birds accounted for 48, 52 and 58% of the adjusted counts of *rubricauda*, *aethereus* and *lepturus*, respectively (figure 3b in Spear & Ainley 2005). Based on these counts, our minimum estimates are about 41 000 *rubricauda* (nearly equally divided between Hawaiian *rubricauda* and the Polynesian/ Pitcairn *rubricauda*), 15 750 *aethereus*, 28 000 southern *lepturus* and 6400 northern *lepturus*.
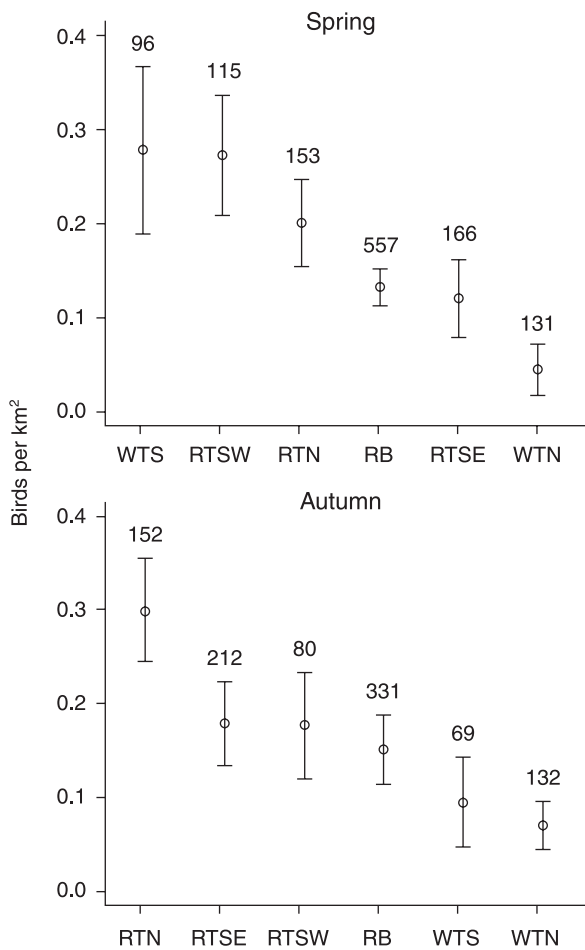
Figure 7. Mean density ± se of six populations of tropicbirds in the eastern Pacific during spring and autumn. RTN = northern *rubricauda*, RTSW = southwestern *rubricauda*, RTSE = southeastern *rubricauda*, RB = *aethereus*, WTN = northern *lepturus*, WTS = southern *lepturus*. The sample unit was one survey-day; numbers adjacent to means are sample sizes. Values pertain only to surveys conducted within the defined range of each population (for definitions, see Results, Tropicbird population delineations).

DISCUSSION

Our abundance estimates for *rubricauda* and *lepturus* are likely to have been underestimated because we did not have complete coverage of the at-sea ranges of these species.

The abundance of northern *lepturus* was the lowest of the six tropicbird populations because only a small group breeds in the North Pacific. Our at-sea estimate of 11 000 birds for this population had a very large CV, but is consistent with the estimated number of breeding pairs (maximum = 2400) from a complete survey on the Hawaiian Islands (Harrison 1990). Demographic information for *aethereus*

Table 2. Between-season comparisons of densities for each of six tropicbird populations. Comparisons by *t*-test.

Population	*t*-value	*P*-value	*df*
Northern *rubricauda*	1.84	0.06	303
Southwest *rubricauda*	1.77	0.07	193
Southeast *rubricauda*	1.79	0.07	376
aethereus	0.57	> 0.5	886
Northern *lepturus*	1.36	> 0.1	267
Southern *lepturus*	2.13	< 0.05	163

(Harris 1977, 1979, and see below) indicates that approximately 60% of that species' population consists of breeders. Assuming that the age-class composition of *lepturus* is similar, the estimated number of breeding pairs we recorded at sea would have been about 3300. This figure is about 1900 pairs of northern *lepturus* if we consider only our minimum abundance estimate (i.e. after adjustment for the effect on count data of these birds' attraction to ships).

In contrast to northern *lepturus*, which breeds on a single archipelago, most of the steep, forested Polynesian islands in the South Pacific support *lepturus* populations. Therefore, our estimated at-sea abundance of 41 500 South Pacific *lepturus*, although constrained by its large CV, is understandable.

The smaller at-sea distributions of southern *lepturus* during the austral spring and of northern *lepturus* during the boreal spring were probably related to them remaining close to or on their nest-sites during their respective breeding seasons. From the higher counts of adults flying over the main Hawaiian Islands it has already been suggested that northern *lepturus* breed during the boreal spring and summer (Harrison 1990). However, prior to this study, we were not aware of evidence indicating that *lepturus* breeding in the southern hemisphere do so primarily in the austral spring (see Spear & Ainley 2005 for further evidence).

Our boreal spring and autumn estimates for eastern Pacific *rubricauda* (82 000 and 87 000 birds, respectively; minimum = 41 000 birds) had very low CVs (9 and 10), and are similar to those of Harrison (1990, estimated to exceed 75 000 birds). Note, however, that this abundance estimate includes waters south of the Equator to 20°S, whereas Harrison's estimate did not. In addition, our estimate for the northern area was obviously incomplete, as demonstrated by the high-density area immediately inside the north and west borders of our survey area, indicating that many birds were probably present in waters beyond it. Our total abundance estimate for the ECP study area, after adjustment for positive bias due to

Table 3. Covariates chosen by the GAMs when modelling distributions and estimating abundance of tropicbirds in the ECP. Dashes indicate that covariate was not significant in the model. Seasons pertain to boreal.

Population: season	Latitude	Longitude	Ocean depth	Distance to: mainland	Distance to: colony
Red-tailed Tropicbird					
Boreal spring					
Total	Smooth	Smooth	Smooth	Linear	Smooth
North	Smooth	Smooth	–	–	Linear
Southwest	Smooth	Smooth	Smooth	–	Smooth
Southeast	Linear	Smooth		Smooth	Smooth
Boreal autumn					
Total	Smooth	Smooth	Smooth	–	Smooth
North	Smooth	–	Smooth	–	Linear
Southwest	Linear	Smooth	Smooth	Smooth	Smooth
Southeast	Smooth	Smooth	–	Linear	Smooth
Red-billed Tropicbird					
Boreal spring	Smooth	Smooth	Linear	Linear	Smooth
Boreal autumn	Smooth	Smooth	Smooth	Smooth	–
White-tailed Tropicbird					
Total	Smooth	Smooth	Smooth	Smooth	Smooth
North	–	Smooth	Smooth	–	Linear
South	Smooth	–	Smooth	–	Smooth

Table 4. Results of generalized additive model analyses to estimate abundance of *aethereus*, three populations of *rubricauda*, and northern and southern *lepturus* in the eastern Pacific Ocean, including 95% confidence intervals (95% CI), and coefficients of variation × 100 (CV). Sample sizes are given in Figure 7. Seasons refer to the boreal time frame, where boreal spring = austral autumn and boreal autumn = austral spring.

Population	Estimate	95% CI	CV
Red-tailed Tropicbird			
Spring total	81 700	51 700–86 500	10.4
North	28 400	22 500–39 100	14.0
Southwest	47 900	27 900–62 300	16.5
Southeast	12 200	10 000–16 700	13.4
Autumn total	86 500	65 800–98 700	9.4
North	46 300	36 500–55 100	11.0
Southwest	23 900	12 900–42 400	29.8
Southeast	23 800	13 200–27 100	15.6
Red-billed Tropicbird			
Spring	26 700	21 500–33 800	12.3
Autumn	33 400	30 900–44 500	11.1
White-tailed Tropicbird			
Total	48 900	32 500–88 600	29.6
North	11 000	5500–21 300	35.5
South	41 500	26 400–78 700	29.7

ship attraction, of 41 000 birds would equate to about 25 000 breeders (assuming that approximately 60% of that species' population consists of breeders; see Harris 1977, 1979, for demography

of *aethereus*), a number similar to that estimated by Gould *et al*. (1974, 31 000 breeders for the ECP), but less than expected when considering the estimate by Harrison (1990) of 24 000 breeders nesting on the Hawaiian Islands alone.

Although the seasonal changes in population densities for the three populations (northern, southwest and southeast) of *rubricauda* were marginally insignificant (*P* values = 0.06–0.07), the differences in abundance estimates themselves deserve comment. First, the 40% decline in estimated abundance of northern *rubricauda* during the boreal spring compared with the boreal autumn, as well as the reduced at-sea range of that population within the study area in spring, is consistent with the location and timing of breeding of that population, which occurs outside the study area, primarily on the Leeward Hawaiian Chain during spring and summer. During spring, the area of moderate density at about 10–20°N on the western side of the study area may have represented breeders from Johnston Atoll as well as subadults from other populations. Subadults would probably, mostly, include birds from the Leeward Chain, as indicated from analyses of band returns (Gould *et al*. 1974). The increase in estimated abundance as well as the ocean area occupied during autumn by *rubricauda* in the North Pacific is thought to represent southward post-breeding dispersal of birds from the

Leeward islands (Gould *et al*. 1974). Indeed, the increase in the proportion of newly fledged young and adults in the northern area during autumn in this study supports that conclusion.

However, the timing of breeding of *rubricauda* in the South Pacific is not well known at most locations. We suspect that the 50% increase in the estimated abundance of the *rubricauda* breeding in the vicinity of the Polynesian Islands (southwest Pacific) group during the austral autumn compared with austral spring reflects a similar pattern to that noted in the northern hemisphere among *rubricauda* breeding there in the boreal spring. Specifically, we suspect that the greater number of Polynesian *rubricauda* during the austral autumn may reflect use of an austral spring breeding season. Thus, with newly fledged young and dispersing adults, this group was more abundant at sea in the austral autumn. The abundance increase during the austral autumn could also result from birds dispersing from colonies on the Polynesian islands west of our study area.

Yet, the chronological pattern suggested above for southwest *rubricauda* differs from that indicated for *rubricauda* in the southeast Pacific, which we assume to have originated primarily from the Pitcairn Islands. That is, the 50% increase during the austral spring in the estimated abundance and range expansion of *rubricauda* found in equatorial waters immediately north of the Pitcairn Islands is consistent with a post-breeding dispersal following an austral autumn breeding season; this timing consistent with that noted by Brooke (1995) for the Pitcairn Archipelago. However, the increase in abundance in the Pitcairn vicinity could also reflect dispersal by birds from the Polynesian Islands to the west (which declined appreciably during austral spring) and even Hawaiian birds from the north. Indeed, the slightly elevated density strip connecting the Hawaiian and Pitcairn high-density areas during the boreal autumn/austral spring (Fig. 2) indicates possible interchange. For that matter, the small and somewhat incomplete hiatus separating Hawaiian from the southwest *rubricauda* is such that interchange could easily occur between those populations (see Gould *et al*. 1974 for a similar conclusion).

The highest densities of *aethereus* occurred in the vicinity of the Galápagos Islands and Peru Current. The more restricted distribution of *aethereus* recorded in the boreal spring is consistent with a predominance of boreal spring/summer breeding of this species within its Pacific range. This idea is also supported by the lower abundance estimate for spring (when adults are attending nests and young have not fledged) compared with autumn (26 700 vs. 33 400 birds), as well as the recording of a significantly higher number of first-year birds during the boreal autumn compared with spring.

Even if we consider only stationary *aethereus* (yielding a minimum 'corrected' abundance estimate of 15 750 birds averaged between seasons), this estimate is larger than expected considering that the estimate for the main breeding area (Galápagos Islands) was 'a few thousand (breeding) pairs' (Harris 1977), and that no other large colonies of *aethereus* have been recorded in the Pacific. Indeed, based on demographic information indicating that (Galápagos) *aethereus* produce on average 0.44 young per breeding attempt, have a non-breeder survival rate of 0.71 and first breed at an average age of 5 years (Harris 1977, 1979), the *aethereus* population would have been composed of 62% breeding adults, or, using the uncorrected at-sea estimates given above, would include 8300–10 400 breeding pairs, or 4900 pairs if we use the minimum estimate after adjustment for the effect of ship attraction.

CONCLUSION

The at-sea distributions of tropicbird species appear to be much restricted in total area (possibly by about 50%) during the breeding compared with non-breeding season. Even during the non-breeding season, most do not appear to disperse more than a few thousand kilometres, making it possible to distinguish between most populations throughout the year.

The results of this study indicate that North Pacific (Hawaiian) populations of *rubricauda* and *lepturus* are probably similar in abundance to that already indicated from censuses on their respective breeding colonies. That of South Pacific (Polynesian) *lepturus* had not been estimated but appears to be in the range of 40 000 birds for waters east of the Gilbert and Samoan islands and north of 20°S. The total abundance (including subadults) of *aethereus* is probably larger than would be expected (16 000–33 000 birds in total) from previous reports. Although no sophisticated censuses have been conducted at the breeding colonies of *aethereus* in the Pacific, our estimate of about 5000 breeding pairs (after adjustment for ship attraction, and application of demographic data to account for the number of non-breeders) is consistent with the estimate of several thousand pairs nesting on the Galapagos, and the existence of breeding colonies on the coasts of Mexico and Central America.

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