

At-sea behaviour and habitat use by tropicbirds in the eastern Pacific

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During the boreal 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 eastern Pacific. Two subpopulations were indicated for both *rubricauda* and *lepturus*, based on distribution hiatuses near the South Equatorial Current (see companion paper). Thus, five populations were examined, two each of *rubricauda* and *lepturus*, and one of *aethereus*. During the boreal spring, when equatorial current systems are less well developed, geographical variables (distance from nearest colony and nearest land) were the most important variables affecting tropicbird occurrence. However, sea-surface salinity and thermal structure of the water column were the primary variables delineating tropicbird occurrence during the boreal autumn. Each tropicbird species utilized different species/sizes of aquatic predators (that make their prey available at the surface) that in turn utilize different oceanographic environments. We suspect that the distribution of aquatic predators is primarily responsible for colony locations and distribution of tropicbird species in the eastern Pacific.

Each of the three species of tropicbird (Phaethontidae) occurs over tropical and subtropical waters of the eastern and central Pacific (ECP): the Red-billed Tropicbird *Phaethon aethereus* (hereafter 'aethereus'), White-tailed Tropicbird *P. lepturus* (hereafter 'lepturus') and Red-tailed Tropicbird *P. rubricauda* (hereafter 'rubricauda'). The at-sea distributions of these species in the ECP have been well described (Spear & Ainley 2005).

The feeding and social behaviours of *rubricauda* and *lepturus* at sea have previously been described briefly (Gould *et al.* 1974, Harrison 1990, Schreiber & Schreiber 1993). However, little information is available on the at-sea behaviour of *aethereus*, nor are we aware of studies describing the responses of these species to the physical environment, either from small-scale (20–60 km; Hunt & Schneider 1987) or larger-scale (> 1000 km) perspectives. Hence, the primary objectives of this paper were to analyse and describe quantitatively: (i) coarse-scale and mega-scale oceanographic affinities of each species in the ECP; (ii) the effect of the El Niño Southern Oscillation (ENSO) while controlling for (and describing) the effects of seasonal changes in the current systems in

the study area; and (iii) at-sea occurrence relative to colony location. Our fourth objective was to provide information on foraging behaviour and at-sea distributions of different age-classes with respect to season.

Our tropicbird data were collected during cruises in 16 years over most of the ECP. We determined tropicbird densities (birds per km² of ocean) while simultaneously monitoring oceanographic parameters. Our surveys included only part of the at-sea ranges of *rubricauda* and *lepturus* in the Pacific, but had extensive coverage of the entire at-sea range of Pacific *aethereus* (Spear & Ainley 2005).

STUDY AREA AND METHODS

Our data are from 26 cruises during 1980–95. We defined two 'seasons': spring/summer (hereafter 'boreal spring' or 'austral autumn') and autumn/winter (hereafter 'boreal autumn' or 'austral spring'). Cruises were nearly equally divided between the two, and sampled tropicbird densities between 20°N and 20°S, and between 176°W and the Americas (hereafter termed 'study area'; see Spear & Ainley 2005; Fig. 1). To include the full range of *aethereus*, the study area also included data gathered between 40°N and 30°S, and, within those latitudes, west to c. 2000 km from the shoreline of the Americas.

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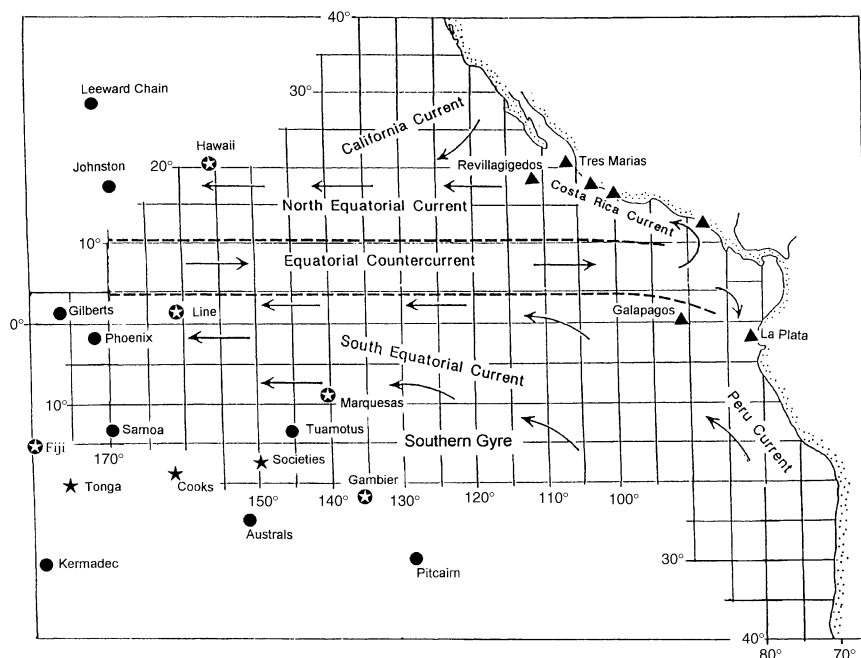


Figure 1. Study area, including current systems. Also shown are islands where 'major' tropicbird colonies (estimated number > 50 pairs) exist: *rubricauda* = solid circles; *lepturus* = stars; both *rubricauda* and *lepturus* = star within circles; and *aethereus* = triangles.

Oceanographic characteristics

The following oceanographic descriptions are from Wyrtki (1966, 1967). Circulation of surface waters in the ECP is dominated by three current systems, the Equatorial Counter Current (ECC), North Equatorial Current (NEC) and South Equatorial Current (SEC, Fig. 1). There are also three coastal currents: two major boundary currents (Peru Current and California Current), and the Costa Rica Current (a branch of the ECC), for a total of six systems in the study area.

Each equatorial current system varies seasonally in location, although they are strongest during the boreal autumn (Wyrtki 1966). The ECC is the only current system that flows eastward (Fig. 1). The ECC lies between about 4 and 10°N. The NEC and SEC lie north and south, respectively, of the ECC, and flow westward. The NEC extends to 25°N, and the SEC to about 20°S, although the latter is strongest between 4°N and 10°S. The Peru Current flows north along South America and merges into the SEC near the Galapagos Islands. The California Current flows south along North America and Baja California, where it flows offshore and merges with the NEC. The Costa Rica Current flows north along Central America and Mexico and also merges with the NEC.

For the purposes of this study, we considered the Gulf of Panama as Costa Rica Current waters because the two regions had very similar oceanographic characteristics during this study. For brevity, we also defined a seventh system, 'Southern Gyre', which is actually southern SEC waters lying south of 10°S and west of the Peru Current (Fig. 1). Being immediately north of the true Southern Gyre, these waters were similar to it but differed appreciably from those of the SEC lying between 10°S and 4°N, owing to the lack of mixing in the water column, higher temperatures and higher salinity of the former.

Thermocline depth (the point where the warm surface layer meets cooler water below) and strength (the rapidity with which temperature changes from warm to cold at the thermocline, where the strongest thermocline has the most rapid temperature change with increase in depth) increase from east to west in the ECP, although thermocline depth and strength are shallow and weak in the three boundary currents and the northern SEC, moderate to strong in the ECC, and deepest and strongest in the NEC and SOG (South Pacific Gyre).

During the study, ENSO (i.e. the oscillation including El Niño, La Niña and 'Neutral' phases; see Trenberth 1997) had a major effect on distributions of seabird species in the ECP, although the effects depended on season, current system, eastern vs.

western sections and foraging guild (planktivore vs. piscivore; Spear *et al.* 2001).

Survey protocol

All tropicbird surveys were conducted using 400–600-m strip transect methods (details in Spear & Ainley 2005). The data analysed in this study are the same as those used by Spear and Ainley (2005) gathered during 1186 days of surveys over 105 546 km² of ocean; 57 346 km² in the boreal spring and 48 200 km² in the boreal autumn.

For each sighting we noted behaviour: sitting on the water, feeding or circling over a potential food source, attracted to the ship, or flying in a steady direction. For the latter, we noted flight direction to the nearest 10°. We recorded as 'attractees' birds that approached the ship from the direction included within a 90° forward quadrant (the one being surveyed) extending towards the horizon. Thus, birds appearing from behind or the opposite side of the quadrant were not recorded. Each attractee was recorded as 0.3 birds (see methods and rationale for counting attractees in Spear *et al.* 2005). We also recorded two categories of age: adult or subadult/fledgling for most birds recorded.

A new transect was started every 30 min during 'offshore surveys' (water depth > 4000 m) and every 15 min for surveys in nearshore waters of shallower depth, where oceanographic conditions changed over a smaller spatial scale than offshore waters. Environmental data recorded for each transect included position, ship speed and course, sea-surface temperature and salinity, thermocline depth and strength, and wind direction (nearest 10°) and speed. Thermocline depth and strength, indices of mixing in the water column, were monitored every 4–6 h with expendable bathythermographs (XBTs). Thermocline depth was visually identified as the shallowest inflection point determined from XBT printouts on which temperature was plotted as a function of depth. Exceptions occurred where there was no inflection

point, when thermocline depth was recorded as being at the ocean surface. We measured thermocline strength as the temperature difference (nearest 0.1 °C) between the thermocline depth inflection to 20 m below it. A region with strong upwelling or a strong front had a shallow, weak, thermocline, and the reverse where little mixing occurred.

Statistical analyses

We considered five tropicbird populations for the habitat analyses: one of *aethereus*, and North and South Pacific populations for both *rubricauda* and *lepturus*. These population designations are those determined when mapping distributions (Spear & Ainley 2005), and also band return information indicating that *rubricauda* originating from the North and South Pacific remain in respective hemispheres (Gould *et al.* 1974).

We adjusted each count of a tropicbird recorded as flying in a steady direction for the effect of movement flux (Spear & Ainley 2005). We used multiple regression to examine mega- and coarse-scale relationships between adjusted tropicbird density (hereafter 'density') and environmental parameters.

We conducted two mega-scale analyses. In the first, we analysed survey data from all five tropicbird populations ($n = 1186$ survey-days, with counts summed across all five populations for each survey-day), for an overall (family, i.e. not species-specific) assessment of tropicbird occurrence as affected by three mega-scale parameters: (1) ENSO phase, (2) current system (see above) and (3) longitude section. Longitude sections were 'east' and 'west'. Western waters are those west of 135°W for waters north of 20°N, and west of 115°W for waters south of 20°N; see Table 1 for ENSO phases occurring during different cruises. The sample unit was one survey day, excluding those with less than 10 km² of ocean area surveyed. The data included 681 survey-days during spring, 505 during autumn, 395 in El Niño, 563 in the Neutral phase and 228 in La Niña.

Table 1. Season and year of the occurrences of El Niño, Neutral and Niña ENSO phases in the ECP during this study (from Trenberth 1997).

	Spring (April–July)	Autumn (September–December)
El Niño	1980, 1987, 1991, 1992, 1993, 1995	1986, 1987, 1991, 1994
Neutral	1984, 1986, 1990, 1994	1983, 1985, 1989, 1990, 1992, 1993
La Niña	1985, 1988, 1989	1984, 1988, 1995

We conducted a second mega-scale regression to compare ENSO and current system relationships among the five populations. We grouped survey data for each population into one data set with 'population' as one of the independent variables. Specifically, we tested interactions of population with ENSO and current system. Mean areas surveyed per day (± 1 sd) were 115 ± 53 km² ($n = 305$ survey days) for northern *rubricauda*, 97 ± 49 km² ($n = 573$) for southern *rubricauda*, 75 ± 51 km² ($n = 888$) for *aethereus*, 111 ± 53 km² ($n = 263$) for northern *lepturus* and 102 ± 52 km² ($n = 165$) for southern *lepturus*. Thus, the sample size for the population-specific mega-scale analysis was the number of survey-days summed across the five populations = 2194 survey-days.

For the two mega-scale analyses described above, we used the same population boundaries for each tropicbird population as used for estimating abundance of North and South Pacific populations of *rubricauda* and *lepturus* (i.e. with a division at the Equator) and used the data for the entire Pacific for *aethereus*.

We also used multiple regression to examine the relationship between density and three coarse-scale environmental variables (sea-surface salinity, thermocline depth and strength) found to be important to piscivorous ECP seabirds in a previous study (Spear *et al.* 2001). We included two geographical variables, distance to colony and distance to nearest point on the mainland, because many colonies of *aethereus* are located on the mainland shoreline. For northern *rubricauda* populations, all distances to colony are those to the Leeward Hawaiian Islands (Midway Island was used as the focal point), where roughly 90% breed (Harrison 1990); for northern *lepturus* we used Kauai. The number of birds is not known for many colonies of southern *rubricauda*, southern *lepturus* or *aethereus*; for those we used distance to the nearest known major colony of each population (Fig. 1). To investigate seasonal differences in responses to these variables (by testing for interactions), season was also included.

As our objective was to investigate tropicbird responses to environmental variables within their areas of occurrence, for each population, we used data collected only within the pelagic ranges observed in this study (Spear & Ainley 2005). Values for environmental variables were averaged across data amassed during several 0.5-h (or 0.25-h for *aethereus*) transects (= one coarse-scale sample), which we term 'one transect segment'. Mean areas surveyed per segment (± 1 sd) were 28.7 ± 7.0 km² ($n = 892$ segments)

for northern *rubricauda*, 29.7 ± 6.5 km² ($n = 906$) for southern *rubricauda*, 28.4 ± 6.3 km² ($n = 942$) for *aethereus*, 28.4 ± 7.1 km² ($n = 300$) for northern *lepturus* and 29.0 ± 6.9 km² ($n = 159$) for southern *lepturus*. No segments had less than 5 km² of area surveyed.

For mega- and coarse-scale analyses, we normalized density using log-transformation (calculated as: $\log[\text{density} + 0.1]/\log[10]$), which is considered appropriate for data having a Poisson distribution (Kleinbaum *et al.* 1988). Not all residuals met the assumptions of normality (skewness/kurtosis test for normality of residuals, $P > 0.05$); however, least-squares regression analysis is a very robust procedure with respect to non-normality (Seber 1977, chapter 6; Kleinbaum *et al.* 1988). Although they yield the best linear unbiased estimator in the absence of normally distributed residuals, P -values near 0.05 must be regarded with caution (Seber 1977, chapter 3). Therefore, we accepted significance in regression analyses at $P < 0.02$ instead of $P < 0.05$.

Using STATA (Stata Corp. 1995), we conducted a principal components analysis (PCA) in conjunction with ANOVA to compare habitat use among the five tropicbird populations on a seasonal basis. Habitat variables and sample size ($n = 3199$) were the same as those used above in the coarse-scale regression analyses, except we added an extra variable: population. Other than providing information about seasonal differences in the responses among tropicbird populations, the PCA is a means of determining which of the five habitat variables were most important in affecting the tropicbird populations as a group.

To test for significant differences in coarse-scale habitat use among the five tropicbird populations, we used two one-way ANOVAs (i.e. Sidak tests, an improved version of the Bonferroni test; SAS Institute Inc. 1985). In the first, we tested for differences among the PC1 scores of the data representing each tropicbird population; in the second, we compared PC2 scores among those data. We considered two populations to differ significantly if either or both of their PC1 or PC2 scores differed significantly.

Tropicbird densities per segment per day were weighted in the PCA and regression analyses by the area surveyed, to control for differences in area surveyed per segment per day. Densities are reported as birds per 100 km², and, unless noted otherwise, were calculated as the adjusted number of birds divided by the area (km²) surveyed, multiplied by 100.

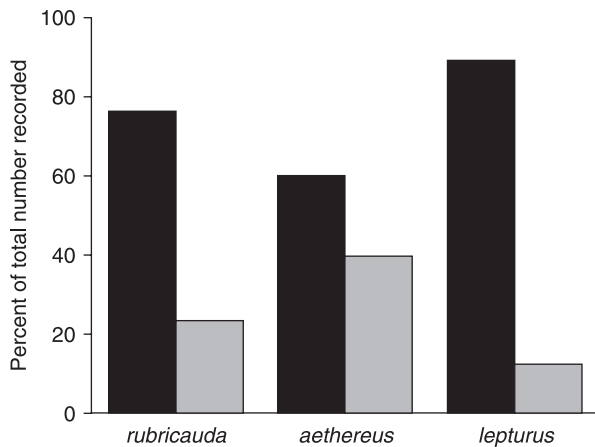


Figure 2. Proportion of three species of tropicbirds seen as singles (dark bars) vs. groups (light bars). Total number of birds recorded was 213 *rubricauda*, 171 *aethereus* and 55 *lepturus*.

Log-likelihood ratio (G) tests were used to compare numerical proportions (i.e. not percentages). Significance was assumed at $P < 0.05$ in these analyses.

RESULTS

Behaviour

Of the 368 sightings, 315 (86%) were of single birds, 43 (12%) of pairs and ten (3%) of larger groups. Hence, 72% of the 439 tropicbirds recorded were singles. The ratio of the number of singles vs. the number in groups differed significantly among species ($G_2 = 22.8$, $P < 0.001$, Fig. 2) owing to the lower proportion of single *aethereus* (60%) and the higher proportion of single *lepturus* (89%).

The proportion of the total unadjusted number of *rubricauda*, *aethereus* and *lepturus* recorded as having been attracted to our vessels was 23% ($n = 48$ attractees), 17% ($n = 29$) and 9% ($n = 5$), respectively (Fig. 3a). These proportions differed insignificantly among species ($G_2 = 4.5$, $P > 0.1$). Within the adjusted counts the proportion was 9, 7 and 4%, respectively (Fig. 3b).

Excluding attracted birds, allocation to three categories of behaviour (i.e. resting on water, feeding, directional flight) was similar across the three species ($G_4 = 6.0$, $P > 0.1$, Fig. 3b). The predominant behaviour among the adjusted counts was directional flight. However, the two stationary behaviours grouped (resting on water and feeding) made up 48, 51 and 58% of the counts for *rubricauda*, *aethereus* and *lepturus*, respectively.

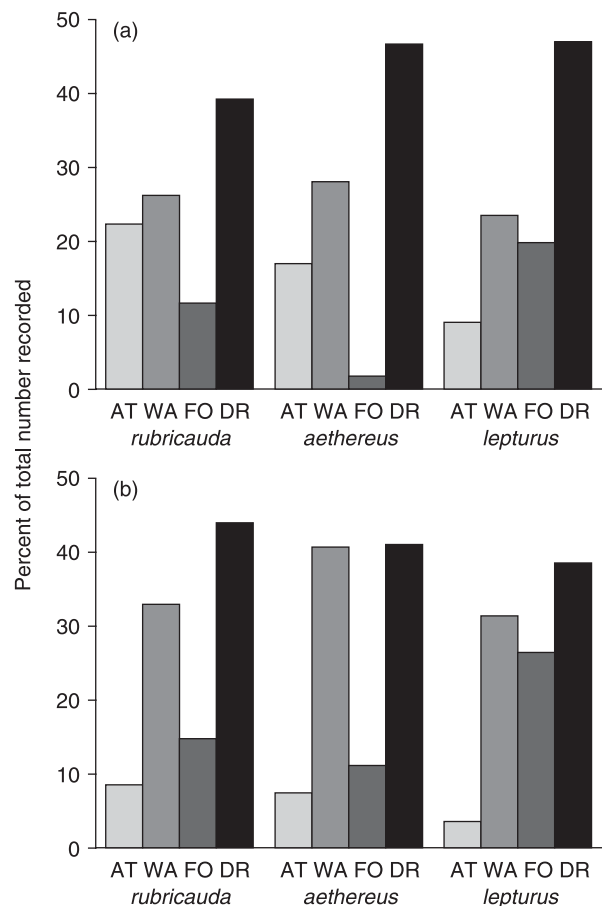


Figure 3. At-sea behaviour of tropicbirds: (a) calculated from unadjusted counts and (b) calculated from adjusted counts (see Methods). AT = attracted to ship, WA = resting on water, FO = foraging, DR = flying in a steady direction. See Results, Tropicbird counts and at-sea ranges, for total unadjusted and adjusted counts.

Feeding associations

None of the 25 foraging *rubricauda* (11 southern and 14 northern) recorded was feeding within multispecies bird flocks feeding over tuna *Thunnus* spp., although eight were feeding < 500 m from large, active flocks (see Gould *et al.* 1974, for similar observations); seven (three southern and four northern) fed solitarily over surface-feeding tuna or Dolphinfinh *Coryphaena hippurus* (that were feeding alone or in small groups), and ten fed where no predatory fishes were seen. Thus, at least 60% of the foraging *rubricauda* fed in the vicinity of surface-feeding predatory fishes, but they avoided feeding flocks.

Similarly, none of the 13 feeding *aethereus* was within seabird flocks, although one was feeding within

100 m of 12 Cook's Petrels *Pterodroma cookii* feeding over a dense school of small fishes leaping at the surface, probably being chased by larger fishes. Four others were feeding 50–100 m from travelling dolphins (two pods of Spinner Dolphins *Stenella longirostris* and one of Bottlenose Dolphins *Tursiops truncatus*). One of these birds caught and ate a 20-cm flyingfish (Exocoetidae) that took flight to avoid the dolphins. Another *aethereus* was feeding over small scombrids (possibly Sierra *Scomberomorus sierra*) or carangids (possibly Yellowtail *Seriola dorsalis*) off the coast of Baja California. Six other *aethereus* fed where subsurface predators were not seen. Thus, 46% of the feeding *aethereus* were utilizing foraging fishes or travelling cetaceans.

In contrast, five of 11 feeding *lepturus* (45%) were associated directly with small, loose-feeding flocks (7.0 ± 3.2 sd birds per flock, $n = 5$ flocks) over small tunas (< 0.6 m). Other than one *lepturus* per flock, flocks included: (1) three White Terns *Gygis alba*; (2) four White Terns; (3) six Sooty Terns *Sterna fuscata* and one White Tern; (4) one Black-winged Petrel *Pterodroma nigripennis*, three Juan Fernandez Petrels *P. externa*, and a Sooty Tern; and (5) ten Sooty Terns and one Juan Fernandez Petrel. The six other feeding *lepturus* were alone; two were each feeding over small Yellowfin *Thunnus albacares*, one over Skipjack *Katsuwonus pelamis*, one over small unidentified scombrids, and two where no aquatic predators were seen. Thus, 64% of the 11 (both northern and southern) *lepturus* were utilizing aquatic predators. When considering all tuna schools identified ($n = 6$) that were being utilized by *lepturus*, 33% were Yellowfin that were 0.4–0.6 m in length and 67% were Skipjack (tunas distinguished by the black strips on the ventral side of the latter species) of similar size as the Yellowfins.

In summary, of the 49 tropicbirds (25 *rubricauda*, 13 *aethereus*, 11 *lepturus*) observed while feeding, 28 (57%) were associated with surface-feeding predators (either dolphins, tuna or dolphinfish).

Effect of mega-scale parameters within tropicbird populations as a group

All mega-scale parameters except season had significant main effects on tropicbird densities within the ECP study area (Table 2a). Overall, tropicbird densities were highest in the Southern Gyre, NEC, Peru Current and Costa Rica Current, although densities differed insignificantly among those four current systems (Sidak tests, all $P > 0.1$, Fig. 4a). With one

Table 2. Results of multiple regression models for the distribution of the five populations of tropicbirds as related to mega-scale environmental variables in the ECP: (a) tested for the overall effect with population counts grouped for each survey day ($n = 1186$ survey-days); (b) tested for interactions between population and the same mega-scale variables ($n = 2194$ survey-days). The dependent variable was tropicbird density ($\log\text{-birds } 100 \text{ km}^{-2}$). For (a), values for main effects were calculated before testing of interactions. All variables were analysed as categorical. Analyses were weighted by area surveyed per day. Significance accepted at $P < 0.2$.

Term	F-value	P-value	df
(a) Model $F_{24,1161} = 8.4$, $P < 0.001$, 15% explained			
Main effects:			
Current system	21.5	< 0.001	6
ENSO phase	5.0	< 0.01	2
Longitude	17.4	< 0.001	1
Interactions:			
ENSO phase * Current system	2.2	< 0.02	12
ENSO phase * Season	5.9	< 0.01	2
Rejected terms:			
Season	4.0	0.05	1
ENSO phase * Longitude	0.9	0.4	2
Season * Longitude	0.6	0.4	1
Season * Current system	1.7	0.11	6
(b) Interactions:			
Population * Current system	14.6	< 0.001	10
Population * ENSO phase	2.7	< 0.01	8
Rejected interaction:			
Population * Season	1.5	0.2	4

exception (see below), densities in the four current systems were higher than those in the ECC, SEC and California Current (all $P < 0.001$). Densities were moderate in the ECC, but did not differ significantly from those of the Peru and Costa Rica currents (all $P > 0.7$). Densities were significantly lower in the SEC and California Current than in other currents, but densities differed little between the two ($P > 0.3$).

Overall, tropicbird densities were significantly lower during El Niño than during Neutral and La Niña ENSO phases (Sidak tests, both $P < 0.01$, Fig. 4b); densities differed little between La Niña and Neutral phases ($P > 0.9$).

The effects on tropicbird density of ENSO phase were also involved in interactions with current system and season (Table 2a). The interaction of ENSO phases with current system reflected high densities during La Niña compared with El Niño in the SEC, ECC, NEC and Southern Gyre, in contrast to higher densities during El Niño compared with La Niña in the California and Peru currents, and high densities only during the Neutral phase in the Costa Rica Current (Fig. 4c). The interaction between ENSO

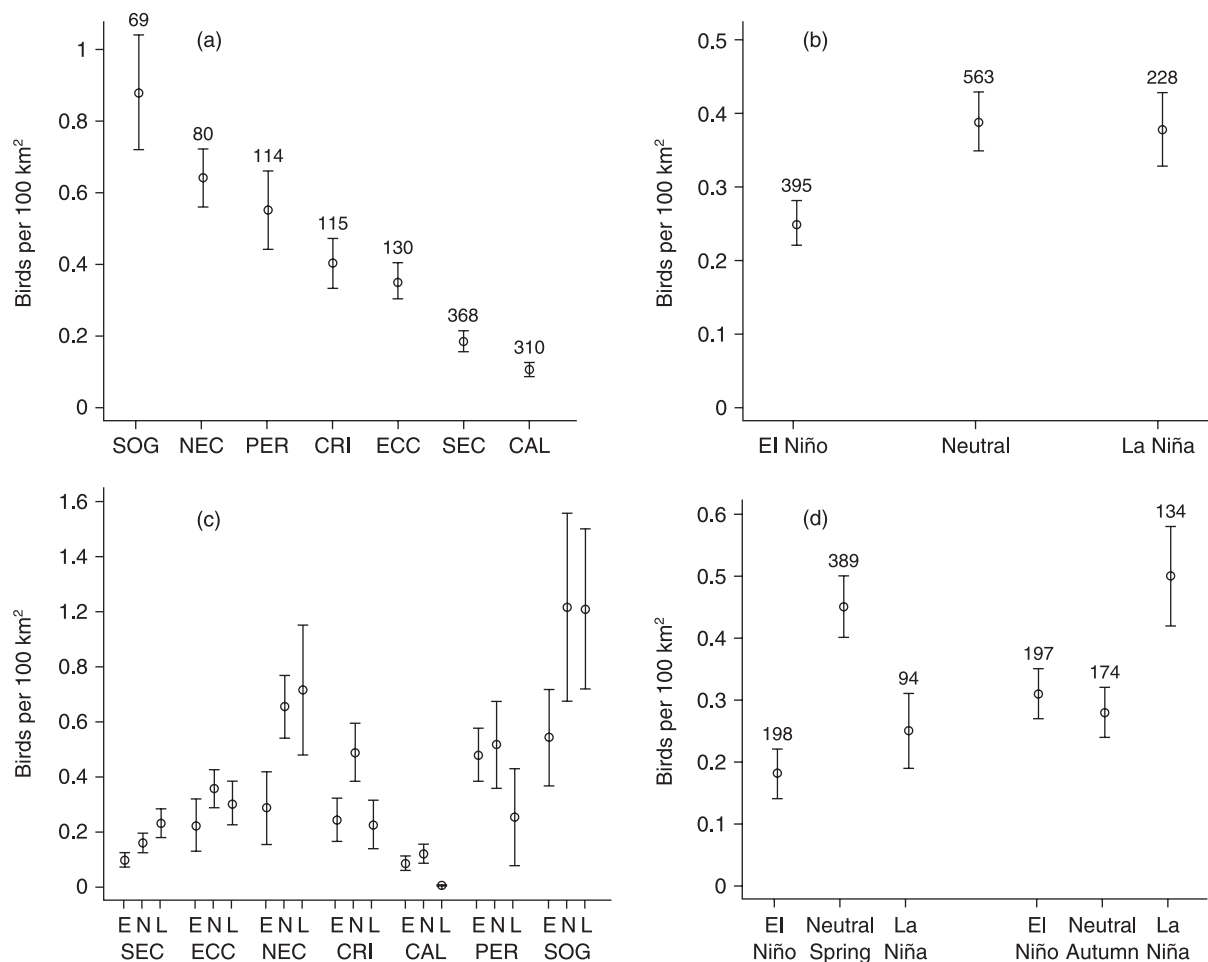


Figure 4. Variation in densities of tropicbirds (populations grouped; mean \pm se) with: (a) current system: SEC = South Equatorial Current, ECC = northern Equatorial Counter Current, NEC = North Equatorial Current, CRI = Costa Rica Current (and adjacent waters), CAL = California Current, PER = Peru Current, SOG = South Pacific Gyre; (b) ENSO phase; (c) current system with respect to ENSO phase (E = El Niño, N = Neutral, L = La Niña); (d) season with respect to ENSO phase. Numbers adjacent to means are sample sizes (survey-transects).

phase and season was due to the highest densities occurring during the Neutral phase in spring, but during the La Niña phase in autumn (Fig. 4d).

Effect of mega-scale parameters compared among populations

The second mega-scale regression revealed two significant interactions when comparing responses among population densities among current systems and ENSO phases (responses pertain only to those observed within the ECP study area; Table 2b). Differences in population densities among current systems reflected the occurrence of the highest values as follows: northern *rubricauda* primarily in the ECC and NEC; southern *rubricauda* in the Southern Gyre;

aethereus in the Costa Rica and Peru Currents; northern *lepturus* in the NEC; and southern *lepturus* in the Southern Gyre (Fig. 5). The differences in the effect of ENSO phase on tropicbird densities reflected highest densities as follows: both populations of *rubricauda* and southern *lepturus* during Neutral and/or La Niña phases; *aethereus* during Neutral and El Niño phases; and northern *lepturus* during El Niño (Sidak tests, all $P < 0.02$, Fig. 6).

Coarse-scale habitat use

Northern *rubricauda*

The multiple regression model for northern *rubricauda* explained 21% of the variation in the at-sea distribution. Density increased with increase in sea-surface

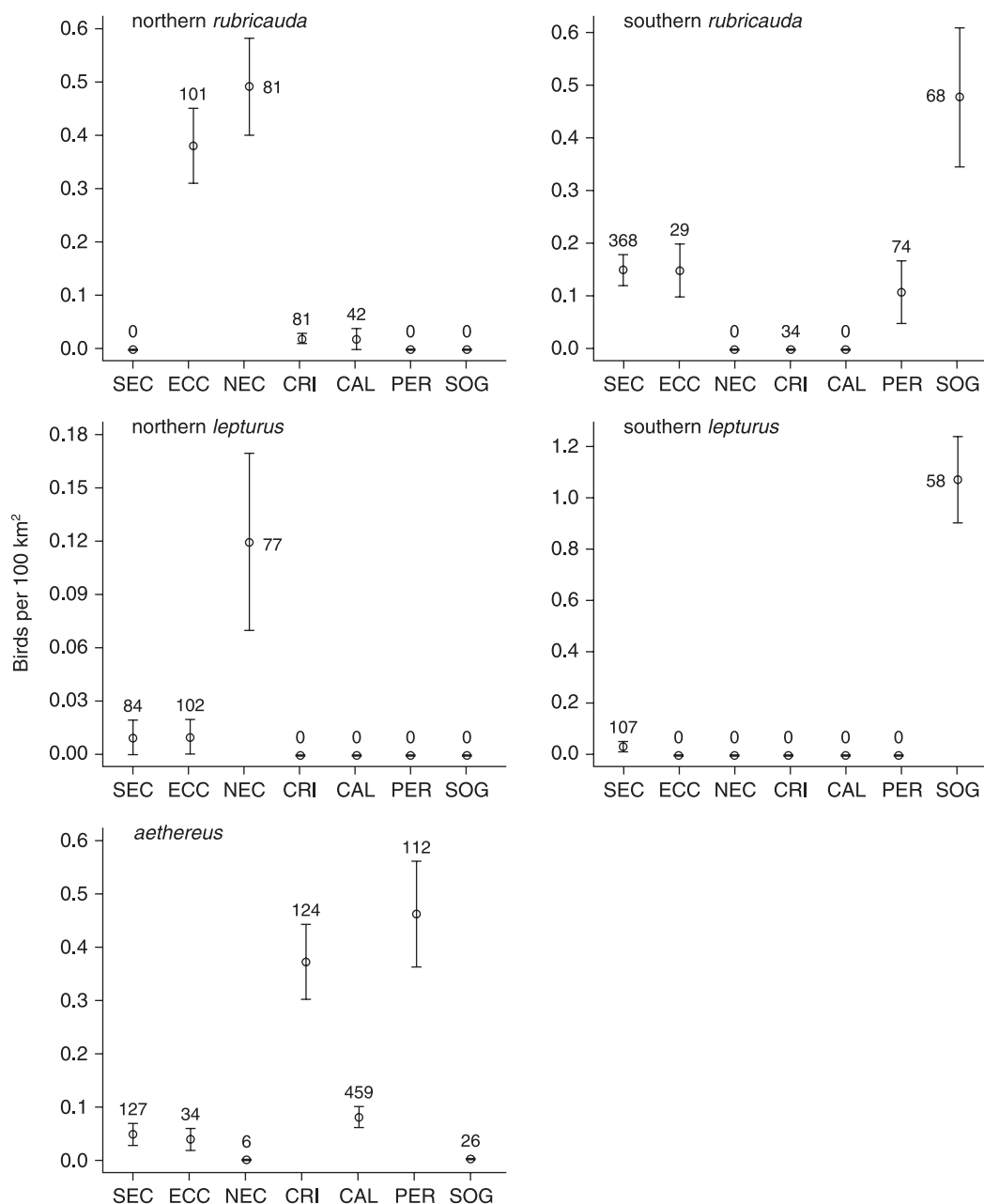


Figure 5. Variation in average densities of five populations of tropicbirds (mean \pm se) observed in each current system within the ECP study area. See Figure 4 for definitions of current system acronyms. Numbers adjacent to means are sample sizes (survey-transects). Zeros indicate that a current system was out of the pelagic range of a population. Sample sizes for a given water mass vary among populations because of differences in pelagic ranges, and thus the ocean area surveyed.

salinity (Table 3). There was a significant interaction between the effects of colony distance and season on northern *rubricauda* density, which was due to a significant linear decrease in density with increase in distance from the Leeward Hawaiian Chain during the boreal spring (Fig. 7a), compared with an insigni-

ficant linear relationship during the boreal autumn (Table 4). In both seasons colony distance was quadratically related to density (Fig. 7a & 7b). In spring this was due to density levelling at distances greater than 4500 km from the Leeward Hawaiian Chain; in autumn the quadratic relationship was due to

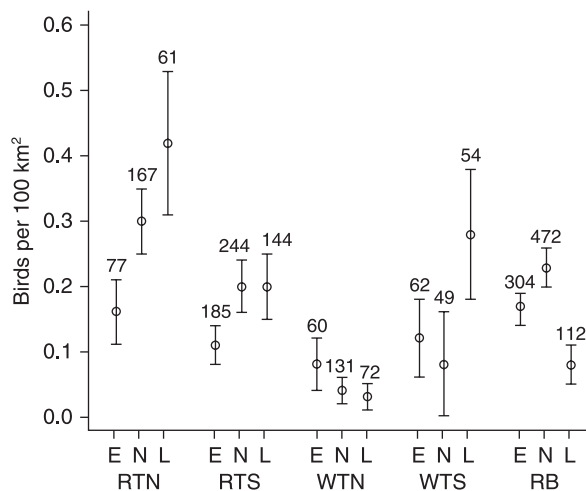


Figure 6. Variation in average densities of five populations of tropicbirds (mean \pm se) with ENSO phase: RTN = northern *rubricauda*, RTS = southern *rubricauda*, WTN = northern *lepturus*, WTS = southern *lepturus*, and RB = *aethereus*. For ENSO phase: (E = El Niño, N = Neutral, L = La Niña). Numbers adjacent to means are sample sizes (survey-days). Sample sizes for a given ENSO phase vary among populations because of differences in pelagic ranges, and thus the ocean area surveyed.

moderately high densities at 1500–2500 km, a density peak at 3500–4500 km and a density decrease at 4501–7000 km.

An interaction between the effects of thermocline strength and season on density of northern *rubricauda* reflected a linear density decrease with increased thermocline strength in boreal autumn compared with lack of a relationship during spring (Table 4).

Southern rubricauda

The regression model for southern *rubricauda* explained 14% of the variation in at-sea density. Densities increased with increase in sea-surface salinity (Table 3). There was also a curvilinear effect of colony distance (Fig. 7c), reflecting a moderately high density at distances up to 1000 km, low densities at 1001–3000 km, a peak at 3001–4000 km and levelling or a slight decline at greater distances. An interaction between season and thermocline strength was due to an insignificant relationship between density and strength in the boreal spring, compared with a significant negative relationship during the boreal autumn (Table 4).

Aethereus

The model for *aethereus* explained 21% of the variation in density. Densities increased with increase in sea-surface salinity and decreased with increase in thermocline depth (Table 3).

A significant interaction of season with distance from land (Table 4) resulted from a significant increase with distance in the boreal autumn compared with a lack of a significant linear effect in the boreal spring (Fig. 7d & 7e). However, in spring there was a quadratic effect of distance to land due to low near-colony densities, a peak at distances of 401–550 km followed by a steep decline at greater distances. Thus, distributions were skewed more towards offshore waters in boreal autumn compared with spring.

An interaction between season and sea-surface salinity was due to a significant increase in density with

Table 3. Results of multiple regression models for the distribution of five tropicbird populations as related to significant environmental variables in the ECP. The dependent variable was tropicbird density (log-birds per 100 km²). Values for main effects were calculated before testing for interactions (see Table 4 for interactions). Values for linear terms were calculated after polynomials for the respective term were removed from the model. Given for each variable are the coefficient sign (i.e. negative or positive slope, in parentheses) followed by the *P*-value. Terms having significant interactions with season are denoted with an asterisk. Terms that were tested but which did not have a significant effect in any of these analyses were sea-surface temperature and wind speed. All numerator *df* = 1. Values of *n* are given in the Methods for 'coarse-scale' analyses.

	Northern <i>rubricauda</i>	Southern <i>rubricauda</i>	<i>aethereus</i>	Northern <i>lepturus</i>	Southern <i>lepturus</i>
Sea-surface salinity	(+) < 0.01	(+) < 0.001	(+) < 0.01*	(+) < 0.001*	(+) < 0.001*
Sea-surface temperature	–	–	–	(–) < 0.001	–
Thermocline depth	–	–	(–) < 0.001	–	(+) < 0.01
Thermocline strength	(ns)*	(ns)*	–	(–) < 0.02*	–
Colony distance					
linear	(ns)*	(ns)	–	(–) < 0.001	(–) < 0.01
quadratic	–	(+) < 0.01	–	(+) < 0.001	(+) < 0.02
Land distance					
linear	–	–	(ns)*	–	(–) < 0.02
quadratic	–	–	–	–	–

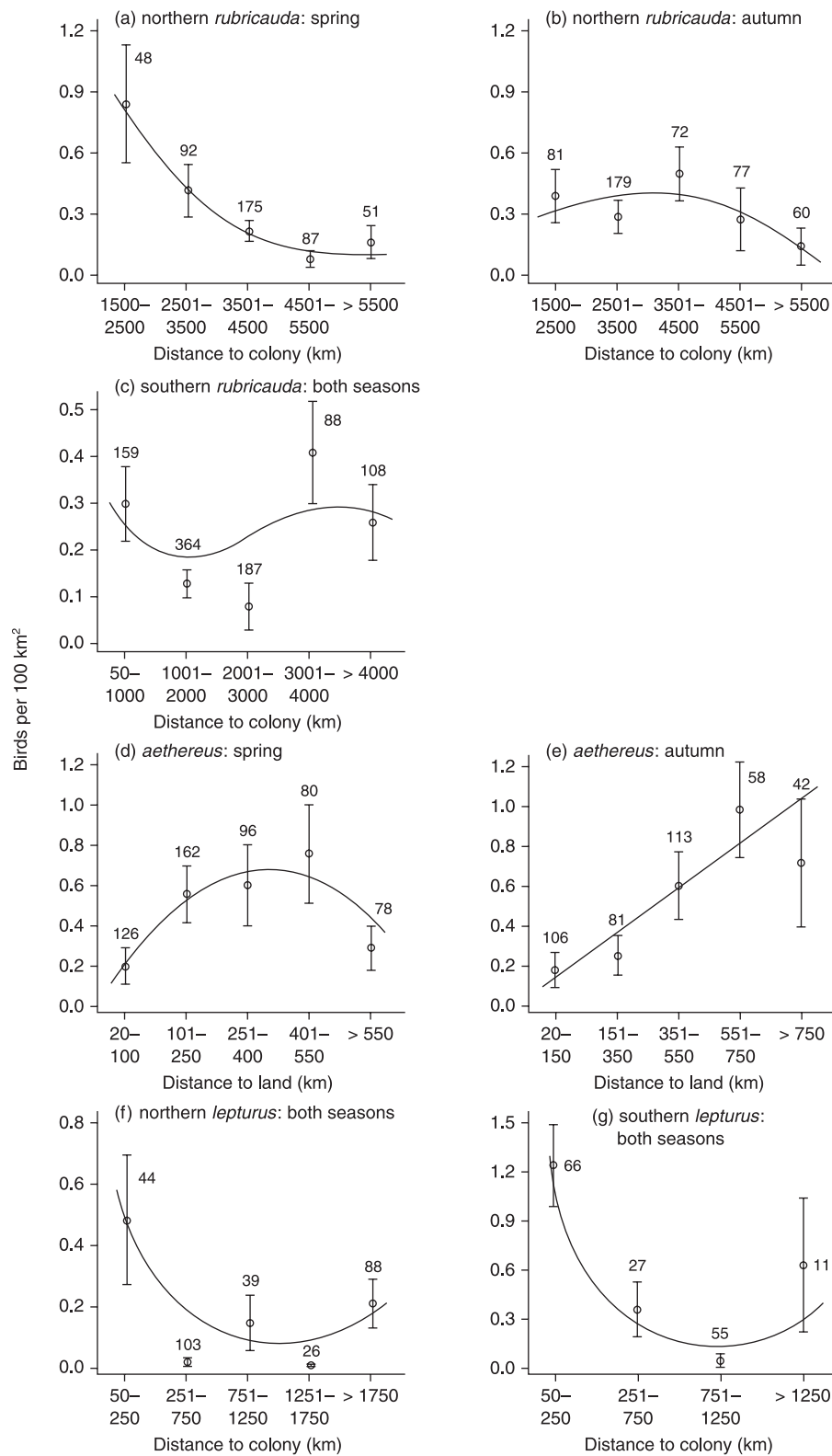


Figure 7. Relation of distance to colony and land with densities (mean \pm se) of five populations of tropicbirds. Sample sizes (number of survey transects) are given adjacent to means.

Table 4. Significant interactions (denoted by two terms separated by an asterisk) between environmental variables and season (boreal timeframe) in their relationship with tropicbird density (log-birds per 100 km²). Interactions were calculated when included in the multiple regression analyses reported in Table 3. Given for the seasonal effect of each variable is the coefficient sign (i.e. negative, positive, or insignificant [ns]) relationship with tropicbird density, given in parentheses) followed by the *P*-value. All numerator *df* = 1. Values of *n* are given in the Methods for 'coarse-scale' analyses.

Northern <i>rubricauda</i>		<i>Aethereus</i>	
Season * Thermocline strength	< 0.01	Season * Sea-surface salinity	< 0.01
Spring	(ns) 0.4	Spring	(ns) 0.2
Autumn	(-) < 0.01	Autumn	(+) < 0.01
Season * Colony distance	< 0.001	Season * Land distance	< 0.01
Spring		Spring	
linear	(-) < 0.001	linear	(ns) 0.6
quadratic	(+) < 0.01	quadratic	(-) < 0.02
Autumn		Autumn	(+) < 0.01
linear	(ns) 0.5		
quadratic	(-) < 0.01		
Southern <i>rubricauda</i>		Northern <i>lepturus</i>	
Season * Thermocline strength	< 0.001	Season * Sea-surface salinity	< 0.01
Spring	(ns) 0.4	Spring	(ns) 0.5
Autumn	(-) < 0.01	Autumn	(+) < 0.001
		Season * Thermocline strength	< 0.02
		Spring	(ns) 0.9
		Autumn	(-) < 0.001
Southern <i>lepturus</i>			
Season * Sea-surface salinity	< 0.001		
Spring	(+) < 0.001		
Autumn	(ns) 0.2		

increase in salinity during boreal autumn compared with lack of an effect in spring (Table 4).

Northern lepturus

The regression model for northern *lepturus* explained 32% of the variation in density. Densities increased with increase in sea-surface salinity, and decreased with increased sea-surface temperature, thermocline strength and distance from the colony (Table 3). There was a quadratic relationship between density and distance to nearest colony (Kauai Island), with high densities near the island (50–250 km distant), and a steep decline and levelling at the ranges of 251–2600 km (Fig. 7f).

Sea-surface salinity and thermocline strength were involved in significant interactions with season (Table 4). These interactions reflected a significant increase and decreases in density with increase in salinity and thermocline strength, respectively, during boreal autumn, compared with lack of an effect during boreal spring.

Southern lepturus

The regression analysis for southern *lepturus* explained 28% of the density variance. Densities increased with sea-surface salinity and thermocline depth, and

decreased with distance from the colony and land (Table 3). The effect of colony distance on density was quadratic owing to a decline in density at distances of 750–1250 km, followed by levelling or a slight increase at greater distances (Fig. 7g). A significant interaction between season and sea-surface salinity reflected a significant increase in density with increase in salinity during boreal autumn in contrast to the lack of a significant relationship between salinity and density during the boreal spring (Table 4).

Coarse-scale environmental characteristics compared among populations

Use of three of the five environmental variables differed significantly between northern and southern *rubricauda* in both the boreal spring and the boreal autumn (Table 5, Fig. 8). Northern *rubricauda* occurred in waters of lower salinity, a more developed thermocline and higher wind speeds than the southern population. The two *rubricauda* populations ranged at similar distances from the nearest land and nearest colony during both seasons.

The two populations of *lepturus* differed significantly for two of the five environmental variables in

Table 5. Ocean habitat characteristics (mean \pm sd) of five populations of tropicbirds in the tropical and subtropical eastern Pacific, 1980–95. For a given population, spring is represented by the upper row of values and autumn by the lower. Values of n are the raw number of birds sighted: northern *rubricauda* – spring and autumn, $n = 42$ and 71 birds, respectively; southern *rubricauda*, $n = 58$ and 42 birds; *aethereus* – spring and autumn, $n = 99$ and 72 birds; northern *lepturus* – spring and autumn, $n = 6$ and 13 birds; southern *lepturus*, $n = 26$ and 10 birds.

Sea-surface temperature ($^{\circ}\text{C}$)	Sea-surface salinity (ppt)	Therm. depth (m)	Therm. strength ($^{\circ}\text{C}$ change)	Wind speed (km/h)	Distance to land (km)	Distance to colony (km)
Northern <i>rubricauda</i>						
26.9 ± 1.2	34.66 ± 0.33	74 ± 26	6.8 ± 3.4	27 ± 6	1032 ± 585	3121 ± 908
26.4 ± 1.9	34.33 ± 0.55	62 ± 34	4.0 ± 2.1	26 ± 12	1279 ± 520	3698 ± 629
Southern <i>rubricauda</i>						
26.1 ± 2.1	35.33 ± 0.56	65 ± 27	3.8 ± 1.7	21 ± 8	1021 ± 489	2376 ± 1747
24.4 ± 1.6	35.49 ± 0.38	83 ± 45	2.3 ± 1.5	28 ± 6	1035 ± 574	1948 ± 857
<i>Aethereus</i>						
24.8 ± 3.5	34.13 ± 1.14	29 ± 22	3.7 ± 2.7	21 ± 9	236 ± 210	245 ± 244
23.2 ± 3.5	34.54 ± 0.79	38 ± 16	4.8 ± 2.5	24 ± 11	379 ± 250	1108 ± 184
Northern <i>lepturus</i>						
24.2 ± 1.3	34.40 ± 0.21	102 ± 38	2.2 ± 0.8	40 ± 17	271 ± 576	302 ± 330
25.2 ± 2.4	34.86 ± 0.24	71 ± 15	2.7 ± 0.7	26 ± 10	1052 ± 770	1245 ± 934
Southern <i>lepturus</i>						
28.2 ± 1.0	35.79 ± 0.50	80 ± 17	2.0 ± 0.3	29 ± 8	331 ± 327	778 ± 631
27.4 ± 0.8	35.79 ± 0.31	114 ± 11	2.6 ± 1.5	24 ± 8	253 ± 280	548 ± 299

	Spring					Autumn				
	High	RTN	RTS	RB	WTN	High	RTN	WTN	RTS	RB
Surface temp.	WTS	RTN	RTS	RB	WTN	WTS	RTN	WTN	RTS	RB
Surface salinity	WTS	RTS	RTN	WTN	RB	WTS	RTS	WTN	RB	RTN
Therm. depth	WTN	WTS	RTN	RTS	RB	WTS	RTS	RTN	WTN	RB
Therm. strength	RTN	RTS	RB	WTN	WTS	RB	RTN	WTN	WTS	RTS
Wind speed	WTN	WTS	RTN	RTS	RB	RTS	WTN	RTN	WTS	RB
Land distance	RTN	RTS	WTS	WTN	RB	RTN	WTN	RTS	RB	WTS
Colony distance	RTN	RTS	WTS	WTN	RB	RTN	RTS	WTN	RB	WTS

Figure 8. Comparisons among five tropicbird populations with respect to association with seven habitat variables. Lines connecting populations indicate insignificant differences (Sidak tests, $P > 0.05$). See Figure 6 for definitions of acronyms.

both the boreal spring and the boreal autumn (Table 5, Fig. 8). Southern *lepturus* were found in waters having higher sea-surface salinity in both seasons. During boreal spring, southern birds were associated with higher sea-surface temperature and, in boreal autumn, with a deeper thermocline. During boreal spring, the distance from nearest land and from nearest colony differed little between northern and southern *lepturus*, but during boreal autumn, the distance to nearest land was greater among northern *lepturus*.

The only environmental variable for which *aethereus* differed significantly from each of the other populations

was thermocline depth; *aethereus* was associated with shallower thermoclines (Table 5, Fig. 8). *Aethereus* were also associated with the lowest sea-surface temperatures and salinities, although these associations did not differ significantly from that of 1–2 other populations in each case.

The northern *rubricauda* population differed significantly from the northern *lepturus* population for three of the five environmental parameters during boreal spring (Fig. 8). Northern *rubricauda* were found in waters having higher temperature and a stronger thermocline. During autumn, northern *rubricauda* were found in waters having lower salinity and a stronger thermocline compared with northern *lepturus*.

Overall effect of coarse-scale oceanographic and geographical parameters

We used the first two PC axes of the PCA to compare overall use of environmental variables among the five tropicbird populations because these axes explained 65 and 66% of the variation among the five during the boreal spring and autumn, respectively (Table 6). In spring, the most important explanatory variables on the PC1 axis were positively loaded variables: distance from the mainland and distance from the

Table 6. Principal component (PC) analyses: including (a) eigenvector (cumulative) proportions of variance explained by (b) five habitat variables affecting at-sea distributions of five populations of tropicbirds. Only oceanographic/geographical data from locations of sightings were used; analyses weighted by tropicbird density. Note that Boreal spring = austral autumn and Boreal autumn = austral spring.

(a) Eigenvalue			(b)				
PC	Cumulative proportion		Habitat variable	Eigenvector loadings:			
	Boreal spring	Boreal autumn		Boreal spring		Boreal autumn	
				PC1	PC2	PC1	PC2
1	0.40	0.37	Sea-surface salinity	0.33	0.64	0.55	-0.39
2	0.65	0.66	Therm. depth	0.39	0.56	0.52	-0.05
3	0.82	0.83	Therm. strength	0.42	-0.37	-0.52	0.20
4	0.93	0.92	Distance to colony	0.58	-0.33	-0.25	0.64
5	1.00	1.00	Distance to land	0.48	-0.19	-0.30	0.63

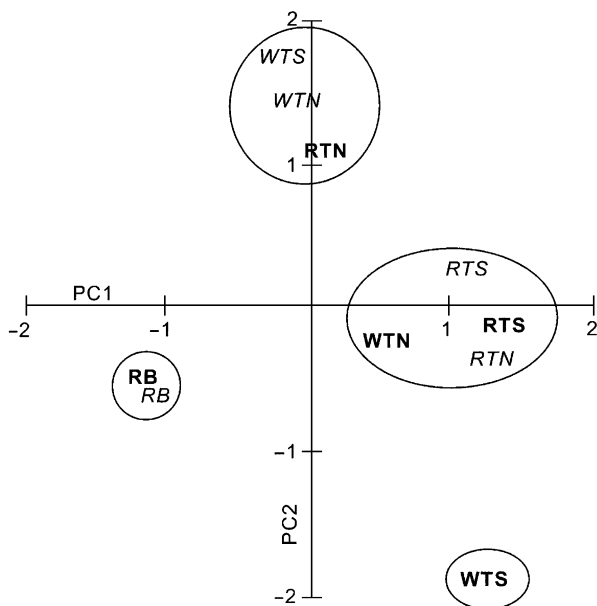


Figure 9. Principal component analysis comparing the overall effect of the five more important environmental variables on the distributions of five tropicbird populations. See Figure 6 for population codes. Spring is denoted with italics; autumn with bold non-italics.

nearest major colony. The most important variables on the PC2 axis were positively loaded sea-surface salinity and thermocline depth. Thus, the elevated positions on the positive side of the PC2 axis of north and south *lepturus* during boreal autumn/austral spring (Fig. 9), and the elevated positions of southern *rubricauda* and *lepturus* on the positive side of the PC1 axis during boreal spring, reflect the long distance relationship of these populations with distance to land and especially distance to colony during respective seasons (see Fig. 7).

During autumn, the most important explanatory variables on the PC1 axis were positively loaded sea-surface salinity and thermocline depth, and negatively loaded thermocline strength (Table 6). On the PC2 axis, the most important variables were positively loaded distance from the nearest major colony and from the land.

Habitat use of *aethereus* and South Pacific *rubricauda* differed little between seasons (Sidak tests, both $P > 0.5$, Fig. 7), whereas that of North and South Pacific *lepturus* and of North Pacific *rubricauda* did (all $P < 0.02$). The five tropicbird populations differed significantly when compared between seasons on either the PC1 and/or the PC2 axis (Fig. 7). North vs. south populations of *rubricauda* and *lepturus* differed significantly on both axes during autumn, but not during spring. During autumn, all five populations differed significantly from one another on one or the other axis.

Aethereus and southern *rubricauda* were the only populations having similar between-season responses to environmental variables (Sidak tests, both $P > 0.5$).

DISCUSSION

Behaviour at sea

During daylight, tropicbird species were seen nearly as often resting on the water as they were in flight. Resting frequency was over twice as great as that of four taxa of procellariids resident in the same waters (Spear *et al.* 1995). Tropicbird parents of large chicks spend 12 h of each 24-h day (night length in tropical oceans) sitting on the water (Schreiber & Schreiber 1993); however, we doubt that the proportion of time spent on the water in our study was influenced

by colony attendance because most of our data were collected more than 50 km from any colony. Higher resting frequencies among tropicbirds are probably due to their exclusive use of flapping flight (in combination with their high wing loading; Spear & Ainley 1997a), a less efficient flight style than that of procellariids (Pennycuik 1989). The latter also make more efficient use of the wind (Spear & Ainley 1997b).

Consistent with the data of Gould *et al.* (1974) and Ballance and Pitman (1999), tropicbirds were mostly solitary at sea. Gould *et al.* suggested, and we agree, that *rubricauda* avoid bird feeding-flocks because they cannot feed effectively within them. The two larger species of tropicbirds surface-plunge from heights of up to 40 m, and a large swirling mass of birds below may present too much interference. Yet avoidance of multispecies feeding-flocks by the two larger species of tropicbirds is in marked contrast to boobies (Sulidae) and frigatebirds (Fregatidae) that plunge dive from even greater heights while feeding in multispecies bird flocks over tuna. Diving tropicbirds, especially the larger *rubricauda* and *aethereus*, do not appear as controlled or co-ordinated as boobies or frigatebirds. Although it is possible that flock avoidance by these two species could be related to avoidance of being involved in a collision with another bird, we have never seen seabirds accidentally collide, or seen an injured seabird, when observing feeding-flocks in the ECP.

In contrast to flock avoidance by *rubricauda* and *aethereus*, 57% of the feeding *lepturus* we observed had joined small feeding flocks that were loosely distributed over smaller, feeding tunas (and see below). This may have been possible because of the small size of those flocks (making it easy for *lepturus* to keep track of flock members), the lower altitudes used by plunging *lepturus* (generally < 20 m; also see Lee & Walsh-McGehee 1988), the infrequent participation by procellariids (that feed from lower altitudes and appear to present most of the potential interference to higher flying Pelecaniformes and Larids), in combination with the smaller size of *lepturus* and, thus, better manoeuvrability than the two larger tropicbird species.

Distribution relative to colony location

Rubricauda had a more extended range from breeding colonies than did *aethereus* and *lepturus* (see also Diamond (1975) and Schaffner (1988) for similar findings regarding *lepturus* and *rubricauda*). Yet

post-breeding (boreal autumn) densities of *aethereus* were highest in waters most distant from nearest colonies and those of northern *rubricauda* were highest at mid-range distances, whereas those of southern *rubricauda* were bimodal with peaks near to, and furthest from, the nearest colonies during both the austral spring and the austral autumn.

During the breeding season of *aethereus* (boreal spring), their densities were highest mid-range, at 100–550 km from the nearest colonies. Thus, the closer mid-range birds, at least, could easily have been represented by a large proportion of breeding birds. Similarly, northern *rubricauda* densities were highest during the boreal spring breeding season in the waters at the western edge of our study area: waters nearest to the primary colony on the Leeward Hawaiian Chain. Although the western perimeter was 1500 km from the reference colony (Midway), these results are consistent with Gould *et al.* (1974), who also reported that the highest densities were in waters near to colonies during the breeding season.

The southern *rubricauda* distribution relative to colony locations was especially interesting because of its bimodality. In this regard, the near-colony peak was likely to have been mainly breeding adults and the more distant peak predominantly subadults. This was indicated by the age-related analysis showing a greater proportion of adults vs. subadults occurring in near-colony waters compared with a greater proportion of subadults in waters more distant from colonies. This pattern is similar to that of other seabird populations in which subadults are more abundant on the periphery of the population's range (e.g. gulls and penguins: Spear 1988, Ainley *et al.* 1995).

Few studies, however, have described dispersal patterns of highly pelagic, tropical seabirds (but see Gould *et al.* 1974). Besides logistic difficulties associated with pelagic studies, dispersal of these species is usually multidirectional and less predictable than that of species breeding in temperate to polar latitudes where, owing to seasonal change in climate, entire populations make relatively synchronized, directional movements.

Important environmental factors affecting at-sea distributions

The breeding seasons of the five tropicbird populations appear to be boreal spring/austral autumn (Spear & Ainley 2005). During that period, the more important variables affecting the at-sea occurrence

of these populations were geographical (including distance from nearest colony and from nearest land). During the breeding period, oceanographic variables (sea-surface salinity and thermal structure of the water column) were of secondary importance. However, these latter variables were the most important ones affecting tropicbird distributions during the non-breeding period in the boreal autumn/austral spring.

Greater importance of the geographical variables in boreal spring vs. autumn is consistent with the results for comparison of PC scores among populations (i.e. the occurrence of a given population relative to the combined environmental variables). For the breeding season, these comparisons indicated insignificant differences between northern and southern populations of the same species (*lepturus* and *rubricauda*), each of which had similar relationships with the geographical variables. This result was also consistent with the fact that most of our data were collected in the northern hemisphere where tropicbirds breed during boreal spring, and thus their distributions are more likely to be constrained by colony location at that time.

By contrast, in the non-breeding period, when oceanographic variables predominated, significant differences existed among the five populations. These differences between seasons are probably related to the more defined oceanographic properties of the equatorial current systems in boreal autumn/austral spring (Wyrтки 1966), in combination with the occurrence of each tropicbird population predominantly in certain current systems having certain conditions (see below).

Population-specific habitat use

The different habitat use made by tropicbird populations was probably related to the preference of each for conditions where the presence of food is most predictable, as well as its proximity to their colonies. For example, *lepturus* and *aethereus* occurred closer to their colonies than did *rubricauda*. Populations of *rubricauda* were most abundant in waters having thermoclines of medium depth and salinity, whereas *lepturus* (particularly southern *lepturus*) were associated with waters having very deep thermoclines and high salinity. The latter difference reflects the association of *lepturus* and *rubricauda* primarily with the NEC, which includes waters surrounding the southeastern Hawaiian Islands, and also south Pacific waters of the SEC (herein termed 'Southern Gyre'),

including waters surrounding the Polynesian Islands (Wyrтки 1966; and see Fig. 1).

In contrast, *aethereus*, particularly during the boreal autumn non-breeding period of that species, differed from the other two species by their occurrence in waters having a shallow thermocline and low salinity, i.e. conditions of the seaward edge of the Peru and Costa Rica currents (Wyrтки 1967).

Yet each tropicbird species had specific foraging and feeding behaviours, that, in the case of *lepturus* and *rubricauda*, did not appear to differ between northern and southern populations (i.e. each population of those species primarily utilized the same species of aquatic predators and the same feeding behaviours) despite the fact that northern and southern populations occurred in different ocean systems. Thus, the question remains as to what environmental factors determine which ocean regimes are occupied by each of two distinct populations of the same species?

If we assess the more important environmental variables for within-species similarities between northern and southern populations, only the distance from the colony and thermocline depth stand out in both spring and autumn. In addition, 57% of the feeding tropicbirds we recorded were associated with subsurface predators, primarily Scombrids (tunas), Coryphaenids (dolphinfish), Carangids (mackerels) and Cetaceans (dolphins).

Significant species-specific relationships with thermocline depth among tropicbirds are consistent with the fact that the structure of the upper water column is importantly involved with the abundance, species/age-class composition and school-structure of tuna (Murphy & Shomura 1972, Brill *et al.* 1999) and the seabirds that depend on them (Spear *et al.* 2001). In particular, the studies of surface-feeding Yellowfin Tuna indicate that they are found in waters with a moderately deep (50–125 m) thermocline. The latter may increase the chances of the day-feeding tuna (Buckley & Miller 1994, Roger 1994) finding prey that hide at depth during the day (Watanabe *et al.* 1999).

In contrast to *rubricauda*, which frequently feed over larger (> 1 m) surface-feeding tunas and dolphinfish (*Coryphaena* sp.), the feeding *lepturus* we observed were feeding over smaller (< 1 m) surface-feeding Yellowfin and Skipjack tuna. We suspect that the difference between *rubricauda* and *lepturus* regarding their use of larger vs. smaller surface-feeding tunas can be explained by: (1) *lepturus* stayed closer to their colony islands; (2) smaller tuna also being more abundant near islands, but replaced

by larger tuna further offshore (Murphy & Shomura 1972), where *rubricauda* predominated; and (3) the prey of *rubricauda* being larger than those utilized by *lepturus* (Harrison 1990, our unpubl. data). Thus, if we assume that larger tuna feed on larger prey, this could also explain the apparent size difference of tuna utilized by *rubricauda* vs. *lepturus*. We suspect that these three factors may be key to understanding the species-specific relationship with colony distance (and thus distributions) of the two tropicbird species.

The feeding *aethereus* we observed did not utilize tuna, but utilized dolphin travelling at the ocean surface, as well as surface-feeding species of smaller Scombrids and Carangids. Specifically, the two fish species that we observed being utilized by *aethereus* (Yellowtail and Sierra) are found nearshore (generally within 5 km) and feed at shallow depths (1–25 m; Miller & Lea 1972, L. B. Spear, pers. obs. from the Sea of Cortez).

Effect of El Niño Southern Oscillation

The effects of the three ENSO phases on the distributions of tropicbird populations were divisible into two types of responses. First, higher densities of both populations of *rubricauda*, and southern *lepturus*, occurred within the ECP study area during La Niña compared with El Niño, indicating that more birds representing these populations remained in or moved into it from waters in the South Pacific during La Niña. Tropicbird responses to El Niño are less clear.

CONCLUSIONS

At sea, tropicbird distributions in the ECP are largely determined by colony location, especially during the breeding season. During the non-breeding season, their distributions are determined primarily by use of different current systems that are delineated by sea-surface temperature and salinity (although the former was not an important factor affecting tropicbird distributions in this study), and thermocline (depth and strength) structure of the top 125 m of the water column.

When foraging, each species except *lepturus* nearly always feeds solitarily. Yet all three species make regular use of larger aquatic predators, species that in turn utilize different oceanographic conditions, and distances from shore. We believe that the latter has a major influence on the distributions of tropicbird species in the eastern Pacific.

Although tropicbirds are partially dependent on predatory fishes to make prey available, because the birds feed solitarily during the day, they search in very low densities for feeding opportunities over wide areas, a foraging pattern consistent with opportunistic feeding.

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REFERENCES

- Ainley, D.G., Nur, N. & Woelher, E.J. 1995. Factors affecting the distribution and size of pygoscelid penguin colonies in the Antarctic. *Auk* **112**: 171–182.
- Ballance, L.T. & Pitman, R.L. 1999. Feeding ecology of tropical seabirds. *Proc. Int. Ornithol. Congr.* **22**: 1–17.
- Brill, R.W., Block, B.A., Boggs, C.H., Bigelow, K.A., Freund, E.V. & Marcinek, D.J. 1999. Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Mar. Biol.* **133**: 395–408.
- Buckley, T.T. & Miller, B.S. 1994. Feeding habitats of yellowfin tuna with fish aggregation devices in American Samoa. *Bull. Mar. Sci.* **55**: 445–459.
- Diamond, A.W. 1975. The biology of tropicbirds at Aldabra Atoll, Indian Ocean. *Auk* **92**: 16–39.
- Gould, P.J., King, W.B. & Sanger, G.A. 1974. Red-Tailed Tropicbird (*Phaethon rubricauda*). In King, W.B. (ed.) *Pelagic Studies of Seabirds in the Central and Eastern Pacific Ocean*: 206–231. Washington, DC: Smithsonian Institution.
- Harrison, C.S. 1990. *Seabirds of Hawaii*. New York: Cornell University Press.
- Hunt, G.L. Jr & Schneider, D.C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. In Croxall, J.P. (ed.) *Seabirds: Feeding Ecology and Role in Marine Ecosystems*: 7–41. Cambridge: Cambridge University Press.
- Kleinbaum, D.G., Kupper, L.L. & Muller, K.E. 1988. *Applied Regression Analysis and Other Multivariable Methods*. Boston: PWS-KENT Publishing Co.
- Lee, D.S. & Walsh-McGehee, M. 1988. White-Tailed Tropicbird (*Phaethon lepturus*). *The Birds of North America*, no. 353.

- 1–24. Philadelphia, PA: The Academy of Natural Sciences, and Washington, DC: American Ornithologists' Union.
- Miller, D.J. & Lea, R.N.** 1972. Guide to the coastal marine fishes of California. *California Fish Bull.* **157**: 1–249.
- Murphy, G.L. & Shomura, R.S.** 1972. Pre-exploitation abundance of tunas in the equatorial central Pacific. *Fish Bull.* **70**: 875–913.
- Pennycuik, C.J.** 1989. *Bird Flight Performance: a Practical Calculation Manual*. Oxford: Oxford University Press.
- Roger, C.** 1994. Relationship among yellowfin and skipjack tuna, their prey and plankton in the tropical west Indian Ocean. *Fish Oceanogr.* **3**: 133–144.
- SAS Institute Inc.** 1985. *SAS User's Guide: Statistics*, 5th edn. Cary, NC: SAS Institute Inc.
- Schaffner, F.C. Jr** 1988. *The breeding biology and energetics of the White-tailed Tropicbird (Phaethon lepturus) at Culebra, Puerto Rico*. PhD dissertation, University of Miami, Miami, FL.
- Schreiber, E.A. & Schreiber, R.W.** 1993. Red-tailed Tropicbird (*Phaethon rubricauda*). In Poole, A. & Gill, F. (eds). *The Birds of North America*, no. 43. 1–24. Philadelphia, PA: The Academy of Natural Sciences, and Washington, DC: American Ornithologists' Union.
- Seber, G.A.F.** 1977. *Linear Regression Analysis*. New York: John Wiley and Sons.
- Spear, L.B.** 1988. Dispersal patterns of Western Gulls from Southeast Farallon Island. *Auk* **105**: 128–141.
- Spear, L.B. & Ainley, D.G.** 1997a. Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis* **139**: 221–233.
- Spear, L.B. & Ainley, D.G.** 1997b. Flight speed of seabirds in relation to wind speed and direction. *Ibis* **139**: 234–251.
- Spear, L.B. & Ainley, D.G.** 2005. At-sea distributions and abundance of tropicbirds in the eastern Pacific. *Ibis* doi:10.1111/j.1474-919x.2005.00411.
- Spear, L.B., Ainley, D.G., Hardesty, B.D., Howell, S.N.G. & Webb, S.W.** 2005. Reducing biases affecting at-sea surveys of seabirds: use of multiple observer teams. *Mar. Ornithol.* In press.
- Spear, L.B., Ainley, D.G., Nur, N. & Howell, S.N.G.** 1995. Population size and factors affecting at-sea distributions of four endangered procellariids in the eastern tropical Pacific. *Condor* **97**: 613–638.
- Spear, L.B., Ballance, L.T. & Ainley, D.G.** 2001. Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline vs. the Equatorial Front. *Mar. Ecol. Prog. Series* **219**: 275–289.
- STATA Corp.** 1995. *STATA Reference Manual: Release 5.1*, 6th edn. College Station, TX: Stata Corporation.
- Trenberth, K.E.** 1997. The definition of El Niño. *J. Am. Meteor. Soc.* **78**: 2771–2777.
- Watanabe, H., Moku, M., Kawaguchi, K., Ishimaru, K. & Ohno, A.** 1999. Diel vertical migration of myctophid fishes (Family Myctophidae) in the transitional waters of the western North Pacific. *Fish Oceanogr.* **8**: 115–127.
- Wyrtki, K.** 1966. Oceanography of the eastern equatorial Pacific Ocean. *Oceanogr. Mar. Biol. Annu. Rev.* **4**: 33–68.
- Wyrtki, K.** 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. *Int. J. Oceanogr. Limnol.* **3**: 117–147.

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