SUBSPECIATION IN THE RED-TAILED TROPICBIRD

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ABSTRACT

This study shows that the Red-tailed Tropicbird (*Phaethon rubricauda*) has a gradual clinal increase in the intensity of the rose-pink suffusion, egg size, culmen length and wing length in breeding populations between Kure Atoll in the northern Pacific and the Kermadec Islands in the southern Pacific. The illusion that birds from this cline comprise three subspecies has long been accepted because the large range of latitude that each subspecies had been arbitrarily given resulted in significant differences in mean measurements. However, as neither the northern *rothschildi* nor the southern *roseotincta* are clearly separable from *melanorhynchos* in the centre of the cline, they must all be one subspecies. Because the mean measurements of the nominate "subspecies" are not significantly different from those of birds from similar latitudes in the Pacific cline, or from *westralis* in the eastern Indian Ocean, there is no valid reason for distinguishing any subspecies in the Red-tailed Tropicbird.

INTRODUCTION

Mayr (1982) has suggested that many of the subspecies described in the first half of this century "did not differ in the slightest and that the recognition of minutely differing populations served, in most cases, no good purpose." Gill (1982) has also suggested that further study of many classical subspecies will lead to their elimination.

Here I examine geographical variation in the Red-tailed Tropicbird (*Phaethon rubricauda*) throughout its Indo-Pacific breeding range. My purpose is to assess the validity of the five subspecific groupings ascribed to the species by Peters (1931) and still in common use: *P. r. rubricauda* in the western Indian Ocean, *P. r. westralis* in the eastern Indian Ocean, *P. r. rothschildi* in the northern Pacific Ocean, *P. r. melanorhynchos* in the central Pacific, and *P. r. roseotincta* in the southern Pacific.

METHODS

The three diagnostic characters originally used to separate the five subspecies were wing length, culmen length and pinkness of plumage. I obtained measurements of these characters mainly from skins in the museums listed in the acknowledgments. Some data were available from the literature (Gibson-Hill 1950, Hindwood *et al.* 1963, Fleet 1974, Diamond 1975). Live birds were measured on Kure Atoll, Sugarloaf Rock, Aldabra Island and Norfolk Island.

I measured the wing held flattened on to a ruler and the culmen from the feather line to the tip. To compare the intensity of pink suffusion in the white feathers I used the scale that Fleet (1974) used to measure seasonal variations of this character on Kure Atoll, Hawaii. The categories are nil, slight, moderate, strong and intense.

These data were compiled so as to compare traditional subspecific and island groupings. By also comparing these data and those for egg size with latitude, I discovered correlations not previously observed.

TABLE 1 — Average wing, culmen and egg measurements from breeding populations

Island	Latitude	Wing Length	S.E.	n	Culmen Length	S.E.	n	Egg Length	S.E.	Egg Width	S.E.	n
Kure	28N	319.2	1.0	71	62.4	0.3	70	64.2	0.2	45.1	0.1	300
Midway	28N	313.8	3.3	12	61.7	0.6	13	64.6	0.6	44.9	0.2	22
Bonin	27N	318.0	1.8	8	58.7	0.5	8	63.1	0.9	45.0	0.5	5
Laysan	26N	314.6	1.4	53	61.2	0.3	58	63.7	0.5	44.6	0.3	33
Lisianski	26N	-	-	-	64.5	-	2	-	-	-	-	-
Necker	25N	319.5	6.5	2	61.8	0.8	2	-	-	-	-	-
Marcus	23N	318.3	1.9	3	61.0	1.0	3	-	-	-	-	-
Kruzenstern	23N	313.5	6.5	2	56.5	0.3	2	-	-	-	-	-
Kauai	22N	322.0	3.5	4	63.7	2.6	3	-	-	-	-	-
Nihoa	22N	327.0	0.0	2	63.7	1.0	2	-	-	-	-	-
Wake	20N	321.6	3.8	5	59.4	1.4	9	67.5	-	45.1	-	1
Pagan	18N	314.0	-	1	58.0	-	1	63.6	0.7	44.2	0.5	8
Nihau	18N	319.5	1.6	2	62.0	4.0	2	-	-	-	-	-
Johnston	17N	316.5	1.7	17	61.5	1.0	12	-	-	-	-	-
Marquesas	10N	331.3	2.1	10	63.6	0.5	10	-	-	-	-	-
Clipperton	10N	320.0	-	1	60.9	-	1	-	-	-	-	-
Marshall	9N	319.0	1.5	3	59.9	1.3	4	-	-	-	-	-
Palmyra	7N	328.5	-	2	61.8	-	2	-	-	-	-	-
Atjah	6N	320.0	-	1	66.0	-	1	-	-	-	-	-
Christmas(Pac)	2N	335.0	2.9	13	64.2	1.1	11	67.4	0.8	46.0	0.4	13
Howland	1N	335.8	2.9	10	63.8	0.7	10	-	-	-	-	-
Jarvis	0	328.8	1.9	16	62.4	0.7	15	-	-	-	-	-
Enderbury	3S	340.0	3.6	3	62.9	0.8	5	63.5	0.7	45.5	0.6	5
Canton	3S	335.3	6.1	4	62.5	1.5	4	65.4	-	42.9	-	1
McKean	4S	-	-	-	60.5	-	1	-	-	-	-	-
Seychelle	4S	342.0	5.7	3	67.3	1.2	3	-	-	-	-	-
Hull	5S	337.6	1.3	31	62.5	2.5	31	67.8	1.0	46.3	0.8	4
Starbuck	5S	-	-	-	60.5	-	1	-	-	-	-	-
Goenoeng Api	7S	321.3	7.0	3	58.3	1.8	3	-	-	-	-	-
Aldabra	9S	335.8	1.4	27	64.0	0.5	29	65.1	-	46.4	-	8
Raine	11S	329.9	4.6	11	65.0	1.2	11	69.0	-	48.5	-	2
Christmas(Ind)	11S	328.2	2.7	21	64.8	0.4	21	69.0	-	48.8	-	5
Cocos-Keeling	12S	333.3	3.5	6	63.5	0.8	21	63.5	-	44.5	-	-
Samoa(Rose)	12S	338.0	1.0	2	62.5	2.5	2	-	-	-	-	-
Suvarov/Takutea	13S	341.1	1.1	49	64.8	1.2	49	68.1	0.4	46.1	0.4	8
Tuamotu	17S	339.0	2.1	31	66.4	1.2	31	67.1	-	46.9	-	34
Madagascar	18S	337.5	3.5	2	65.5	0.5	2	-	-	-	-	-
Mauritius	20S	330.3	2.7	10	66.0	0.8	13	64.9	1.2	46.9	0.7	7
Rodriquez	20S	327.0	-	1	67.0	-	1	-	-	-	-	-
Tonga	20S	338.4	3.1	11	64.8	1.2	11	-	-	-	-	-
Brampton	20S	-	-	-	67.5	-	2	-	-	-	-	-
Gambier	21S	338.0	-	1	66.0	-	1	-	-	-	-	-
New Caledonia	22S	323.0	-	1	65.0	-	2	-	-	-	-	-
Wreck	23S	331.0	1.0	2	67.5	1.5	2	-	-	-	-	-
Oeno	24S	345.0	1.6	8	67.6	0.9	8	67.0	0.8	46.6	0.3	10
Henderson	24S	342.4	4.4	7	64.3	0.9	7	-	-	-	-	-
Ducie	25S	345.8	3.2	5	67.3	1.1	6	66.6	1.1	46.6	0.4	14
Austral	25S	343.0	-	1	65.0	-	1	-	-	-	-	-
Rapa	27S	341.0	2.2	8	66.7	0.6	8	-	-	-	-	-
Easter	27S	330.0	-	1	-	-	-	-	-	-	-	-
Abrolhos	28S	335.6	2.5	8	66.5	0.8	8	66.0	-	48.0	-	6
Norfolk/Phillip	29S	348.9	1.8	41	66.4	0.4	41	67.7	3.9	47.7	0.3	22
Kermadec	31S	343.9	1.2	58	66.2	0.3	55	67.2	0.9	47.4	0.7	6
Lord Howe	32S	341.3	1.5	45	67.6	1.9	46	65.4	1.8	47.6	1.0	3
Broughton	33S	325.0	-	1	63.0	-	1	-	-	-	-	-
Sugarloaf	34S	342.2	2.7	14	64.8	0.4	30	65.6	1.1	46.8	0.5	7
TOTAL				654			698					524

RESULTS

Table 1 gives average bird and egg measurements for every island from which I could get data. Although the sample sizes vary, the larger samples are evenly spread over the latitudes.

As the previously accepted subspecies were based on certain groupings of the island populations, I have examined the data under these divisions.

P. r. westralis

There is no significant difference between the mean exposed culmen lengths ($t = 0.545$, $P > 0.1$, $df = 104$) or mean wing lengths ($t = 2.082$, $P > 0.1$, $df = 93$) of *rubricauda* and *westralis*. *P. r. rubricauda* has a wing of 334.84 ± 1.23 mm ($\bar{x} \pm$ SE, $n = 43$) and an exposed culmen of 64.86 ± 0.39 mm ($n = 48$); whereas *westralis* has a wing of 333.33 ± 1.68 mm ($n = 52$) and a culmen of 64.25 ± 0.38 mm ($n = 68$).

Skins of *rubricauda* show no pink suffusion. Diamond (pers. comm.) verified this in the field, although he found one or two birds with a slight suffusion of pink. In the eastern Indian Ocean (Sugarloaf Rock) I found nesting birds of all intensity scalings, although the average was moderate (Tarburton 1977).

P. r. rothschildi

Specimens from the northern Pacific are smaller and less pink than those from the southern Pacific. For example, the average exposed culmen and wing lengths of 71 birds (Fleet, pers. comm.) from Kure Atoll (the northernmost Pacific colony) are significantly smaller (Table 2) than those of 41 birds from Norfolk Island (one of the southernmost Pacific colonies). The intensity of the pink tinge (Table 3) is also significantly different ($P < 0.01$) between the two islands.

TABLE 2 — Statistical differences in measurements for birds from populations at the extremes of the cline in the Pacific Ocean

	Norfolk Population (Average ± SE)	Kure Population (Average ± SE)	t	P
Wing	348.9 ± 1.8	319.2 ± 1.0	14.62	<0.001
Culmen	66.4 ± 0.4	62.4 ± 0.3	14.92	<0.001

TABLE 3 — Statistical differences in the intensity of the pink suffusion in live birds from populations at the extremes of the cline in the Pacific Ocean

		Intense	Strong	Moderate	Slight	Nil	χ^2	P
Norfolk	(O)	9	8	11	4	0		
Kure	(E)	3	7	28	4	0	22.46	<0.01

TABLE 4 — Measurements of diagnostic characters for currently accepted subspecies

	Character	x̄	SE	n
	Wing			
rothschildi		317.30	0.67	180
westralis		334.55	1.70	49
rubricauda		334.84	1.23	43
melanorhynchos		337.20	0.69	210
roseotincta		342.30	0.99	163
	Exposed Culmen			
rothschildi		61.58	0.20	185
westralis		64.25	0.38	68
rubricauda		64.86	0.39	48
melanorhynchos		64.43	0.20	212
roseotincta		66.40	0.24	164
	Pinkness			
rothschildi		2.28	0.11	96
westralis		3.17	0.08	42
rubricauda		1.06	0.04	31
melanorhynchos		1.02	0.02	139
roseotincta		3.16	0.19	55

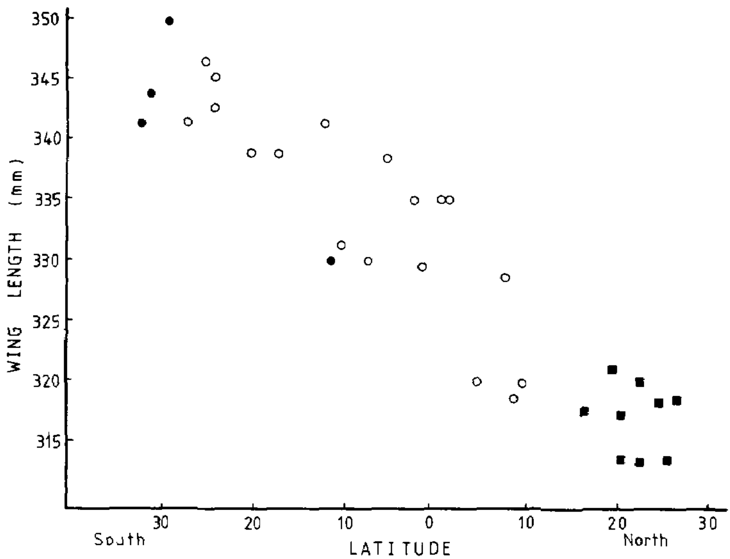

FIGURE 1 — The clinal relationship between wing length and latitude in Pacific Ocean populations. Solid circles represent samples from those populations originally designated as *P. r. roseotincta*. Hollow circles represent *P. r. melanorhynchos*, and solid squares represent *P. r. rothschildi*

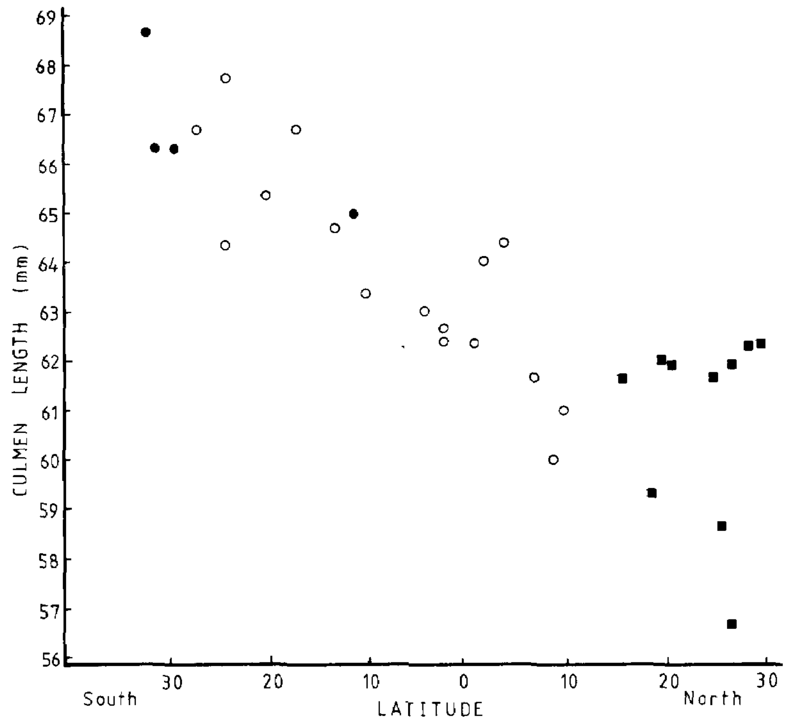

FIGURE 2 — The clinal relationship between exposed culmen length and latitude in Pacific Ocean populations. Solid circles represent samples from those populations originally designated as *P. r. roseotincta*. Hollow circles represent *P. R. melanorhynchos*, and solid squares represent *P. r. rothschildi*

The average for the total sample of *rothschildi* (Table 4) shows that they have a smaller wing ($t=20.7$, $P<0.001$, $df=388$) and exposed culmen ($t=9.6$, $P<0.001$, $df=395$) and have significantly more pink ($t=11.3$, $P<0.001$, $df=234$) than *melanorhynchos*. However, both culmen and wing measurements are clinal (Figures 1 and 2), and so these differences are not sharp distinctions.

P. r. roseotincta

This subspecies has a larger wing ($t=4.2$, $P<0.001$, $df=371$) and exposed culmen ($t=6.1$, $P<0.001$, $df=374$) and is significantly more pink ($t=58.6$, $P<0.001$, $df=193$) than *melanorhynchos*.

P. r. melanorhynchos

Although the average lengths of culmen and wing for the total sample of *melanorhynchos* are significantly different from those of *rothschildi* and *roseotincta*, Figures 1 and 2 show that the averages for the island populations within this "subspecies" form a gradual cline between those at the extreme latitudes of the Pacific. In addition, *melanorhynchos* is not significantly different from the nominate subspecies *rubricauda* in wing ($t = 1.2$, $P > 0.1$, $df = 251$), exposed culmen ($t = 1.0$, $P > 0.1$, $df = 258$), or intensity of pinkness ($t = 0.9$, $P > 0.1$, $df = 168$). Neither is *melanorhynchos* significantly different from *westralis* in wing ($t = 1.4$, $P > 0.05$, $df = 255$) or exposed culmen ($t = 0.42$, $P > 0.25$, $df = 278$).

Average egg size for each island also varied with latitude. Significant correlations were found between latitude and egg length ($r = 0.49$, $P < 0.01$, $n = 25$) and latitude and egg width ($r = 0.74$, $P < 0.01$, $n = 25$). These correlations are graphed in Figures 3 and 4.

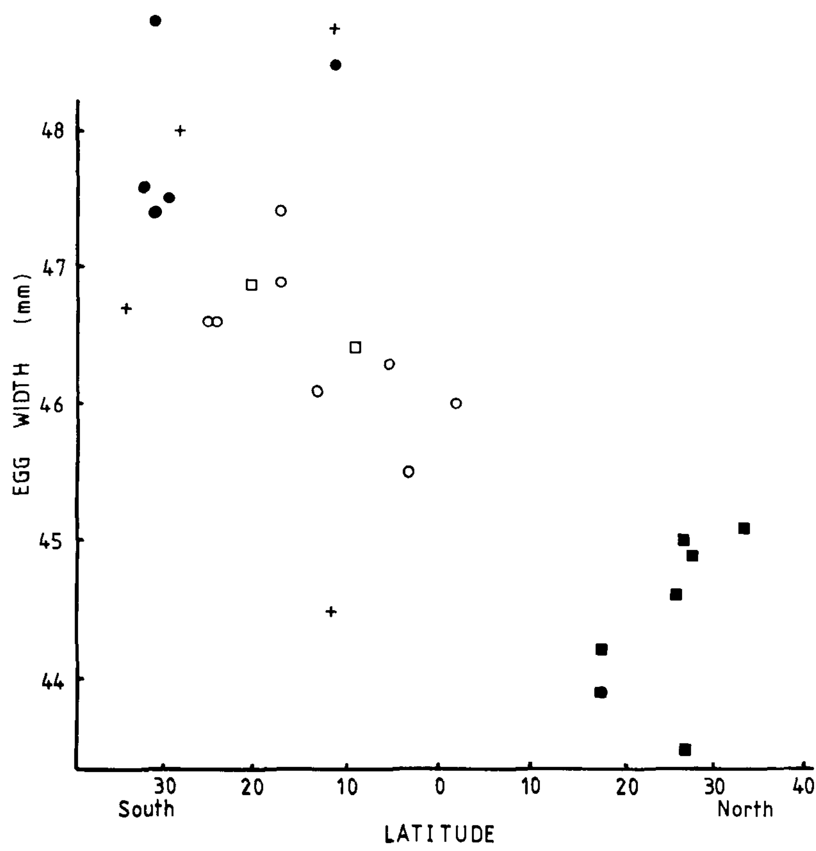

FIGURE 3 — The clinal relationship between egg width and latitude. Solid circles represent samples from those populations originally designated as *P. r. roseotincta*. Addition signs represent *P. r. westralis*, hollow circles represent *P. r. melanorhynchos*, hollow squares represent *P. r. rubricauda*, and solid squares represent *P. r. rothschildi*

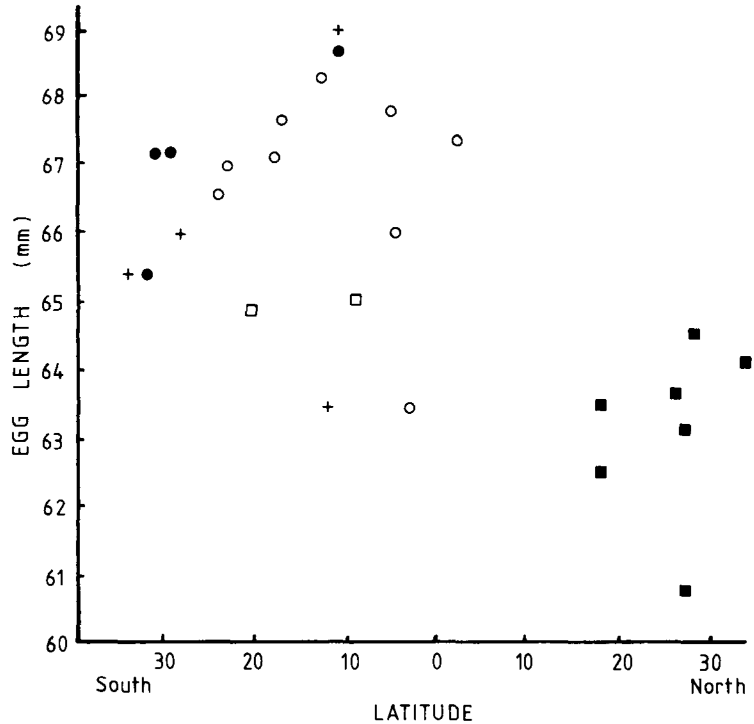

FIGURE 4 — The clinal relationship between egg length and latitude. Solid circles represent samples for those populations originally designated as *P. r. roseotincta*. Addition signs represent *P.r. westralis*, hollow circles represent *P. r. melanorhynchos*, hollow squares represent *P. r. rubricauda*, and solid squares represent *P. r. rothschildi*

DISCUSSION

P. r. westralis

The type specimen of *rubicauda* was described by Boddaert in 1783 and, even though it and several other specimens were taken from Mauritius, the subspecific range was given as the western Indian Ocean (Peters 1931). Rothschild (1900) was the first to record that birds from the eastern Indian Ocean (Christmas Island) were different from those nesting in the Western Indian Ocean. However, he acknowledged that a larger series was needed before the impression could be confirmed. Later, the sample from the eastern Indian Ocean was enlarged by the addition of some specimens from the Abrolhos Islands (Mathews 1914-15: 305, although on p.302 Mathews gave their origin as Rottnest Island). They were together described (Mathews

1912, 1914-15) as the subspecies *westralis.* Mathews said those specimens ascribed to the new subspecies had rosier coloration, a rather smaller bill, and a longer wing than the type. The measurements he gave supported the difference in bill size because the two ranges did not overlap. However, the wing lengths he gave (*rubricauda* 320-336, *westralis* 320-341) overlapped greatly.

Gibson-Hill (1950), in assigning two birds from the Cocos-Keeling Islands to *westralis,* continued the subspecific distinction. It is clear, from comparing the data in Mathews (1912, 1914-15) and Gibson-Hill (1950) with the skins from which these were taken (in the Western Australian Museum and University of Singapore), that Gibson-Hill kept this distinction largely because the bill measurements given by Mathews were mistakenly accepted as those of the exposed culmen. Mathews also gave culmen measurements for *rubricauda,* and these were similar to those Gibson-Hill made on *westralis.* The small bill of three birds from Goenoeng Api in the south Banda Sea (van Bemmel & Hoogerwerf 1940) and of several new birds from Christmas Island (Chasen 1933) had also been used to place these birds with *westralis.* In both instances the wing measurements were considered unsuitable for distinguishing *westralis* from *rubricauda* because of considerable overlap.

By comparing larger samples from the western and eastern Indian Ocean I have shown that there is no significant difference in those characters that were used to establish *rubricauda* and *westralis* as separate subspecies. Because my culmen and wing measurements were taken from live specimens as well as skins, they may be biased. However, Table 5 demonstrates that the mean measurements for skins are not significantly different ($P > 0.05$ in all four comparisons) from those made on live birds.

TABLE 5 — A comparison between measurements made on skins and live birds from the Indian Ocean

		westralis		*rubricauda*	
		Culmen	Wing	Culmen	Wing
Live	$\bar{x}$	64.71 ± 0.46	334.48 ± 1.86	64.30 ± 0.6	337.29 ± 1.56
	SD	3.06	12.50	2.90	6.42
	n	44	45	19	17
Skin	$\bar{x}$	65.02 ± 0.64	333.32 ± 1.60	65.3 ± 0.5	333.23 ± 1.71
	SD	3.02	7.52	2.8	8.71
	n	22	22	26	26
	t	0.39	0.47	1.64	1.75
	P	>0.1	>0.1	>0.1	>0.05

Certainly, the intensity of the pink suffusion in both the body and wing feathers does vary between the two subspecies. However, three factors make this character alone inadequate to support the continued differentiation of the two populations in the Indian Ocean:

1. The pink suffusion is in part a condition of new plumage and the birds' age. As it fades during the breeding season (Fleet 1974), the time of the year as well as the birds' maturity when collected would need to be known to make comparisons valid.
2. In most museums the pink suffusion does not last for more than a few years. I have seen this when comparing skins from the same islands in different museums.
3. I am not able to assign to a particular subspecies those birds taken at sea in the Indian Ocean with only slight or no suffusion. Moreover, birds collected at sea need not be breeding in the area of collection. A bird banded by Jenkins (1969) north-east of Sumatra in May 1965 was recovered near Mauritius in September 1968. Thus, the range of one "subspecies" includes the breeding islands of the other "subspecies". Because of the distance this bird had travelled (4344 km), one could not even be sure that such birds had bred in the Indian Ocean at all.

If none of the three diagnostic characters originally used to separate *rubricauda* and *westralis* are reliable, the continued use of the trinomials is unwarranted.

P. r. rothschildi, P. r. melanorhynchos and P. r. roseotincta

Whereas Mathews and Rothschild were incorrect in dividing the Indian Ocean population into two subspecies on the basis of few specimens, they were correct in stating that the Hawaiian birds (*rothschildi*) were distinguishable from those found in the Kermadec, Norfolk, Lord Howe and Raine Islands (*roseotincta*). Rothschild (1900) stated, on the basis of 28 skins from the Kermadec Islands and 15 from Hawaii, that those from the Kermadecs (he also included those from Norfolk and Lord Howe Islands) had more rosy-red tinge in their plumage as well as longer bills and wings than the Hawaiian birds.

However, no matter how different the Hawaiian and south-west Pacific birds are, they cannot be valid subspecies if the two populations grade into a continuous cline (Monroe 1982, O'Neill 1982). When Mathews (1914-15) defined the geographical distribution of *melanorhynchos* in the central Pacific as being between that of the other two subspecies, he did express caution. He did this, however, because the topotypic examples were not available for comparison, not because he was aware that they might form part of a long series of slightly different adjoining populations.

Gmelin (1789) based his type description for *melanorhynchos* on birds from Turtle (Christmas Island, Pacific Ocean) and Palmerston Islands. Mathews (1914-1915) noted that the Society Islands were geographically the nearest to Palmerston and Christmas Islands and inferred that birds from the Society Islands should belong to *melanorhynchos*. Society Island birds have ever since been accepted uncritically as *melanorhynchos*. Common usage has subsequently included birds from Austral, Ducie, Tonga, Tuamotu, Samoa, Marquesas, Phoenix, Line, and the Cook Islands under *melanorhynchos*.

The earliest hint of a cline was by Gould *et al.* (1974), who noted that the size of *rubricauda* taken in the northern Pacific tends to correlate with latitude north, being smaller from the equator northwards. What they did not realise was that the cline continued south of the equator as well. One logical expectation would be that culmen and wing would become smaller also for birds found at increasing distances south of the equator. However, this is not so, for the birds from the equator southwards continue to increase in size. Thus, genetic factors or different environmental factors in the Southern Hemisphere may produce larger birds. A similar trend has been found in the White Tern (*Gygis alba*), which breeds over a similar latitudinal range in the Indo-Pacific (Holyoak & Thibault 1976). Those breeding populations of the White Tern fitting into the cline have been united as one subspecies.

The continuous nature of the clinal gradients in both wing and culmen for individual island populations are clearly shown in Figures 1 and 2. In addition there are significant correlations between latitude and wing length ($r = 0.93$, $P < 0.001$, $n = 15$) and latitude and culmen length ($r = 0.78$, $P < 0.001$, $n = 15$).

As the correlations vary inversely with latitude in the Northern Hemisphere and proportionally with latitude in the Southern Hemisphere, Bergman's rule (Mayr 1956) on size related to heat conservation cannot apply. The continuous nature of the cline across the equator suggests gene flow is implicated.

For the White Tern, Holyoak & Thibault (1976) explained exceptions to the size cline by colony or island size; presuming that competition for nests favoured larger birds on larger islands. Increased density in the nesting colony or in the feeding ground is the more likely factor, rather than island size itself. That this is not a contributing factor in the size cline of the Red-tailed Tropicbird is suggested by the significant inverse correlations between wing size and colony size ($r = 0.69$, $P < 0.005$, $n = 16$) and culmen length and colony size ($r = 0.67$, $P < 0.005$, $n = 16$).

Another contributing factor might be the amount of available food. However, if a larger colony depletes its food supply, which in turn decreases bird size, how does the colony become so large in the first place?

In spite of the marked north-south size cline there does not appear to be an east-west cline. Two explanations are plausible:

1. The birds tend to disperse further along latitude than along longitude. The measurements from a large sample of Red-tailed Tropicbirds taken at sea, far from the nearest island, correlate with those expected for the latitude at which they were found (Gould *et al.* 1974). It is also supported by the recovery of a Red-tailed Tropicbird in the western Indian Ocean that had been banded in the eastern Indian Ocean (Jenkins & Robertson 1969).
2. The birds seem to return to their natal breeding sites. Most breeding birds return to the same nests at Kure (Fleet 1974), Sugarloaf (Tarburton 1977), and Norfolk Island (Tarburton, unpubl.).

CONCLUSIONS

As all of the five "subspecies" of the Red-tailed Tropicbird are clearly part of a north-south cline and cannot be separated from adjacent subspecies, there is no valid reason for continued use of the trinominals. The origin of this north-south cline is not clear. Evidence for considerable gene flow in the east-west direction and little gene flow along the north-south cline indicates that the cause of the cline might be genetic, although environmental factors cannot be ruled out.

ACKNOWLEDGMENTS

I thank the ornithologists at the following institutions for providing measurements: Academy of Natural Sciences; American Museum of Natural History; Auckland Institute and Museum; Australian Museum; Bernice P. Bishop Museum; British Museum of Natural History; California Academy of Sciences Museum; Carnegie Museum; Denver Museum of Natural History; Field Museum of Natural History; Los Angeles County Museum of Natural History; Museu e Laboratorio Zoologico e Antropolocico Lisboa; Museum of Comparative Zoology, Harvard University; Museum National d'Histoire Naturelle, Paris; Museum of Vertebrate Zoology, University of California; National Museum of Natural History, Smithsonian Institution; National Museum of New Zealand; National Museum of Victoria, Melbourne; Peabody Museum of Natural History, Yale University; Queensland Museum; Rijksmuseum van Natuurlijke Historie, Leiden; Royal Ontario Museum; South Australian Museum; University of Singapore; Western Australian Museum. I also thank R. Fleet, and A. W. Diamond for measurements from live birds.

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