

The Peregrine Falcon *Falco peregrinus* in Fiji and Vanuatu

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ABSTRACT

We studied the Peregrine Falcon *Falco peregrinus* in Fiji 1985-1997 and in Vanuatu 1993-1995. Based on preliminary findings in 1985-86 and data from Fergus Clunie, Fiji Museum, we projected a population of about 100 pairs for Fiji. By 1987 we had adjusted our population projection downward to about 70 pairs and based on the history of inactivity and our continual checking of various regions we concluded that perhaps only 20 effective breeding pairs were a reasonable estimate for Fiji, although in any one year possibly 30 pairs breed. In 1994 of 6 nesting sites checked only 1 was active, and 2 had lone females; of 6 checked in 1997, 2 were active. Through time we have seen a reduction in occupancy of nesting sites. If our sample is indicative of the entire population in Fiji, especially for places we have not checked such as much of Vanua Levu, Kadavu, and the Lau Group, then the species is extremely rare and may be down to a few pairs within Fiji. We discuss other interpretations that might explain our findings of an apparent downward trend in occupancy rate, speculate on this aspect of their biology, and compare it with better known northern hemisphere populations. Breeding chronology in Fiji has been regular with young leaving the nest about early to mid-September while in Vanuatu the phenology is *ca.* 6 weeks later despite being on the same latitude. Effects of such factors as food and weather in regulating breeding, as opposed to photoperiodic control, are discussed. Peregrines in Fiji, Vanuatu and New Caledonia are allocated to the same subspecies (*F. p. nesiotes*). Those in Fiji show signs of inbreeding and we discuss the DNA differences and similarities between those of Fiji, Vanuatu, and Australia. Such differences are important from the point of view of conservation if in fact the Peregrine in Fiji has declined and this will be discussed.

INTRODUCTION

While allusions to the breeding of the Peregrine Falcon *Falco peregrinus* in Fiji were made as early as 1877 (Gordon 1897-1912) there was no clear consensus in the literature (Mayr 1941), even as late as 1968 (Brown & Amadon 1968), that they even occurred in Fiji. It was not until the studies of Clunie (1972) that some of their breeding status and biology was chronicled. His study was first restricted to a single breeding pair on Joske's Thumb. Clunie suggested breeding for Viti Levu, Vanua Levu, Wakaya, Ovalau, and Kadavu but little else was known about their breeding distribution. While the Peregrine may be among the most studied and best known species of birds in many parts of the northern hemisphere, and while in the southern hemisphere they are well studied in temperate

South America, Africa and Australia, little has been done on the species in tropical climates. The species is cosmopolitan in distribution and in Fiji represents the easternmost outlier in Oceania and thus a peripheral population. Since the species had also been affected by synthetic chemicals (mainly chlorinated hydrocarbons) in the northern hemisphere, and in some places declined into extinction, its status within Fiji was of interest.

With this in mind we started to study the birds in some detail in 1985. The questions we had in mind were: 1) what is their breeding density and geographical distribution? 2) what is their breeding chronology for a tropical population of the species? 3) what do they eat? 4) have they been affected by synthetic chemicals in a similar fashion to populations of the northern hemisphere? 5) to which population are they most closely related evolutionarily (phylogenetically)? and 6) what effect do the above parameters have on their long term conservation in Fiji? Some of these questions have been briefly explored in White *et al.* (1988, 1993).

MATERIALS AND METHODS

Field Work

Peregrines normally nest on cliffs and in the northern hemisphere, at least, cliff size is important with large (high) cliffs having priority selection. In 1985 we spent 10 hours with a helicopter examining major cliff areas, over the range of types of cliffs Peregrines occupy, on Viti Levu, Vanua Levu (part), Moturiki, Ovalau, Wakaya, Makogai, Koro and Kioa islands. Three observers (including the pilot) examined each cliff closely for nesting ledges with excreta (faecal stain) on them and for falcons. We flew the helicopter about 10 kph past cliffs and perhaps 20-50 m from them. When a falcon flushed from a cliff we searched the cliff slowly for an eyrie. Locations and observations were plotted on maps and elevation and orientation of each cliff was recorded. We later visited several accessible areas on foot and by car. Cliffs visited were recorded as small (<50 m tall), or large (>50 m tall). Values for the numbers of cliffs examined were somewhat arbitrary as it was often hard to determine exactly where one cliff ended and another began. Islands without cliffs were not examined. Extrapolations on distribution in the Lau group came mainly from Clunie (northern Lau), from Fijians, and from P. Geraghty, none of which we were able to confirm. In 1986, 6.5 hours were spent in a helicopter examining most eyries on Viti Levu, Wayaka and Kioa and some eyries on Vanua Levu. Food remains and eggshell fragments were gathered from 6 eyries and the shell fragments were examined for their thickness at the Western Foundation of Vertebrate Zoology. In 1989 only eyries that could be visited from automobile and by foot were examined. In 1991 helicopter was again used and in addition to visiting all known eyries we examined other parts of Viti Levu not previously seen, Taveuni, and the Mamanuca-I-Cake, Mamanuca-I-Ra, and Yasawa Groups. In 1993 only 4, 1994 only 7, and in 1997 only 6 easy of access eyries were examined.

We worked in Vanuatu between 18-30 August 1993, and surveyed by helicopter some 30% of the linear area (24% of the land area) covered by islands in Vanuatu. Within that area, however, some islands without cliffs such as Emae, of 33 km² area, were not examined. Large inland regions devoid of cliffs were also not examined so in some cases only shorelines were surveyed. We used Efate (ca. 17° 45' S. Lat.) as a starting point because of helicopter service, and from there examined cliffs on 21 islands from Tanna (ca. 19° 30' S. Lat.) in the south to Epi (ca. 16° 30' S. Lat.) in the north. This covered a linear distance of about 310 km. Cliffs were categorized into 3 groups based on estimated heights; 1) 20 m or less, 2) 20-70 m, and 3) over 70 m. Numbers of cliff, by size, were recorded for each island. Only those cliffs that were devoid of heavy vegetation were examined. We timed our survey to occur during what we deemed to be the peak of fledgling development (1-4 wk old young). This was based on the breeding chronology at the same latitude in Fiji (White *et al.* 1988) and locations 10° latitude farther south in adjacent Queensland, Australia (Czechura 1984). In 1994 we examined 6 eyrie locations (Efate and Erromango) from helicopter and climbed into 1 eyrie to look for eggshells and get blood samples. In 1995 our helicopter pilot examined 3 locations from helicopter and we obtained a blood sample from 1 bird.

Molecular Data

DNA was extracted from a variety of tissues; primarily aliquots of whole blood or pectoral muscle stored at ambient temperature (some later frozen) in an equal volume or larger volume of Blood Lysis Buffer (0.1 M Tris-HCl-pH 8.0; 0.1 M EDTA; 0.1M NaCl; 0.5% SDS). Samples from Vanuatu included a pectoral muscle sample in formalin, feather tips, and egg contents ranging from embryonic material to egg membrane. Aliquots of clotted whole blood or finely chopped pieces of tissue (*ca.*20µg) were resuspended in 650µl SET (150mM NaCl, 50mM Tris/HCl pH 8.0, 1mM EDTA Na2) with 15µl of 10mg ml⁻¹ Proteinase K solution, 7.5µl of 25% SDS (w/v), and 7.5µl 10% Triton 100 followed by two phenol, two phenol/chloroform and one chloroform extractions with subsequent ethanol precipitation. The DNA was dried at 37°C for 30 minutes and resuspended by overnight incubation in 150µl TE (1mM EDTA Na2, 10mM Tris/HCl pH 8.0).

PCR amplification of the two microsatellite loci *Fpeµ1* & *Fpeµ2* was achieved using 30ng of DNA per 25µl PCR reaction comprising 20 pmoles of each primer, 0.2 mM each of dATP, dGTP, dTTP and 0.05 mM dCTP, 0.25mCi[alpha-³²P]-dCTP, 3mM MgCl₂, 20mM (NH₄)₂SO₄, 0.01% (w/v) Tween, 75mMTris-HCl pH 9.0 and 1 unit "Red Hot" DNA polymerase (Advanced Biotechnologies). After an initial denaturing step of 180 seconds at 94°C, the reaction proceeded for 30 cycles as follows; 45 seconds at 94°C, 60 seconds at 58°C then 90 seconds at 72°C (DNA Thermal Cycler PTC-100, MJ Research). The PCR products were electrophoresed through 6 or 7% denaturing polyacrylamide gels and visualized by autoradiography after an overnight exposure. Allele sizes were determined by reference to standards.

RESULTS

Cliffs Examined-Fiji

Of the various surveys, the primary areas not checked were major cliffy areas in east and west Vanua Levu, Kadavu, and the Lau Group. Overall more than 263 total cliffs were examined. On Viti Levu those cliffs checked varied in elevation from 122-920 m; mean elevation for a sample of 49 large cliffs was 598 m and mean for 49 small cliffs was 483 m in elevation. More than half of the inland cliffs were checked but very small (< 8 m) coastal cliffs were not. As an indication of the distribution of cliff sizes examined, other than on Viti Levu, a sample is: 35 large and 55 small cliffs on Vanua Levu, 6 large and 15 small on Ovalau, 1 large and 2 small on Wakaya (all the cliffs), 3 small on Kioa (all the cliffs), 2 small on Matage. Of the 33 cliffs checked in the Mananua and Yasawa Groups about half were considered large.

Cliffs Examined-Vanuatu

While numbers of cliffs in each category were recorded by island we do not present the data for each island. Cliffs in many cases were extensive and nearly continuous, with only short breaks, and it was at those places we divided them for convenience. Therefore, the numbers of cliffs are only approximate since the determination of the end of one cliff and the start of the next was often arbitrary. We suspect the number of cliffs 20 m or less is overestimated because from the helicopter angle and distance from the cliff, the actual size is misleading and thought to be smaller. The 70 m category may be correspondingly underestimated. It may well be that the 20 m or smaller category is 20-30% fewer and those in the 70 m over may be 15-20% more. A large number of cliffs in the 70 m or more category were higher than 100-125 m. Numbers of cliffs by island varied greatly. For example, Ewose in the Shepherd Island group and Veto Manung near Erromango, are small islands of less than 1 km² in area and completely ringed with cliffs 20-40 m in height. Most cliffs are on the perimeter of islands. Tanna and Erromango contained the most cliffs, probably partly because of their size. Although Efate and Erromango have about the same land area, the former had 28 and the latter 123 coastal cliffs. In all, 421 cliffs were examined; 85 (20 m or less), 181 (20-70 m), and 155 (70m or more).

Numbers of Falcons

For Fiji during the breeding season usually only those falcons associated with cliffs are seen (Clunie 1976, pers. obser.). The 12 locations where we found young or other positive signs of nesting or where we knew that eyries occur are shown on Table 1. For the total 263 cliffs examined falcons were at only about 7%. In addition, however, there are several areas with typical falcon faecal staining on cliffs on eastern Vanua Levu and behind Lautoka on Viti Levu where falcons doubtless nest but we never found eyries. Overall, falcons were found by us or collaborators or reported by Fijians (not all were documented eyries but most presumed to be) at 42 locations (see White *et al.* 1988 for earlier discussion of this); we only have some "history" of occupancy for 12 (Table 1). The eyrie at Sawa-i-Lau has long been talked about but we never found young there as clear proof of nesting. Based on the total numbers we originally estimated about 100 pairs for Fiji but as we continued to search and look at cliffs over and over again our data suggest that perhaps only 30 pairs nest in any one year and the average effective population size may only be 20 pairs or less. We lack data from Kadavu and the Lau group, however. The decreasing eyrie occupancy rate of our sample will be discussed below.

Table 1. Occupancy¹ rate of Peregrine eyries² visited in Fiji (F) and Vanatu (V), 1985-1997.

Eyrie name		Year Visited (1985-1997)								
		85	86	89	90	91	93	94	95 ³	97
Joske's Thumb	(F)	2	2	---		---	--- ⁶	---		
Namosi	(F)	2	2	2			--- ⁶			
Nausori Road	(F)	2	1	2		2	1	1		2
Wakaya	(F)		2			---				
Kioa	(F)	2	2			---				
Sigatoka	(F)		2	2		2	---	1		---
Nalato Range	(F)		2 ⁴			2				---
"The Saddle"	(F)		2 ⁴			---		2		---
Raki Raki	(F)		2 ⁴		2 ⁵	2		---		2
Matagi	(F)					2		2		---
Swa-i-Lau	(F)		2 ⁴	---		---				
Lautoka	(F)		2 ⁴					---		
Nguna	(V)						2	---	2	
Goat Island	(V)						2	---		
Erromango I	(V)							2	2	
Efate	(V)						2	---	2	
Tongoa	(V)						2			
Erromango II	(V)						2	---		
Tanna Volcano	(V)						---	2	2	

¹Occupancy by pair, usually breeding=2; only single adult found although pairs may have been present but not breeding=1. Eyries visited but no breeding falcons seen=---. Blank areas indicate eyrie was not checked. Presumed eyries on Vanua Levu had no falcons, were never checked again, and are not on table.

²Eyries are defined as areas with evidence of use and breeding (faecal stains, "whitewash" in eyrie) and falcon seen nearby.

³Checked by G. Cloete

⁴Found by C. Anderson

⁵Young found by Fijians

⁶Checked by helicopter pilots

Peregrines have been recorded on 13 of the more than 83 named islands of Vanuatu (Diamond & Marshall 1976, Pickering 1982, Bregulla 1992, W. Eakle pers. comm.). In all, we found 11 peregrines, 4 pairs, 2 single adults (1 male, 1 female) and 1 sub-adult female occupying cliffs; about a 2% cliff occupancy rate. All pairs or adults, the latter we believe to have been at breeding stations because of their behaviour, were only on islands where they were previously known even though we searched 15 islands where they had not been recorded. We include as part of Erromango, where we found 2 pairs and a single bird, a small volcanic upthrust (less than 1 km area and 1.5 km offshore) called locally Goat Rock or Veto Manung, where we also found falcons. The rock is not specifically mentioned in any of the above literature as having falcons but it also may have been included with Erromango in that literature. We found a sub-adult female on Mataso, for which falcons were also not listed, but she showed no signs of being a breeder. Although the literature lists Peregrines for 12 islands we do not doubt that they may breed on many other islands with cliffs, especially in areas difficult of access where ornithologists have not visited.

After our departure, a pair was found by Garrett Cloete on Emae, an island that we considered to be poor because of the lack of good cliffs. Falcons had not before been recorded and perhaps the pair seen were post-breeding wanderers or were from nearby neighbouring Nguna, where they do breed. Cloete also saw a lone falcon on Ambryum, another island where they had not been recorded and found a pair on Tanna near the volcano.

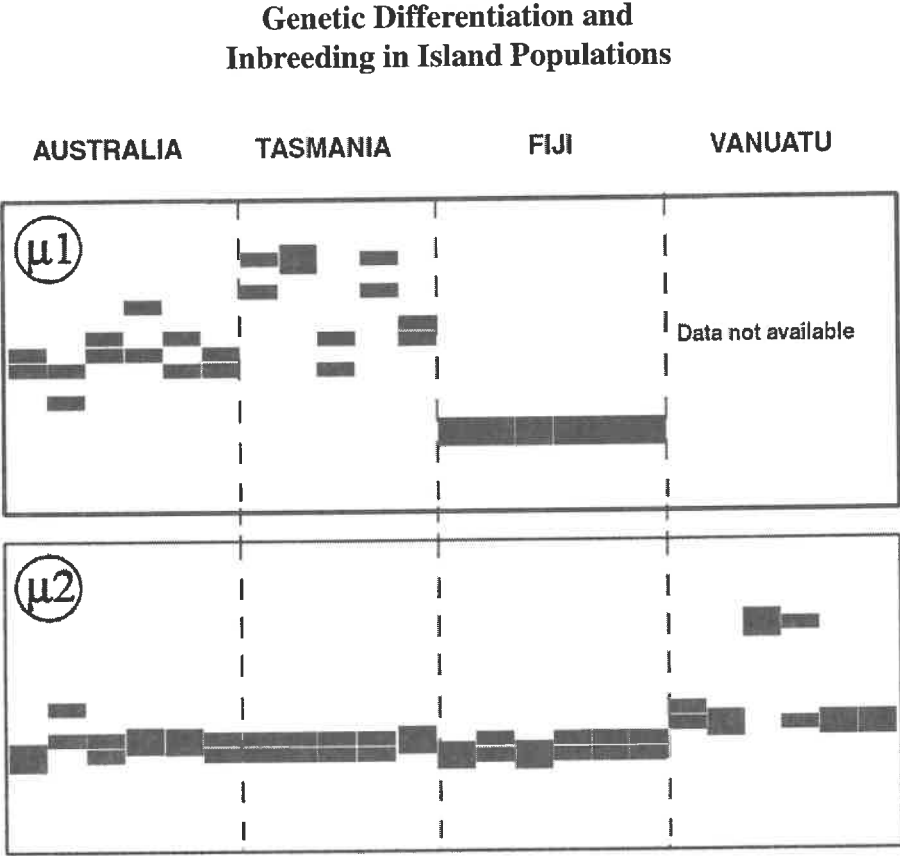
Breeding Chronology and Success

All the nests with young we examined on Fiji between 1985-1997 have been well synchronized relative to the month of fledging. Most young are of fledging age by early September; eggs were then laid during the first part of July. Clunie (1972), however, found that eggs in the Joske's Thumb eyrie were laid in the first week of August 1971. If that was the first clutch then young would have fledged the second week of October. All young we have seen are within 2 to 2-1/2 weeks age of one another and it is difficult to believe that in any one year some pairs lay in June and others in August. There may, however, be variation from year to year, the timing of which is dictated by some of the factors we discuss below. If there were considerable variation from pair to pair within any one year the absence of pairs and young in eyries that are visited in late August might be explained. This will also be discussed below. The 5 active eyries examined in 1986 all had young for an average of 2.6/eyrie. In 1994, when only 1 eyrie of 6 checked had young, they too were near fledging on 15 September.

Based on our Fiji work we were surprised to find falcons either incubating eggs or not yet having laid on Vanuatu in mid-August. On 20 August the pair at Nguna had c/3, and on 28 August a pair at Erromango had c/3. On 20 August we found a pair inland on Efate that flew together as a territorial pair, but clearly had not laid eggs. Upon returning on 30 August the female flushed from a ledge after the helicopter was but 7 m from it and had been so for several seconds. She flew back past the ledge and looked at it in the common practice of falcons "checking" eggs or young. Her intensity at trying to return to the ledge indicated that she was on eggs. We could not, however, see the ledge adequately from the helicopter because of a screen of vegetation on it but subsequently found young on that ledge. A second pair at Erromango and a pair on Veto Manung were territorial and "aggressive" at our presence but clearly had not laid (or had lost clutches?). A male on Tongoa was very territorial but we could not flush a mate from the cliff. Lastly, at a third location on Erromango, a female flushed from a cliff was territorial but nonetheless acted as though she had not laid eggs. The female at Nguna was still incubating with great intensity on 30 August. She was so intent on returning to the clutch after she was first flushed that she flew under the helicopter and landed on the ledge while the helicopter was about 15 m from the ledge. She then commenced to incubate while the helicopter hovered there and even moved to within about 6 m of her, without flushing. After our departure, G. Cloete checked the eyrie on Nguna and inland on Efate but could not determine the latter's contents. At one eyrie young were 3-4 d old on 16 August and on Efate there were 2 young about one week from fledging on 23 September. The eyrie on Nguna produced 3 young but only 1 survived.

Overall, the breeding cycle on Vanuatu was in the pre- to mid-incubation stage in late August. This breeding schedule averaged about 6 weeks behind Fiji even though on the same latitude and with essentially the same temporal climatic patterns. In 1986, in 5 eyries on Fiji, the largest young (a female) was about 1 1/2 weeks from fledging on 22 August [tail *ca.* 60 mm, wt. 680 g., (adult female wt. *ca.* 850 g.)], and the youngest nestlings in 5 eyries were about 1 week old (wt. 200 g.) on 23 August. On 31 August 1991 on Fiji we found young ranging from those with tail feathers out 55 mm (3 weeks old) to those within a week of fledging (4 eyries). Unfortunately, we could not verify the breeding stage in Fiji on 2 September 1993, the year we first examined Vanuatu, because no eyrie checked was occupied. The breeding schedule on Fiji, however, has been within this same time period on 5 surveys between 1985 and 1997 and there was no reason to expect they would not have been on that timing in 1993.

Figure 1. Comparison of genetic (DNA) diversity at two microsatellite loci, *Fpeμ1* and *Fpeμ2* in *Falco peregrinus macropus* (Australia and Tasmania) and *Falco peregrinus nesoites* (Fiji and Vanuatu). Five to six individuals were used at each locus for each population. At locus *Fpeμ1*, Vanuatu data were too faint to interpret. The falcons indicated by the term Australia were from the state of Victoria.



Molecular Findings

As was described earlier for DNA fingerprinting analysis (White *et al.* 1993) Peregrines from Fiji show essentially no genetic variation and high inbreeding (though perhaps not deleterious) based on that technique. The microsatellite technique presented here (Fig. 1) confirms the earlier data. This is especially graphic when compared to the Australian (state of Victoria) and adjacent Tasmanian samples; typical of large outbred populations. The differences in frequency of the observed genetic variants between Victoria and Tasmania suggests restricted gene flow although the 2 locations are only separated by the narrow (200 km) Bass Strait. Recoveries of ringed birds also indicate no movement between the two locations (W.B. Emison, C.M. White ms). The little genetic data available indicate that Fiji falcons may be more inbred than those of Vanuatu. This makes sense if one looks only at isolation as the principal factor. Unfortunately we obtained no data from the *Fpep1* locus to see if falcons from Vanuatu possess similar genetic variants to those of Fiji. In order to gain better insight to their relationship this would be important to know. Further analyses of other loci may help resolve that point. Based on this analysis we were also not able to resolve the question of relationships among the Australian/Vanuatu/Fiji groups and thus the question of origin of the Fiji population remains open.

DISCUSSION

Genetic Information

We had hoped that the genetic information might have provided at least two sorts of information. 1) What is the extent of genetic variability within the subspecies *nesoites* (Fiji and Vanuatu) and 2) What might have been the source of the populations on Fiji/Vanuatu/New Caledonia that differentiated into the subspecies *nesoites*; Australia (*F.p. macropus*) or Solomon Islands/New Guinea (*F.p. ernesti*) of which *nesoites* is nearly morphologically intermediate? To date we have not been able to resolve those questions.

Breeding Density

Earlier we suggested that Peregrines might be as frequent on Vanuatu as on Fiji provided that food and nesting resources were as abundant (White *et al.* 1988). However, based on our results, Peregrines appear to be less frequent on Vanuatu, by more than half, given the abundant habitat, than they were on Fiji. We also suggested earlier, based on our Fiji experience, that if habitat and food resources were similar on Fiji, Vanuatu and New Caledonia then the subspecies *nesiotes*, whose range encompasses those islands, may contain 200-250 pairs. We now believe that to be a significant overestimate. Y. Letocart (pers. comm.) indicated that the Peregrine was encountered very infrequently on New Caledonia and that the Loyalty Islands contained most of the likely Peregrine habitat. Our experience now, having examined some of both Vanuatu and Fiji, suggests that the subspecies *nesiotes* may not consist of more than 100 pairs being scattered over 51,610 km² of land area that itself occurs over many times that amount of ocean surface. *F. p. nesiotes* is thus a rare subspecies of the Peregrine.

Our misestimate of nesting chronology for Vanuatu came as a complete surprise. We may have missed some pairs because during our survey some females may have been sitting tightly on clutches. Males, however, should have been "on guard" near eyries and we think we missed few areas where they are known. For example, Aniwa is a small island (8 km² area) where Peregrines have been recorded and has a limited series of easily examined cliffs. We found none, however, suggesting they did not nest the year of our survey. We have good confidence in our findings although a larger sample may have altered our views of temporal sequence.

On Fiji in 1986 of 263 cliffs examined we located 7 cliffs with pairs or territorial birds and several other obvious eyries, in distinct territories, without pairs. For Vanuatu, twice the number of cliffs were examined and 7 locations (probably representing 6 pairs) were found. In Fiji, many of the cliffs used were black volcanic rock making white faecal stains easy to see which resulted, in part, in

our being able to find used cliffs even though falcons were not present (see discussion in White *et al.* 1988 on cliff use by birds in general on Fiji). In Vanuatu, however, many of the coastal cliffs (e.g., Erromango) were of uplifted marine limestone, white in colour, thus making it difficult to see faecal stains even when pairs were present. Not being able to find even unused eyries adds to the impression of rareness. Nonetheless, if our results are a rough indicator of density then not more than 20-30 pairs occur in Vanuatu; considerably fewer than we expected. We are thus as perplexed, as we were by Fiji data, at the low numbers of falcons. Peregrines may, however, be inexplicably spotty in what is seemingly excellent habitat. Kodiak Island, in the Gulf of Alaska for example, appears "identical" in habitat quality and food base abundance to the adjacent Aleutian Islands. Yet Kodiak has only about one-fourth the number of breeding pairs of falcons for amount of habitat available and examined (C.M. White, R.J. Ritchie, pers. observ.)

Table 2. Comparative densities per pair of Peregrines expressed as linear distances and areas (see text for discussion of area comparisons). Linear distances are shorelines, rivers or simply average straight line distances between a sample of eyries. Areas are for entire land masses, not just regions where falcons occur.

Name	Islands (Location)		Name	Mainlands (Location)	
	Linear (km)	Density Area (km ²)		Linear (km)	Density Area (km ²)
Zembra (Mediterranean Sea)	0.9	0.04	Spain	8.7 ²	300
Amchitka (Aleutian Islands)	10.1	136	Arctic Canada	3.3 ³	17
Buldir (Aleutian Islands)	2.6	0.40	Victoria (Australia)	16 ⁴	700
Tasmania (Australia)	13.8 ¹	939	New South Wales (Australia)	6.1 ⁵	154
Vanuatu	130	507	Transvaal (South Africa)	6.4 ⁶	7150

¹Sample of 10 eyries (Mooney & Brothers 1988)
²Sample of 41 eyries in southern Spain (Heredia *et al.* 1988)
³Sample of 18-26 eyries over several years (Court *et al.* 1988)
⁴Sample of 14 eyries (Emison *et al.* 1988)
⁵Sample of 21 eyries (Olsen & Olsen 1988)
⁶Sample of 4 eyries in a river canyon (Tarboton & Allen 1984)

Peregrines' territories can become rather dense with averages of about 4-6 km apart over large portions of their worldwide range. It is difficult to calculate a density for Fiji because of the scattered nature of cliffs and because some likely areas with cliffs were not examined. Within Vanuatu the most realistic way to calculate Peregrine density is by linear shoreline distance since most cliffs are on island perimeters. Calculation by area, as in much of the literature, can be misleading because large regions may not have cliffs; pairs per km² has little meaning and in part accounts for the large variance of values in Table 2. Since Peregrines frequently have a clumped distribution, distances between pairs in areas where falcons occur, often have quite similar average nesting densities. For comparative purpose, however, we have presented data in linear distances (where available) and also by area (Table 2). Some of the highest densities known are on the island of Zembra in the Mediterranean Sea off the coast of Tunisia where 10-12 pairs of Peregrines occur along 9.5 km of coastline (Thiollay 1988). In some regions such as Africa, Peregrine densities are unexpectedly thin

and tend to be spotty or regional (Hustler 1988, Mendelsohn 1988, Tarboton & Allen 1984, Thomson 1984). For the Transvaal of South Africa the average might be 1 pair / 9533 km² (Tarboton & Allen 1984) whereas south of the Transvaal Peregrines have still lower densities until again near the Cape (Jenkins 1991). North of the Transvaal in Zimbabwe some local populations are extremely dense. The low overall densities for Africa are surprising, especially in relation to densities in other parts of the southern hemisphere such as much of Australia and southern Chile and Argentina. The low densities for Vanuatu are likewise surprising because of the abundance of habitat. For Africa, such factors as competition with congeners (Lanner Falcons, *Falco biarmicus*), nest sites in short supply, and limited amounts of appropriate foods have been hypothesized to explain the rareness of Peregrines there; all logical factors. In Vanuatu there are no congeners or other cliff nesting raptors. Appropriate cliffs for nest sites are in superabundance and not limiting. In addition to cliffs, however, suitable nesting ledges on the cliffs are necessary. While many cliffs, especially on Fiji, are more or less smooth basalt without horizontal ledges, this was not the case on Vanuatu; the majority of cliffs we examined had suitable ledges. As with Fiji, we are left with the possibility of some form of food dictated breeding limitation. There are at least 45 widespread bird species in Vanuatu, however, that are in the size class and taxonomic composition that Peregrines feed on elsewhere. Seven are doves and pigeons and 2 are parrots; high preference foods for Peregrines. While we did not see many birds flying above the canopy, from the helicopter we saw forest pigeons and kingfishers "commonly" on Erromango and parts of Tanna in 1993 and fruit bats (at least three species) were abundant in large camps at least on southwestern Efate and Tangoa. In fact they were so abundant in Tangoa that on several occasions we were afraid they would collide with the helicopter. After our departure large numbers of bats were seen on Erromango in inland areas where we did not visit. On a similar flight in 1994 we saw few if any birds. Aside from bats, we have no good impressions about the vulnerability of likely prey species; but in fact we saw no bat remains in eyries.

Breeding Chronology

We are also at a loss to explain the difference in timing of breeding between 2 locations on essentially the same latitude (and thus the same photoperiod) with similar climatic and ecological conditions. In addition to photoperiodic control of breeding, we are aware that environmental cues, such as weather (rain, temperature) and food, may also drive reproductive cycles (Cody 1971, Murton & Westwood 1977). Although rainfall varies considerably, depending on the side of the island, both island groups are within the same precipitation range (1800–4000 mm). The lee and windward sides of islands in Fiji were on the same breeding schedules. Wet and dry and hot and cold seasons occur essentially over the same period on both island groups. Cyclones hit both island groups during a similar temporal period. Thus, the difference in timing is especially difficult to understand, because breeding on Fiji has been so constant in timing over a 10 year spread. On the other hand, Peregrines in equatorial regions have reduced photoperiodic cues and so breeding cycles must be driven largely by environmental factors. At 1 eyrie in Ecuador, at nearly 2400 m, egg laying varied between late June and mid-December (Hilgart 1988) and in Kenya egg laying occurred between June and December (Thomsett 1988). Both authors concluded that food availability was the factor determining onset of laying.

It was suggested to us that cyclones early in 1993 in Vanuatu were so disturbing to fruit bats that they became largely unavailable as food to Peregrines. However, by the time falcons were ready to breed (June, July) bats were once again in large camps as we found them. Both Peregrines and bats have had a long evolutionary history together on the islands in the presence of temporally regular cyclones. Falcon breeding seasons in general are quite regular on Fiji and there are no data to suggest they would not be on Vanuatu. We saw no evidence that cyclones caused Peregrine food shortages in 1993 that might have affected onset of breeding and, further, the breeding schedule was the same in 1994.

One factor that might alter onset of breeding of an entire population in one direction or the other is rainfall. For example, in temperate Australia, a dry, warm winter may shift egg laying earlier, but by less than a week (Olsen & Olsen 1989b). Wet years were those in which the mean increase in

rainfall came within two months of the normal onset of laying. However, in Queensland, Australia, onset of laying has been as early as July and as late as early November (the latter date was one case, anomalous and perhaps a replacement clutch, Czechura 1984). Australian birds in general, however, are noted for being very dependent on weather related breeding responses and in Australia weather is varied. We encountered the "normal" variation in weather in Fiji (some "wet," some "dry" seasons) over the 10 years of looking at breeding, but because of the few nests could not "measure" any real difference or relationship in onset of laying. Certainly mean differences were not more than 2 weeks apart. Generally speaking, our experience is that food abundance or quality drives either onset of laying or clutch size while environmental conditions affect success of the nesting attempt or fledging rate (see also Olsen & Olsen 1989a)

Lack of Breeding

We are disturbed by our findings in Fiji between 1985 and 1997 of the gradual decrease (perhaps actually only extreme variation) in occupancy of nest sites. In mid-October 1985, we found flying young and adults at 4 locations and observed 6 other nest sites that appeared active. Adjusting survey time in 1986, based on age of young the previous year, we covered most of the same area except for parts of Vanua Levu and located young in nests in late August at 7 locations, 4 at the same places from 1985. In 1986 pairs were seen at 3 other locations by colleagues but eyries were not found. In 1989, we covered the same area as previously on Viti Levu and found 2 eyries containing young and 1 had flying adults but no young. In 1991, we made a thorough examination of the cumulative total of 10 eyries with some history of activity and the results are shown on Table 1. Following 1989 there was a rather sharp drop in activity, representing about a 50% overall inactivity rate. In 1993 we checked 2 reliable eyries that had been active on all previous years and two were checked by our helicopter pilots; there was no breeding although a solitary female was at one. If the rest of Fiji (e.g., Kadavu, Lau group, parts of Vanua Levu) has a similar inactivity rate to our sample then the falcon has become extremely rare as a breeding species in Fiji.

We are at a loss to explain the gradual loss in activity of these eyries over such a short period of time. But F. Clunie (pers. comm.) found that the eyrie on Joske's Thumb was used intermittently and D. Watling (pers. comm.) mentioned the inactivity (see White *et al.* 1988) of the eyrie we called "Signatoka" in Table 1. The latter may have been because of human disturbance since the eyrie is relatively accessible and can be walked to. Generally, there is no evidence that direct human interference at eyries is involved since most of the eyries are relatively inaccessible. However, we heard of several cases of adults being shot. In 1995 we know of 1 adult shot by a farmer during the breeding season, prior to our visit, near a known eyrie. That eyrie was unoccupied that season. The same farmer told us he had shot 3 others over the previous 4 years as they sat in trees at his farm.

There are several events that might have happened to explain our findings. First, adults were lost at a higher rate (perhaps a result of human shootings) than they could be replaced because of an extremely low floating, non-breeding population. Second, pairs might have had early egg loss and thus not been attached to breeding stations on a permanent basis so they were not seen. Third, the single birds we saw at eyries in 1994 could be a result of either one of these. Lastly, they may be tied to variable weather and food resources as they are in Australia; this could result in non-breeding or at least adjustments in the breeding cycle as in Queensland. In Australia, for example, breeding dynamics of some raptors have evolved to compensate for periodic weather phenomena, such as El Niño events of which there have been a series over the past 4-5 years (Trenberth & Hoar 1996), that in turn affect food availability and thus their breeding condition. Weather, however, seems to have been "average" through this time period except for the especially wet typhoon Kina that occurred in January 1993. In a species with naturally low adult mortality one evolutionary strategy used when food is undependable or periodically affected, is to have intermittent breeding (many northern hemisphere raptors do just that). As with the Australian populations (Sherrod 1983), falcons in Fiji and Vanuatu may also have long juvenile dependency periods that help increase survivorship of young as a response to that very situation. On Vanuatu, we were at a nest containing a newly hatched young when a juvenile of the previous year came food begging from the flying adults. It was not driven away by the pair as would be the case in other populations we have studied.

Population Dynamics-A Scenario

Based on the fact that Peregrines seem to be, 1) poorly suited or adapted to tropical climates and generally occur in low densities there, 2) that few year-old birds are seen away from eyries (Clunie in White *et al.* 1988) suggesting a low floating population and that, 3) there seemed to be variable amounts of breeding year to year. A plausible scenario for those island populations might be as follows: Adults have evolved to be relatively long lived once reaching breeding age because mortality is high in the years prior to breeding. A relatively substantial pre-breeding age mortality may be related to food availability. Food availability (or perhaps choice or vulnerability) require that young have an extended period of dependence on adults (our observations in Vanuatu; Sherrod 1983). Food or weather vagaries, rather than interaction for nest sites or with adults, thus account for the major mortality of young. All of this then results in a low density non-breeding (floating) population to act as replacements at eyries once adults are lost. Under normal compensatory mortality rates (mortality adjusted so that there is a balance with carrying capacity) population density is maintained at a given level. However, once additive mortality (mortality over and above the natural compensatory levels) increases, from shooting of adults for example, replacement populations are not sufficient to maintain eyrie activity. Some adults may occur at eyries (our observations of lone adults) without finding mates for a time period. Slowly the population builds up and eyries are reoccupied again.

IMPLICATIONS FOR BIODIVERSITY AND CONSERVATION

There are at least 3 important items that emerge from the data on Peregrines from Fiji and Vanuatu. First, the race *Fp. nesiotus* occurs in low densities and breeding pairs are widely scattered. However, Peregrines may occur in very low densities over long time periods if adult survivorship is not drastically altered or if mortality is not additive. Effective breeding populations of only a few pairs persisted in some regions of North America for apparently a couple of decades during the pesticide era in the 1960's-70's. The subspecies *madens*, confined to the Cape Verde Islands, may contain 10-12 pairs and *furuitii* is apparently confined to one island in the Volcano Islands, North Pacific Ocean, so far as is known (King 1978,79). Second, even if such small populations may persist over some time periods it gives us little comfort with regards to Fiji if our impressions of a highly fluctuating breeding population are accurate (Brimm 1994), especially because of the lack of any feasible scenario causing such changes. This is especially alarming in the face of a rapidly developing island nation. Because of the falcon's presence, its historical roots and folklore within Fiji (the *ganivatu* of legend), the loss of the species from Fiji would certainly diminish the biodiversity by more than simply the loss of one species. Perhaps annual census data over at least one falcon breeding generation is necessary to understand breeding phenology and to help answer the questions of any relationship between the loss of eyrie occupation we have witnessed and disturbance, weather, food, and the regularity of breeding. An Australian population near Melbourne with 21 eyries steadily declined 25% between 1976-1984 and the regression line predicted nearly a 50% decline by 1992. However, a survey in 1992 showed nearly a 90% reoccupancy again (Emison & Hurley 1995). Also, during the exceptionally dry year of 1994 over 50% of a well studied sample of 22 eyries near Canberra, Australia, did not occupy breeding sites but were back to the previously high occupancy rate (around 90%) the following year (P.D. Olsen, pers. commun.). Overall, this population generally had a 82-100% occupancy per year by at least one bird. Annual eyrie occupancy rates in continuously monitored populations may be extremely different from region to region and from one another as shown in a sample of studies in Table 3. No particular relationship between occupancy rates and food or weather was established for these studies although the Utah sample is in a region of inordinately abundant food resources. Thus, better knowledge is needed on the control of breeding dynamics in tropical or southern latitudes and assumptions based on northern hemisphere breeding biology may not be accurate. Third, the impact of inbreeding on population viability is not understood especially for populations that may have successfully passed through several "bottlenecks" and where the breeding strategy may be one of inbreeding. Regardless, genetic variability (and the so-called hybrid vigour) may help the populations we have studied. The notion of infusion of genes from Vanuatu

Table 3. Examples of variation in eyrie occupancy rates between regions as compared with Fiji. Occupancy is defined as the presence of at least one falcon at the eyrie whether breeding took place or not. The South African sample¹ was specifically used because all sites were checked in a given year and the regions had more or less distinct populations. Percent occupancy is for a constant sample except in Fiji where it represents occupancy of those that were checked and the sample size varied from year to year.

Region	Percent by Year						
	Yr.	Yr.	Yr.	Yr.	Yr.	Yr.	Yr.
	1	2	3	4	5	6	7
So. Africa 1 (n=10)	70%	80%	90%	90%	90%	90%	100%
So. Africa 2 (n=6)	100%	100%	100%	100%	100%	100%	83%
So. Africa 3 (n=7)	86	71%	71%	57%	71%		
Utah ² (n=7)	100%	100%	100%	100%	100%	100%	100%
Fiji	100% (n=4)	100% (n=11)	60% (n=5)	50% (n=10)	25% (n=4)	57% (n=7)	40% (n=6)

¹Unpublished data provided, at our request, by Andrew Jenkins from his study areas.

²Data were taken from "hack" towers around the shores of the Great Salt Lake from which falcons had been originally released for a reintroduction programme. Data furnished by Don Paul.

into Fiji by translocating birds, and *vice versa*, may be a worthwhile consideration for populations declining or in low densities. Based on a phylogenetic analysis of morphological traits (White & Boyce 1988) it was not clear if Peregrines from Australia or those from the New Guinea/Solomon Islands complex are the source gene pool although *nesoites* did cluster with that clade. So far, genetic analysis has also not been adequate to resolve this question. The likely answer may lie in a broader DNA analysis of birds from New Caledonia, northern Australia, and the Solomon Islands.

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