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THE POPULATION STATUS, LONGEVITY AND MORTALITY OF THE WHITE-RUMPED SWIFTLET IN FIJI

M. K. TARBURTON

Department of Botany and Zoology. Massey University. Palmerston North, New Zealand

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The population size of the White-rumped Swiftlet *Aerodramus spodiopygius* in five Fijian caves has been estimated by up to five methods. The averages of these methods for 1974 are: Dry Cave, 413; Waterfall Cave, 20 994; Ono Cave, west entrance, 345; east entrance, 10 365; Waiyala Cave, 8 430; Cikobia-i-lau, 210. The largest annual average estimated population was 32 526 for Waterfall Cave in 1975. Although the population of Dry Cave declined between 1974 and 1984 the recapture rate of marked birds remained high. These data show an average survival rate of 64%, though a survival rate of 73% (which is determined when data taken in the abnormal years of 1976 and 1982 are deleted), may be more realistic. The higher rate, which gives an adult further life expectancy of 3.2 years is higher than most passerines, some seabirds and one other species of swift. Higher adult life expectancies have been shown for four other swift species. Juvenile mortality is shown to be too high to replace the adult population and it is reasoned that human interference in Dry Cave is responsible for the high juvenile mortality. Adult mortality is low and arises from predation and accidents caused by conspecifics The current longevity record in this study is at least 12 years.

INTRODUCTION

It might be assumed that if a population is large, its survival is not threatened, but without census data only guesses can be made as to its long term viability.

Knowing something of the stability of the population upon which manipulation (Tarburton 1987) and longevity studies were made, could help in the interpretation of the results of those experiments. The ability of the swiftlets to obtain adequate food for themselves and their chicks is the basis of both studies. In the former, the growth rates of chicks in artificially enlarged broods of three was compared with the growth rates for single chicks and those in broods of two young. It was reasoned that a population in balance with its food supply would not be able to gather enough food to feed an additional chick. On the other hand it has been suggested that for the Lesser Black-backed Gull *Larus fuscus* (Harris and Plumb 1965) and the North Atlantic Gannet *Sula bassana* (Nelson 1964), the ability to raise broods artificially larger than normal was at least in part facilitated by an increased food supply, resulting in a period of considerable population growth prior to and during the time the manipulation experiments were being conducted.

Alternatively, a population that is either stable or in decline, as a result of a limiting food supply is unlikely to be able to raise a larger brood than that normally produced.

In this paper the population trends in two Fijian (18°S., 179°E.) caves where manipulation experiments and longevity studies were conducted, are determined. The populations of these and three other Fijian caves are estimated and the locality of the nesting sites are mapped for four of the caves. Together five caves on two islands (Nasinu Caves [Waterfall Cave and Dry Cave], Ono Cave, and Waiyala Cave are on the island of Viti Levu, while Ono-i-Lau Cave is on the island of Ono-i-Lau), were incorporated into the study. The further life expectancy of adults is calculated and that measure, survivorship and longevity are discussed in relation to the stability of each population and are compared with those for a range of other birds. Finally, causes of mortality are identified and their relative importance discussed with a view to preserving these South Pacific populations of the White-rumped Swiftlet.

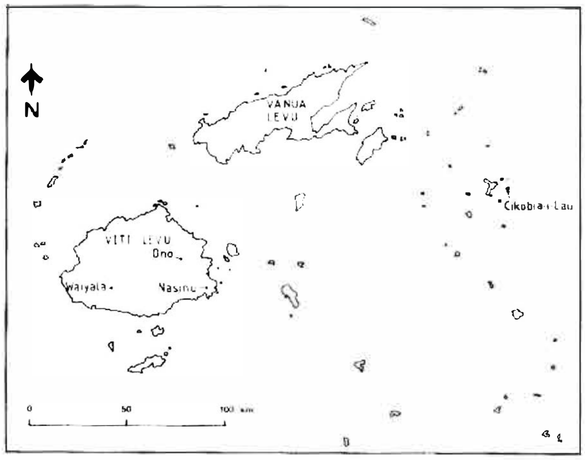

Figure 1. *Location of White-rumped Swiftlet colonies studied in Fiji.*

METHODS

The location of the five Fijian caves visited in this study are shown in Figure 1. All caves are in limestone and although Ono Cave has several levels of development none has reached the stage of collapse that allows light to enter internal passages or chambers. The majority of nest and roost sites are in the totally dark portions of each cave. The cave on Ono-i-lau is the only one without running water and it and Dry Cave are the only two that do not pass completely through the base of a hill to provide a second entrance.

Dry and Waterfall Caves were the most frequently visited in the course of this and other studies with a total of 59 visits to Waterfall Cave and 45 to Dry Cave. ●no Cave was visited 10 times while Waiyala and the cave on Ono-i-Lau were visited once.

Five methods of estimating population size have been used in this paper. Counting the sleeping birds late at night, once they had ceased entering the cave, was the first method of census and is only possible with small populations in small caves. Thus this was only feasible in Dry Cave, Nasinu and the sole cave on Cikobia-i-Lau. This method of estimating a population assumes that all birds that roost and breed in a particular cave enter it each night. To check this, estimates made by direct counting in Dry Cave were compared with a nest count and two capture-recapture analyses; Jolly's Stochastic method and the Modified Petersen method (Begon 1979). As the Petersen method does not allow for deaths, the number of marked birds estimated by this method was reduced at the end of each year by 29 per cent, being the estimated annual mortality rate for each of the first 2 years after banding.

In the Waterfall Cave, very few recaptures were made so the Schnabel method as well as those of Petersen and Jolly were applied to the recapture data and each result compared with the nest count.

In the larger caves the swiftlet populations were estimated by counting nests, most of which remained intact and were used from year to year. The sampled area in the Waterfall Cave at Nasinu contained just over three birds to each nest. An assumption was made that a ratio of three birds to each nest, held for all parts of the cave as well as for other caves, the larger ones being censused within a week of completing the Waterfall Cave census.

RESULTS

Cave Population and Population Trends

Dry Cave, Nasinu

Data from the Dry Cave alone are sufficiently comprehensive to be analysed by Jolly's Stochastic method. The results of this probablistic method are shown in Table 1. The raw capture and recapture data and preliminary computations are shown as Appendices 1, 2 and 3.

The four estimates made in 1974 using Jolly's method indicate an average population of 397 ± 51 ($\bar{x}$ ± SE). Close to this estimate is that of the Modified Petersen estimate of 430 ± 32. The two estimates for 1975 average 339 ± 79 which is similar to the Petersen estimate of 346 ± 56. The 11 recaptures made in 1976 provide an estimated population of 305 ± 37 using Jolly's method and 204 ± 28 from Petersen's method. These estimates differ considerably but both indicate a marked decline. This decline has continued, as the nest and bird count data in Table 2 indicate. Nests declined from 163 in 1974 to 49 in 1983. Bird counts indicated that the population declined from 200 in 1974 to 90 in 1983 but was maintained at 94 in 1986. Nest positions in the cave are shown in Figure 2.

TABLE 2

Population of Dry Cave, Nasinu.

	No. of Nests	Nests ×2	Nests ×3	Jolly's Estimate ±SD	Modified Petersen ±SD	Bird Census
1974	163	326	489	430 ± 51	430 ± 32	200
1975	—	—	—	339 ± 79	346 ± 56	—
1976	142	284	426	305 ± 37	204 ± 28	88
1978	—	—	—	—	—	91
1979	—	—	—	—	—	94
1980	—	—	—	—	—	82
1981	61	122	182	—	—	—
1983	49	98	147	—	—	90
1986	—	—	—	—	—	94

TABLE 1

Population estimates of the Dry Cave population.

	Jolly's Estimates			Modified Petersen		
Sample Date	$\dot{M}i$	n	$\dot{N}i$ ± SE	$\dot{O}i$	$\dot{B}i$	$\dot{N}i$ ± SE
8 Aug. 74	0	48	— —	—	—	— —
18 Aug. 74	54.75	72	438 ± 158	0.47	233	389 ± 115
4 Sept. 74	106.46	115	515 ± 100	0.54	238	522 ± 118
27 Oct. 74	178.2	36	356 ± 78	0.91	330	387 ± 90
19 Dec. 74	143.72	34	279 ± 57	0.90	29	420 ± 201
23 Nov. 75	155.85	58	418 ± 78	0.93	30	401 ± 157
4 Dec. 75	155.87	19	260 ± 55	0.96	11	290 ± 115
10 June 76	157.87	91	138 ± 12	0.78	36	219 ± 70
13 June 76	254.82	91	378 ± 44	0.90	39	322 ± 52
7 Oct. 76	213.66	60	214 ± 25	0.93	16	308 ± 59
14 Oct. 76	157.86	16	335 ± 98	0.95	18	340 ± 154
17 Oct. 76	196.96	43	234 ± 28	0.98	6	132 ± 45
22 Oct. 76	174.62	18	221 ± 41	1.04	−8	163 ± 57
25 Oct. 76	213.2	9	237 ± 75	1.00	1	90 ± 46
29 Oct. 76	191.5	12	244 ± 61	0.99	3	63 ± 34
7 Nov. 76	312.0	88	463 ± 82	0.92	38	153 ± 52
9 Nov. 76	421.0	15	561 ± 300	0.99	7	235 ± 70
11 Nov. 76	271.11	43	328 ± 94	0.98	8	220 ± 33

Key: $\dot{M}i$ = number of marked birds at risk.
n = sample size.
$\dot{N}i$ = population size on day i.
$\dot{O}i$ = stochastic survival rate.
$\dot{B}i$ = additions between i and i+1.

Waterfall Cave, Nasinu 9 Mile

Although 2 545 birds were banded in the Waterfall Cave, the population is so large that it was the fifth evening visit before any recaptures were made. The average number of recaptures thereafter was 5.8 from an average sample size of 192. This recapture rate was so low that population estimates using Jolly's method ranged from 11 332 to 408 165 having standard errors of 5 692 to 445 128. The resulting average of 91 054 ± 41 796 (± SE) seems less realistic than the average derived by using only those estimates with standard errors less than the means. These averaged 25 690 ± 6 078 and are more in line with the Petersen and Schnabel estimates shown in Table 3. (Computations for Schnabel's method are shown in Appendix 4). The final column of this Table is an average of all methods used in estimating the population and indicates a population increase between 1974 and 1975 but no significant change into 1976.

As no bands were recovered from this cave after 1976 (not an unexpected result with only about 8% of the population marked), the 1981 nest count is the only method for assessment of the population size at the time the manipulation experiment was run (470 birds were caught in an effort to make recaptures). This estimate indicates that the 1981 population was similar in size to that of 1976 and 1975, though the occurrence of intervening fluctuations cannot be disproved. Nest numbers and positions are shown in Figure 2.

Ono Cave, Wailotua

The west entrance to this large cave has only a small colony. There were 115 nests in 1975, giving an estimated population of 345. This is much smaller than the 1 211 given by the average of five Modified Petersen estimates. This is probably explained by a high level of band loss as a result of the band being placed on the tarsus during the first few trips. Bands were subsequently placed on the tibia, once recaptures revealed that the hind toe does not prevent bands from slipping down over the other three toes and presumably in some cases slipping off the leg completely. No birds were ever found flying the 390 m between the closest west and east colonies, but as in the Nasinu Caves, a small level of exchange may have taken place through the separate entrances.

The population at the east end of the cave had 3 455 nests giving it an estimated size of 10 365 birds. Nest positions in the cave are shown in Figure 3. The Modified Petersen estimate was 17 909 ± 7 202, from four recaptures in a total catch of 167. Another estimate when only one recapture was made in a catch of 138 birds was 37 909 ± 24 432. A subsequent capture of 298 birds made no recaptures. Perhaps this disparity is due to some birds staying out at night, though the small sample sizes (<3%) in this case may also influence the accuracy.

Waiyala Cave

Only one visit was made to this cave (February, 1975) and the best estimate of its population size is made from the count of 2 800 nests giving 8 430 birds. The position of these nests is shown in Figure 4.

Cikobia-i-Lau

Seventy nests were counted on 7 January, 1976 making an estimated population of 210 birds.

TABLE 3

Population of Waterfall Cave.

	Nests	3× Nests	Modified Petersen ± SE	Schnabel ± SE	Jolly	Average Of All Estimates
1974	3 660	10 980	22 266 ± 5 273	26 040 ± 2 121	24 688	20 994 ± 3 428
1975	—	—	45 032 ± 14 868	30 753 ± 2 844	21 792	32 526 ± 6 767
1976	7 370	22 110	37 045 ± 12 613	32 890 ± 965	29 143	30 292 ± 3 170
1981	7 140	21 420	—	—	—	—

Survival and Further Life-expectancy

It is in the context of a declining swiftlet population in Dry Cave that the data from 502 banded birds have been used to determine survivorship and further life-expectancy of adult birds and hence the results should be regarded as conservative. Of the 446 banded adults 261 were subsequently recaptured. This represents a recapture rate of 59 per cent and contrasts with the nestling recapture rate of 17 per cent. Four adults were recaptured 11 times; one was captured nine times; three, eight times; four, seven times; 11, six times; 22 five times; 18, four times; 41, three times; 42 twice and 115 only once.

The 675 recoveries of these 261 birds show a range of annual adult survival of 41 to 77 per cent and an average of 64 per cent (Table 4). The lowest annual survival was that of 1976, the year that the Dry Cave population had the most visits by me and to my knowledge the most disturbance from other people. Nevertheless none of 99 clutches observed in the manipulation experiment (Tarburton 1987) were deserted and no chicks from the 130 observed in the same experiment died of starvation.

TABLE 4

Survivorship of adult birds in Dry Cave as at 1 September, 1983.

	Number of Banded Birds Present	Number Still Present 1 Year Later	% Survival
1974	69	52	75
1975	119	91	76
1976	160	66	41
1977	88	65	74
1978	65	44	68
1979	44	34	77
1980	34	23	68
1981	23	17	74
1982	17	10	59
1974-1982	629	402	64%

Further adult life expectancy for all years

$= \frac{2-m}{2m} = \frac{1.64}{0.72} = 2.3$ years

(m = mortality)

Further life expectancy excluding the poor years of 1976 and 1982

$= \frac{1.73}{0.54} = 3.2$ years.

Even though the two Nasinu caves were only 18 m apart few birds made the short transfer. On each banding visit to Dry Cave more than half the birds present were captured, yet only three of the 2 545 birds banded in Waterfall Cave were found among them.

Thirty-five of 48 birds taken from Dry Cave and released at Fulton College, 21 km to the north, on 10 June, 1976, were subsequently recaptured at Dry cave. This represents a recapture rate of 73 per cent which is identical to the average adult recapture rate for this population. Hence my handling of birds, whether breeding or non-breeeding does not cause desertion of the breeding cave.

When the data for all 9 years are used the expected further adult life expectancy is determined to be 2.3 years. When the data for 1976 and 1982 are excluded, the expected further adult life is estimated to be 3.2 years.

DISCUSSION

There has been some discussion of the accuracy of Lack's method for population analysis. For example Piper, Mundy and Ledger (1981) found estimates on vultures using Lack's method were lower than those of Haldane (1955) and Piper *et al.* (1981) which allow for the incompleteness of data from bands yet to be recovered. Yet Seber (1972) states that it can be shown mathematically that the methods of Haldane and Lack still hold if the recoveries are ignored for an initial period of any length. In this longevity study banded swiftlets were not counted as present unless they were recovered subsequent to the 1 September following their initial recapture. As all eggs hatch before the end of February all birds would be at least seven months old before being included in the calculations. These data then should be reasonably accurate and in any case are comparable with the data for the other species mentioned, as the same method was used to determine their mortality. As all of the apodid species have similar feeding and breeding ecologies, comparisons within the family should be reasonably valid.

The adult recapture rate of 59 per cent in this study contrasts with the recapture rate of 2.1 per cent for adult Common Swifts *Apus apus* in Britain between 1909 and 1969 (Spencer 1971). However, a Russian study on the Common Swift (Kashentseva 1982) had better returns than the

Figure 2. *Nasinu Caves showing the location and numbers of White-rumped Swiftlet nests. (broken hatching = water, closed broken line = areas of nesting with the number of nests indicated, bold broken line = point at which twilight is replaced by darkness).*

Figure 3. *Wailotua Cave showing the location and numbers of White-rumped Swiftlet nests. (broken hatching = water, closed broken line = areas of nesting with the number of nests indicated).*

Figure 4. *Waiyala Cave showing the location and numbers of White-rumped Swiftlet nests. (broken hatching = water, closed broken line = areas of nesting with the number of nests indicated, bold broken line = point at which twilight is replaced by darkness).*

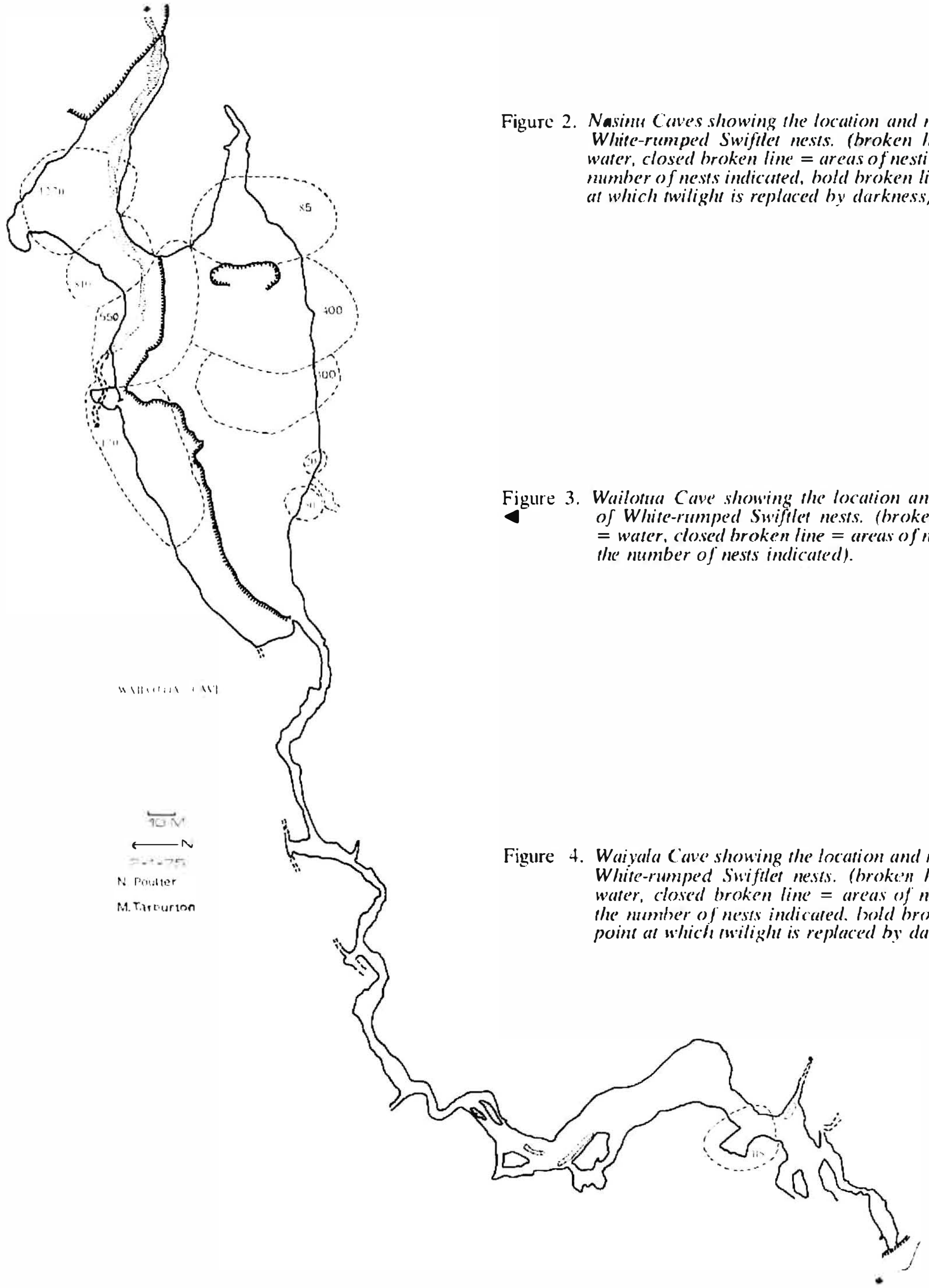

Figure 3

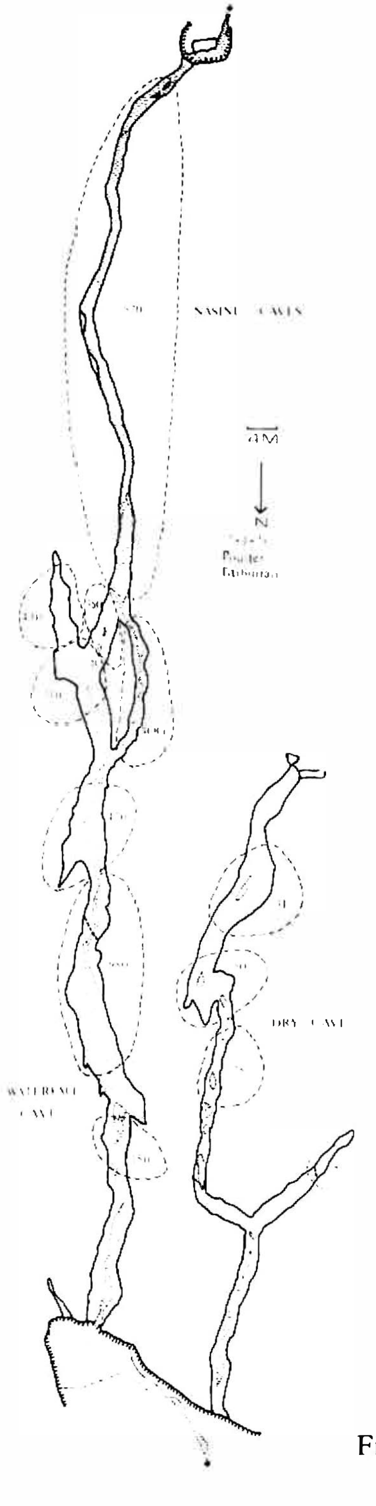

Figure 2

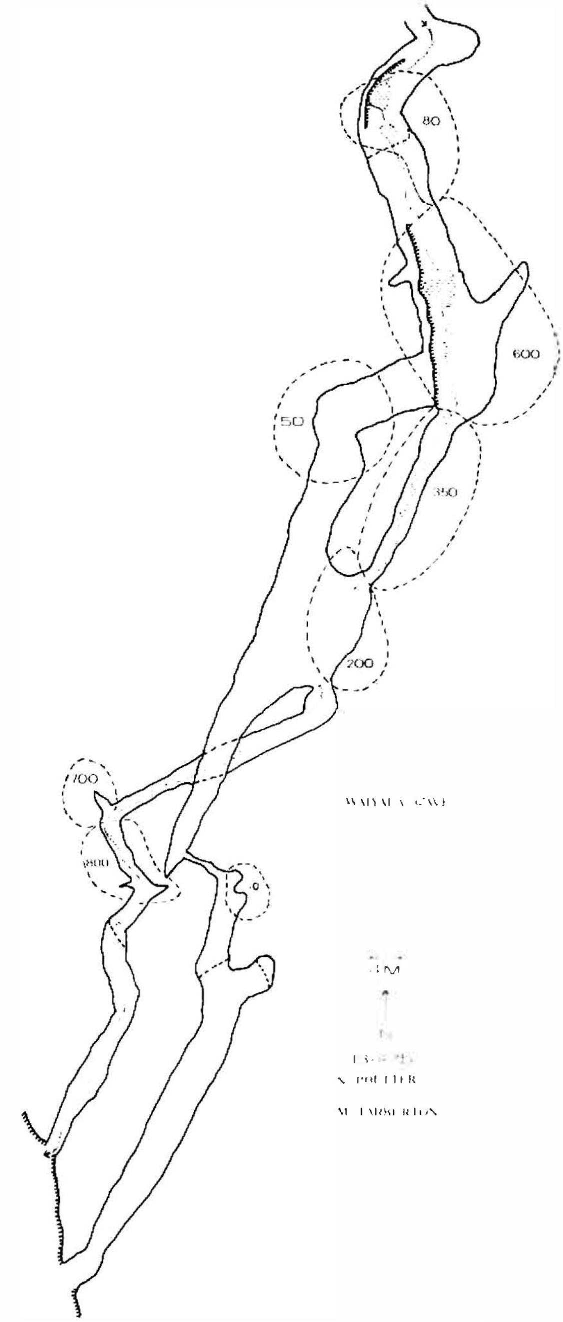

Figure 4

total British banding scheme. Betweeen 1950 and 1979, 4.1 per cent of juveniles and 40.1 per cent of adults were recaptured from 667 banded swifts. Both the Russian study and this study have much higher returns than normal, recovery rates of all bird species banded in Britain and America being usually less than 4 per cent (Botkin and Miller 1974).

That frequent or severe human disturbance and low survival may be related is suggested by several authors finding that distrubance causes avoidance of the site of capture by up to one third of the Common Swift population (Lack 1956). Lack qualified this statement by adding that some birds taken from their nests for banding and measuring deserted but when the birds were banded on the nest desertion was most uncommon.

It might be reasoned that birds deserting one of the two Nasinu Caves as a result of being disturbed would be more likely to go to the other cave as the two caves are only 18 m apart, whereas the next nearest cave is 10 km away. From the proportion of birds banded in the Waterfall Cave and caught in Dry Cave it is estimated that six birds banded in the Waterfall Cave would have subsequently been caught in the Dry Cave if all birds present had been captured at the time of each visit. If it is assumed that the same percentage move in the reverse direction and that there is no movement between the caves before the birds are handled for banding, then only one of the 502 birds banded in the Dry Cave will have transferred to the Waterfall Cave.

However, the observable effect of disturbance in the two caves may not be equal. The Waterfall Cave is quite large in cross-section (most birds are out of reach of a hand-net), is long (178 m) and has two entrances. Birds banded and released in the Waterfall Cave may just relocate within that cave and would thus be rarely recaptured in the Dry Cave. Dry Cave on the other hand is small in cross-section (all nests and most birds can be reached by the hand-net), is short (90 m) and has only one entrance. This means that in Dry Cave a greater percentage of birds will be caught or otherwise disturbed at each visit, than is the case in the Waterfall Cave. If birds from Dry Cave relocated in the Waterfall Cave there would be little chance of their recapture and hence little chance of determining whether members of the Dry Cave population were deserting more frequently due to their greater disturbance.

It is also possible that some birds may change caves periodically whether disturbed by humans or not. If this is the case the three birds banded in Waterfall Cave and retrapped in Dry Cave can be used to estimate the total movement of swiftlets from the Waterfall Cave to the Dry Cave. The retrapped birds are counted as six to allow for that (almost) half of the birds present each visit that were not caught. The 2 545 birds banded in the Waterfall Cave make 8.4 per cent of the estimated total population of 30 292. Thus 71 birds are likely to have moved from the Waterfall Cave to Dry Cave. However, unless a greater percentage move in the reverse direction we can still only account for one bird moving from the Waterfall Cave as a result of 'random' movement, for almost all birds in the Dry Cave were banded by the end of 1976.

The above reasoning assumes random movement, but that this does not always exist in swifts is shown by the regular use of two chimneys during the northward movements of Chimney Swifts *Chaetura pelagica* in Texas whereas only one of the chimneys is used during their southward movements in autumn (Michael and Chao 1973). That swiftlets caught in Dry Cave may sometimes sleep elsewhere cannot be discounted.

Since the Dry Cave allows for a far higher percentage capture of birds present than does the Waterfall Cave, this activity itself possibly creates greater disturbance with more birds leaving the cave after human activiy in it. A small post-disturbance exodus is possible, as each of the methods used for estimating the population and shown in Table 2 give consistently higher estimates through the 1970's than the numbers of birds found to be in the cave. But there are other possibilities.

It is likely that some birds were still to return after the time of the visit. I have recorded arrivals as late as 2230 hours, the latest I have made observations. The rate of arrival at that time of night is however very low, though it may continue for some time as Medway (1961) has recorded Black-nest Swiftlets *Aerodramus maximus* returning as late as 0310 hours. That birds may delay their return to the roost is substantiated by the first reported night feeding for the White-rumped Swiftlet. Jim Pierce who is familiar with this swiftlet told me of its feeding on insects flying around fluorescent lights at the Williamstown mining camp 25-30 km south-west of Mungana, Queensland. These swiftlets were seen feeding amongst the bats for an hour or so after sunset on at least two nights in September 1985.

Some birds may stay in the field. Several Fijians have told me swiftlets will sleep in the coil of a young banana leaf. Another Fijian whom I consider reliable, once saw a swiftlet enter such a banana leaf during the day and leave it a short time later. The Fijian belief, that swiftlets sleep in the roll of a young banana leaf may have developed from sightings such as this. After all, the Fijian belief that the swiftlet has no legs appears to have developed from the observation that the birds never land on tree branches.

Watling (1982) suggests some swiftlets probably sleep on the wing but no supporting evidence is given. I presume the view is simply a transfer of Lack's report that the Common Swift sometimes sleeps on the wing.

That alternative sleeping places may exist does not, however, mean that they are used, nor does it mean that they are used more when the birds are disturbed frequently at their normal roost site in the cave. However, such possibilities do allow for the discrepancy between the population estimates and the number of birds counted.

My high recapture rate for all adults (including those held overnight and taken some distance away) caught in Dry Cave suggests my handling of the birds was not causing a significant decline in the population. However, disturbance through nest destruction, which is quite possible in Dry Cave (due to other persons visiting it), could cause a population decline in three ways. Birds having to rebuild their nests could experience greater physiological stress, resulting in higher mortality. Birds losing their nests and clutch or brood may be more likely to abandon the colony. This has been suggested to explain the persistent decline of Black-nest Swiftlets in Madai Cave (Sabah, Malaysia), where the nests are harvested for human consumption (Dalton). Finally replacement nests may not be as large or as strong as the original nest, resulting in higher egg or chick losses from the eggs, chicks and/or nests falling to the ground. Replacement nests in the Edible-nest Swiftlet *Aerodramus fuciphagus* are inferior in this way (Gibson-Hill 1948), though the effect on breeding success is not known.

If we consider the disturbances of 1976 and 1982 to be abnormally excessive and so delete the data for these years, we obtain an average adult survival rate of 73 per cent instead of 64 per cent. The consequent average mortality of 27 per cent (range 16-32%) means the White-rumped Swiftlet does considerably better than the Barn Swallow *Hirundo rustica* (63%) and 12 other passerines (41-72%) but less than the Alpine Swift *Apus melba* (18%), and the Common Swift (20%) (all in Lack 1954). Two other studies on the Common Swift found mortalities to be between that which Lack found for the Common Swift and those found in this study. In the USSR, mortality was 24.4 per cent (Kashentseva 1982) and in Britain it was 21 per cent. Two other swifts also have lower mortality than the White-rumped Swiftlet. These are the White-throated Swift *Aeronautes saxatalis* of the United States, which has an annual mortality of about 20 per cent (Collins 1973) and the Chestnut-collared Swift *Cypseloides rutilus*, which in Trinidad has 15 to 17 per cent mortality (Collins 1974). While the recapture rate for the White-tipped Swift *Aeronautes montivagus* in Venezuela (Collins unpub.) is about 65 per cent, Collins' work on this species leads him to believe that the real figure is about 82 per cent. It appears that both a disturbed bird and its mate are likely to lose the nest site and leave the colony, hence avoiding recapture (Collins, pers. comm.). If this is correct (as is to be expected, for larger birds tend to live longer), the only swift with higher mortality than the White-rumped Swiftlet is the Chimney Swift of the United States, which has an annual mortality of 38 per cent (Henny 1972). The White-rumped Swiftlet has lower mortality than 15 other non-passerines, including two seabirds and is only bettered from those non-passerines given in Lack (1954) by the Royal Albatross *Diomedea epomophora* and the Yellow-eyed Penguin *Megadyptes antipodes*, which have annual mortality rates of 3 per cent and 10 per cent respectively.

Both estimations for further adult life expectancy (2.3 years and 3.2 years) appear reasonable when compared with 1.1 years for the Barn Swallow and 4.6 years (Magnusson and Svardson 1948) and 5.6 years (Weitnauer 1947) for the Common Swift. However, because of the declining population in Dry Cave even the life expectancy of 3.2 years should correctly be regarded as conservative.

Just how conservative an adult life expectancy of 3.2 years is, can be estimated by calculating the number of years it would take for parents to replace themselves with breeding offspring at variously selected mortality rates. By using the annual fledging success data (1.1 chicks per pair per year) from the stable population of the Waterfall Cave and the 80 per cent survival rate of adult European and American swifts, it would take 2.3 years for parents to replace themselves. With 74 per cent survival (the average of Fijian swiftlets without the two abnormally poor years) replacement would take 2.5 years. With 64 per cent survival (the average of all years for Fijian swiftlets) replacement would take 2.9 years. Clearly each of these replacement rates could be achieved in the 3.2 years of further adult life estimated from the declining population of Dry Cave. However, as juvenile mortality is usually higher than adult mortality, lower survival rates than those used should be expected. The proven first year survival of 21.25 per cent (from 74 banded chicks) in the declining Dry Cave population would require 8.6 years to replace parents and can be regarded as below the minimum of that in a stable population. If we raise the juvenile survival to 50 per cent the parents would be replaced in 3.6 years, which is the average longevity of the adult Common Swift in Russia (Kashentseva 1982).

The Common Swift also has an adult mortality similar to that of the White-rumped Swiftlet, and so (assuming no net migration gain or loss) if the same ratio of juvenile to adult mortality holds for the swiftlet, 50 per cent mortality between fledging and breeding may be realistic. If it is realistic, then disturbance of the birds by the suspected destruction of their nests and contents in Dry Cave has considerably reduced juvenile survival and has led to the decline observed in that population.

Maximum Recorded Longevity

At the time of writing (March 1986) the oldest recorded bird from the 502 banded in Dry Cave was 013-69752 banded on 4 September 1974 and last recaptured on 27 February 1986, 137 months having elapsed. As the bird was an adult when banded it would have been at least 12 years old at the time of recapture. Two other adult birds have been recaptured 112 months after banding, making them at least nine years old when last recorded.

There are few longevity records for Apodidae with which to compare this record for this species. The oldest recorded Chimney Swift was 13 years (Hight 1953). The record for the Alpine Swift is 16 years (Rydzewski 1962) and 21 years for the Common Swift (Rydzewski 1962). The oldest recorded Common Swift in the Russian study is 11 years (Kashentseva 1982) and in a Czechoslovakian study 12 years 11 months and 21 days (Beklova 1976). The records for two swallows in this last study show that they only live about half as long as the Apodidae. The longest records for Hirundine longevity are 7 years for the Barn Swallow and 6 years 5 months for the House Martin *Delichon urbica*.

Mortality and its causes

Because the survivorship of the White-rumped Swiftlet is here shown to be greater than most other similarly sized land-birds studied so far, it naturally follows that its mortality will be low compared to theirs. Adult mortality was shown to average 27 per cent for 7 years. If the years (1976 and 1982) showing abnormally high mortality are included the average mortality for the 9 years rises to 36 per cent. It can be reasoned that the practice of being airborne all day and of roosting and breeding in what may be thought of as the safe environment of a cave would help reduce mortality. However, mortality remains, and some observations and discussion regarding its causes will help clarify whether the feeding, roosting and nesting habits do enhance longevity, not only for this species but possibly also for other species having similar ecological habits.

That man has little direct effect on the mortality of this bird outside the caves is evidenced by the fact that whereas numerous bands from those I have placed on similar numbers of other bird species in Fiji have been returned, none of the 4 554 swiftlets I banded in Fiji were ever recovered away from the caves they use for nocturnal roosting and breeding. The small size of this swiftlet means man is not interested in it as a food source. Though some indigenous Fijians are very good at collecting birds by throwing stones at them I have heard only once of their collecting a swiftlet in this manner. The extreme difficulty I had in trying to mist-net this swiftlet in the field also demonstrated that their keen eyesight and rapid manoeuvrability make them much harder for man to capture than most land birds.

Even the caves offer protection from man when the birds are roosting. Indians are reticent to enter caves for fear of snakes and Fijians rarely enter alone, giving as their reason that the devil lives there. However, when a group of Fijians do go in to catch the Long-tailed Fruit-bat *Notopteris macdonaldi* for food, numbers of swiftlets may also perish. In Ono Cave at Wailotua village in the Wainibuka Valley, bamboo is burnt to drive the bats (and birds) into small dead-end passages and if this is done when swiftlets are present, swiftlet mortality may result.

Apart from man the White-rumped Swiftlet in Fiji has few predators. A Pacific Python *Enygrus bibranii*, a little over a metre in length, was found sleeping on a rock below nests in the eastern end of Ono Cave. It would be unreasonable to expect that pythons would feed on anything but chicks and eggs that fell from nests. American Cockroaches *Blattaria americanus* and large fresh-water eels do the same, though the cockroaches also feed on the saliva that glues the nests to the wall. Although cats are reported to capture swiftlets when flying low (Clunie 1984), most birds feed over the forest where such a fate is not likely.

The Barn Owl *Tyto alba* does take adult and nestling swiftlets. It was said to be responsible for the abandonment of several score of nests placed in the twilight zone of the upper entrance (south end) of the Waiyala Cave (see Figure 4). Many eggs lay on the guano below the nests and villagers from Waiyala said they had seen the Barn Owl chasing swiftlets in this entrance. I have found a Barn Owl feather in the entrance to Waterfall Cave and Clunie (1972) has seen a Barn Owl catching swiftlets at the entrance to a cave in Navosa. I have picked up several freshly dead and concussed birds from the stream in the entrance of Waterfall Cave. However, they were probably victims of head-on collisions in the zone where the birds fly their fastest, though the possibility that they were struck by a Barn Owl could not be ruled out. Even in Europe where there are abundant data for avian predation on the Common Swift the diurnal predators take few swifts compared to other species. The Common Swift forms only 1 per cent of the prey of the Sparrowhawk *Accipiter nisus*, 1.5 per cent of the prey of the Peregrine Falcon *Falco peregrinus* and 2.25 per cent of the prey of the Hobby *Falco subbuteo* (Lack 1956). Clunie (1972b, 1976) has shown that swiftlets comprise only a small portion of the diet of the Fijian Peregrine Falcon.

In short, the low mortality rate of the White-rumped Swiftlet results from the inability of terrestrial predators to reach them and the limited effect of aerial predators on their numbers. (Neither Barn Owls nor Peregrine Falcons flock at cave entrances). So apart from periodic interference from man, the availability of food appears to be the main regulator of Fijian populations of the White-rumped Swiftlet. As no chicks starved in the manipulation experiment, even in the artificially enlarged broods of three (Tarburton 1987), pressure from a lack of food does not appear to be critical in a normal brood situation and one is left with the likelihood that a period when available food is low such as in a prolonged cyclone, and/or a period of excessive human interference may individually or in unison increase mortality.

It is probably predatory pressure from Barn Owls that has encouraged the majority of swiftlets to nest beyond the twilight zone in the five Fijian caves I have examined. That swiftlets increase their speed at cave entrances (Tarburton 1986), supports this view. This view is contrary to Watling's (1982) statement that most nests are built in the twilight zone of caves. In Waiyala only 4 per cent of nests were in the twilight zone, the rest in total darkness. In Dry Cave only 1 per cent and in Waterfall Cave only about 27 per cent were in the twilight zone. At Ono Cave, 36 per cent of nests were in the twilight zone but none of the nests in the cave on Cikobia-i-Lau were in the twilight zone. The position where twilight gives way to total darkness is shown as a dotted line across the passage on each map.

Death may result from the activity of conspecifics. I found five adults dead at their nests. Their wings had been glued by saliva to their neighbour's nest. This presumably happened while they slept but the hardened saliva held them suspended in the air when they attempted to fly, thus preventing them from feeding. Two other birds had not been long in the same predicament and were rescued. This problem is clearly caused by high density nesting.

CONCLUSIONS

Population size of the White-rumped Swiftlet in Fiji correlates with island size, except that a small colony may be found even on the largest island if it is close to another colony. Because most nests are in total darkness and on overhanging cave walls and roofs, brooding birds, eggs and chicks are safe from most natural predators. Handling of the birds or their young does not cause desertion, but the marked decline in the population of Dry Cave, where all nests can be reached by humans is thought to have occurred as the result of wilful destruction of nests, eggs, chicks and possibly adults by man. The other small colony in this study is not under threat as the villagers on Ono-i-Lau protect the site and the birds. The large colonies are not considered to be in danger either, as most nests are out of easy reach and there is little interest in catching such small birds.

The factors that have made the Dry Cave population vulnerable to human predation have also brought higher percentages of band recoveries in this longevity study than in all other studies on apodids. It is concluded that my activity in collecting the data that show an expected further adult life of 3.2 years has not significantly reduced the bird's survival and that the estimate is close to reality. However, the lower than expected juvenile survival is attributed to the destruction of eggs and young by other visitors to the cave.

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APPENDIX 1

Raw Data for use in Jolly's Population Estimate of the Dry Cave Population, 1974 to 1978.

				Time of release of marked birds ($_j$)																	
Date	Day_i	n_i	r_i	18 Aug. '74	4th Sept. '74	27 Oct. '74	19 Dec. '74	23 Nov. '75	4th Dec. '75	10 June '76	13 June '76	7th Oct. '76	14 Oct. '76	17 Oct. '76	22 Oct. '76	25 Oct. '76	29 Oct. '76	7th Nov. '76	9th Nov. '76	11 Nov. '76	20 May '78
8 Aug. 74	1	—	48						Number of Marked Birds Recaptured (m_{ij})												
18 Aug. 74	2	71	71	8																	
4 Sept. 74	3	115	115	8	15																
27 Oct. 74	4	37	36	2	6	10															
19 Dec. 74	5	34	34	3	1	11	2														
23 Nov. 75	6	58	58	3	5	5	4	4													
14 Dec. 75	7	19	19	0	1	4	0	3	3												
10 June 76	8	90	90	1	2	9	8	6	10	7											
13 June 76	9	91	89	6	4	7	1	2	11	5	25										
7 Oct. 76	10	60	60	0	2	3	0	2	2	1	15	17									
14 Oct. 76	11	16	16	0	0	0	0	0	1	0	3	1	2								
17 Oct. 76	12	43	41	2	2	2	2	2	3	1	6	3	10	3							
22 Oct. 76	13	18	18	0	1	1	0	1	1	0	1	2	1	2	4						
25 Oct. 76	14	9	9	1	0	0	0	1	0	0	1	3	0	1	0	1					
29 Oct. 76	15	13	12	0	0	0	0	0	1	0	2	0	1	2	2	1	1				
7 Nov. 76	16	88	88	0	0	3	1	1	2	0	3	8	15	3	9	6	2	6			
9 Nov. 76	17	15	15	0	0	0	0	0	0	0	0	2	1	0	2	1	0	0	5		
11 Nov. 76	18	45	43	1	1	6	1	1	0	0	4	5	2	3	3	2	0	1	6	0	
20 May 78	19	92	92	0	1	1	1	0	5	2	5	3	4	1	5	2	2	1	13	3	9

Key: n_i = number captured on day i, r_i = number marked and released on day i, m_i = number of marked recaptures on day i.

APPENDIX 2

Preliminary Computations for Jolly's Estimate of the Dry Cave Population.

Day i	r_i	m_i	y_i	z_i
1	48	—	35	—
2	71	8	41	27
3	115	23	62	45
4	36	18	20	89
5	34	17	22	93
6	58	21	40	93
7	19	11	16	122
8	90	43	76	97
9	89	61	45	98
10	60	42	36	103
11	16	7	14	132
12	41	36	27	106
13	18	14	13	116
14	9	8	5	114
15	12	10	8	121
16	88	59	24	69
17	15	11	3	82
18	43	37	9	49
19	92	58	—	—

Key: r_i = number of marked birds released on day i (Appendix 1).
m_i = number of marked birds recaptured on day i.
z_i = number of birds marked before day i, but not recaptured until after day i.
y_i = number of r_i individuals subsequently recaptured.

APPENDIX 3

Results using Jolly's Estimate of the Dry Cave Population.

Sample	$\hat{M}_i$	$\hat{N}_i$	SE $\hat{N}_i$	$\hat{O}_i$	$\hat{B}_i$
1	0				
2	54.76	438	158	0.47	233
3	106.45	515	100	0.54	238
4	178.20	356	78	0.91	330
5	143.72	279	57	0.90	29
6	155.85	418	78	0.93	30
7	155.87	260	55	0.96	11
8	157.87	158	12	0.78	36
9	254.82	378	44	0.90	39
10	213.66	214	25	0.93	16
11	157.86	333	98	0.95	18
12	196.96	234	28	0.98	6
13	174.62	221	41	1.04	−8
14	213.20	237	75	1.00	1
15	191.50	244	61	0.99	3
16	312.00	463	82	0.92	38
17	421.00	561	300	0.99	7
18	271.11	328	94	0.98	8

Key: $\hat{M}_i$ = the estimated number of marked birds at risk on day i.

$\hat{N}_i$ = the estimated population using the modified Petersen formula:

$$\hat{N}_i = \frac{\hat{M}_i(n_i+1)}{(m_i+1)}$$

$\hat{O}_i$ = the estimated stochastic survival rate.

$\hat{B}_i$ = the estimated additions between i and i+1.

SE $\hat{N}_i$ = the standard error of the estimate, for method of estimation see Begon (1979).

APPENDIX 4

Computation for estimates of Population in Waterfall Cave — Schnabel's Method.

Date	A Number Trapped	Number Newly Marked and Released	B Number Already Marked in Population	A×B	(A×B)	C Number Recaptures	C	Estimate of Population $\frac{(A\times B)}{C}$
7 Apr. 74	27	27	0					
8 Aug. 74	83	83	27					
18 Aug. 74	165	165	110					
24 Aug. 74	129	129	275					
27 Oct. 74	121	121	404	48 884	48 884	2	2	24 442
26 Dec. 74	264	264	525	138 600	187 484	6	8	23 436
29 Dec. 74	299	299	789	235 911	423 395	6	14	30 243
								26 040±2121
22 June 75	164	164	796	130 544	448 090	7	18	24 894
16 July 75	235	235	1031	242 285	690 375	6	24	28 766
23 Nov. 75	75	75	1106	82 950	773 325	1	25	30 933
4 Dec. 75	202	201	1307	264 014	1 037 339	2	27	38 420
								30 753±2844
10 June 76	237	237	1270	300 990	1 089 368	8	31	35 141
13 June 76	208	208	1478	307 424	1 396 792	13	44	31 745
23 Sept. 76	182	182	1660	302 120	1 698 912	11	55	30 889
7 Oct. 76	127	126	1786	226 822	1 925 734	2	57	33 785
								32 890± 965

Note: This commonly used method estimates the size of a population by taking the sum of all birds captured (A), multiplied by the number of birds already marked (B), and dividing that by the sum of the number of marked birds captured. Like many methods Schnabel's assumes that the population is stable.