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Survival among Birds of the Understorey in Lowland Rainforest in Papua New Guinea

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Recapture rates of birds netted at Brown River, Papua New Guinea, are analysed. Newly-banded birds have a much lower recapture rate than birds banded one year or more. Recapture rate of newly-banded birds is lowest in those with high breeding success and large clutches (mostly hole-nesters) and highest in those with low breeding success and small clutches (mostly open-nesters). Nectarivores appear to be as sedentary and long-lived as insectivores. Survival rate increases in the second year from banding and drops after the fifth or sixth year. Rate of recruitment is estimated at 10-20% annually. The results are similar to that for other tropical forest areas.

Fry (1980) compared the longevity of passerine birds in tropical areas with those in the Holarctic, by analysing recovery records of banded birds. He stated that individuals of about 50 species of passerines had survived for seven or more years after banding in each of Australia, Europe and North America even though at that time the numbers of birds banded in Australia was only one hundredth of those banded in each of the other two continents. The Migratory Animal Pathological Survey in Asia had, in only eleven years, yielded twenty passerine species with individuals surviving more than seven years after banding. In New Guinea Filewood (1971) reported a high survival rate and a strong fidelity to territory among birds of a lowland forest plot. Bell (1971) banded* sixteen birds in one day at one montane locality in New Guinea in 1967 and Dr J. M. Diamond, unaware of this, recaptured five of these in a single day's netting, exactly two years later. At Brown River, Central Province, Papua New Guinea, intermittent banding has occurred since 1962 and some 1 500 birds have been banded in at least four different sites spread over six km. Despite this sporadic effort long-term recoveries include seven species at over seven years, three at six years and four at five years (Anon. 1971, 1977, 1978; pers. obs.).

I present here information on survival of birds netted from July 1975 to March 1978 at the Three Mile Experimental Plot, Brown River.

Study Area and Methods

The study area at Three Mile Experimental Plot was 2.5 ha and was covered in lowland tropical forest with emergents to 40 m high, bounded on one side by the Hiritano Highway, which cut through a large expanse of relatively undisturbed forest. Rainfall at the Forestry Station, 4.5 km away, averages 2 010 mm annually with most falling between December and April. The vegetation, climate, and information on the ecology of the birds are described elsewhere (Bell 1982b, 1982c, 1982d).

* Bands used were provided by the Australian Bird-banding Scheme, Division of Wildlife Research, CSIRO.

During my main study from December 1975 to November 1976, I netted regularly for at least 150 net-hours per month. (One net-hour = one 13 m mist-net set near ground level which was opened for one hour.) From December 1976 to November 1977, I netted for 100 net-hours per month, but also expanded the number of net-sites into additional areas. Net sites were regularly rotated, but at a much lower rate during the second year. I also netted outside the study period, from July to November 1975, and from December 1977 to March 1978, involving about 100 net-hours. All birds caught were banded with bands provided by the Australian Bird-banding Scheme and released after particulars about them were recorded.

I recorded 165 species of birds on the site; of which 57 were netted, and a further twenty at least, are known to occur (Bell 1982b). Breeding, particularly of small passerines, occurred mainly in the Austral spring and early summer, i.e. in the late dry and the early wet seasons (Bell 1982c). Filewood (1971) had operated a banding station 300 metres from my site. He also banded some birds at my site, from 1970 onwards, so some banded birds were already present.

Nomenclature follows Rand and Gilliard (1967), amended in some cases to conform to current Australian usage.

Results

Because of the well-defined breeding season at Brown River it is convenient to divide the data into three seasons, July 1975-June 1976, July 1976-June 1977, and July 1977-March 1978. Caution must be exercised in interpreting my data because banding effort was not equal in each year (see Table 1), either in my study, or in Filewood's. I extended the area of coverage in the second, and again in the third season. Thus many of the new birds netted in those seasons may have been old birds already present when I first started. Because my banding area was extended but net-hours reduced, the chances of retrapping banded birds in the initial area of coverage was much reduced. However these shortcomings would work against my conclusions that there is a high loss of newly-banded birds but a very low loss of older ones.

Table 1 gives data on recaptures, divided into the years in which the birds were banded and the year in which they were recaptured. All species are included. Catch-rates (birds netted/100 net hours) were highest in the first year, possibly because net-shyness increased as netting progressed, as was also found by Lovejoy (1974) in Brazilian rainforest.

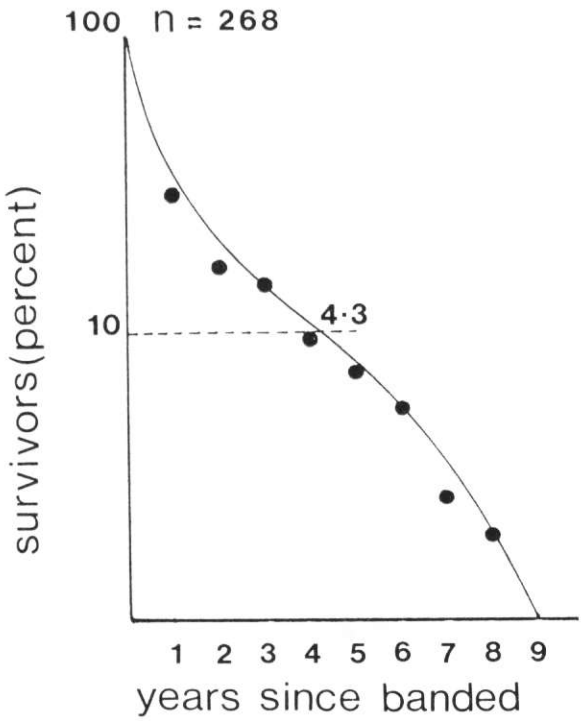
Table 1 shows that birds banded for one year or more have a better chance of survival than those newly-banded. The survival of the older birds could have been even higher, had I maintained the intensity of netting at all sites. The low recapture rate for newly-banded birds could be because many were young of the year. Forty-seven percent out of 305 known adults, but only 26% out of 39 known immatures were subsequently recaptured.

TABLE 1

Numbers of individual birds banded and subsequently recaptured in each year (July-June) at Three Mile Plot 1975/1978.

Banded	Year recaptured 75/76	76/77	77/78
1968/69	2	2	—
1969/70	1	1	—
1970/71	6	5	2
1971/72	9	8	5
1972/73	5	4	2
1973/74	4	4	2
1974/75	16	10	8
1975/76	75	36	20
1976/77		193	38
1977/78			85
Total birds caught	118	263	162
(including new birds)	(75)	(193)	(85)
Net-hours	327	1 438	723
Number of net-sites	14	18	24
Birds netted/ 100 net hours	36.1	18.3	22.4
% of birds banded in previous year recaptured	Not known	48%	20%
% of 'older' * birds recaptured	Not known	79%	56%

* = banded more than one year.



• Figure 1. *Survival curve of all birds banded at Three Mile Plot, Brown River, plotted as % on log scale against number of years between initial banding and last recovery, and showing mean age reached by 10% of the population.*

Figure 1 is a survival diagram based on the data in Table 1. The curve has been constructed from composite life table data in the form of minimum ages of birds mist-netted and banded usually as unaged 'adults' and recovered live or dead at known intervals thereafter (Fry 1980). This illustrates the higher loss in the first year, compared with subsequent years.

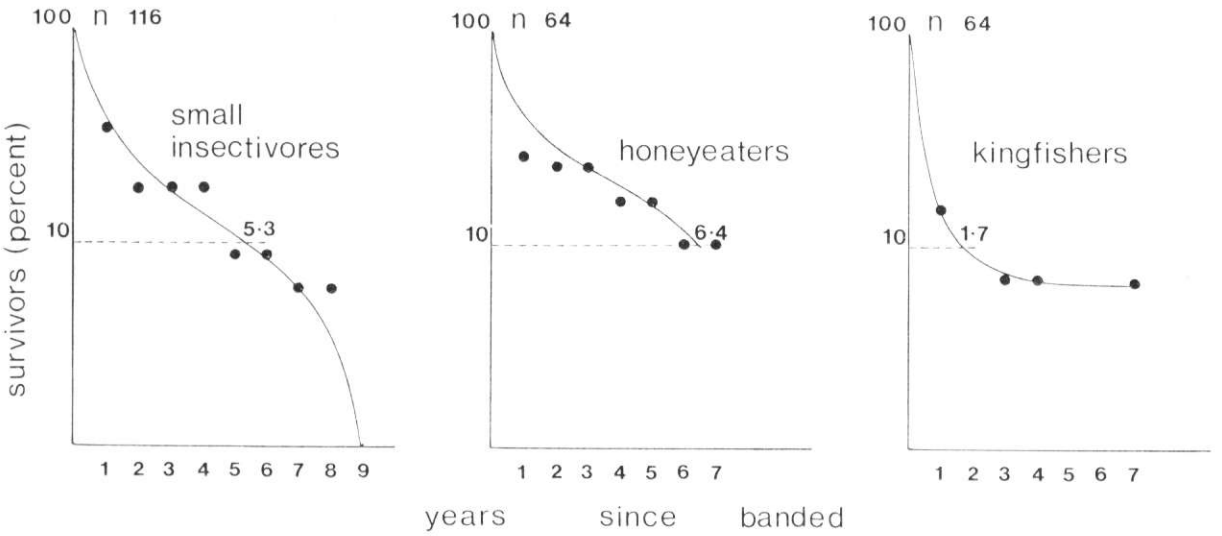
There are differences in the recovery-rate of kingfishers, honeyeaters, small insectivorous passerines and an individual species, the Little Shrike-thrush *Colluricincla megarhyncha* (Table 2, Fig. 2). The trend in all cases is for the older birds to survive better. The high recapture rate for honeyeaters was at first surprising because the aggregations of honeyeaters at flowering trees suggests that they are highly mobile. In fact most species, and in particular the Long-billed Honeyeater *Melilestes megarhynchus* and Grey-bellied Longbill *Toxorhamphus iliolophus,* showed high fidelity to territory. The only recoveries of the Red-spot Myzomela *Myzomela eques* and Spotted Xanthotis *Xanthotis polygramma,* both species of the canopy, were over a year from banding in the same net-sites where they had been first netted. Kingfishers, however, showed a significantly lower survival of newly banded birds compared to the overall total than did the other groups (X^2 (1), $P < 0.05$).

TABLE 2

Percentage of banding age-classes * that survived for at least one further year.

Years from banding		0	1	2	4	5	6	7	8	9
All species	n	268	52	14	9	13	14	6	3	2
Survived:	%	28	58	86	67	77	71	50	67	—
Kingfishers	n	64	14	2			2	2		
Survived:	%	14	56	100			100	—		
Honeyeaters	n	64	10	2	2	7	8	2		
Survived:	%	27	90	100	50	100	62	—		
Small passerine insectivores	n	116	17	2	2	2	3	3	3	2
Survived:	%	34	53	100	100	50	100	67	100	—
Little Shrike-thrush	n	33	8	4		1	4	3		
Survived:	%	40	75	100		100	100	67		

* A cohort of birds banded for the same number of years



• Figure 2. *Survival curves of small (< 32 g) insectivores; honeyeaters and kingfishers at Three Mile Plot, plotted as % on log scale against number of years between initial banding and last recovery, and showing mean age reached by 10% of the population.*

Table 2 shows the percentage survival rates, of all birds, kingfishers, honeyeaters, small insectivorous passerines and the Little Shrike-thrush by banding age-class. (A banding age-class is a cohort of birds that have carried bands for the same number of years.) In all groups of species the lowest proportions known to have survived are for the first year after banding. For example, I caught eight Grey-bellied Longbills that had been banded by Filewood, one of them six years before, and recaptured all again during my study, but of the twenty-eight banded by me only nine were recaptured. I caught five Black Berrypeckers *Melanocharis nigra* banded by Filewood, two of them six years, and one five years previously. Four of the five were recaptured again but of the fifteen new birds banded by me only one was recaptured.

Discussion

It is not surprising that newly-banded, and therefore presumably mostly young birds, should have a lower recapture rate than older and more experienced ones. The missing birds may have moved elsewhere, but none of the hundreds of birds banded by Filewood at his site 300 m away were caught by me at my plot. Yet a netting-day conducted by the PNG Bird Society at his plot, over two years after he ceased operations, produced 50% retraps out of the ten birds caught. McClure and bin Othman (1965) showed, in Malayan rainforest, that birds evicted from their territory mostly disappeared, presumably perished, or in a few cases displaced other birds from adjacent territories. Given the sedentary nature of most species of the understorey, which are those most frequently netted, and their high densities (Bell 1982b), most of each year's young birds, unless they can find a vacancy caused by the death of an old one, must be either evicted or perish. Fogden (1972) gave evidence of starvation among young of the year, once the optimal feeding conditions (in his area, the wet season) had passed. I recorded several cases of recaptured immature kingfishers showing serious losses of weight at the onset of the dry season (Bell 1980).

The survival curves in Figures 1 and 2 conform generally to those given by Fry (1980) for other tropical areas and the humid parts of Australia. Although the samples for some classes are small, Table 2 supports the trend found by

Fry (1980) that the survival rate actually increases up to the fifth year, and then sharply declines.

From Table 2 the average annual mortality, after the first year, i.e. of potentially breeding birds, was about 20% for all birds combined. The Little Shrike-thrush showed a mortality rate of only 12% annually. From observations of territories I calculated the annual mortality of adult Common Paradise Kingfishers *Tanysiptera galatea* as 25-33%, but for various reasons considered this greatly inflated (Bell 1980). Fogden (1972) in Borneo and Snow (1962) in the Neotropics estimated an annual recruitment of 10% for some species and Thiollay (1974) 20% for West Africa. I believe that the rate in New Guinea is probably around 20% because my loss rates were probably artificially increased by my reduced intensity of netting per unit area in the third season.

The clutch-sizes of open nests in New Guinea average about 1.4 eggs per nest, and the success rate of such nests is 12.5% (Bell 1982c), although in both cases the sample sizes are small. I assume that unsuccessful pairs will try at least a second time in one season, and saw a banded pair of Chestnut-bellied Fantails *Rhipidura hyperythra* make four attempts. A success rate of 12.5% for an average of two attempts per season would replace an annual mortality of 10-20% of adults

Builders of dome-shaped nests have large clutches, by New Guinean standards, but my sample is too small for analysis of success rates, although all three nests found were successful. It is possible that most species in New Guinea that build such nests will turn out to be co-operative breeders, such as the Black and White Wren-warbler *Malurus alboscapulatus* (Coates 1976), Wallace's Wren-warbler *Todopsis wallacii* (Bell *et al.* 1979), Rufous Babbler *Pomatostomus isidori* (Bell 1982a), and Yellow-bellied Gerygone *Gerygone chrysogaster* (pers. obs.). If their rate of success is high then some of the additional birds could be absorbed into territories as extra helpers. Among the dome-shaped nesters pittas may be an exception. They appear to be monogamous and they lay large clutches. Banding and retrap data held by CSIRO shows that of 33 pittas banded at Brown River only two Black-headed Pittas *Pitta sordida* have been recovered more than one year later, a very low rate compared to other species netted in similar numbers. Pittas are territorial and it would be surprising that even if migratory they did not return to the same territory each breeding season, so there may be a high rate of mortality. Being ground-feeders pittas are vulnerable to predation, but other ground-feeders e.g. Lowland Eupetes *Eupetes caerulescens*, show a high recapture rate. Perhaps the apparent seasonal movements of pittas (Bell 1982c) result in high mortality. McClure (1974) showed that pittas in south-east Asia, even excluding the Palaearctic-breeding Blue-winged Pitta *P. brachyura*, have a very low rate of recapture in proportion to the thousands netted.

Hole-nesters have the largest clutches and highest success rates (Bell 1982b). The Common Paradise Kingfisher produces 1.5 fledged young per adult each season and those young that are unable to find vacant territories, i.e. most, are evicted by the adults (Bell 1980). It is therefore not surprising that kingfishers show a loss of newly-banded birds even higher than that for other groups (see Fig. 2).

I conclude that, in common with other tropical areas, birds in lowland rainforest in New Guinea have high adult survival and a low breeding success and rate of recruitment.

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