

Survey Methods and Monitoring Within Crocodile Management Programmes

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THIS chapter is essentially divided into two sections. The first is an introduction to surveying and monitoring, which will hopefully assist people getting into the field for the first time. It deals in a simplified fashion with the fundamental principles behind sampling animal abundance, the definitions of terms used, the common problems encountered and the ways in which some of them may be avoided. The approach taken is a personal one, and thus some readers may disagree with what are basically my own biases and leanings.

The second section examines the results of experiments aimed at validating the methods used to estimate the abundance of saltwater crocodiles (*Crocodylus porosus*), in the tidal wetlands of the Northern Territory. It is essentially a series of experimental case histories. The rate at which *C. porosus* populations have been recovering is quantified from spotlight count indices. A mark-recapture experiment is used to estimate the real population size in three tidal habitats. The relationship between spotlight count indices and the real population size is examined and both average and size-specific correction factors are derived. The relationship between spotlight counts and helicopter counts is examined also, with the view of using the latter to survey inaccessible habitats at reasonable cost. These results are of course specific to *C. porosus*, mainly in tidal habitats, but the approaches taken are by no means species or habitat specific. Hopefully they will be of use to others faced with specific management problems in other parts of the world.

DEFINITIONS, PROBLEMS AND APPROACHES

Management and Survey Objectives — Levels of Resolution

The right choice of survey method and the ultimate assessment as to whether it was useful or not, depends entirely on whether the management objectives of the survey were realised. In the management of a single-species population, such as a crocodilian, there are only three specific management objectives (Caughley 1977):

1. *Conservation*. The treatment of a small or declining population to raise its density;
2. *Harvesting*. The exploitation of a population to take from it a sustained-yield; and,
3. *Control*. The treatment of a population that is too dense, or which has an unacceptable high rate of increase, to stabilise or reduce its density.

The management of wild cocodile populations may involve elements of all three objectives, as occurs with *C. porosus* in the Northern Territory at present (see Webb *et al.* Chapter 11).

At a crude level of resolution, there are two basic objectives of a population survey in terms of the three management objectives outlined above. The first of these is:

1. *To determine distribution and abundance*. Basically we ask *where* the animals are and *how many* there are. This is a descriptive approach and is a necessary first step in any population study whose aims are management or otherwise. At a finer level of resolution we may ask what are the factors that determine distribution and abundance? This is a functional approach and may not be necessary for a population's management, depending on the nature of the problem. This artificial dichotomy is useful when allocating scarce resources to management problems. In terms of contributing truth to science the distinction is trivial. However, experimental ecology, the only objective approach, has yet to triumph over theoretical dogma and the insatiable drive to collect more and more data of the same kind.

Hence a population manager may need only to focus on what happens to treated and untreated populations, rather than search for causalities. I do not argue here against the "search for truth" or the level of detail that different biologists take. Rather, I argue that many population management problems can be solved by taking the simple descriptive and/or experimental approach. Even this needs careful

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scrutiny, as an easier solution may be found in executing a commonsense political or bureaucratic value judgement.

The second objective of a population survey can be:

2. *To monitor changes in abundance and distribution.* Basically we ask whether the population is *increasing, decreasing or stable*. That is, regardless of inherent variability in animal numbers, what is the average trend over a number of years? The most powerful and useful measure of a population's dynamics is the rate of increase statistic. It is a direct and concise summary of all population processes — fecundity and survival by age and sex and immigration and emigration. It is the essence of population dynamics and provides the only unambiguous measure of demographic vigour or a population's well-being. It is summarized below as the differential between births (b) and deaths (d), and immigration (i) and emigration (e).

$$r = (b - d) + (i - e)$$

A simple measure of r is the change in numbers between two points in time, usually a year. It can be expressed as a finite or exponential rate. A more useful estimate is the average exponential rate of increase (\bar{r}) and this is obtained by regressing a series of logged (natural) density indices over time. The slope of the line estimates exponential \bar{r} per unit time.

There are many indirect indices of rate of increase, for example, fat storage, body weight and size, age and sex ratios etc. However, often it is easier to obtain a direct measure of rate of increase than an indirect one, and a direct measure will usually suffice for solving most population management problems. Indirect measures of demographic vigour may also be difficult to interpret, as has been pointed out by a number of authors. Verme and Ozoga (1980a,b) demonstrated experimentally that White-tailed Deer *Odocoileus virginianus*, produced substantial fat reserves despite undernutrition and a negative energy balance — lipogenesis was an obligatory seasonal, physiological event. Caughley (1974) demonstrated by simulation that age-ratios can often provide ambiguous information and that their facile interpretation can lead to serious management blunders. There are numerous studies showing great variability in the size of animals at different ages, both between and within populations, and this is especially so in crocodylians (Webb *et al.* 1983); yet size is often used as an index of age in order to estimate age distributions and hence rate of increase (but see Caughley 1974 for further problems).

Measuring Abundance

The point made above, is that our management and hence survey objectives should be crystal clear. We cannot manage populations if we don't

know what it is we wish to manage. To obtain such clarification, at any level of resolution, we need some measure of abundance. This may seem relatively simple, but there are many formidable problems of methodology which reinforce the view that "life wasn't meant to be easy". The main ones are outlined below:

1. *Population Boundaries and the Scale of Study.*

The first step is to define the boundaries of the population to be studied, which comes from resolving the scale of the study that will be needed to satisfy the management objectives. There needs to be a very clear understanding of the relationship between the objectives of the study, the necessary scale at which to operate (and hence the boundaries of the study area), and the usually discontinuous distribution of the animals within it.

The Australian submission to CITES for the transfer of *C. porosus* from Appendix I to Appendix II (Webb *et al.* 1984) affords an example. It required information and input from all States in northern Australia. It needed statistics describing the broad distribution and abundance of *C. porosus* in the Northern Territory, and others describing the increasing numbers since protection; these were the cornerstones of the document. The objectives were national, hence the population boundary was necessarily defined by the geographic distribution of the animal itself. Yet survey figures of crocodile numbers and nests in selected tidal river systems were used to demonstrate specific points. Hence it provided a broad-scale picture across Australia, and a detailed picture for some river systems in the Northern Territory; it used two extreme scales of study as its *modus operandi*.

However, it also raised important questions that were somewhat independent of scale. How representative is the available information? What proportion of a crocodile population in a typical tidal system inhabits the river mainstream (which is usually surveyed), relative to the smaller side-creeks and associated floodplain swamps and billabongs (which are not usually surveyed)?

2. *Measures of Abundance.* Having chosen a scale of operations, and hence defined our population boundaries, what is the most appropriate measure of abundance? Abundance can be measured in three ways:

- i. *Absolute value.* The total number in a population within a defined boundary: e.g. 40,000 crocodiles in the Northern Territory;
- ii. *Relative density index.* An index of the true density: e.g. 100 crocodiles spotlighted per 10 km of river stream;
- iii. *Absolute density.* The true density: e.g. 140 crocodiles per 10 km of river stream or 10 crocodiles per km² of swamp.

Estimates of absolute density have no intrinsic value in themselves; in fact in many studies they are an unnecessary luxury. Most population management problems can be solved with relative indices of density, particularly those linked with habitat use, rate of increase, dispersal and the reaction of populations to management treatments. However, if the management objective is to calculate sustained-yields, in the traditional fisheries sense, then absolute values or density estimates are required to match against absolute offtake levels.

The most important assumption of any relative density index is that there is a linear relationship between it and absolute density, and that this relationship is stable over time. Nearly always this assumption is not validated because control populations of known size are as rare as "hens teeth". However, relative indices are extremely powerful if survey techniques are rigidly standardized. They facilitate important comparisons of populations between different countries, river systems, management treatments and times. Some relative densities of crocodilians from different parts of the world are compared on Table 1.

Nest Counts. The number of nests is a special case of an index of abundance. As well as indexing

breeding success, nest counts index the abundance of breeding females in a population and hence indirectly, but not completely, its rate of increase: it is really only related to births and says nothing about deaths or dispersal. However, Chabreck (1966) used nest counts as an indirect method to estimate the number of American alligators, *Alligator mississippiensis*. He derived the following formula:

$$P = N/MFB$$

where N is the number of nests, M the sexually mature proportion of the population, F the proportion of females among mature alligators, B the proportion of nesting mature females, and P the population size of alligators occupying the area in which nests have been counted.

Sampling Errors

Once we have chosen an appropriate measure of abundance, we must next decide whether to do a *total* or *sample count*:

1. *Total counts.* An attempt is made to count all animals in the survey area. This is usually prohibitive because of the huge costs in surveying large areas.

Table 1. A comparison of crocodilian density indices (spotlight indices per km of river or shoreline) in different parts of the world (after Turner 1977; Montague 1983; Messel *et al.* 1981; Webb *et al.* 1984). As far as is known, most do not account for visibility biases which are probably very different from each other.

Country and Location	Species	Relative density	Date
USA	<i>Alligator mississippiensis</i>		
Central Florida		9.4	1971
Miami Canal		0.6-4.3	1954-68
Everglades National Park		18.1	1977
ETHIOPIA	<i>Crocodylus niloticus</i>		
Upper Awash River		7.0	1972
Lake Margherita		1.3	1972
Blue Nile		2.4	1972
UGANDA			
Albert Nile		0.4	1970
Victoria Nile (below Murchison Falls)		26.3	1970
KENYA			
Lake Rudolf		13.4	1971
Upper Lorian Swamp		8.5	1971
TANZANIA			
Grumeti River		2.2	1971
N.T. AUSTRALIA	<i>Crocodylus porosus</i>		
Adelaide R.		1.85	1977
Adelaide R.		2.65	1984
South Alligator R.		1.25	1977
South Alligator R.		2.45	1984
Habgood R.		4.59	1975
Habgood R.		9.39	1984
Glyde R.		0.61	1975
Glyde R.		2.46	1984
Blyth/Cadell R.		4.21	1974
Blyth/Cadell R.		4.00	1984
PAPUA NEW GUINEA	<i>C. porosus</i> and <i>C. novaeguineae</i>		
Mid. Strickland R.		2.23	1979
Tomm R.		0.16	1979
Aiema R.		0.07	1979

2. *Sample counts.* A representative proportion of the survey area is counted and total population size, or an index of population size, is estimated from this sample.

There are strengths and weaknesses in both approaches and the value of each must be weighed in terms of costs and the original management objectives. Nearly all population surveys fall into the category of sample counts because it is usually impossible to count all animals in all space and time within the defined boundary. This fact plunges most population managers into the field of sample statistics, a complex often intimidating field. Fortunately, much of the apprehension is unnecessary, because coping with sample statistics requires only the realization that there are three basic sources of errors (White *et al.* 1982):

1. *Precision errors.* The standard error of a sample mean estimates its repeatability, precision or consistency;

2. *Accuracy errors.* The difference between the sample estimate and the true value. If the estimates are inaccurate, they are biased. In most surveys of animal abundance, estimates are usually biased downwards because not all animals are detected. This is called visibility bias.

3. *Random errors.* Errors due to chance variation.

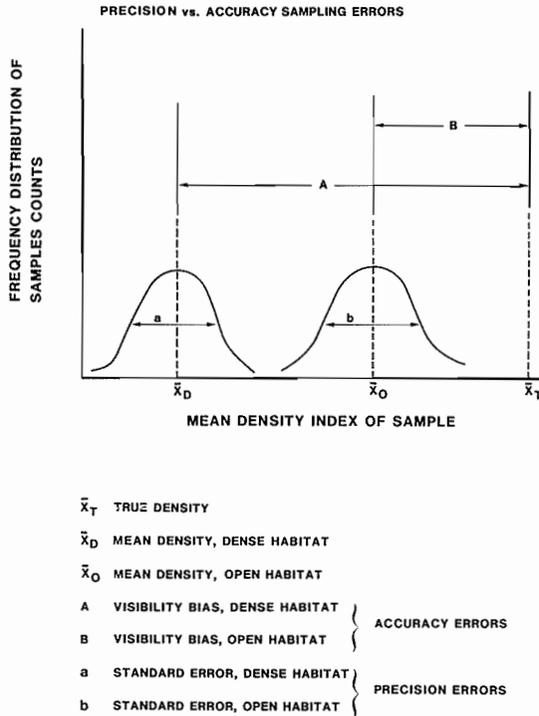


Fig. 1. A theoretical example demonstrating the difference between precision and accuracy in sampling errors.

The important difference between precision and accuracy sampling errors can be illustrated with a hypothetical example (Fig. 1). The absolute density

of crocodiles is the same in two habitat types ("open" and "dense" with regard to vegetation covering the water), but because of the many factors that prevent all animals being detected, both mean estimates of density (relative densities) are biased downwards from the true value. Less crocodiles are seen in the dense habitat than in the open one and hence the estimate is more biased. Note that the dispersion or spread of points about the mean, as measured by the standard error, could be the same in both habitats: it is clearly not a measure of accuracy. This example cautions against facile comparisons of indices of crocodile density from different habitats, and applies to Table 2.

Differential visibility bias can be caused by other things besides the density of vegetation in a habitat. For example, the effects of hot and cold weather on animal behaviour (Bayliss and Giles 1985), state of the tide (Messel *et al.* 1981), observer and lighting condition (Short and Bayliss 1985), wariness (discussed later in this chapter) and so on.

Before we sample an animal population we must therefore have a clear understanding of the difference between the three types of sampling errors, and some idea of the variables that are likely to affect the precision and accuracy of the sample counts.

Some of the variables that may affect the consistent detection of animals on a survey are outlined in Figure 2. A biologist familiar with a particular animal and the many different survey techniques available, can draft a more appropriate chart for any specific problem.

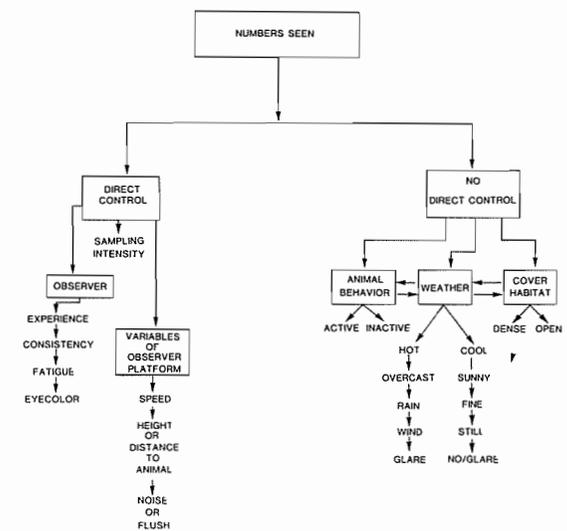


Fig. 2. Factors that may affect the consistent detection of animals on a survey.

If the management problem requires that population trends only need to be monitored, then relative indices of abundance will suffice. Particular attention needs to be paid to all the factors affecting

precision; e.g. sampling intensity, standardization of counting procedures, standardization of observers, weather conditions, types of habitat and so on. The degree of visibility bias is unimportant as long as it is held constant by *rigidly standardized survey procedures*. A major problem occurs when the visibility bias is uncontrolled and hence not constant. The resulting relative density indices are unstable and in many cases are probably useless.

If the management problem requires a sustained-yield harvest, then accurate estimates of numbers are required to match offtake levels to real density. Hence we need not only to obtain good precision (low standard errors) but accuracy. The causes of visibility bias must be identified (usually via simple experiments), the bias measured, and the relative indices adjusted via a multiplier or correction factor. This procedure obviously only relates to sources of error that can be controlled; those that cannot are rendered to the random error category.

Removal Experiment to Estimate Population Size

Many biologists working with crocodylians will probably be confronted at some time with the unique opportunity to indirectly measure population size. Crocodiles are often "removed" for commercial reasons (hunted), scientific reasons or nuisance reasons (as around waterholes visited by tourists), or may be added through restocking. Population size can be measured before and after known numbers of animals are added or removed. All we need is an index of density (I_1) before the removal (or addition), an index after the event (I_2), and the number of animals added (+ C) or removed ($-C$).

The pre-event population size (N_1) will always be:

$$N_1 = \frac{I_1 C}{I_2 - I_1}$$

The post-event population size (N_2) is:

$$N_2 = \frac{I_2 C}{I_2 - I_1}$$

The fundamental assumption is that the population remains closed during the experiment, and thus it needs to be run over as short a time interval as is possible.

CASE HISTORIES — SURVEYING AND MONITORING CROCODILE POPULATIONS IN THE NORTHERN TERRITORY

Indices of Abundance — Spotlight Counts

The recovery rate of *C. porosus* since protection in 1971 has been monitored by relative indices of abundance derived from spotlight counts, particularly in tidal rivers. The best data are those from the Blyth-Cadell river system in Arnhem Land, which encompass 11 years of consistent counts (Messel *et al.* 1981; Webb *et al.* 1984).

1. *Methodology*

Crocodiles are counted from aluminium boats between 3 and 5 m long. The banks and waters surface are scanned with a powerful spotlight and crocodiles are identified to species (*C. porosus* or *C. johnstoni*) and have their sizes estimated. They are recorded as "eyes only" if they cannot be identified or have their sizes estimated. Surveys are typically timed to coincide with a falling tide as more crocodiles are visible with an increase in the amount of exposed mud bank (Messel *et al.* 1981).

2. *Rate of Increase*

Within the context of the first part of this chapter, we can note the following points about the Northern Territory spotlight counts:

- i. *Management Objectives*. In 1971 the management objective for saltwater crocodile populations in Australia was defined broadly as "conservation". Commercial hunting was banned. Populations were extremely low and the objective was to raise densities. The whole sequence of events, from unrestricted hunting for 26 years to protection, and the subsequent recovery, can be viewed as a time series experiment on a grand scale: the control being the hunted populations and the treatment, the protected populations. Unfortunately there are no spotlight indices before 1974, and we can only assume that hunted densities were very low. However, there is strong anecdotal evidence to support this assumption: the catch rate of commercial crocodile hunters dropped to zero in heavily hunted areas; rivers that previously supported large numbers of crocodiles were virtually crocodile free.
- ii. *Population Boundary and Scale of Study*. The population boundary was delineated by the geographic distribution of *C. porosus* in the Northern Territory, and included all major river systems. Each river system was treated as a discrete population, and crocodiles present in mainstreams and in the major side-creek habitats were assumed to represent the whole population. It was mistakenly assumed that these habitats contained nearly all of the crocodiles within a wetland river system. It was also assumed that the crocodile populations in the rivers surveyed represented those in rivers not surveyed.
- iii. *Measure of Abundance*. An appropriate measure of abundance was chosen — all crocodiles seen on a spotlight survey along fixed lengths of river or creek. The total spotlight count is therefore a relative index of abundance because not all crocodiles are seen.

iv. *Sampling Errors.* The spotlight counts in the mainstream and major side-creeks are sample counts because only a proportion of the total available habitat is surveyed. It is also inaccurate because of visibility bias — not all crocodiles present during a survey are seen. It is not possible to calculate the level of precision of these surveys as counts were not usually replicated — hence we cannot calculate a mean and standard error. However, when spotlight counts have been replicated (Messel *et al.* 1981; Bayliss *et al.* 1986) a high precision (low standard error) was usually achieved with a low number of samples.

Hence the spotlight surveys within the Northern Territory provided relative indices of abundance for representative river systems, and these can be used to monitor trends in crocodile numbers.

For the rivers in which more than three years survey data were available, densities were transformed to natural logarithms and regression analysis was used to calculate the average annual exponential

rates of increase (\bar{r} p.a.) (regression analysis requires at least 3 datum points for significant testing with 1 degree of freedom). The results are summarized in Table 2, and they indicate that all populations are “healthy” — \bar{r} is either positive or zero and no populations are decreasing significantly (see Fig. 3 for selected examples).

Rates of increase which were found to be significantly different from zero varied between +0.051 and +0.072 p.a., indicating an annual increase of between about 5% and 7% respectively. The \bar{r} for *C. porosus* within the Northern Territory as a whole was calculated by combining all available data; it was estimated as 0.080 p.a., indicating an annual increase of approximately 8%. If this average rate remains constant, the Northern Territory population of salt-water crocodiles can be expected to double every 8.7 years. Hence, depending on the river system, crocodile populations have either recovered from the effects of sustained hunting for 26 years, or are still recovering. Given that protection was only introduced 13 years ago, it indicates *C. porosus* was resilient to the intensive hunting effort of the past.

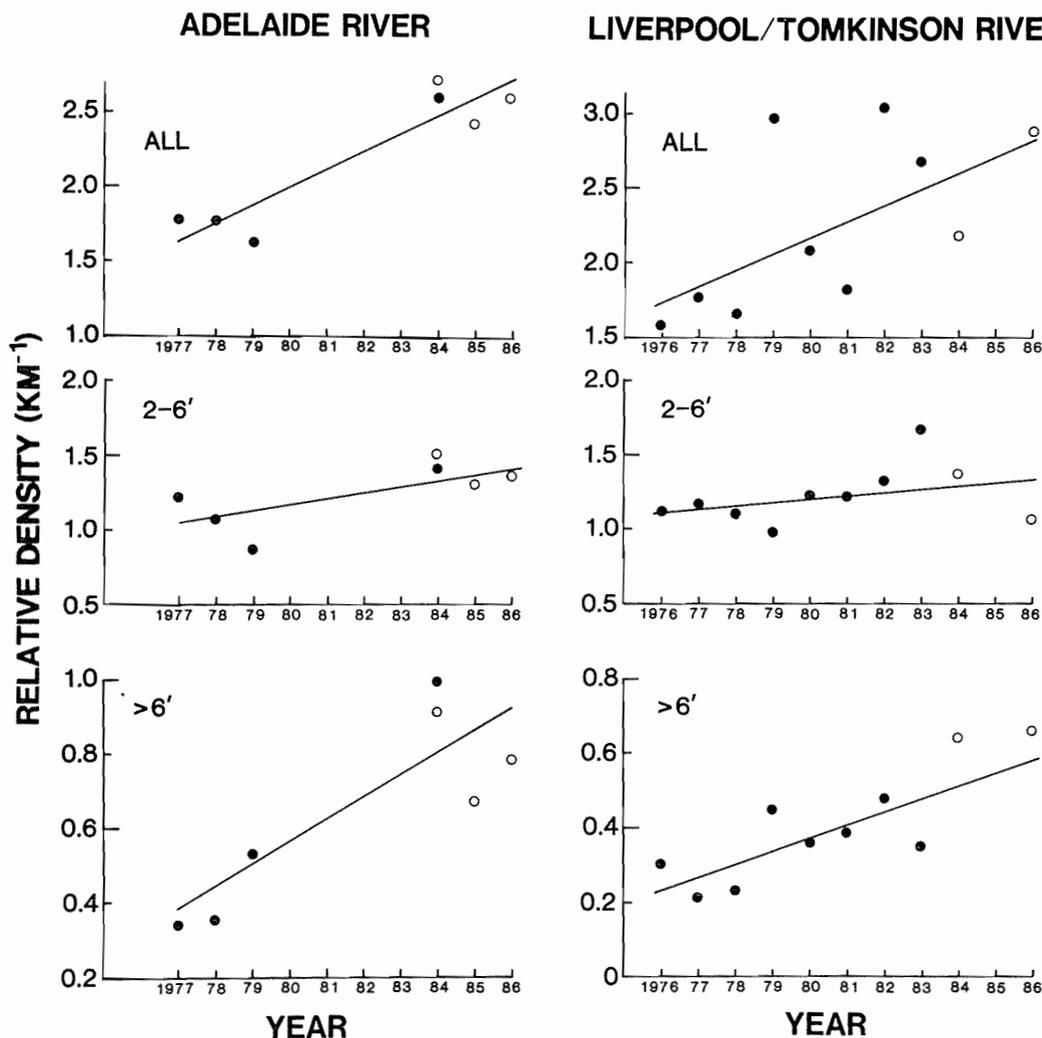


Fig. 3. Average rates of increase (\bar{r} p.a.) for different size classes of *Crocodylus porosus* in the Liverpool-Tomkinson and Adelaide Rivers system. Rates of increase are calculated by regression analysis.

Table 2. The average annual exponential rates of increase (\bar{r} p.a) for *Crocodylus porosus* in rivers of the Northern Territory that have been surveyed at least three times over a period of years. Raw data and locations are in Messel *et al.* (1981), Webb *et al.* (1984), and unpublished data.

River/Creek	\bar{r} p.a	R ²	N	Sig.	Period
Adelaide	+0.055	0.84	7	P<0.01	1977-86
All-Night	+0.271	0.39	3	NS	1975-79
Andranangoo	+0.072	0.96	5	P<0.10	1975-84
Baralminar	+0.096	0.89	3	NS	1975-84
Bath	+0.134	0.74	4	NS	1972-84
Blyth-Cadell	+0.002	0.00	13	NS	1974-86
Burungbirinung	+0.096	0.52	3	NS	1975-84
Cato	+0.015	0.25	3	NS	1975-84
Crab	+0.001	0.00	3	NS	1981-83
Darwarunga	+0.129	0.89	3	NS	1975-84
Dongau	+0.016	0.03	6	NS	1972-84
East Alligator	+0.072	0.64	9	P<0.01	1977-85
Glyde	+0.143	0.78	4	NS	1975-84
Gobalpa	+0.075	0.83	3	NS	1975-84
Goomadeer	+0.016	0.06	8	NS	1975-84
Goromuru	+0.006	0.06	3	NS	1975-84
Habgood	+0.081	0.89	3	NS	1975-84
Habgood Ck	+0.001	0.00	3	NS	1975-84
Johnston	+0.113	0.56	4	NS	1972-84
King	+0.240	0.74	4	NS	1975-79
Liverpool-Tomkinson	+0.054	0.45	10	P<0.05	1976-86
Majarie	+0.040	0.18	7	NS	1975-84
Murgenella	+0.096	0.57	4	NS	1977-84
Ngandadauda	+0.029	0.92	3	NS	1975-83
Nungbulgarri	+0.089	0.48	8	NS	1975-84
Peter John	-0.018	0.03	3	NS	1975-84
South Alligator	+0.225	0.27	10	NS	1977-84
Tinganoo	+0.181	0.73	5	NS	1972-84
West Alligator	+0.051	0.99	4	P<0.05	1977-84
Wildman	+0.098	0.98	7	NS	1978-84
Wurugojj	+0.139	0.38	7	NS	1975-84
TOTAL N.T.	+0.080				1972-86

Regardless of any potential source of error associated with these spotlight indices, they still provide important insights into the conservation "status" of *C. porosus* populations before and after protection:

- i. Unrestricted commercial hunting severely reduced saltwater crocodile numbers;
- ii. Since protection numbers of saltwater crocodiles increased rapidly, exhibiting demographic vigour;
- iii. No riverine population surveyed is declining, nor have crocodiles disappeared from any part of their former range;

Crocodile populations therefore seem to be very resilient to hunting. The response to protection after 26 years of intensive, unrestricted exploitation was relatively 'rapid', and the populations did not irreversibly collapse past some threshold to very low densities, as has happened to many commercial fisheries. Their innate wary nature in combination with a hostile, inaccessible and patchy habitat, probably provided refuges for part of the hunted population. Hence a significant number of animals were able to escape "predation" by humans to provide the breeding core needed for recolonization and recovery. Resilience to habitat changes (e.g. damage to wetlands by feral buffalo) is a more important consideration.

Correcting Spotlight Indices to Estimates of Absolute Numbers via a Mark-Recapture Experiment

Whilst standardized spotlight surveys can provide precise indices of abundance, a major limitation is that they are inherently inaccurate because of visibility bias; observers do not see *all* the crocodiles on an average spotlight survey. Some of the factors associated with visibility bias are:

1. The density of vegetation on the banks or overlying the water (Figs 4 and 5);
2. The width of a river or stream;
3. The number or frequency of bends in a stream (sinuosity) (Fig. 6);
4. The position of crocodiles (floating, submerged, resting on the bank, etc.) relative to the observer; and,
5. The degree of "wariness" in the crocodiles.

Most important is the relationship between factors 1-4 and factor 5, the wariness of crocodiles. Webb and Messel (1979) found that in *C. porosus*, size is a reasonably good index of wariness; the older and larger crocodiles are usually more wary and hence more difficult to detect.

In July 1984 we conducted an experiment to measure the extent of visibility bias in spotlight counts of *C. porosus*, in different habitats, within a

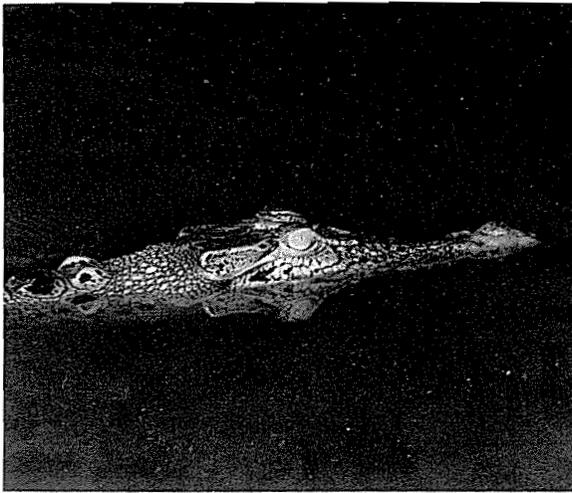


Fig. 4. In tidal rivers, *Crocodylus porosus* that are not wary and are in shallow water at the edge of the bank, can be approached closely.



Fig. 5. *Crocodylus porosus* amongst vegetation on the banks in tidal rivers are more difficult to detect in spotlight surveys.

tidal river (the Adelaide River). We used a mark-recapture experiment to estimate the total population in each of the habitats, and then quantified the proportion missed during spotlight counts. This allowed *sighting fractions* to be derived for each habitat which were essentially *correction factors* for converting spotlight count indices to estimates of total numbers. For example, if we saw 50% of crocodiles on a spotlight count in a particular habitat, the correction factor would be 2.0.

The ultimate objective of this experiment was to obtain a crude estimate of the total population of *C. porosus* in the Northern Territory, through correcting spotlight count indices to absolute estimates. The total population estimate itself was part of the information required by CITES before the Australian population of *C. porosus* could be shifted back to Appendix II (Webb *et al.* 1984); it had been shifted to Appendix I in 1979.

However, the whole question of visibility bias in spotlight count indices of *C. porosus* was in need of clarification. Previous to the experiment there was

little incentive to accurately measure visibility bias because spotlight surveys were thought to reliably monitor changes in abundance. However, the data of Webb and Messel (1979) suggest a strong relationship between body size, wariness and thus the probability of detection. As the size structure of the recovering populations has been continually changing in the direction of there being more large crocodiles each year, size-based correction factors could be essential for interpreting survey results over time. A spotlight index not adjusted for differential visibility due to size would be inconsistent and hence unstable over time; a spotlight index of abundance in 1972 would not necessarily be comparable to one in 1984 which contained increased numbers of larger, wary crocodiles. Failure to account for such a bias could lead to spurious interpretations, although it would further enhance the recovery shown on Table 2.

A potential "spin-off" from the experiment relates to sustained-yield harvesting. If in the future it is incorporated into the management programme for the species, absolute population estimates will be needed; the experiments provide the groundwork for them.

1. Study Area

Three distinct habitats were chosen within the tidal part of the Adelaide River (upstream, downstream and side-creeks), which differed from each other in physical and vegetative characteristics. Each was 10 km long and they were chosen because they appeared to offer a range of crocodile visibility characteristics, from good to bad (Table 3; Fig. 7).

Table 3. Characteristics of the three study areas in the Adelaide River where visibility bias in counts of *Crocodylus porosus* was examined. All river and creek sections were 10 km long (after Bayliss *et al.* 1986). Vegetation density (%) refers to the amount of obstructive vegetation cover on the water and bank.

Area	River Width	Sinuosity	Vegetation Density (%)	Visibility Rank
Downstream (10 km length)	Wide (100 m)	Few wide bends (7)	50	Good
Upstream (10 km length)	Narrow (50 m)	Many sharp bends (16)	80	Bad
Side-creeks (two 10 km lengths)	Very narrow (10-20 m)	Many sharp bends (26)	100	Very Bad

2. Spotlight Indices

Standard spotlight counts for each habitat were replicated twice on consecutive nights (Table 4) prior to the mark-recapture experiment. In the upstream river section we lumped sightings of *C. johnstoni* and *C. porosus* together. A mean spotlight index with high precision was obtained with only two counts in all habitats (Table 4). The spotlight



Fig. 6. Highly sinuous tidal side-creeks off the Adelaide River mainstream, N.T.

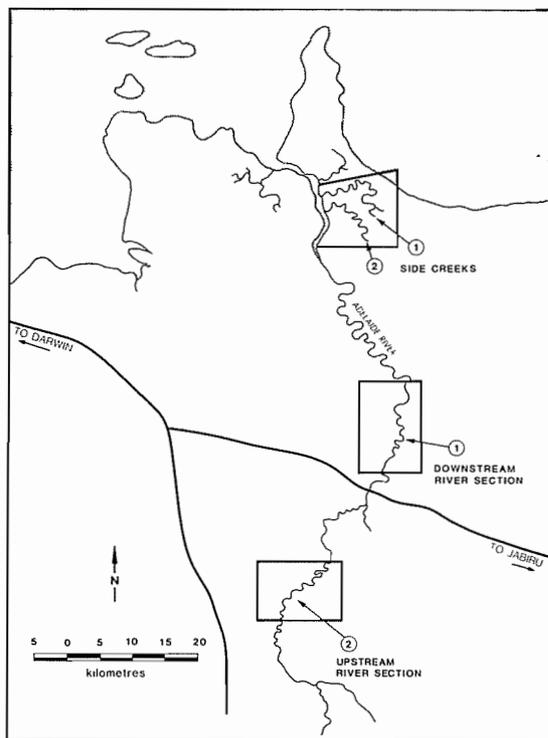


Fig. 7. Map of study area on the Adelaide River where the mark-recapture experiment was undertaken in July 1984 (from Bayliss *et al.* 1986).

counts showed low numbers of crocodiles in each of the two side-creeks, hence the data from them were pooled and analysed together (i.e. the population estimate refers to a total of 20 km of side-creek).

3. Marking and Recapturing Crocodiles

Crocodiles were approached with a spotlight beam held on their eyes. Those longer than 3 ft were marked by driving a barbed shaft containing a numbered plastic cattle tag into the skin of the neck (Fig. 8). The barb was held loosely in a socket in the end of a harpoon pole, and the tag was attached by jabbing the crocodile. Smaller crocodiles were caught by hand and tagged with a wire inserted through a scute on the neck. Successful insertion of a tag was recorded as the initial capture. Recaptures required that the crocodile be approached to a distance permitting the tag number to be read, which was equivalent to that required to insert the tag. If a crocodile could not be captured or recaptured on the first attempt, it was left. Captures and recaptures were recorded throughout the tidal cycle, and observers estimated the size of each crocodile marked or recaptured.

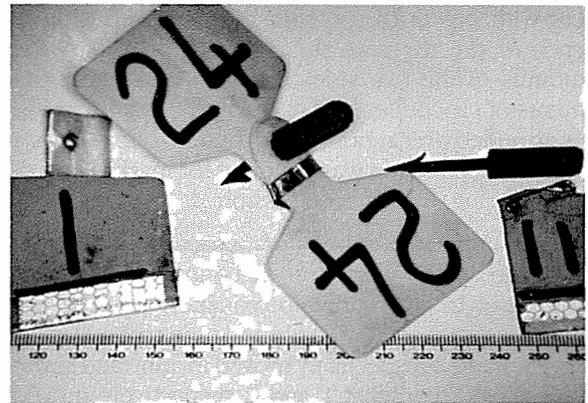


Fig. 8. Tags used for marking different sized *Crocodylus porosus* during a mark-recapture experiment: hatchlings (right): animals <3' long (left); animals >3' long (centre).

4. Recapture Statistics

The recapture statistics are summarized in Table 5. There were a total of 11 sessions in the downstream river section, seven in the upstream river section, and six in the side-creeks: all in three nights over a period of seven days. The important point to emphasize in this table is the high recapture rates in all habitats.

Table 4. Mean spotlight count indices for *Crocodylus porosus* in each of the study areas on the Adelaide River. Errors are standard errors (SE). *Crocodylus johnstoni* and animals sighted as "eyes only" are tabled separately.

Study Area	Index night 1	Index night 2	Mean index	±SE (%)	Mean "eyes only"	Mean <i>C. johnstoni</i>
Downstream	88	89	88.5	0.5(0.6)	12	0
Upstream	31	33	32.0	1.0(3.1)	9	5
Creeks (N=2)	30	31	30.5	0.5(1.6)	0	0

Table 5. A summary of the capture and recapture statistics obtained during a mark-recapture study of *Crocodylus porosus*: n = number in the sample; m = number recaptured; y = recapture rate; and, u = the number of unidentified tags (after Bayliss *et al.* 1986).

Session	Downstream					Upstream					Side-creeks				
	n	m	y	u	Date	n	m	y	u	Date	n	m	y	u	Date
1	73	—	—	—	20/7	21	—	—	—	13/7	28	—	—	—	22/7
2	41	19	0.46	9		22	5	0.23	2		26	12	0.46	1	
3	27	16	0.59	4		11	3	0.27	3		20	15	0.75	2	
4	13	5	0.38	6		19	6	0.32	3		10	7	0.70	1	
5	34	23	0.68	10		15	7	0.47	4	14/7	18	14	0.78	2	23/7
6	51	36	0.71	10		16	9	0.56	2		18	14	0.78	2	
7	37	24	0.65	10	21/7	12	7	0.58	4						
8	34	21	0.62	6											
9	22	13	0.59	5											
10	62	34	0.55	12	27/7										
11	52	32	0.62	8											

5. Sources of Experimental Bias

There are three important sources of bias that could affect the population estimates derived from the mark-recapture data, depending on which population model we choose to analyse it with. We attempted to account for them in the following ways:

i. *Movement into or out of the study area.* Observers with powerful spotlights were placed at both ends of the downstream river section and at the mouths of the two side-creeks, to monitor movements of crocodiles into and out of the study areas. As an added precaution, a 5 km buffer zone on either side of each section was searched for marked crocodiles during or after each session.

The small number of crocodiles in the downstream river section that moved out of the study area in one night approximately equalled the number that moved in (eight and nine crocodiles for nights 1 and 2 respectively moved in, nine and seven crocodiles for nights 1 and 2 respectively moved out). There was no positive sightings of tags on any crocodiles that moved out, and nor were any tagged crocodiles detected in the 5 km buffer zones. We assume from these results that movement was a trivial event and that any possible bias on the mark-recapture population estimates would be insignificant.

ii. *Tag Loss.* Five large crocodiles were double-tagged to provide a measure of tag loss. However, none of these animals lost a tag during the short time interval of the study. No small crocodiles were double-tagged, but as each one was tagged by hand, and tagged animals were sighted three weeks later; we assumed no loss.

iii. *Equal Catchability.* An important assumption of most mark-recapture models used to estimate population size is that all animals are equally catchable. We examined our data for signs of unequal catchability by testing for significant deviations from the observed recapture frequencies and the expected frequencies generated by the zero-truncated Poisson, geometric and negative binomial distributions (Seber 1973; Caughley 1977;

see Appendix II). Zero-truncated means that the distribution of recapture frequencies does not include a zero class, i.e. the frequency of those animals that were not caught. We used the χ^2 test for significance.

If the recapture frequencies (how many times individuals were recaptured) can be significantly rejected ($P < 0.05$) from a Poisson model then this is a strong argument in favour of unequal catchability between individuals. If it cannot be significantly rejected ($P > 0.05$) the result is consistent with equal catchability, although a non-significant result is really ambiguous. The results (Table 6) were not significant for all three habitats, and this favours the assumption of equal catchability.

If the recapture frequencies can be significantly rejected from either of the other two models then this strengthens the assumption of equal catchability. The negative binomial model was rejected for the recapture data in all three habitats. The geometric model (Table 6) was significantly rejected for the side-creek recapture data, indicating equal catchability, but not for the upstream and downstream habitats. This favours unequal catchability in those two habitats.

Overall, the results are ambiguous. These conventional tests for equal catchability were inconsistent and hence inadequate.

On the assumption that size-related wariness would be the main contributing factor to unequal catchability between individuals, we based a further examination of equal catchability on a one-factor analysis of variance (ANOVA) of mean recapture rate by 1-foot size classes (Fig. 9). The recapture rates of crocodiles in the downstream area varied significantly between 1-foot size classes, with most of this difference being attributable to crocodiles greater than 6'. However, variability in recapture rates within 1-foot size classes accounted for 82% of the total variance, also indicating unequal catchability within the population as a whole.

The recapture variability within 1-foot size classes was also large in the upstream habitat, and in the two side-creeks, but the mean recapture rates between

Table 6. The χ^2 values testing the goodness of fit of the observed *Crocodylus porosus* recapture frequencies to a zero-truncated Poisson distribution and to a zero-truncated geometric distribution, for all study sites. Mean recapture rates (\bar{x}) and number of sampling sessions (N) are included (after Bayliss *et al.* 1986).

Area/Model	χ^2	df	Significance (p)	Mean recapture rate (\bar{x})	Number of sessions N
POISSON					
Downstream	9.33	6	$p < 0.10$	3.33	12
Upstream	1.66	2	$p < 0.25$	1.89	7
Side-creeks	2.44	2	$p < 0.25$	2.36	4
GEOMETRIC					
Downstream	10.10	6	$p < 0.10$	3.33	as above
Upstream	2.20	2	$p < 0.25$	1.89	as above
Side-creeks	8.22	2	$p < 0.02$	2.36	as above

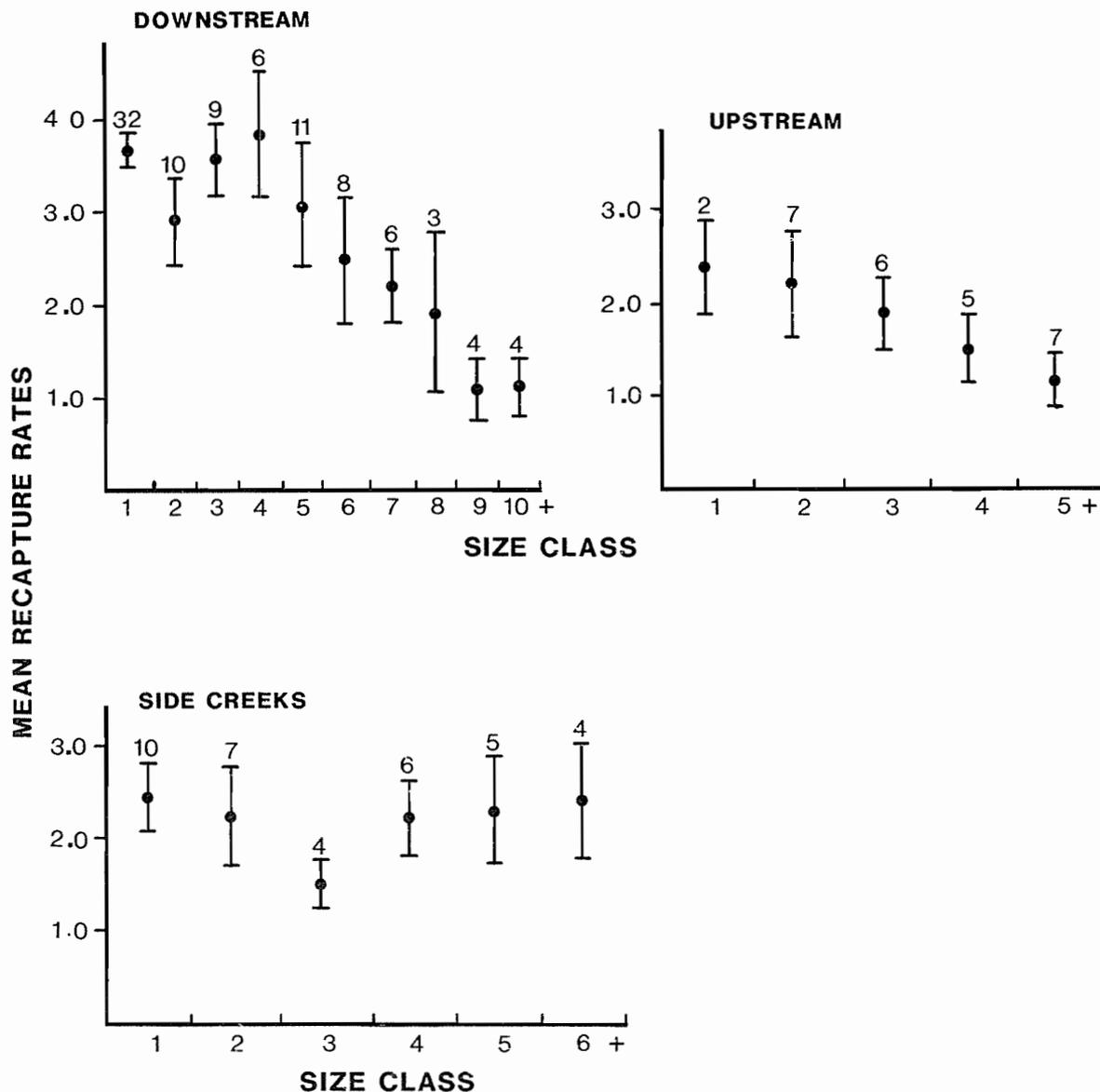


Fig. 9. Mean recapture rate of *Crocodylus porosus* in 1' size classes, for three study areas within the Adelaide River, July 1984 (from Bayliss *et al.* 1986). Vertical bars are standard errors; numbers are sample sizes.

1-foot size classes were not significantly different (although a downward trend in mean recapture rates with increasing size is apparent in the upstream area; Fig. 9).

Taken together, the results suggest that standard capture-recapture models may be appropriate for the upstream river and side-creek habitats, but a model that accounts for unequal catchability may be

more appropriate for the downstream river section. However, Magnusson *et al.* (1978) found that unequal catchability does not necessarily bias a Petersen population estimate.

6. Sighting Fractions, Correction Factors and Population Estimates

All mark-recapture data were analysed using four different models (Table 7), each with their own strengths and weaknesses (see Appendix II). These are the Petersen Estimate, as modified by Bailey (1951, 1952), Schumacher's Method, the Jolly-Seber Method, and Frequency of Capture Models. A series of population estimates were calculated for all available sessions, for all models, for all habitats. For each model, a one-factor ANOVA indicated that successive population estimates were not significantly different. Hence a more precise estimate was obtained for each model by averaging all estimates and merging the variances (Appendix II). These estimates could be biased because of the absence of independence between successive mark-recapture estimates. However, Caughley and Grice (1982) show that lack of independence does not necessarily bias population estimates derived from the Petersen Model if the capture probabilities are greater than 0.45. In fact the population estimates from all methods (Table 7) are very similar and the standard errors associated with them are low.

The average sighting fraction for each study area, and the resulting correction factors, were estimated by comparing the population estimates with the mean spotlight indices. The spotlight indices included the number of "eyes only" sightings, whilst all recapture analyses excluded them, because they obviously could not be classed as tagged or untagged: these crocodiles were assumed to have been part of the unseen population in each session.

The average sighting fractions reflected the differences in visibility of crocodiles in each habitat. The more structurally complex the habitat, the less the chance of detecting crocodiles; there is a very low probability of detecting crocodiles in mangrove-lined, narrow, highly sinuous side-creeks. An important consideration when assessing these data is the high recapture rates that were obtained in each habitat. In reality, this fact alone is likely to overwhelm minor violations of most assumptions associated with each model.

7. Size-based Correction Factors

The sighting fractions previously estimated are an average for each population at the time of survey. Accordingly, their application is limited to populations with the same size structure and with the same levels of inherent wariness. To develop a size-based sighting fraction for each habitat we examined the relationship between detection and crocodile size using the downstream recapture data which involved the largest numbers of animals. We use the geometric probability of capture at least once (q) (see Appendix II), because a previous analysis (Fig. 9) had already demonstrated unequal catchability between and within 1-foot size classes.

The probability of capture varies relatively little for crocodiles less than 6' (Fig. 10), but drops precipitously after that. We fitted a second-order polynomial curve to the data to predict size-based sighting fractions and their appropriate correction factors (Table 8).

8. Summary

The results of the mark-recapture experiment indicate that great caution needs to be exercised in extrapolating sighting fractions derived from one habitat and one population, with a given age-size distribution, to other habitats and other populations.

Table 7. A summary of the total population estimate (N) of *Crocodylus porosus* in each study area, generated by each model, and the estimated correction factors (CF) derived from the sighting fractions (P) needed to correct spotlight indices to total populations. SE = standard error; EO refers to animals sighted as "eyes only"

Model	Study Area	N	SE (%)	$P(+EO)$	$CF(+EO)$	Authors' Choice
Petersen's Estimate	Downstream	135	5 (3.7)	0.66	1.51	
	Upstream	54	6(11.1)	0.59	1.69	
	Side-creeks	43	3 (6.6)	0.35	2.86	*
Schumacher's Method	Downstream	145	6 (4.2)	0.61	1.64	
	Upstream	56	5 (8.1)	0.57	1.75	
	Side-creeks	44	2 (4.4)	0.34	2.94	
Jolly-Seber	Downstream	133	5 (3.8)	0.67	1.49	*
	Upstream	56	10(17.8)	0.57	1.75	*
	Side-creeks	46	2 (4.2)	0.33	3.03	
Frequency of capture:						
Geometric	Downstream	133	—	0.67	1.49	
Poisson	Upstream	35	—	0.57	1.75	
Poisson	Side-creeks	41	—	0.37	2.70	

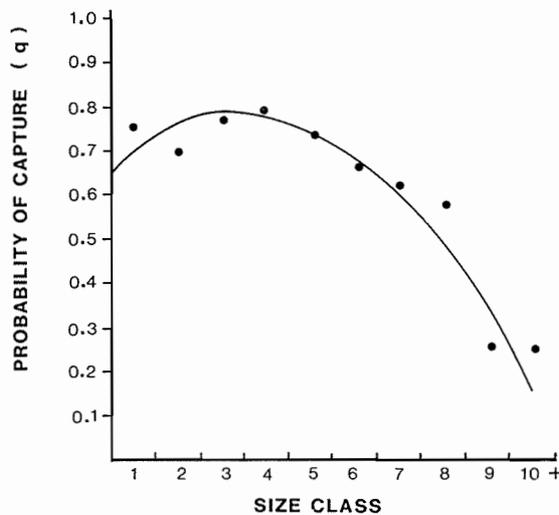


Fig. 10 The geometric probability (q) of capture at least once for 1' size classes (s) of *Crocodylus porosus* in the downstream section of the Adelaide River, July 1984. $q = 0.613 + 0.094S - 0.015S^2$ ($r = 0.89$, $n = 10$, $p < 0.001$). (From Bayliss *et al.* 1986)

Table 8. Size-specific correction factors (CF) for scaling spotlight counts in tidal rivers to absolute counts of the total "sightable" population. H = hatchlings, p = the probability of being sighted on any one survey (Webb *et al.* 1984) (see Fig. 10)

Size Class	p	CF
1-2' (H)	0.693	1.443
2-3'	0.745	1.342
3-4'	0.769	1.300
4-5'	0.765	1.307
5-6'	0.733	1.364
6-7'	0.673	1.486
7-8'	0.585	1.709
8-9'	0.469	2.132
9-10'	0.325	3.077
10' +	0.153	6.536

A Comparison of Helicopter and Spotlight Counts

Spotlight surveys from boats have other major disadvantages besides inherent visibility bias. They are time consuming, expensive, often dangerous, and are by necessity restricted to habitats that allow easy boat access. There are huge slabs of potential crocodile habitat in the Northern Territory that have not been surveyed due to poor or impossible boat access. In an attempt to overcome these problems we examined the feasibility of using helicopters to count crocodiles in tidal and freshwater wetlands during the day, and compared the results to spotlight surveys by boat in terms of cost and suitability for extensive surveys of crocodile habitat.

Visibility bias is also inherent in aerial surveys, but here we are only concerned with obtaining a reliable relationship between spotlight and helicopter counts for the purpose of monitoring population trends over time. If such a relationship exists,

then the results of the mark-recapture experiment may also be cautiously applied to helicopter counts to improve their accuracy.

1. Calibration of Spotlight and Helicopter Counts

Crocodiles were counted during low tide from a Jet Ranger (Bell 506) in a 40 km section of mainstream and in four tidal side-creeks, all within the Adelaide River. These counts were matched to recent spotlight counts at spring low tide in the same areas (Fig. 11 illustrates the mainstream habitat type).



Fig. 11 *Crocodylus porosus* as seen from a helicopter in the Adelaide River, N.T.

The river mainstream was surveyed twice by helicopter, once during a spring low tide and again during a neap low tide to test the relationship between visibility and the state of tide (the amount of exposed mud bank; Messel *et al.* (1981). A constant survey height (20 m) and speed (93 km h^{-1}) were maintained 100 m towards midstream along one bank. Crocodile densities were similar on both banks, but this relationship does not necessarily hold for other parts of the river, nor for other rivers. Other effects on the visibility of crocodiles could not be completely standardized. The effects of ambient temperature on crocodile basking behaviour and hence visibility are unknown. Temperatures were cool during the spring tide survey (18°C) and warm during the neap tide survey (27°C).

All side-creeks were surveyed at neap low tide and ambient conditions were warm (27°C). Acute visibility bias caused by severe glare and deep shade was reduced by surveying between 0900 and 1500 hours, however neither effect could be completely eliminated.

i. *Observer bias.* Two tandem observers counted in 1 km units of river and creek, and a mark-recapture model (Magnusson *et al.* 1978; Caughley and Grice 1982; see Appendix III) was applied to these simultaneous counts to estimate the proportion of "potentially visible" crocodiles that each observer missed in their common field of view. Observer correction factors derived from these proportions were used only to standardize observer bias when different observers were used. The corrections do not account for submerged crocodiles and those in dense bank vegetation because these are never sighted ("marked" in the context of the mark-recapture model). The corrected counts are therefore only an improved index used to standardize observer differences.

Each tandem observer recorded the position (bank, waters' edge, midstream) and size of each crocodile, and this helped reduce bias in the mark-recapture analysis which may result from the assumption that both observers saw the same animals.

A total of 75 km of river and 45 km of densely vegetated side-creek were surveyed throughout the calibration study. One observer (PB) participated in all counts and two other observers (GW and KD) shared the tandem position. The classification of crocodiles as being seen by one ("marked") or both ("recaptured") observers was substantially improved in patches where crocodiles were in high densities by recording their size and position in the field of view.

This model was originally applied to groups of animals rather than counts of individuals. Crocodiles did not occur in groups, but were found in high and low densities. Fortunately, the effects of unequal catchability (here due to variations in density on the probability of capture) do not necessarily affect the validity of the model which uses a Petersen Estimate (Magnusson *et al.* 1978).

The results (Table 9) indicate that the probability of seeing crocodiles from a helicopter varied between observer and habitats but not between spring and neap low tides in the river mainstream. Hence the proportion of crocodiles missed by a given observer was constant regardless of numbers seen and this supports the findings of Magnusson *et al.* (1978) that unequal catchability should not affect the model. The results show also what we expected: crocodiles are much more difficult to detect in side-creeks lined with dense mangroves than along open river banks.

Table 9. The probability (p) of each tandem observer detecting crocodiles, at both spring and neap low tides, in two sections of the Adelaide River (the downstream part of the mainstream, and side-creeks lined with dense mangroves) and the correction factors (CF) needed to standardize their counts. No data exist for spring low tide in side-creeks (after Bayliss *et al.* 1986).

Habitat/Observer	Spring low tide		Neap low tide	
	P	CF	P	CF
Downstream				
PB	0.80	1.25	0.80	1.25
GW	0.80	1.25	—	—
KD	—	—	0.67	1.49
Side-creeks				
PB	—	—	0.67	1.49
GW	—	—	—	—
KD	—	—	0.25	4.00

ii. *The Relationship between Total Spotlight Counts and Helicopter Counts.* Hatchlings (<2') were rarely detected from the helicopter, hence the resulting count was matched to the spotlight counts of non-hatchlings. The helicopter counts of one observer were then paired to recent spotlight counts in units of river length increasing from 1 km to 5 km. The unit length which produced the lowest residual variance in a regression (passing through the origin) of the helicopter counts on spotlight counts was used to derive calibration equations. This procedure was necessary to account for mismatched pairs resulting from inaccuracies in navigation in either method of survey. The relationship between spotlight and helicopter counts in the river mainstream applied to counts of both banks during the spotlight survey and one bank during the helicopter survey. Counts were paired in 5 km units of river because this yielded the lowest residual variance in the calibration regression equations for spring and neap low tides (Table 10).

Table 10. The results of regression analyses (through the origin) between total mean spotlight counts (Y) and helicopter counts (X) of *Crocodylus porosus*, in both the mainstream (downstream part) and in side-creeks of the Adelaide River (July 1984). Spotlight counts included both banks, whereas helicopter counts included both banks in the side-creeks, but only one bank in the wide mainstream section. All data were collected at low tide. Helicopter counts were corrected for observer bias and then paired to spotlight counts in 5 km units. Hatchlings were excluded from the spotlight counts (after Bayliss *et al.* 1986).

Area/Tide	Equation	95% C.I. of slope	R^2	df	Significance
Downstream					
Spring	$Y = 2.07X$	1.78-2.37	0.98	5	$p < 0.001$
Neap	$Y = 3.18X$	2.61-3.76	0.96	6	$p < 0.001$
Side-creeks					
Neap	$Y = 0.55X$	0.43-0.68	0.99	2	$p < 0.001$

The four creeks were surveyed at a constant height (20 m), but aircraft speed was kept as slow as possible (25-27 km h⁻¹). The total helicopter counts

at neap low tide were paired with the total spotlight counts at spring low tide because of low crocodile densities. Although only four creeks were surveyed, the relationship is significant (Table 10), however, more replication is needed to determine its stability.

The results show that helicopter counts in the mainstream at spring low tide, when doubled to account for both banks, are similar to spotlight counts under the same tidal conditions. Neap low tide helicopter counts (doubled for both banks) were 37% less than spotlight counts at spring low tide. However, total helicopter counts in the side-creeks at neap low tide were 45% higher than the spotlight counts at spring low tide. Overall, the results show that despite variation in absolute numbers of crocodiles sighted with tide, habitat, and observer, the helicopter counts at spring and neap low tide on the Adelaide River were consistently related to spotlight counts at spring low tide. Hence helicopter surveys in tidal river systems can provide comparable population indices of crocodile abundance, and an abrupt change of survey technique from boats to helicopter would not invalidate comparisons of past and future surveys.

Three freshwater billabongs of the Mary River were surveyed by helicopter, and these counts were compared to recent spotlight counts. Each billabong varied in the amount of floating and bank vegetation. Most of the crocodiles counted were freshwater crocodiles, *C. johnstoni*. No calibration was attempted due to low replication, however a ratio of helicopter to spotlight counts is presented as an index of visibility from the air (Table 11). The number of crocodiles seen from a helicopter in the two billabongs with dense and floating vegetation was very low compared to spotlight counts (see Fig. 12). More surveys are needed to develop helicopter census methods in these habitats, however the high sighting fraction for the open billabong is encouraging.

Table 11. A comparison of helicopter counts (HC) and spotlight counts (SC) in some freshwater billabongs of the Mary River (July 1984). Data include both *Crocodylus porosus* and *C. johnstoni*; percentage vegetation cover of the water and bank was estimated by eye.

Billabong name	Bank and floating vegetation (%)	HC	SC	HC/SC
Bridge	90	40	222	0.18
Rockhole	70	32	112	0.29
Corroboree	10	48	60	0.80

2. Feasibility Survey

A Bell-47 helicopter was used between Melville Island and the Western Australian border (8-10 August) to count crocodiles from samples of coastline (see Fig. 13), coastal creeks, tidal rivers and river side-creeks. All survey variables were standardized as per the calibration surveys, and we assumed



Fig. 12. Aerial counts of crocodiles in freshwater billabongs with floating mats of vegetation extending out from the shore gave reduced counts relative to spotlight counts in the same areas.

no difference in counts between the different helicopters used. Counts were standardized for observer bias in each habitat and then converted to relative spotlight densities (numbers per km of coastline, numbers per km of creek, numbers per km of river including both banks) using the appropriate tidal calibration equation. (The conversion factor depended on whether one or both banks of a river were surveyed).



Fig. 13. *Crocodylus porosus* as seen from a helicopter on the coast.

Table 12. The results of a helicopter survey of *Crocodylus porosus*, in different tidal habitats, between Melville Island and the Western Australian border: *N* = the number of creeks or sections of coast sampled; *HC* = helicopter counts; *SI*(corrected) = helicopter counts corrected for observer bias and then adjusted to spotlight densities using neap tide corrections; *RD* = the spotlight relative density; and $\pm SE$ = the error of *RD*. Large creeks are those wider than 20 m at their mouth (after Bayliss *et al.* 1986).

Area	Habitat	km	HC			$\pm SE$ (%)
			<i>N</i>	(corrected)	<i>SI</i>	
Darwin to W.A. border	Large coastal creeks	37	15	35	28	0.76 (44)
	Large river creeks	60	5	27	22	0.37 (26)
	Coastline	244	4	7	11	0.05 (45)
Melville Island	Coastline	114	2	9	15	0.21 (2)

The results show that habitats had substantially different densities (Table 12). The density of crocodiles on the coastline of Melville Island was four times that on coastline south of Darwin, possibly reflecting better habitat. Crocodiles were detected only in large creeks (>20 m wide at the mouth), and none were seen in 32 small creeks (<20 m wide at the mouth) sampled. In the tidal section of the Moyle River, the helicopter (3.83/km) and spotlight (3.44/km) indices of density were similar.

The cost of a helicopter survey in remote areas is approximately \$7/km of habitat surveyed, which includes hire (fuel and pilot), wages, travel expenses (three people) and dead travel time. In contrast, the cost of a boat survey in remote areas is approximately \$28/km of habitat surveyed. Boat surveys require capital equipment and entail maintenance costs, high wage costs (more people and time), insurance and many hidden administrative overheads.

3. Summary

Aerial survey is much cheaper and less time consuming than boat survey, yet it provides a population index comparable to that obtained by spotlighting. A further advantage of helicopters is the ability to obtain and/or improve precision of a population index rapidly by replication, at a reasonable cost.

Failure to detect hatchlings from the air is not necessarily a significant disadvantage in monitoring the rate of increase of a crocodile population. Recruitment to the populations can be assessed by long-term trends in the larger size classes and associated helicopter surveys of nesting effort.

Aerial survey offers a realistic way of achieving one of the monitoring aims of the management programme — to survey more kilometres of more habitat in a very much shorter period of time at less cost.

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APPENDIX I

(taken from Seber 1973, Caughley 1977; symbols are those used in Caughley)

TESTS FOR EQUAL CATCHABILITY

1. Leslie's Test

This test is used where animals are marked on a single occasion and recaptured on subsequent occasions. The test rejects information from the first and last capturing occasion, and all the recapture records of animals not caught on the last occasion.

If catchability is equal, the recapture frequencies will form a binomial distribution: the hypothesis is tested by comparing the observed variance with the expected binomial variance using χ^2 with $(\sum f) - 1$ degrees of freedom.

$$\chi^2 = \frac{\sum fi^2 - (\sum fi)^2 / \sum f}{\sum fi / \sum f - \sum n^2 / (\sum f)^2}$$

where n is the number of recaptures, i is the number of times it was recaptured and f is the number of animals. A significant result is a good indication of unequal catchability, whereas a non-significant result is ambiguous — unequal catchability perhaps occurring, but cannot be demonstrated.

2. The zero-truncated Poisson Test

If the period between first and last capturing occasions is short, and natural mortality is low or zero, then all capture records can be used in this test. Since all catching occasions are included, each arrival has been caught at least once. We do not therefore have a zero frequency class as in the Leslie Test. If catchability is equal (constant) the distribution of recapture frequencies will form a zero-truncated Poisson distribution when the number of sampling occasions is large relative to the mean recapture rate. A truncated Poisson distribution is fitted to the observed frequencies and the fit is tested by χ^2 . Expected frequencies are calculated from the

mean, \bar{X} , of the complete Poisson distribution which is related to the mean of a zero-truncated Poisson by:

$$\bar{x} = \frac{\bar{X}}{1 - e^{-\bar{X}}}$$

if $\bar{x} > 2$, then $\bar{X} = \bar{x} - Z - Z^2 - 1.5Z^3 - 2.6Z^4 - 5.2Z^5$

where $Z = \bar{x} e^{-\bar{x}}$, and

where $\bar{x} = \sum fi / \sum f$

The expected frequency $E(f)$ for each i is calculated as

$$E(f) = \frac{(\sum f) e^{-\bar{x}} \cdot \bar{x}^i}{(1 - e^{-\bar{x}}) i!}$$

TEST FOR LOST TAGS

Marks or tags always drop off, hence leading to biased results. The proportion of double-tagged animals that lose one tag could be used as an index of tag loss. A group of animals is double-tagged with similar single tags. A sample of animals sometime later will comprise four classes.

1. B_2 animals that retained both tags;
2. B_1 animals that retained only one of the original tags;
3. B_0 animals that retain neither tag;
4. animals that are not members of the double tag fraternity

B_0 is estimated as:

$$B_0 = (B_1^2 / 4B_2)$$

The probability that an animal originally marked with one tag would lose it over the same time period is estimated as:

$$p = (B_1 / 2B_2 + B_1)$$

This estimate of p can be used to correct records of recaptured animals originally marked with one tag

APPENDIX II

A. SOME MODELS TO ESTIMATE POPULATION SIZE FROM MARK-RECAPTURE DATA

(taken from Seber 1973, Caughley 1977; symbols are those used in Caughley)

1. Petersen Estimate (as modified by Bailey 1951, 1952)

This requires marking on one occasion and recording the proportion of marked animals in a sample captured on a second occasion. The assumptions are:

- i. no animal is born or immigrates into the study area;
- ii. marked and unmarked animals die and leave the study area at the same rate;

- iii. all animals are equally catchable;
- iv. no marks are lost.

If the number of marked animals to be recaptured is not decided prior to recapturing then

$$N = \frac{M(n + 1)}{m + 1}$$

Appendix II — cont.

where M animals are marked in a population of size N (unknown) and m marked animals are recaptured in a subsequent sampling of n animals.

The standard error of this estimate is approximated by

$$SE = \sqrt{\frac{M^2(n+1)(n-m)}{(m+1)^2(m+2)}}$$

If the number of animals is decided before recapture commences a different formulation for population size and variance is required (see Caughley 1977, pg 143).

The Petersen Estimate is biased upwards by births and immigration.

2. Schumacher's Method

If enough animals cannot be marked on a single occasion then marking on several occasions becomes necessary. The population size is estimated from the rate at which the proportion of marked animals rises as more are progressively marked.

$$N = \frac{\sum M_i^2 n_i}{\sum M_i m_i}$$

Where N is the unknown population size, M is the number of individuals marked prior to the i th sampling occasion, and n is the number of individuals captured on the i th occasion of which m had been marked previously.

The standard error (SE) of N is calculated indirectly from the SE of $1/N$

$$SE(1/N) = \frac{s}{\sqrt{\sum M_i^2 n_i}}$$

$$\text{where } s^2 = \frac{\sum (m_i^2/n_i) - (\sum M_i m_i)^2 / (\sum M_i^2 n_i)}{j-1}$$

and j is the number of recapture samples.

This method allows a check on the assumption of equal catchability. If the assumption holds, the regression of m_i/n_i on M_i is linear through the origin with a slope of $1/N$. The method assumes that the population maintains a constant size during the experiment, and that no animal dies or leaves the area, or is born or immigrates.

3. The Jolly-Seber method

If animals are recaptured on two or more occasions, a stochastic analysis developed by both Jolly and Seber can be used. All previous models are deterministic. The method requires that each animal's history of recapture is known — animals must be serially marked with time-specific tags, or individuals must have unique tags (e.g. numbered tags). In the calculations:

N_i = estimated population size;

n_i = size of sample;

M_i = number of marked animals in the population immediately preceding the i th occasion;

m_i = number of marked animals in the sample;

R_i = number of animals marked and released;

r_i = number of animals of the R released that are subsequently recaptured;

Z_i = number marked before the i th occasion that were not recaptured on the i th occasion but were recaptured subsequently;

a_i = proportion of marked animals in the population at the i th sampling.

The size of the population at each time of sampling, other than the first, is estimated as:

$$N_i = n_i + \frac{n_i Z_i R_i}{m_i r_i}$$

Each estimate has a formal standard error (SE) of:

$$SE = \sqrt{\left[\frac{N_i(N_i - n_i)}{n_i} \left(\frac{M_i - m_i + R_i}{M_i} \right) \cdot \left(\frac{1}{r_i} + \frac{1}{R_i} \right) + \frac{1 - a_i}{m_i} \right]}$$

where $a_i = \frac{m_i}{n_i}$ and $M_i = m_i + \frac{Z_i R_i}{r_i}$

The probability that an individual alive at the moment of release on the i th occasion will survive and/or not emigrate from the study area before capture on the next sample is:

$$p_i = \frac{M_{i+1}}{M_i - m_i + R_i}$$

The number of animals joining the population by birth or immigration between the i th and $i+1$ occasion, and which are still alive at the end of this interval, is estimated as:

$$A_i = N_{i+1} - p_i(N_i - n_i + R_i)$$

Population size on the first and last occasion cannot be directly estimated. However, an approximation can be obtained by linear extrapolation (forwards or backwards) from an estimated rate of increase between sampling occasions.

The main advantage of the Jolly-Seber Method is that the assumptions of the model are less constrained than the previous deterministic models.

4. Frequency of Capture Models

Violations of the assumptions of all the previous mark-recapture models are more the rule than the exceptions. Most attempts at improving the models have been directed at developing models of frequencies of capture that relax the requirement of equal catchability. Frequency of capture analyses use data on the number of times an animal is caught once, twice, three times, etc., over a number of capturing occasions. These data form a zero-truncated frequency distribution of captures, the

Appendix II — cont.

missing zero class representing the unknown number of animals that were never caught. The method attempts to estimate the frequency of the zero class from the shape of the truncated distribution. Population size is then estimated as the number of animals caught at least once plus the estimated number that were never caught. Only three frequency models are discussed here. The Poisson model assumes that catchability is constant, however, the negative binomial and geometric models allow for unequal catchability generated in different ways.

i. Poisson Estimate (see Appendix I)

$$N = \frac{\sum f_i}{\bar{X}}$$

This model assumes equal catchability and zero or trivial mortality.

ii. Negative Binomial Estimate

$$N = \frac{\sum f_i}{\bar{X}}$$

$$\text{where } \bar{X} = \bar{x} - \left[\frac{s^2 f_i}{\bar{x}(\sum f_i - f_i)} \right]$$

where f_i is the observed frequency of single captures and

$$\bar{x} = \frac{\sum f_i i}{\sum f_i}, \text{ and}$$

$$s^2 = \left(\frac{1}{(\sum f_i) - 1} \right) \left(\frac{\sum f_i i^2 - (\sum f_i i)^2}{\sum f_i} \right)$$

The observed fit to this model is calculated using a χ^2 test on observed and expected frequencies. First of all two extra parameters need to be calculated, w and k .

$$w = \frac{\bar{x}}{s^2} \left(1 - \frac{f_i}{\sum f_i} \right)$$

$$k = \frac{w\bar{x} - f_i / \sum f_i}{1 - w}$$

Expected frequencies of a zero-truncated negative binomial distribution are calculated as:

$$E(f_i) = \sum f_i \cdot \frac{w^k}{(1-w)^k} \cdot \frac{\Gamma(k+i) \cdot (1-w)^i}{\Gamma(k)!}$$

where Γ means the gamma function, E means expected and $!$ means factorial. Gamma functions are calculated by

$$\log_e \Gamma(x) = (x - 1/2) \log_e x - x + 0.91767 + \frac{1}{12x} - \frac{1}{360x^3}$$

(iii) Geometric Estimate

$$N = \frac{\sum f_i}{q}$$

$$\text{where } q = \frac{\sum f_i - f_i}{f_i - 1}$$

$$\text{and, } E(f_i) = (\sum f_i) (1 - q) q^{i-1}$$

B. MERGING VARIANCES OF POPULATION ESTIMATES

If there are k independent population estimates (N , for 1 to k sessions) and a one-factor ANOVA shows that there is no significant difference between them, then a more precise population estimate and variance may be obtained.

$$\hat{N} = \frac{N_1 + N_2 + \dots + N_k}{k}$$

$$VAR(\hat{N}) = \frac{1}{k^2} (VAR1 + VAR2 + \dots + VARk)$$

The standard error of N is simply:

$$SE = \sqrt{VAR(N)}$$

APPENDIX III

THE MARK-RECAPTURE MODEL USED TO CALCULATE OBSERVER BIAS FROM TANDEM AERIAL COUNTS OF CROCODILES

(see Caughley and Grice 1982; Bayliss 1986)

The notations used in this model are:

S_1 = the number of crocodiles seen by the first observer but missed by the second;

S_2 = the number of crocodiles seen by the second observer but missed by the first;

B = the number of crocodiles seen by both observers;

\hat{p}_1 = the probability of a crocodile being seen by the first observer.

\hat{p}_2 = the probability of a crocodile being seen by the second observer.

CF_1 and CF_2 = the estimated correction factors for observer one and two respectively, which standardize crocodile counts between observers.

The model is:

$$\hat{p}_1 = B/(B + S_2)$$

$$\hat{p}_2 = B/(B + S_1)$$

with $CF_1 = 1/\hat{p}_1$

and $CF_2 = 1/\hat{p}_2$