CLIVE MINTON

165 Dalgetty Road, Beaumaris, Victoria 3193, Australia, e-mail: mintons@ozemail.com.au

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I emphasise the importance of wader banders designing and carrying out their fieldwork programmes in a manner that will enable catch data to be utilised as a means of monitoring, on a long-term basis, the reproductive rates of migratory waders. Reproductive and survival rates are the two key demographic factors that govern population levels, and hence knowledge of them is essential to understanding the causes of any observed changes.

BACKGROUND

Wader banding - which commenced in the Scandinavian countries in the late 1940s, in the UK in the 1950s and in the USA, Africa and Asia in the 1960s - was initially focused mainly on determining migration routes and destinations of the different species and populations. Subsequently biometric measurements, especially weight and moult studies, have assisted this process on an ever-widening scale. More recently, the widespread use of colour leg-flagging to identify migration routes has also greatly advanced our understanding of migration strategies over the last ten years, especially in the East Asian/Australasian and the North/ South American Flyways. Now, at least an outline - and in some cases a very detailed understanding - is known of the migration of most of the main species in each flyway and, most importantly from a conservation perspective, the principal stopover sites and non-breeding areas have been identified.

While much more information is needed before we can claim to understand migration strategies fully, banders can afford – in fact, need – to turn their attention more to the collection of other critical conservation-related data: demographics. Count data reveal whether population levels are changing or are stable but only contemporaneous monitoring of survival rates and reproductive rates will enable us to understand the reasons for any changes. Furness & Greenwood (1993) emphasised that monitoring population levels *per se* was relatively valueless unless research that facilitates an understanding of the results is carried out in parallel. If survival and reproductive rates both remain unchanged, and if current population size is considered satisfactory, then there is no need to worry about a population as its continuity is ensured (Goss-Custard *et al.* 2002).

Much effort has been directed at methods of measuring survival rates in waders, especially based on capture/recapture data using, for example, the Jolly-Seber model and subsequent variations (Sandercock, this volume). Considerably less effort has been directed at determining reproductive rates, the other key demographic factor. This is partly because of the practical difficulties of collecting such data. This paper concentrates on reproduction rate measurement, and compares the various methods.

It should be noted that most of the methods considered here are measures of recruitment into the non-breeding population rather than true reproductive rates. The results may therefore be affected by variations in mortality experienced during the first migration from the breeding grounds to the sampling area. However, it would appear that such variability is probably small in comparison with year-to-year fluctuations in breeding success.

METHODS

Methods of determining breeding success, and their relative merits, are:

a) On the breeding grounds

Measuring breeding success by observing the number of young that fledge is a time-consuming process and is generally only practical, especially on a long-term basis, in temperate regions. Direct measurement of breeding productivity on the more remote northern, especially arctic, breeding grounds is both difficult because of the terrain and virtually impossible on a long-term basis because of the time and expense involved. The monitoring of a defined area of the Taimyr Peninsula in Arctic Russia by Pavel Tomkovich (and many others) and of some locations in northern Canada (e.g. Jehl & Lim 2001) are the main examples of attempts to monitor productivity in the arctic. However, both studies found that monitoring the number of breeding pairs was far more practical than measuring the annual production of chicks.

b) By field observation

Reproduction rates – or, more precisely, recruitment rates – can be measured if the proportion of juvenile/first-year birds in a population can be determined. First-year waders are only easy to identify by observation in the field when extensive amounts of characteristic juvenile plumage are retained. In many species, ageing in the field becomes difficult after the end of October as the juvenile plumage is moulted into non-breeding plumage similar to that of adults. Thus scanning flocks systematically with a telescope to determine age composition cannot easily be undertaken later in the season. Many juveniles do not reach their non-breeding areas and mix with the adults until November. Therefore, the proportion of juveniles is best measured when the population is relatively stable in December–February. As most juveniles are no longer

recognisable by then, the feasibility of determining age composition by scanning in the field is very limited.

c) By counts at migratory stopover sites

Some measure of relative annual breeding success can be obtained by observation and counts during southward migration in early autumn. Distinguishing between adult and juvenile birds at this time is relatively easy. In addition, there is often a timing difference between the migration of the two age groups, adults preceding juveniles by several weeks in many species. Generally, however, such data are at best only qualitative. Frequently the rapid turnover of such transient populations means that it is impossible to obtain hard quantitative age-ratio data for the population as a whole. Thus years when unusual numbers of juvenile Curlew Sandpipers Calidris ferruginea and Little Stints Calidris minuta occur in the British Isles in late August/September are thought to be associated with "good" breeding years, though weather conditions play a part in these influxes as well (Stanley & Minton 1972). Therefore quantitative comparisons with other years are not necessarily valid.

d) By counts at non-breeding locations

One-year-old birds of many wader species, especially those that migrate to non-breeding areas in the Southern Hemisphere, do not return to the breeding grounds. A comparison between the number of such birds left behind (in the Austral winter) when the adults have migrated northwards and the total numbers of birds present in the previous non-breeding season (the Austral summer) can therefore be a relative measure of breeding success in the previous year. In species where breeding commences uniformly at age two and where, in addition, there is little movement of one-year-old birds away from their nonbreeding location, this measure can give a good quantitative indication of reproductive success. However, universal use of such a method is constrained:

- i) because in some species young birds breed at the end of their first year
- ii) because in some species young birds do not breed until they are three or more years old, and
- iii) because in some species first year birds make considerable movements (up to several thousand kilometres), away from their non-breeding area, even though they do not actually return to the breeding grounds.

e) From the proportion of juvenile/first year birds in banding catches

This is potentially the most practical quantitative method of measuring breeding productivity – either in absolute terms or in a comparative year to year and species by species manner. However, like many field data, it is susceptible to known, and possibly unknown, biases. To minimise these, conditions should be standardised as far as possible. For example:

i) Only one capture technique should be used.

In Victoria/South Australia and in the Broome/ Eighty Mile Beach region of NW Australia only cannon net catches are used in the % juvenile statistics. It has frequently been reported that mist netting generally produces catches with a higher proportion of juvenile birds than are caught by cannon-netting (Pienkowski & Dick 1976) or are present in the population (Goss-Custard *et al.* 1981). This is thought to be associated with the lower awareness or greater naivety of young birds.

ii) For each species, catches should be made at the same location, or preferably the same range of locations, each year.

Marked and relatively consistent differences have been found in % juveniles caught at different locations. If several locations are sampled the figures are more likely to be representative of the population as a whole.

iii) Catches should be made around the same time each year, after all juveniles have arrived on the nonbreeding grounds and before the departure of adults back to the breeding grounds has commenced.

Existing banding data will generally show what these dates are for each species/location. Thus, for example, in SE Australia the optimum period is December–February – virtually all juveniles having arrived by the end of November and mobility within this period being minimal. In many species, where departures are known not to commence until late March/April, samples obtained in the first 2–3 weeks of March can also be used.

In NW Australia, a wider window of opportunity for sampling is possible with juveniles arriving there several weeks earlier on southward migration and northward departures not commencing until the last week in March (except Eastern Curlew *Numenius madagascariensis*).

In European non-breeding ("wintering") areas other constraints on timing may be relevant e.g. the post primary moult as well as the westward dispersal in October/November of species such as Dunlin *Calidris alpina* and Red Knot *C. canutus* may preclude accurate assessment of % juveniles before about late November.

iv) Data from catches obtained after prolonged disturbance ("twinkling" in cannon-netting parlance) should be used with caution.

Experience has shown that cannon net catches made after extensive disturbance of birds – to try to get them into the catching area – may contain a greater than normal proportion of young birds. The same effect can be obtained if a catch is made at a location soon after a previous catch there. The probable explanation is that older birds recognise the signs of cannon-netting activity and are more likely to avoid the catching area. Most cannon net catches involve some twinkling and it is only when this is unusually prolonged that significant biases in the data are likely to occur.

POTENTIAL BIAS: NON-UNIFORM DISTRIBUTION

The three areas of potential bias in assessing the proportion of juveniles in the population from catch data, which are most difficult to assess or circumvent, are those associated





with the possible non-uniform distribution of young birds:

- 1) on a macro-scale within the non-breeding area
- 2) on a local scale in a particular habitat or at a particular location
- 3) on a micro-scale within a high tide roosting or feeding flock

There is considerable evidence that all of the above occur to at least some extent in some species and/or at some locations. Examples are given below.

In a variety of species there are well-documented cases of marked differences in the non-breeding areas of adult and juvenile birds. For example, in several species of terns (notably Common Terns *Sterna hirundo* in the West Atlantic Flyway (Hayes *et al.* 1997) and Roseate Terns *Sterna dougallii* in the East Asian/Australasian Flyway) the "wintering" areas of the age groups are almost completely exclusive.

In waders, perhaps the best example is Red Knot in Australasia. Most juveniles of the race *rogersi* spend their first year in E and SE Australia and only make the additional journey to the non-breeding areas in New Zealand at the beginning of their second year. Thus the proportion of first year birds in the populations in E Australia is particularly high (with up to 70% in years of high breeding success) whilst in New Zealand only a low proportion of first year birds is ever recorded in the Austral summer.

At a local scale, segregation of age groups may also be marked on occasions. For example, at Eighty Mile Beach, NW Australia, juvenile Bar-tailed Godwits *Limosa lapponica* may be seen in October and November wandering around the upper beach at high tide, searching for food, while the adults are concentrated in large roosting aggregations elsewhere. Similarly a greater proportion of young birds tend to occur in places such as sewage farms compared with adjacent shore habitats, e.g. at Broome in NW Australia (Bartailed Godwits, Grey-tailed Tattlers *Heteroscelus brevipes*) and at the old Wisbech Sewage Farm in the U.K (Dunlins).

An uneven distribution of age groups in high tide roosting flocks of Red-necked Stints C. ruficollis and Curlew Sandpipers has been observed in October and November at Werribee Sewage Farm, Victoria, SE Australia (D. Rogers & M. Barter pers. comm.). There are other observations suggesting that young birds have a tendency to be located at the periphery of roosting flocks. The considerable mixing that takes place when birds are being extracted from a cannon net and being placed in keeping cages makes this difficult to measure. However, there has been at least one occasion when it was clear that birds were segregated into age groups within the catching area of a net. In this case, the Red-necked Stints that were high up the beach, close to the net after the birds had been disturbed away from the net for safety reasons, contained a much higher proportion of juveniles than the body of the catch. However, it is not possible to tell whether this was because the juveniles were less wary or were differently positioned within the flock.

In the field, it is not usually possible to decide which section, or what proportion, of a roosting flock should be caught in order to give the most accurate representation of the ageclasses. Equally it is not possible to estimate the extent of macro or local segregation of age-classes within a flock. This means that the proportion of juveniles caught may not be an accurate representation of the proportion in the population as a whole. However, if annual samples are obtained in a reproducible and standard way, and especially if multiple samples are obtained, potential biases will be minimised and the data on the proportion of juveniles should at least be comparable from year to year so as to give an index of annual breeding success.

RESULTS

Summers & Underhill (1987) were the first to publish extensive data on the proportion of juveniles in waders. They used count and catch data from South Africa to show that there were marked annual variations in apparent breeding success of three wader species, generally following the same threeyear cycle observed in Brent Geese *Branta bernicla*. They attributed the variation to the lemming/predator cycle occurring in the parts of N Siberia where all four species breed.

The Victorian Wader Study Group and the Australasian Wader Study Group have been collecting data on the proportion of juveniles in cannon net catches since 1978 (SE Australia) and 1981 (NW Australia) respectively. Results in recent years have been published in the *Arctic Newsletter* (Minton *et al.* 2000, 2001 and 2002). The longest dataset on recruitment rates relates to Red-necked Stints and Curlew Sandpipers (Minton *et al.* 2002). Similar data on Sanderling *Calidris alba* and Turnstone *Arenaria interpres* was incorporated in a paper on Sanderling biometrics and moult by Gosbell & Minton (2001). These data series have now been extended and are presented here (Table 1) to illustrate the sort of information that can be obtained from a targeted approach to catching aimed at obtaining useable samples annually over a prolonged period.

It is not the purpose of this paper to analyse these data in detail but a few key conclusions may be of interest.

- 1. Apart from Ruddy Turnstone and Curlew Sandpiper, which breed together in the Yakutia region of N Siberia, the four species show only a low, non-significant correlation between their annual recruitment rates each year (Table 2, Fig. 1). Presumably this reflects variation in arctic breeding conditions from place to place.
- 2. The regular three-year cycle observed in Brent Goose reproductive success (Summers 1986), and partially present in some wader species which visit South Africa (Summers & Underhill 1987), is not particularly followed by the four species.
- 3. 1991 was apparently a universally good breeding season, as reported for other arctic breeding species and for other locations around the world (Ganter & Boyd 2000).
- 4. 1992 was a very poor breeding season. Ganter & Boyd (2000) attributed this to poor breeding conditions (high predation and poor weather) in much of the arctic. They associated the adverse weather with huge eruptions of Mount Pintubio and the consequent higher-than-usual cloud cover plus the heat masking effect of unusually high particle levels in the atmosphere. However, the figures in Table 1 suggest that the 1989 breeding season in the Siberian Arctic was even poorer than 1992.
- 5. Three of the past five years have been unusually productive for Red-necked Stints. This tallies well with record high population levels shown by population monitoring counts.
- 6. Curlew Sandpipers had an exceptional three-year run of poor breeding success from 1994 to 1996. Low success





Table 1. Percentage of juveniles in cannon net catches of waders in SE Australia. All catches between 18 November and 20 March are
included (except for Curlew Sandpipers where the end date is 28 February).

Year	Red-necked Stint		Curlew Sandpiper		Ruddy Turnstone		Sanderling	
	Total caught	% Juv	Total caught	% Juv	Total caught	% Juv	Total caught	% Juv
1978–79	871	17						
1979–80	3229	6.4	1922	6.9				
1980-81	2205	5.6	279	10				
1981–82	2542	16	210	9.5				
1982-83	1518	8.0	842	15				
198384	1515	6.5	730	7.4				
1984–85	3640	18	1175	4.7				
1985–86	2280	18	832	8.9				
1986-87	2795	6.8	1333	4.9				
1987–88	4896	21	942	17				
1988–89	5436	13.8	879	32				
1989–90	2314	0.7	889	0.3	109	0		
1990–91	3824	14	963	11	140	11	208	14
1991–92	1994	29	437	45	152	80		
1992–93	4340	3.8	2232	0.3	78	2.6	35	17
1993–94	6015	15	1239	17	14	7.1	161	14
1994–95	3191	19	954	9.6	185	6	49	12
1995–96	1804	25	506	5.9	108	9.3	192	3.1
1996–97	3526	12	636	8.8	197	6.1	404	1.5
1997–98	4232	7.8	934	21	331	40	271	30
1998–99	4854	32	737	4.1	177	6.2	110	10
1999–00	4885	23	1016	20	51	29	462	13
1900–01	5815	13	381	6.8	181	10	243	2.9
1901-02	6351	35	419	27	118	9.3	483	10
1902–03	3357	13	402	15	89	17	459	43
Median		14		9.5		9.3		12.5
Mean		15.2		12.9		16.7		14.25

in 1992 year, only just before this, meant that four years out of five were poor. It is not surprising therefore that there has been a major decline (in some areas to 25% of former levels) in the Australian population.

DISCUSSION

Knowledge of annual recruitment rates can be a key factor in explaining observed population changes and hence in determining if remedial actions to halt or reverse population declines are possible.

Data on Eurasian Oystercatchers *Haematopus ostralegus* on The Wash showed that mortality associated with a severe shortage of shellfish food was the prime cause of a major population decline and that decreased breeding productivity played only a minor role (Atkinson *et al.* in press). However, part of the population decrease was also thought to be due

Table 2. Correlation between the recruitment rates of the speciesmentioned in Table 1.

Species pair	N (years)	R _s S	ignificance
Red-necked Stint & Curlew Sandpiper	24	0.360	ns
Curlew Sandpiper & Ruddy Turnstone	14	0.760	p<0.01
Ruddy Turnstone & Red-necked Stint	14	0.300	ns
Red-necked Stint & Sanderling	12	-0.380	ns
Ruddy Turnstone & Sanderling	12	0.343	ns
Curlew Sandpiper & Sanderling	12	0.311	ns

to young birds moving to better feeding grounds elsewhere. On the other hand, Boyd & Piersma (2001) showed that Red Knot populations wintering in Britain had exhibited marked variations over a 30-year period and that some of these variations appeared to be caused by changes in breeding success,



Fig. 1. Annual percentage of juveniles in Curlew Sandpipers and Ruddy Turnstones caught by cannon net in SE Australia between 1989 and 2003. The datasets are significantly correlated (see Table 2).

measured by data on the proportion of juveniles, rather than changes in survival rates.

Although adult survival has been shown to be a key factor determining population levels in many species (Sandercock, this volume), the data presented here show that breeding productivity can also have an important impact on populations in both Red-necked Stint and Curlew Sandpiper.

While major short- or medium-term changes in population levels may be explicable with relatively short series of proportion of juveniles data, detection of long term changes, such as those associated with climate change, will need data sets obtained over a prolonged period. Long-term data sets become ever more valuable as time passes.

CONCLUSION AND RECOMMENDATIONS

Careful planning of banding operations can provide consistent annual data on the breeding success of wader species. Capture/recapture information obtained at the same time can facilitate estimates of annual survival rates. These key demographic factors are fundamental to interpreting count data.

From both scientific and conservation viewpoints, wader banders are exhorted to carry out their banding operations in a way that provides data on recruitment rates or to initiate new banding programmes designed to generate such data for population monitoring purposes.

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