Measuring wader breeding success in the non-breeding season: the importance of excluding immatures

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Estimating the breeding success of waders in the non-breeding season is subject to error if based on the percentage of juveniles in samples caught because it does not take account of the fact that in many species one-year-old birds do not breed, and therefore do not contribute to breeding success. A method is proposed for adjusting the figures to take this into account. Various alternative ways of expressing breeding success are compared. While these differ, in the dataset examined, they all show the same pattern of variation in breeding success from year to year.

INTRODUCTION

Increased attention is being focused on the use of wader catch data to estimate reproduction rate, one of the two key demographic parameters necessary for understanding population trends (Minton *et al.* 2000, Boyd & Piersma 2001, Minton *et al.* 2000, 2001, 2002a,b, 2003a,b, Atkinson *et al.* 2003, Minton *et al.* 2004a,b,c, Rogers *et al.* 2004a).

For a variety of reasons, the percentage (or proportion) of juveniles in non-breeding wader populations is currently considered the most practical method of measuring recruitment rate, especially for long-term, year-to-year monitoring in a range of migratory species (Minton 2003). Sampling protocols have been developed to minimise potential biases in data collection and methods of data analysis and statistical procedures have been investigated (Clark *et al.* 2004, Rogers *et al.* 2004b). These processes produce an estimate of the rate of recruitment of juveniles into the population.

However, this estimate differs in two ways from 'true breeding success' (the number of young produced, at the time of fledging, per breeding pair). First, as it is measured 4–7 months after the juveniles were fledged, it does not take account of any difference there may be between the survival of adults and juveniles over that time. It would seem very likely that the survival of inexperienced juveniles is lower than that of adults, which may mean that the result is an underestimate of true breeding success. However, adult/juvenile survival over this period has not yet been measured in any arctic-breeding wader so it is not possible to evaluate its impact. Therefore, this possibly important aspect is beyond the scope of this paper, but it is one that needs to be measured and should always be borne in mind as a caveat.

Second, in many species, particularly those spending the northern winter in the Southern Hemisphere, the adults and juveniles become mixed with immatures hatched the previous year which have not bred. These are mostly indistinguishable from adults, but they need to be excluded if the true recruitment rate is to be established. My purpose is therefore to describe a method of calculating the number of surviving juveniles per surviving breeding pair. I will illustrate this using data on Red-necked Stints *Calidris ruficollis* caught in Australia.

METHODS

Where waders are caught systematically each year, the immature component of the adult-plus-immature population can be estimated from age-ratio data collected the previous year. For species in which age of first breeding is two years, the adjustment is relatively straightforward. In species that do not start breeding until the third year or later, or where age of first breeding is spread over a range of years, more complex calculations are necessary.

Here I illustrate a method for estimating recruitment rate using data on Red-necked Stints caught by the Victorian Wader Study Group (VWSG) in SE Australia during the 13 non-breeding seasons from 1991/92 to 2003/04.

I make the following assumptions:

1. *All one-year-old Red-necked Stints remain in Australia and all migrate to breed in the arctic starting in their second year.* VWSG data shows that this is virtually certain because the only birds caught during the breeding season are one-year-olds that are easily aged as such by plumage and moult characteristics.
2. *The survival of adults and juveniles from one non-breeding season to the next is similar and does not vary from year to year.* This is by no means certain. The adults, though more experienced, carry out a long, hazardous round trip to their arctic breeding grounds, whereas the juveniles are more or less sedentary during the year from age 6–18 months. Almost certainly the data exist to show whether adult and juvenile survival rates differ, but this analysis has not yet been carried out. When it has, it will be possible to refine the calculations to take this into account.

The juveniles that remain in the non-breeding area during their first northern summer (i.e. their first potential breeding season) and survive until their second non-breeding season become 'immatures' that are virtually indistinguishable from the adults that have bred (but quite different from the new season's juveniles). However, the ratio of immatures to adults can be estimated by reference to the ratio of juveniles to adults-plus-immatures the previous year. In this way it is possible to estimate the ratio of adults that bred in any year to the juveniles they produced. This can be expressed in a number of ways, including 'surviving young per surviving breeding pair'. This is the same parameter as true breeding success, but with the qualification that there may be differential survival as mentioned above. This is calculated as follows:

The percentage of juveniles in year 1 is $(J_1 / C_1) \times 100$ where C_1 is the total catch and J_1 is the number of juveniles.

In year 2, the number of breeding adults (B_2) in the total catch is:

$(C_2 - J_2)(1 - J_1 / C_1)$

where C_2 is the total catch in year 2 and J_2 is the number of juveniles caught in year 2.

Thus in year 2 the number of juveniles expressed as a percentage of the breeding adult plus juvenile population is:

$(J_2 / (B_2 + J_2)) \times 100$.

Alternatively this can be expressed as the number of juveniles as a percentage of the number of breeding adults $((J_2 / B_2) \times 100)$ or as the ratio of juveniles to breeding adults $(J_2 : B_2)$ or as surviving juveniles per surviving breeding pair $(2 \times J_2 / B_2)$.

RESULTS

During the 13 non-breeding seasons from 1991/92 to 2003/04, the number of Red-necked Stints caught per year by the VWSG varied between 1,994 and 6,351, with an average of 4,142 (Table 1). Breeding success, as measured by the percentage of juveniles in each year's catch, ranged from 3.8 to 34.5%, with a mean of 18.9% and a median of 16.7%.

The number of juveniles expressed as a percentage of the calculated number of adults that had bred plus the juveniles ranged from 5.2 to 37.7%, with a mean of 22.2% and a median of 19.9%. Expressed as a percentage of the breeding adults only, the juveniles ranged from 5.5 to 60.6%, with a mean of 28.6% and a median of 24.9%. This corresponds to 0.11 to 1.21 surviving juveniles per surviving adult breeding pair (mean 0.57, median 0.50).

When the three measures of breeding success for the twelve non-breeding seasons 1992/93 to 2003/04 are plotted together (Fig. 1), it is shown that the effect of excluding the immatures is to increase the magnitude of breeding success. However, in the present dataset, the overall pattern and direction of year-to-year change remains the same whichever measure is used.

DISCUSSION

The effect of excluding the immatures from measures of breeding success fluctuates depending on breeding success the previous year (Fig. 1). In the year following one with high productivity the adult-plus-immature population will contain a higher than usual proportion of immatures that have not contributed to the production of juveniles. Therefore, if the immatures are not excluded, the true breeding performance of the adults will be greatly underestimated. In contrast, in the year after one with poor productivity, there will be a much smaller difference between the adjusted and unadjusted figures. This is evident from Fig. 1, which shows the measures including and excluding immatures systematically diverging and converging subsequent to good and poor breeding seasons respectively.

Detailed examination of the data illustrates the way in which these fluctuations occur. In the 1998/99 non-breeding season, for example, the percentage of juveniles measured in both the traditional way (as a percentage of the total population) and adjusted to exclude the immatures was close (32.4 and 34.2% respectively) (Table 1). This was because the season followed a year of poor productivity. Thus, with only 7.8% juveniles in 1997/98, the effect of excluding the immatures was small. In contrast there was a larger difference between the two figures in 1999/2000 (22.7 and 30.3%).

Table 1. Age parameters of Red-necked Stints caught in SE Australia during the non-breeding season (austral summer) from 1991/92 to 2003/04 by the Victorian Wader Study Group.

Non-breeding season	Total catch (C)	Total juveniles (J)	Total adults (including immatures) (C–J)	Juveniles as percentage of total catch (J/C) × 100	Calculated no. of breeding adults (see text) (B)	Juveniles as a % of the breeding adults plus juvenile population (J/(B+J)) × 100	Juveniles as a % of the breeding adults (J/B) × 100	Breeding productivity: surviving juveniles per surviving breeding pair (J/B) × 2
1991/92	1,994	580	1,414	29.1	–	–	–	–
1992/93	4,340	163	4,177	3.8	2,962	5.2	5.5	0.11
1993/94	6,015	892	5,123	14.8	4,931	15.3	18.1	0.36
1994/95	3,191	594	2,597	18.6	2,212	21.2	26.9	0.54
1995/96	1,804	452	1,352	25.1	1,100	29.1	41.1	0.82
1996/97	3,526	421	3,105	11.9	2,327	15.3	18.1	0.36
1997/98	4,232	331	3,901	7.8	3,435	8.8	9.6	0.19
1998/99	4,854	1,572	3,282	32.4	3,025	34.2	52.0	1.04
1999/00	4,885	1,108	3,777	22.7	2,554	30.3	43.4	0.87
2000/01	5,815	770	5,045	13.2	3,901	16.5	19.7	0.39
2001/02	6,351	2,188	4,163	34.5	3,612	37.7	60.6	1.21
2002/03	3,357	438	2,919	13.0	1,913	18.6	22.9	0.46
2003/04	5,470	1,259	4,211	23.0	3,662	25.6	34.4	0.69
Total	**53,840**	**10,188**	**43,652**		**35,634**			
Mean				**18.9**		**22.2**	**28.6**	**0.57**

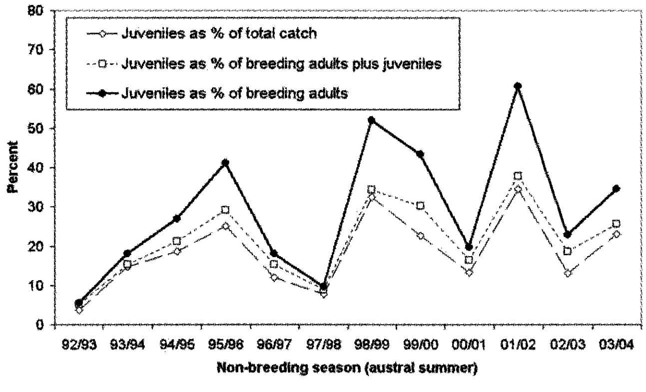

Fig. 1. Three measures of the annual breeding success of Red-necked Stints caught during the non-breeding season (the austral summer) in SE Australia.

This is because of the higher productivity in 1998/99 which fed through to a higher percentage of immatures in the adult-plus-immature population in 1999/2000.

It is encouraging that the various methods of calculating breeding success give annual indexes which follow a broadly similar pattern. This means that for long-term monitoring purposes it may not be critically important which measure is used as long as it is employed consistently. Since juveniles as a proportion or percentage of the total population is the most easily calculated measure and since there is already a substantial volume of data published in this form, it may be best to keep to this for the general ongoing monitoring of productivity. However, when breeding success is being monitored in relation to detailed demographic studies to determine, for example, whether recruitment or survival is driving population trends, or when comparing breeding success across species, the exclusion of immatures is essential.

There is a case for using juveniles as a proportion of breeding adults (or the juvenile:adult ratio) as the standard for year-to-year comparisons of breeding success because it is a truer indication of breeding output. Moreover it accentuates the difference between good and bad years. Thus the difference between the worst and the best breeding years for Red-necked Stints, 1992/93 and 2001/02 respectively, is a factor of 7.25 when juveniles are expressed as a percentage of the breeding adults plus juveniles (5.2 versus 37.7%) but 11.0 when juveniles are expressed as a percentage of breeding adults alone (5.5 versus 60.6%).

The method of measuring breeding success described here is subject to two important caveats: (1) it is not the same as true breeding success monitored on the breeding grounds because of the unknown subsequent mortality of adults and juveniles which is probably juvenile-biased and (2) it assumes that there is no difference between the survival of juveniles and adults from one non-breeding season to the next. Eventually it is hoped that these parameters can be quantified so that estimation of true breeding success will be possible.

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