The role of breeding success and parental care in determining sexual differences in the timing of southward migration of the Curlew Sandpiper *Calidris ferruginea* through Tunisia

J. FIGUEROLA

Department of Applied Biology, Estación Biológica de Doñana, CSIC, Avda. Maria Luisa s/n, E-41013 Sevilla, Spain. jordi@ebd.csic.es

The effects of breeding success on the timing of Curlew Sandpiper *Calidris ferruginea* southward migration through Tunisia were analysed using ringing data collected from 1971 to 1981. In years of low production and high predation pressure on the breeding grounds, female migration occurred on dates similar to male passage. In years with high breeding production, female migration occurred later in comparison with poor breeding years. No such relationships occurred in the timing of male migration. It is concluded that breeding success and patterns of parental care correlate with the timing of female migration, and annual fluctuations in breeding success with differences in the timing of passage of males and females.

INTRODUCTION

In many species of birds, males and females differ in their timing of migration (Terrill & Able 1988). Several hypotheses have been proposed to explain these patterns, based on differences in the onset or rate of migration (Chandler & Mulvihill 1990). One of the reasons for the occurrence of differences in the onset of southward migration could be sexual differences in patterns of parental care (Figuerola & Bertolero 1996). Various models have been proposed to understand the mechanisms and patterns of migration in birds (Alerstam & Lindström 1990, Weber *et al*. 1998). Some of these models assume that the optimal strategy for birds is to initiate migration as soon as free from parental care duties. However, no study has demonstrated this preference for early postbreeding migration. Such evidence could be provided if, for example, failed breeders initiated migration earlier than successful breeders. However, such data are hard to obtain given the difficulty in following individuals during both breeding and migration.

Productivity cycles have been described for several species of waders and geese breeding in the arctic, with large annual fluctuations in breeding success resulting from changes in predator pressure upon bird clutches (Summers & Underhill 1987, Underhill *et al*. 1993). The Curlew Sandpiper *Calidris ferruginea* is one of these species, which additionally shows a female-biased parental care system, in which males leave females to incubate and tend the young, and depart from the breeding grounds 3–4 weeks before females (Portenko 1959). This provides a good background to test the hypothesis that birds initiate migration as early as possible, because female passage through stopover areas should be earlier in seasons when most clutches fail. Also, if patterns of parental care are an important factor determining sexual differences in the timing of autumn passage, these differences should be smaller in years with poor breeding success than in years with good breeding success.

MATERIAL AND METHODS

Curlew Sandpipers breed in Arctic tundra north of 65°N in central Siberia, and migrate to spend the nonbreeding season in Africa, southern Asia and Australasia. In Africa, most birds migrate to West and southern Africa, and only a few hundred birds remain in Tunisia for the nonbreeding season (Wilson *et al*. 1980, Cramp & Simmons 1983). However, Tunisia is an important stopover area during southward migration (Wilson *et al*. 1980).

In 1968–85, regular ringing was done at the Lagune de Tunis at Radès, Tunisia (36°52'N 10°18'E). Variable numbers of walk-in-traps were operated by ringers of the Club de Baguage de Radès (see Spiekman 1992 for a detailed description of trapping methods). Individuals were aged according to plumage characters, although age was not recorded for many birds, mainly in the first years of field work. From 1971 onward, wing and bill length of most individuals were recorded, enabled the sex of each bird to be assigned, using the discriminant formula of Wymenga *et al*. (1990).

This analysis is restricted to the period 1971–81; during this period, sample sizes were large, and wing and bill measurements were recorded for most individuals. No ringing took place in autumn 1975, and the number of sexed individuals, in relation to the number of trapped adults, was small in 1978 (only 2.3%, compared to over 35% in all other years). Excluding these two seasons, nine years of data were available for analysis (Table 1).

Two indices of annual breeding success were used. The first was the proportion of juveniles out of the total number of aged individuals trapped in Tunis in each year. The second was derived from a three-level index of 'inferred predation pressure', based on lemming abundance scores (Schekkerman *et al*. 1998), with estimated predation pressure increasing from score one to three.

One-tailed statistical tests were used because the direction of the expected correlation was clearly derived from the hypotheses being tested.

Table 1. Mean date of capture (days since 1 January) at Rades, Tunisia, of adult males and females trapped, percentage of young trapped in the sample, percentage of adults trapped that were measured (and consequently could be sexed from measurements) and annual index of inferred predation pressure in the breeding grounds (Schekkerman *et al.* 1998). Number of aged individuals presented in brackets.

Year	M	F	% young	% sexed	Predation pressure
1971	254.7	259.5	40.1 (137)	37.8	3
1972	228.3	240.1	32.3 (585)	93.9	2
1973	227.0	239.6	0.0 (123)	55.3	1
1974	224.2	227.0	0.5 (219)	88.5	3
1976	213.0	251.0	30.0 (10)	42.9	1
1977	218.4	229.3	19.3 (332)	53.4	3
1979	211.6	266.3	41.2 (34)	70.0	1
1980	229.5	235.0	6.3 (63)	62.7	3
1981	219.5	218.6	0.0 (18)	77.8	2

Fig. 1. Relationship between mean date of male (open circles and solid line) and female (black circles and dashed line) passage, and relative proportion of young individuals in trapped in the study area.

RESULTS

Breeding success and timing of passage

The proportion of young individuals trapped in Tunisia correlated positively with mean date of female passage (Pearson correlation, $r_8 = 0.84$, $P = 0.002$, Fig. 1), but not with date of male passage ($r_8 = 0.14$, $P = 0.35$). The index of predation pressure was statistically unrelated both to date of female passage (Kendall Rank correlation, $\tau = -0.33$, $n = 9$, $P = 0.13$) and of male passage ($\tau = 0.46$, $n = 9$, $P = 0.94$).

Breeding success and sexual differences in timing of passage

A positive relationship was detected between differences in mean time of male and female passage and the percentage of juveniles trapped in Tunisia ($r_8 = 0.62$, $P = 0.04$). Similarly, differences in timing of passage of the sexes were smaller in the years with higher predation pressure in the tundra ($\tau = -0.59$, $n = 9$, $P = 0.02$).

DISCUSSION

The timing of migration is determined by endogenous mechanisms (Berthold & Terrill 1991, Gwinner 1996), but exogenous factors, such as body condition or temperature, can also affect timing of migration (Alerstam 1990, Dugger 1997). The relationships between differences in male and female passage and breeding success suggest that breeding productivity also affects timing of migration. In addition, females could advance the start of migration when released from parental care duties, supporting the hypothesis that birds attempt to start southward migration as early as possible. Breeding productivity correlated positively with mean date of female passage, but not male passage. Only a weak, non-statistically significant correlation with timing of migration in females was found when using an index of estimated predation pressure. This effect could be less clear because several other factors could affect this variable, such as variability in mean date of breeding, related mostly to spring weather conditions (e.g. Zandt *et al.* 1990). The lack of correlation between male migration and breeding success, suggests that the patterns reported are not due to an early start of breeding in years with reduced breeding success, but are due rather to factors linked to female and not male biology.
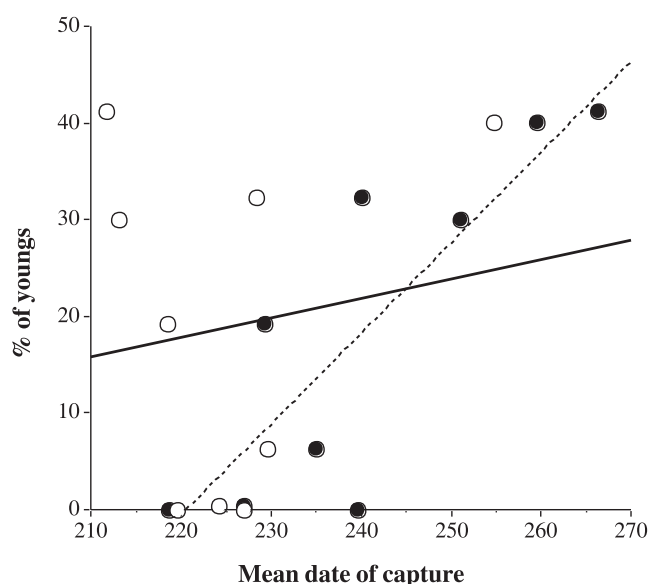
In conclusion, circumstantial evidence suggests that sexual differences in the timing of passage of Curlew Sandpiper are determined by patterns of parental care and are affected by annual fluctuations in breeding success. However, weather could have affected both breeding success and timing of migration, and therefore the patterns reported in this paper need more rigorous investigation and testing.

ACKNOWLEDGEMENTS

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