# ARRIVAL OF PIED AVOCETS *RECURVIROSTRA AVOSETTA* AT THE BREEDING SITE: EFFECTS OF WINTER QUARTERS AND CONSEQUENCES FOR REPRODUCTIVE SUCCESS

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Pied Avocets *Recurvirostra avosetta* breeding in the same colonies on the German Wadden Sea are known to winter in France, the United Kingdom and The Netherlands ('the North') or about 1000 km further south west in Portugal, SW Spain and Morocco ('the South'). Using data of 537 individually colour ringed Avocets, the influence of age, sex and winter quarter on arrival date at three study sites was studied in N Germany, and the relationship between arrival date and breeding success was investigated. Avocets up to an age of four years arrived later than their older conspecifics. The arrival dates of first year Avocets coincided with hatching dates, which were the best opportunities to collect information on the quality of colonies. Avocets wintering in the North arrived significantly earlier at their breeding sites than Avocets wintering in the South. Females arrived later than males. In contrast to females and to males wintering in the North, males wintering in the South had individually consistent arrival dates between years. Arrival dates of males wintering in the North were significantly more strongly related to spring temperatures than arrival dates of males wintering in the South. Early arrival corresponded with a higher breeding success.

Key-words: *Recurvirostra avosetta* – arrival at breeding site – spring migration – winter quarters – timing of migration – reproductive success

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## INTRODUCTION

For many migratory birds the timing of arrival at the breeding grounds is crucial for the breeding success (Myers 1981; Oring & Lank 1982; Møller 1994; Kokko 1999). The trade-off between costs and benefits of arriving early, however, may be very different for birds of different age and sex (Reynolds *et al.* 1986; Cristol 1995). Potential costs of arriving early are often related to weather factors. The climate of north western Europe is characterised by a distinct seasonality but also by a low predictability of weather conditions in late winter and early spring when most migrants arrive. Some species can directly adjust the timing of their migration to weather conditions (Richardson 1978), others control their migration through endogenous factors and predictably changing factors like day length (Gwinner 1986). Long distance migrants are supposed to fall typically in the latter group whilst short distance migrants are more expected to belong to the first group. Within a species, the influence of the winter quarter on arrival dates has received little attention yet, and there is also little evidence for the individual consistency from year to year in migration patterns (Rees 1989; Potti 1998).

The winter quarters of Pied Avocets *Recurvi-*

*rostra avosetta* cover a huge range of latitudes (Glutz von Blotzheim *et al.* 1977; Cramp & Simmons 1983). Individuals breeding in the same colony and even partners of the same pair are known to winter in different countries (Hötker 1998a). Pienkowski & Evans (1984) hypothesised that migrants tend to winter as close as possible to their breeding grounds in order enhance their reproductive success. An early arrival at the breeding site would be one of the benefits gained by wintering close to the breeding site. In order to test the hypothesis of Pienkowski & Evans, arrival patterns of individually colour-ringed Avocets breeding in Northern Germany were studied. The wintering sites of some of these Avocets were known to be either in western Europe, mainly in France but also United Kingdom and The Netherlands, or on the south western part of the Iberian peninsula in Portugal and Spain (one in Morocco). The distance to the breeding sites were about 1.000 km and 2.000 km respectively. There are indications, that most Avocets travel from their European winter quarters to their breeding sites without long stop-overs or even without any stop-overs. First, there are no sightings of colour ringed Avocets on a stop-over areas. Second, countings on potential stop-over sites gave no evidence for resting Avocets on spring passage (Yésou 1992; Mennebäck & Zang 1995; R. Mahéo; pers. comm.). The following questions were tried to be answered: When do Pied Avocets arrive at the breeding sites? How does age and sex influence the arrival dates? Is there a relationship between winter quarter and arrival date? Are arrival dates individually consistent between years? Does the arrival date influence breeding success?

## STUDY SITES AND METHODS

The study was carried out in three breeding sites of Pied Avocets on the Wadden Sea coast of Schleswig-Holstein in Northern Germany (Fig. 1) between 1989 and 1999. Beltringharder Koog (54°22'N, 8°57'E), Ockholmer Westerkoog (54°39'N, 8°51'E), and Fahretofter Westerkoog (54°42'N, 8°48'E) are all polders which have been embanked between 1985 and 1988. Pied Avocets mostly bred on islands within the polders but gathered on intertidal mudflats outside the embankments for foraging. The study is based on 1477 Pied Avocets that had been individually marked with combinations of colour-rings mostly within the study sites during 1988-99. Of these, 345 had been marked as adults and 1132 as chicks. All study sites and the adjacent mudflats were checked for colour ringed Pied Avocets about every five days between the beginning of March and the End of April of each year between 1989 and 2000. Observations were made with telescopes, usually from the dike or from roads. From May to July less frequent controls took place. Pied Avocets were checked in their winter quarters in France and on the Iberian Peninsula in the winters of 1990/91, 1991/92, 1992/93, 1995/96, 1996/97, 1997/98, and 1998/99 (for details see Hötker 1998a). In addition many sightings of colour ringed Pied Avocets by the public could be included in this study. Wintering sites of Pied Avocets in Portugal, Spain or Morocco were named 'south' and sites in France, the United Kingdom and The Netherlands were named 'north'.

The date of first sighting of an individually colour marked Avocet was taken as its date of arrival. The true date of arrival usually was earlier than this date because study sites were not checked every day and not all colour marked Pied Avocets could be identified during each visit to the study sites. There are, however, reasons to believe that most Pied Avocets sighted in the study sites for the first time in a year before the onset of breeding (end of April, beginning of May) had not yet visited other breeding sites before in the same season. The evidence for this comes from two observations. First, there were no peaks in numbers of Pied Avocets resting at other potential breeding sites in the pre-breeding season (Mennebäck & Zang 1995, pers. observ.), and second, extensive studies of arriving Pied Avocets in Schleswig-Holstein in 2001 revealed, that most individuals did not visit more than one site before

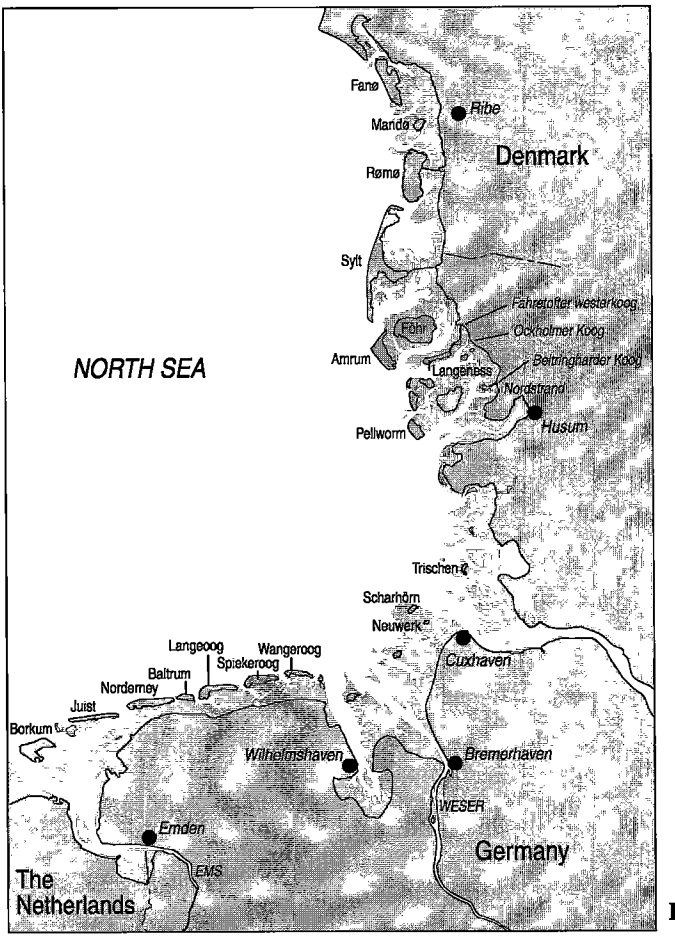


**Fig. 1.** Position of the study sites.

settling down for the first time (Neuhalfen and Weber, pers. comm.). Thus, the first sighting of a colour ringed Avocet in the study site seems to be a good indication for its arrival date from spring migration. Pied Avocets arriving from early May onwards, may however have attempted breeding elsewhere.

Breeding success could be estimated for individually colour-ringed Pied Avocets. A colour-ringed Avocet was considered to be successful in a given year if it was observed to attend chicks over an estimated age of ten days. Although mortality of chicks can occur after the first ten days of life, most mortality occurs before chicks are ten days old (own unpubl. data). Breeding success was probably underestimated because many chicks escaped our attention and some families left the study site. Weather data for the study sites were obtained from the weather station of Deutscher Wetterdienst on the Island of Föhr. In addition data from weather stations near the most important wintering sites (Portugal: Lisbon airport; France: La Rochelle) were used. In the study sites the springs of most study years were mild with the exception of 1996. The spring of 1996 was extremely cold and parts of the intertidal mudflats next to the breeding colonies were ice-covered until the end of March. Statistical analyses were performed SPSS 7.5 for Windows. For many individuals arrival could be recorded for more than

one year. Repeatabilities were calculated according to Lessells & Boag (1987). If not stated otherwise one case per individual was selected by using random numbers (Microsoft Excel).

## RESULTS

Altogether, 1289 arrival dates for 537 individual Pied Avocets could be recorded. Arrival occurred from the beginning of March until the beginning of July (Fig. 2). Arrival dates were strongly related to age. First year birds ($P < 0.001$), second year birds ($P < 0.001$), third year birds ($P = 0.001$) and fourth year birds ($P = 0.014$; Mann-Whitney-U-Tests) arrived significantly later than older birds (age 5 or older and birds ringed as adults). The age-dependency of arrival could be seen in many individual histories (Fig. 3). Because of the age-dependency of arrival dates, birds younger than five years were omitted from all following analyses. In order to avoid confusion with second breeding attempts, only arrival times before 1 May were used in the following section. The distribution of arrival times (before 1 May) did not differ significantly from a normal distribution (Kolmogorov-Smirnov-Test; $Z = 0.806$; $P = 0.53$).

Arrival dates depended on sex. The mean (± SE) arrival date of males was day 99.6 ± 1.8 of the year (10 April; $n = 152$), and females arrived significantly later ($P = 0.009$; $z = 6.921$; Mann-Whitney-U-Test), on day 107.1 ± 1.8 (17 April; $n = 117$). As male Pied Avocets are bigger than females (Glutz von Blotzheim *et al.* 1977) and males tended to winter closer to their breeding sites than females (Hötker 1998a), the sex difference in arrival times might have been confused by effects of winter quarter and/or body size. In total 84 data sets of adult Pied Avocets were analysed which included arrival time, winter quarter (of the winter preceding the recording of arrival) and wing length (as a measurement of body size). Data for all years were pooled because there was no significant effect of year (ANOVA; $F_{6,77} = 1.661$; $P = 0.14$). An ANCOVA (factors sex and winter quarter, covariate wing) revealed a significant effect of winter quarter ($F_1 = 9.661$; $P = 0.003$) and of the interaction of sex and winter quarter ($F_1 = 4.058$; $P = 0.047$). Sex itself ($F_1 = 1.791$; $P = 0.19$) and wing length had no significant effect ($F_1 = 0.493$; $P = 0.49$). In all years except 1996, a year with a very cold and late spring, males which had been

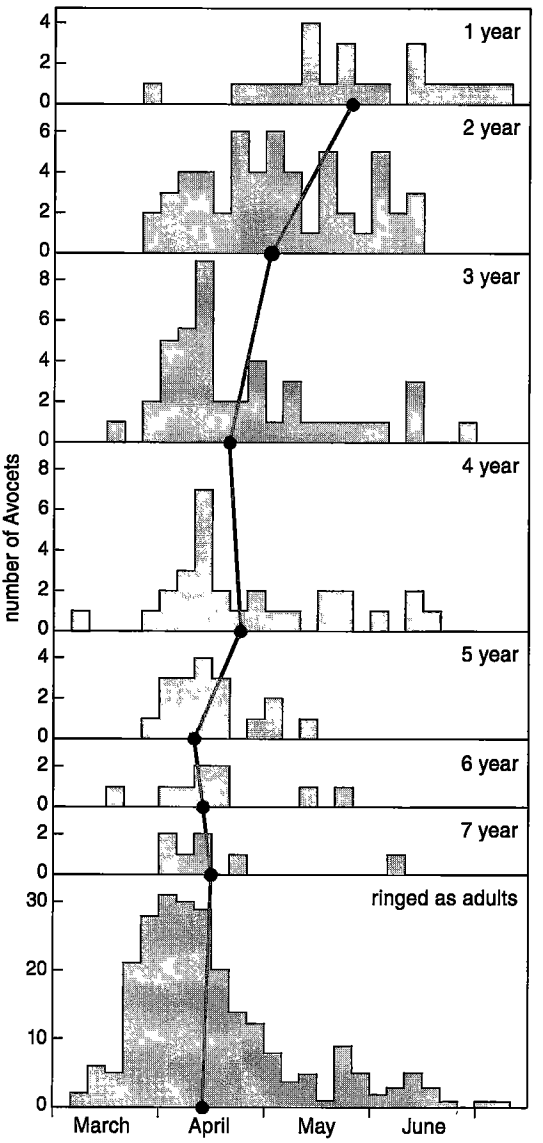


**Fig. 2.** Arrival dates of Pied Avocets of different age in the study sites. The dots mark the arithmetic means. All data pooled.

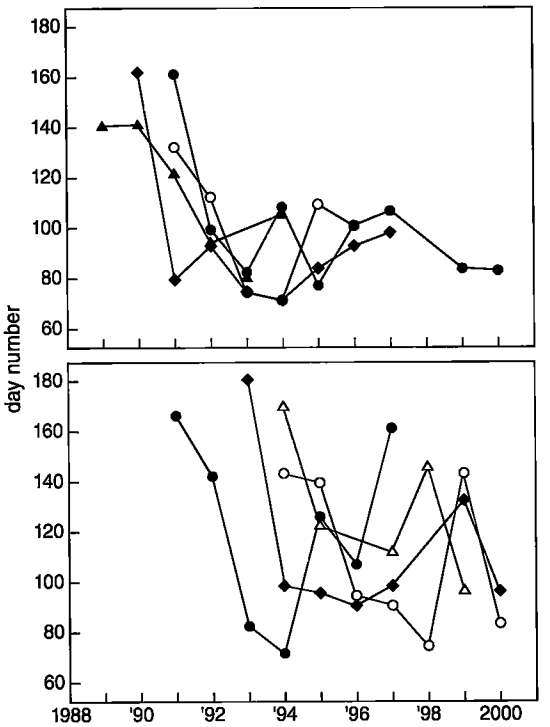


**Fig. 3.** Individual histories of arrival dates of the eight best documented individual Pied Avocets of the study. Each individual is represented by different symbols connected by lines. Each line starts with the first year of life.

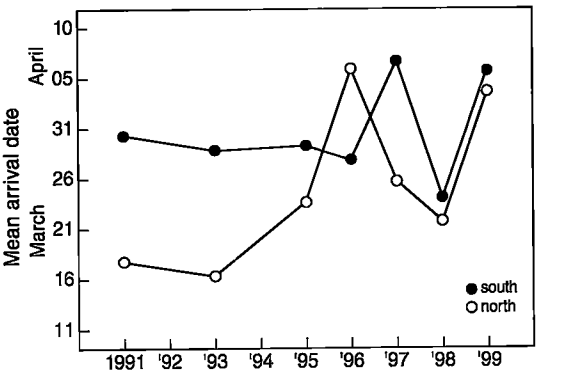


**Fig. 4.** Annual mean arrival dates of males wintering in the North (open dots) and in the South (solid dots). All data from all individuals pooled. Years with insufficient data were omitted.

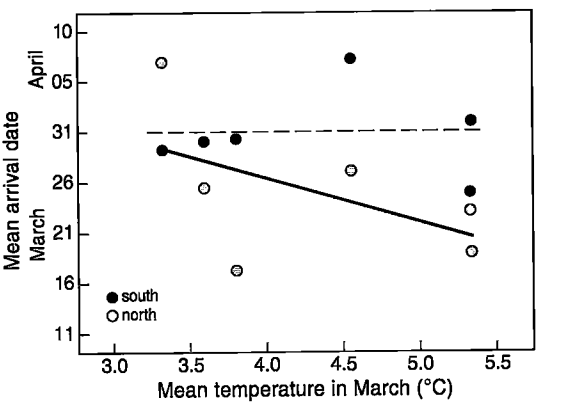


**Fig. 5.** Relationship between mean temperature in March in the study site and mean arrival dates of males wintering in the North (open grey dots) and in the South (solid dots). All data from all individuals pooled. The lines show the linear regressions for males wintering in the North (solid line) and for males wintering in the South (hatched line).

sighted in northern winter quarters the winter before arrived earlier at their breeding sites than males that had been sighted in southern winter quarters the winter before (Fig. 4).

Males wintering in the south had individually constant arrival dates, i.e. the variance in arrival dates within individuals between years was significantly smaller than the variance between individuals (ANOVA; $F_{30,60} = 1.831$; $P = 0.023$, repeatability 0.29, SE = 0.11). This was neither the case for males wintering in the North (ANOVA; $F_{27,58} = 0.635$; $P = 0.90$, repeatability 0.09, SE = 0.11) nor for females wintering in the South (ANOVA; $F_{26,53} = 1.118$; $P = 0.36$, repeatability 0.05, SE = 0.11) or in the North (ANOVA; $F_{14,20} = 1.094$; $P = 0.42$, repeatability –0.08, SE = 0.18). Annual mean arrival dates of males wintering in the North showed some (however statistically non significant) relationship to temperature on the breeding ground. In contrast, annual mean arrival dates of males wintering in the South were not correlated with temperature on the breeding grounds (Fig. 5). The regression coefficients for the temperature relationships of northern and

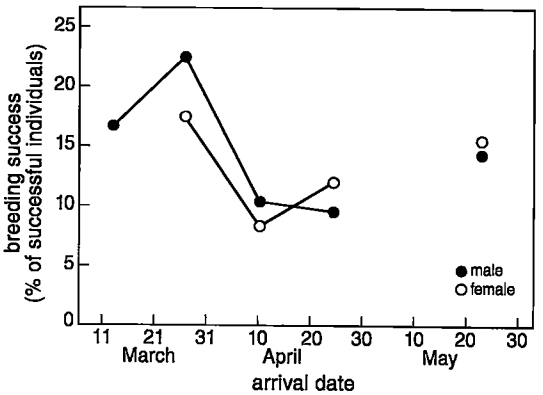


**Fig. 6.** Relationship between arrival dates of male (solid dots) and female (open dots) Pied Avocets and reproductive success in the same year.

southern males differed significantly ($t = 5.117$; $P < 0.001$). There was a clear relationship between arrival date and breeding success in the same year (Fig. 6). In Pied Avocets arriving before May, breeding success was significantly affected by time of arrival (Logistic regression; Arrival: Wald statistic = 4.520, $P = 0.033$).

## DISCUSSION

Which factors determined the arrival dates of Pied Avocets? Many Pied Avocets arrived long before the onset of laying (end of April, beginning of May), and early arriving had a strong positive effect on breeding success. Why arriving early was so beneficial for successful breeding has not yet been studied sufficiently. Pied Avocets were not territorial before actually choosing a nesting site, and choosing a nesting site took place a few days before the onset of laying. Early arrival thus was not related to the acquisition of a high quality territory. There were also neither clear relationships between arrival date and social status (Greve pers. comm.) nor between arrival date and the number of nesting sites inspected before the start of laying (Neuhalfen, Weber pers. comm.). Pied Avocets arriving early faced certain risks, which were associated with predators and adverse weather (Fig. 7). Wintering Peregrine Falcons *Falco peregrinus* were the only predators of Pied Avocets that were commonly present in the breeding sites. Peregrines left late in April and there was no indication that their presence had an influence on arrival time of Pied Avocets. The earliest Pied Avocets arrived at a time when their maintenance metabolism reached its annual maximum. If they arrived earlier, their energy expenditures would not have been higher but probably even slightly lower (Hötker 1998b). Energy expenditure alone therefore did not seem to be a factor actually limiting the date of arrival. Pied Avocets, however, did not arrive before ice days (days with maximum temperature below 0°C) were gone. On

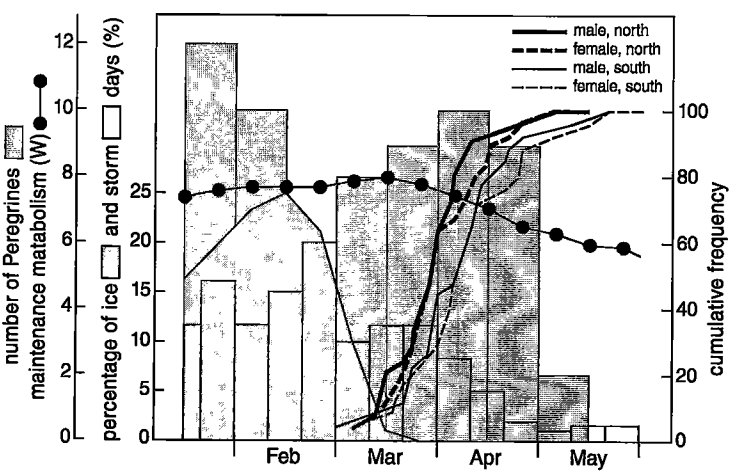


**Fig. 7.** Arrival of adult male and female Pied Avocets from different winter quarters (cumulative frequencies) compared to the bimonthly means of Peregrine numbers (grey columns) in the Beltringharder Koog (Bruns & Hötker 1997), frequency of ice days (daily maximum temperature below 0°C, shaded polygon), frequency of storm days (daily mean wind speed above 12 m $s^{-1}$, open bars) and maintenance metabolism of adult avocets (from Hötker 1998b, dots).

ice days the upper parts of the mudflats, which are often visited by foraging Pied Avocets, usually start to freeze. Even if ice covers only part of the mudflats it severely reduces the availability of food. There is also relatively little overlap in the occurrence of Pied Avocets and the probability of storms. Storms also reduce the feeding activity of Pied Avocets (Hötker 1999). Ice days and storms can thus be regarded as an indication of food availability. Food availability, therefore, seems to be the factor setting some limit to the earliness of the arrival on the breeding grounds.

Pied Avocets breeding on the Wadden Sea coast of Schleswig-Holstein usually started breeding when two to five years old (own data). Many first year Pied Avocets spend their first summer close to the wintering sites (Edelstam 1971; Salvig 1995). Few first year Pied Avocets were seen in the study site, and they arrived much later than the majority of older birds. One possible reason for the late arrival dates of young birds could be the fact that first year birds did not visit the breeding sites for breeding but for prospecting and for collecting information on the quality of breeding sites (Danchin *et al.* 1991). This may also have been the case for some Pied Avocets in their second, third year or even forth year. If Pied Avocets want to investigate the quality of a breeding site they should observe the breeding success on that site. Gaining information on breeding success, however, is difficult because places where Pied Avocets raise their chicks may be several kilometres apart from nesting colonies. Observing chick-rearing territories does not reveal reliable information on the quality of nesting colony sites because it is not clear from which nesting colony the chicks came. The first choice first breeders have to make, however, is a choice on nesting site, and nesting sites greatly differ in quality (Hötker & Segebade 2000). The only way to combine the information on both colony site and on chick raising grounds is to be present at hatching, when some pairs are still breeding and others are already guiding their chicks to the feeding grounds. The timing of arrival of first year Pied Avocets coincides rather well with the seasonal pattern of

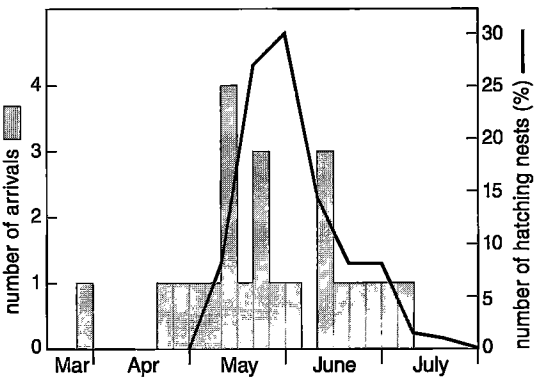


**Fig. 8.** Arrival dates of first year Pied Avocets (columns) and hatching dates in the study sites (polygon).

hatching dates in the study site (Fig. 8). Arrival seems to take place when the best information on the quality of breeding sites is available (Boulinier *et al.* 1996).

Age explains some but not all of the huge variance in arrival dates. Even in older Pied Avocets arrival dates were not at all synchronised. According to the models of Kokko (1999) a high synchronisation of arrival dates is expected if there are gaps in the quality distribution of resources, e.g. late arriving birds have no chance to reproduce because they are excluded from access to some vital resources. This was obviously not the case in this study. The chances of reproductive success diminished rather smoothly with time and even very late arrivals had at least some chance to breed successfully. The relationship between winter quarter and arrival time supports the hypothesis of Pienkowski & Evans (1984). Pied Avocets wintering closer to the breeding sites arrived earlier, and early arrival enhanced breeding success. It has been shown earlier (Hötker 1998a) that Pied Avocets wintering in the North had a significantly higher breeding success than their conspecifics wintering in the South. The question why not all Pied Avocets then winter in the North is not yet answered, differences in survival rates between the North and the South obviously do not exist (Ganter, pers. comm. and own data).

The results of this study indicate that male

Pied Avocets use two different mechanisms for controlling their arrival time. The males wintering in the North seemed to be able to react to the weather conditions in the breeding sites and those wintering in the South had fixed individual arrival times and did not show much reaction to the weather in the breeding site. How could Pied Avocets wintering 1000 km away react to the weather in the study site? Mean daily temperatures in March were used from Lisbon, La Rochelle and the study sites. There was no relationship between the March temperatures 1990-1996 in Lisbon and the study site, nor for the data pooled from all years ($r$ = - 0.02; $P$ = 0.79) neither in the single years. Temperatures in La Rochelle and the study sites had a somewhat stronger but still non-significant correlation ($r$ = 0.08; $P$ = 0.25). In the extremely cold March of 1996, however, temperatures in La Rochelle were significantly correlated with those of the study site ($r$ = 0.40; $P$ = 0.024). The west coast of France and the Wadden Sea coast of Schleswig-Holstein often share the same weather systems, whereas weather systems in Portugal and northern Germany are often independent (Häckel 1993). It therefore seems likely that Pied Avocets wintering in France could adjust their departure to the weather in the breeding sites by observing the weather in their wintering grounds. Pied Avocets wintering in Iberia did not have this option.

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## SAMENVATTING.

De aankomstdatum van trekvogels in het broedgebied kan enorm binnen een soort variëren: sommige vogels komen vroeg in het voorjaar aan, andere pas laat. Wat bepaalt nu de aankomstdatum van een individu in het broedgebied? Om dit te begrijpen zijn Kluten *Recurvirostra avosetta* in Noord-Duitsland van kleurringen voorzien, waarna ieder jaar is gekeken wanneer ieder individu in het broedgebied aankwam. Noord-Duitse Kluten overwinteren langs de kusten van Zuid- en West-Europa. Van veel geringde vogels is uit aflezingen in het winterkwartier bekend of ze zuidelijk (Marokko, Spanje, Portugal) of noordelijk (Frankrijk, Verenigd Koninkrijk, Nederland) overwinteren. De Kluten bleken de eerste vier levensjaren later op de broedplaatsen terug te keren dan oudere vogels, maar in de loop van die vier jaar kwamen ze wel steeds iets eerder aan. Jonge vogels kwamen het eerste jaar pas in het broedgebied aan rond het moment dat de nieuwe generatie uit de eieren kwam. Op deze manier zouden de eerstejaars vogels een idee kunnen krijgen van de kwaliteit van de verschillende broedkolonies en daarop dan de keuze van hun toekomstige broedkolonie kunnen baseren. Vogels die noordelijk overwinterden, kwamen eerder in het broedgebied aan dan individuen die zuidelijk overwinterden, terwijl mannetjes eerder arriveerden dan vrouwtjes. Voor mannetjes gold dat zuidelijk overwinterende vogels een veel constantere aankomstdatum hadden dan noordelijk overwinterende vogels. Dit is terug te voeren op het feit dat de aankomstdatum van noordelijk overwinterende mannetjes een relatie heeft met de temperatuur in het broedgebied. Mannetjes die dicht bij de broedgebieden overwinteren, kunnen namelijk een betere inschatting maken van de omstandigheden die dan in de broedgebieden heersen. Op deze manier kunnen ze in warme jaren vroeger aankomen en in koude jaren wat langer wachten voordat ze naar de broedgebieden terugkeren. Vogels die zuidelijk overwinteren, vliegen waarschijnlijk in één vlucht naar hun broedgebieden terug. In deze winterkwartieren is het slecht te voorspellen wanneer het in Duitsland voorjaar wordt. De noordelijk overwinterende vogels zijn waarschijnlijk in het voordeel, omdat ze hun terugkeer kunnen afstemmen met de situatie in het broedgebied en vroeg terugkerende vogels een hoger broedsucces hebben. Dit gaat dan echter wellicht ten koste van een wat lagere overleving tijdens koude winters in Noordwest-Europa. (CB)