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Bar-tailed Godwits (*Limosa lapponica*) in the Sylt-Rømø Wadden Sea: which birds, when, from where, and where to?

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In the Sylt-Rømø Wadden Sea, a tidal catchment area in the northern Wadden Sea, Bar-tailed Godwits of two different populations stop over on migration between wintering and breeding areas. The Afro-Siberian population, which winters in West Africa and breeds in Siberia, uses roosts on the mainland coast only for one month each in spring and summer, whereas the European population, with wintering areas in Western Europe and breeding grounds in Fennoscandia, occurs mainly for three months in spring on the islands. Some birds also stay from autumn until late January. The European population was studied in detail in the Königshafen area at the northern end of the island of Sylt. Morphometric as well as ringing data confirmed that birds belonged to the European population with 13 out of 15 ringing recoveries in or from Great Britain. During the spring stopover, birds moulted from winter to breeding plumage in 43 days. On autumn migration, Bar-tailed Godwits arrived already with ¼ winter plumage. Moult back into complete winter plumage took 28 days. Sex ratio was 1:1 throughout the year apart from i) the second half of May, when males left before females and ii) winter, when more males than females left the study area to overwinter in milder regions like the Dutch Wadden Sea or Great Britain. However, birds identified by colour rings in winter did not differ in size from all other birds colour ringed and not wintering in the Königshafen area. In spring, most colour marked birds arrived before the 24th of March and left after 30 – 40 days on the 3rd or 4th of May. A higher turnover of birds was observed in May as compared to March and April when Bar-tailed Godwits from other areas seem to concentrate in the northern Wadden Sea before final departure to the Fennoscandian breeding grounds. In autumn most marked birds arrived before 14th August. However, some birds arrived in early September, when a high turnover of birds occurred, since a proportion of the early arriving birds left for other wintering areas. On spring migration Bar-tailed Godwits seemed to be highly site-faithful whereas in autumn less than 25 % of the birds ringed in spring were resighted. Assuming 100 % site faithfulness in spring, maximum mortality rates ranged between 17.4 and 26 % for adults which is far below previously published figures.

Key words: biometrics, Bar-tailed Godwit, *Limosa lapponica*, migration, mortality, moult, return rates, seasonal occurrence, turnover rates, Wadden Sea

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1. Introduction

The seasonal occurrence of large numbers of birds in the Wadden Sea and their migration between southern wintering and northern breeding sites fascinates natural scientists for more than a century (e.g. DROSTE-HÜLSHOFF 1869, HOMEYER 1880). Some 10 – 12 million waterbirds use the Wadden Sea during their annual cycle. For 41 species of waterbirds, the area is an internationally important stopover or wintering site (MELTOFTE et al. 1994). The Bar-tailed Godwit (*Limosa lapponica*), a long-distance migrant, on an annual average contributes 4 – 5 % in numbers to this waterbird community (SMIT 1980, SCHEIFFARTH & NEHLS 1997). Two different populations (classified as subspecies by ENGELMOER & ROSELAAR 1998) of the species occur in the Wadden Sea. The European population breeds in Fennoscandia and winters around the North Sea, mainly in the western part of the Wadden Sea and Great Britain (SMIT & PIERSMA 1989, DRENT & PIERSMA 1990, ENGELMOER & ROSELAAR 1998). The Afro-Siberian population has breeding areas on Taymyr and Yamal and wintering sites in West Africa, mainly the Banc d'Arguin, Mauritania and Guinea-Bissau (SMIT & PIERSMA 1989, DRENT & PIERSMA 1990, WYMENGA et al. 1990, ENGELMOER & ROSELAAR 1998).

As a basis for the understanding of the stopover ecology of Bar-tailed Godwits, parameters describing the birds present in a study area have to be known. In particular a classification with different populations is important since different constraints act on the different populations, resulting in distinct behavioural patterns (SCHEIFFARTH et al. 1993, SCHEIFFARTH & BAIRLEIN 1998). This paper summarizes basic population parameters, as the seasonal occurrence, morphology, moult into breeding and back into winter plumage, turnover and return rates for Bar-tailed Godwits using the Sylt-Rømø Wadden Sea as a stopover and wintering area in the northern Wadden Sea, where both populations occur.

2. Material and methods

2.1. Study area

This study was carried out in the Sylt-Rømø Wadden Sea, a tidal basin in the northern part of the Wadden Sea in the German-Danish borderland with an area of 411 km^2 (Fig. 1). The islands of Sylt and Rømø, which protect the area from the North Sea, are both connected to the main land by causeways. Detailed studies were carried out in the Königshafen, a shallow tidal bay at the northern end of Sylt with a total area of ca. 6 km^2. For a detailed description of the area, see GÄTJE & REISE (1998).

2.2. Bird counts

Birds were counted during high-tide at each spring-tide (approx. every 15 days) from dikes, dams or dunes between 1989 and 1995 (for a description of the spring-tide counts, see RÖSNER & PROKOSCH 1992). Additional counts were conducted during the migration periods in the subareas Königshafen and Nielönn (s. Fig. 1 for location of the subareas). During some periods, birds in the Königshafen were counted daily. Phenologies are presented on a monthly or fortnightly basis. For each time interval, first the mean number of birds per year was calculated and in a second step for each time interval the mean across all years. This method of calculation accounts for the variation between years and eliminates the variation within years for each time interval.

2.3. Moult of body feathers

To follow the progress of body moult in spring and autumn, males in foraging flocks were scanned with telescopes. Extension of breeding plumage was recorded on a 7 point scale (PIENKOWSKI 1980, see also PROKOSCH 1988, PIERSMA & JUKEMA 1993) for each male in the flock (1: winter plumage, 2: traces of breeding plumage, 3: ¼ breeding plumage, 4: ½ breeding plumage, 5: ¾ breeding plumage, 6: traces of winter plumage, 7: complete breeding plumage). On average, flocks consisted of 72 males (range: 12 – 258 males). For each sample a mean plumage score was calculated.

2.4. Catching, measuring, marking, and resighting of birds

Between 1991 and 1993 a total of 129 adult and 18 juvenile Bar-tailed Godwits were caught by cannon nets (IRELAND et al. 1991, see also PROKOSCH 1988) at the water line in the Königshafen area. Birds were aged and sexed according to PRATER et al. (1977). Wing length was measured to the nearest mm as described in ENGELMOER & ROSELAAR (1998). Tarsus+toe was also measured to the nearest mm, excluding the claw from total length (PRATER et al. 1977, in contrast to ENGELMOER & ROSELAAR 1998). Bill length (culmen, from bill tip to feathering) was measured to the nearest 0.1 mm with a vernier calliper according to PROKOSCH (1988) and ENGELMOER & ROSELAAR (1998). Body mass was recorded to the nearest gram with an electronic balance.

Besides metal rings, 120 adult birds got individual colour ring combinations for subsequent identification in the field. Additionally, 88 adult birds were marked with a yellow dye (picric acid) in March 1992 to enhance the chance of resighting as well as the determination of the number of marked birds in a flock. Mainly during the migratory periods in spring (March – April) and autumn (August – October), flocks of foraging Bar-tailed Godwits or birds moving from or to the high-tide roost were controlled for marked individuals.

Since Bar-tailed Godwits show a strong sexual dimorphism (Fig. 5, PROKOSCH 1988, ENGELMOER & ROSELAAR 1998), the sexes can easily be distinguished in the field. To determine the sex-ratio of the local population, flocks of foraging Bar-tailed Godwits were scanned with a telescope and the sex of each individual was determined on the basis of the relationship between estimated bill length and body size (cf. ZWARTS et al. 1990). Mean size of observed flocks was 241 birds (range: 46 – 530 birds).

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3. Results

3.1. Phenology and distribution of Bar-tailed Godwits in the Sylt-Rømø Wadden Sea

Bar-tailed Godwits used eight areas in the Sylt-Rømø Wadden Sea as main high-tide roosts (Fig. 1). Two types of roost sites can be distinguished on the basis of the phenologies (Fig. 2): i) sites along the mainland coast, which are only used during migratory stopover in May and August to October ('Ballum saltmarsh', 'Margrethe/Rickelsbüller Koog', 'Rømø-dam'). According to the phenolo-

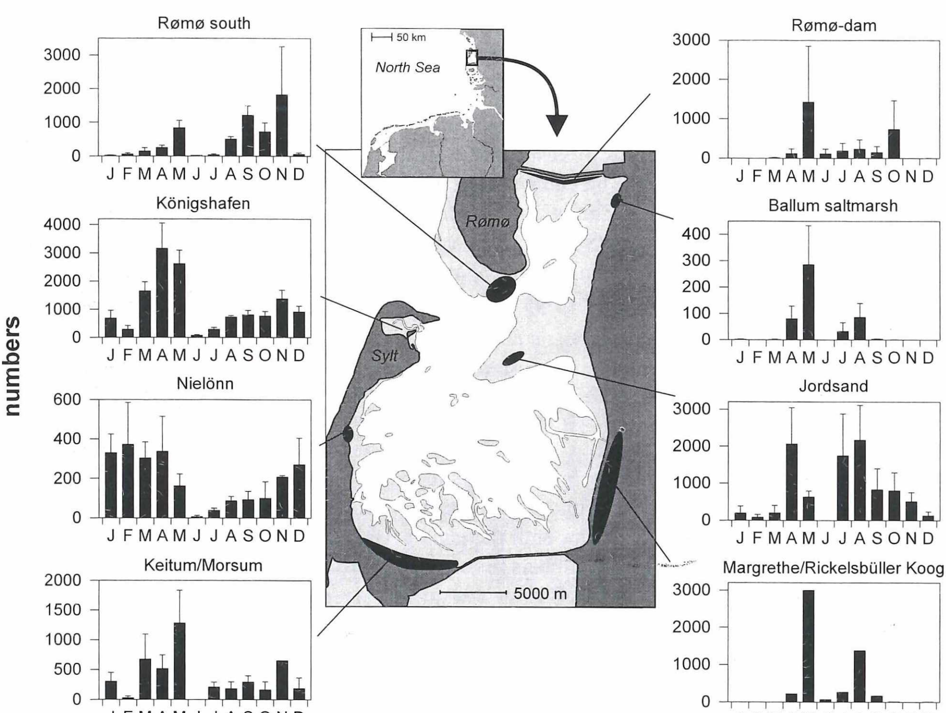

Fig. 1: Seasonal occurrence of Bar-tailed Godwits at different high-tide roosts in the Sylt-Rømø Wadden Sea. Monthly means + SE from 2 – 5 years.

Abb. 1: Phänologie der Pfuhlschnepfen an verschiedenen Hochwasserrastplätzen im Sylt-Rømø Wattenmeer. Dargestellt sind monatliche Mittelwerte + SE aus 2 – 5 Jahren.

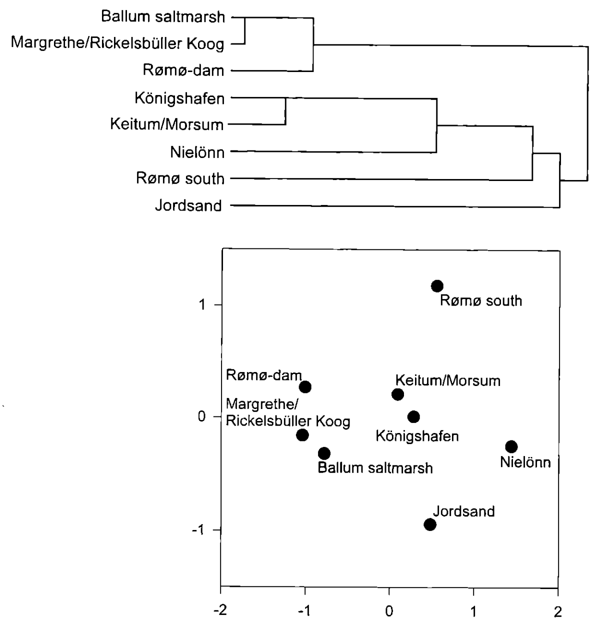

Fig. 2:
Cluster analysis and Multiple Dimensional Scaling (MDS) plot to demonstrate similarities between the phenologies at different high-tide roosts in the Sylt-Rømø Wadden Sea. Similarities were calculated with the cosine measure (BACKHAUS et al. 1990). Stress of MDS plot: 0.061; $r^2 = 0.976$.

Abb. 2:
Cluster Analyse und Multiple Dimensionale Skalierung (MDS), um Ähnlichkeiten zwischen den Phänologien an verschiedenen Hochwasserrastplätzen im Sylt-Rømø Wattenmeer aufzuzeigen. Die Ähnlichkeiten wurden mit dem Cosinusmaß berechnet (BACKHAUS et al. 1990). Stress der MDS Abbildung: 0,061; $r^2 = 0,976$.

gies, Bar-tailed Godwits occurring at these sites are supposed to belong to the Afro-Siberian population (PROKOSCH 1988, PIERSMA & JUKEMA 1990). ii) sites on the islands, which are attended during the entire year apart from the breeding season in summer. On Sylt in particular, highest numbers occurred during the spring migration, which lasts for three months from March to May in contrast to the mainland. The sites on Sylt show the typical phenology for the European population (PROKOSCH 1988). Within this second group of roosts representing the islands, 'Jordsand' and 'Rømø south' each form a distinct subgroup with phenologies showing a mixture of the patterns on the mainland and on Sylt.

3.2. Phenology, moult, sex ratio and morphology of Bar-tailed Godwits in the Königshafen

In August, after the breeding season, bird numbers in the Königshafen increased only moderately and stayed on a constant level from mid-September until mid-January (Fig. 3). In mid-February, birds returned with increasing numbers until the end of April/early May. Bird numbers decreased rapidly during May, resulting in low numbers in June. Owing to this phenology, Bar-tailed Godwits in the Königshafen were studied in detail being considered as representative of the European population.

Male Bar-tailed Godwits in the Königshafen moulted from winter plumage to breeding plumage during their stopover in spring (Fig. 3). The first bird with traces of breeding plumage appeared on 7th March and the first male with a complete breeding plumage was observed on 12th April. On 27th March 50 % of the males showed traces of breeding plumage whilst by 8th May 50 % of the males present were in complete breeding plumage. Taking the two 50 % dates as the average start and endpoint of moult for the population, this results in an average moult duration of 43 days in spring.

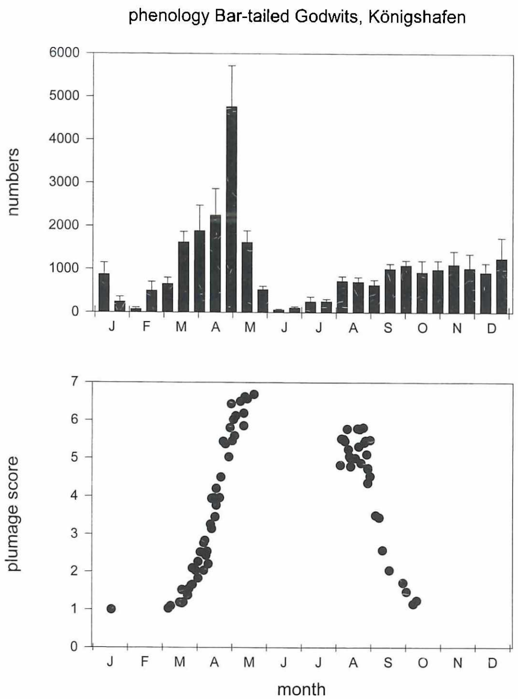

Fig. 3:
Upper graph: Phenology of Bar-tailed Godwits in the Königshafen 1990 – 1995 as fortnight means (+ SE). Lower graph: Progress of moult into breeding resp. winter plumage of male Bar-tailed Godwits in the Königshafen area. Plotted are mean plumage score of flocks of birds scanned with a telescope (mean number of males in flocks: 72). Extent of breeding plumage was recorded on a 7 point scale from 1: winter plumage to 7: complete breeding plumage (PIENKOWSKI 1980).

Abb. 3:
Obere Abbildung: Phänologie der Pfuhlschnepfe im Königshafen in den Jahren 1990 – 1995 als 14-tägige Mittelwerte (+ SE). Untere Abbildung: Entwicklung des Gefieders ins Brut- bzw. Winterkleid von männlichen Pfuhlschnepfen im Königshafen. Dargestellt sind mittlere Gefiederklassen von Trupps, die durch ein Spektiv beobachtet wurden (mittlere Anzahl Männchen in Trupps: 72). Die Ausprägung des Brutkleides wurde in 7 Kategorien von 1: Winterkleid bis 7: komplettes Brutkleid aufgenommen (PIENKOWSKI 1980).

When Bar-tailed Godwits arrived in the Königshafen in August, more than 50 % of the birds already had started to moult into the winter plumage. Furthermore, mean plumage score fluctuated largely in August, indicating a high turnover rate of birds in the Königshafen. From the end of August onwards, a continuous moult of the male population into winter plumage could be observed. Although the first male in complete winter plumage was seen on 29th August, on 28th August 50 % showed still ³/₄ or more of the breeding plumage. On 1st October 50 % of the male Bar-tailed Godwits were in complete winter plumage resulting in an average duration of 35 days from more than ³/₄ of breeding plumage to winter plumage. This period is slightly longer than in spring, when birds needed 28 days for moult from winter to more than ³/₄ of the breeding plumage.

During most of the year the population present in the Königshafen consisted of similar numbers of males and females (Fig. 4). There were only two exceptions: In the second half of May clearly more females were present than males since males left the area earlier than females (cf. PROKOSCH 1988), and also in January more females than males were present.

Bar-tailed Godwits caught in March showed a strong sexual dimorphism, with females being larger (Fig. 5). They had 5.7 % longer wings (K-S test, $D_{76,42} = 0.826$, $p < 0.01$), 23 % longer bills (K-S test, $D_{76,43} = 0.964$, $p < 0.01$), 7.2 % longer 'legs' (tarsus+toe, K-S test, $D_{73,43} = 0.681$, $p < 0.01$), and 21.4 % more mass than males (K-S test, $D_{59,34} = 0.954$, $p < 0.01$).

No Bar-tailed Godwits were caught in winter but since birds were individually marked with colour rings, it was possible to check whether Bar-tailed Godwits staying in winter in the northern part of the Wadden Sea differed in morphology from the average of birds caught in spring and not controlled in January/February (Fig. 6). For all morphometric variables tested, no differences were found in either males or females (bill, wing, tarsus+toe, K-S test, for all variables $p > 0.1$). Thus, birds staying in January/February in the area are supposed to be of the same size as migrants present in March.

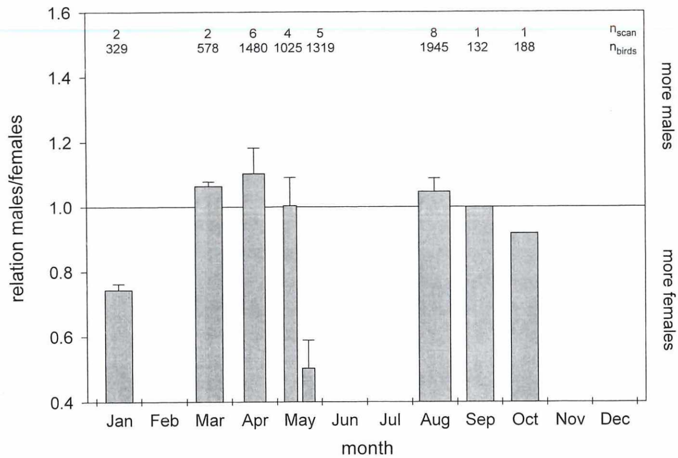

Fig. 4: Sex ratio ($n_{males}/n_{females}$) of Bar-tailed Godwits in the Königshafen area ($\bar{x}$ + SE). Flocks (mean flock size: 241) of birds were scanned with a telescope.

Abb. 4: Geschlechterverhältnis ($n_♂/n_♀$) der Pfuhlschnepfen im Königshafen ($\bar{x}$ + SE). Die Trupps (mittlere Truppgröße: 241) wurden mit einem Spektiv durchgemustert.

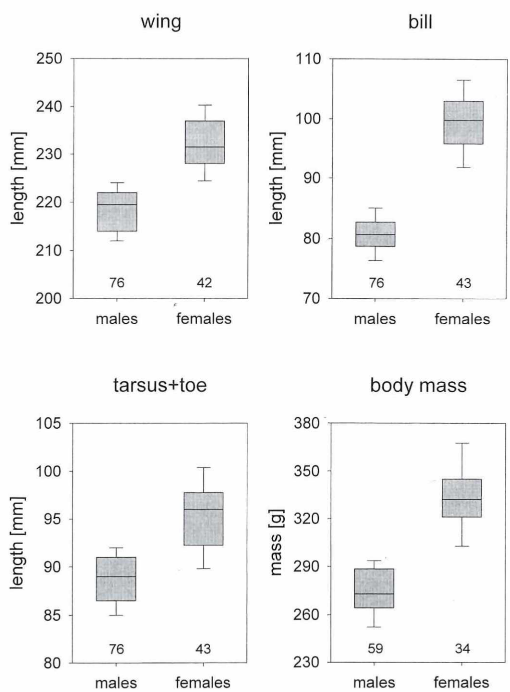

Fig. 5:
Box plot (line = median, box = 50 % interval, error bars = 90 % interval) of morphometric parameters of Bar-tailed Godwits caught in March in the Königshafen. Numbers below boxes denote number of birds measured.

Abb. 5:
Box Plot (Linie = Median, Box = 50 % Intervall, Fehlerbalken = 90 % Intervall) morphologischer Parameter von Pfuhlschnepfen aus dem Königshafen, die im März gefangen wurden. Zahlen unter den Boxen geben die Anzahl gemessener Vögel an.

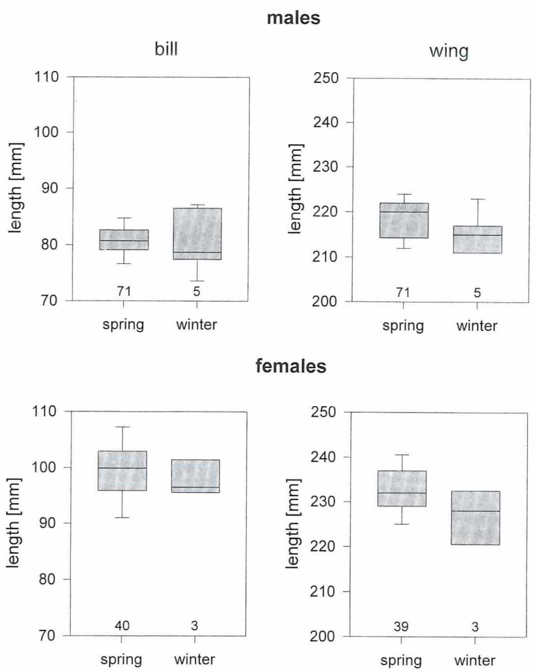

Fig. 6:
Comparison of bill and wing length between Bar-tailed Godwits caught in March and present in January/ February (winter) and all other birds caught in March and not observed in winter in the Königshafen area. See Fig. 5 for statistics.

Abb. 6:
Vergleich der Schnabel- und Flügellängen von im März gefangenen Pfuhlschnepfen, die auch in darauffolgenden Wintern (Januar/Februar) anwesend waren und sämtlichen anderen Märzfänglingen, die nicht im Winter beobachtet wurden. Statistik s. Abb. 5.

3.3. Controls of ringed birds outside the Sylt-Rømø Wadden Sea

From 137 Bar-tailed Godwits marked with metal or colour rings, 11 were recorded in other areas. Four birds ringed as adults and one as juvenile with metal rings in Britain were controlled during the catches in the Königshafen and colour ring combinations from two other birds ringed as juveniles in England were identified (Fig. 7).

The majority of controls (15 out of 18) originated from Great Britain, most of them from the British east coast. Six of these birds were either ringed or controlled in winter, one in early spring, three in early autumn and the remaining five birds in late autumn. Additionally, one bird was found dead in the Dutch Wadden Sea in March and another bird was controlled in July in southern Norway.

3.4. Turnover and residence time of migratory Bar-tailed Godwits in the Königshafen area

The proportion of marked birds in the local population fluctuated between 4.2 % and 0.3 % (Fig. 8). The maximum proportion of marked birds observed in the field depended on the number of birds actually marked and on the resighting efforts which both differed between seasons. Thus, proportions between years and seasons are not comparable. Apart from spring 1993, within one season the resighting effort was, however, on the same level. In spring, the proportion of marked birds in the local population decreased from April onwards, indicating that most of the marked individuals arrived and left earlier than the phenology of total numbers suggests. In autumn the proportion of marked birds showed a pronounced decrease between the end of August and the middle of September with a subsequent increase in the following fortnight period indicating some turnover of the marked birds.

In spring, most of the individually marked birds arrived in the Königshafen area before the 24th March (Fig. 9, 10, Table 1). In spring 1994 with a high effort for controls, most birds were ob-

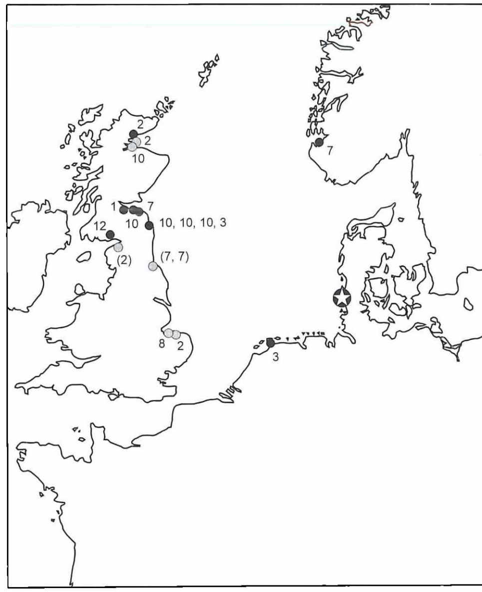

Fig. 7:
Controls of Bar-tailed Godwits ringed outside the Sylt-Rømø Wadden Sea (grey dots) and birds ringed in the Königshafen (star) and controlled elsewhere (black dots). Numbers denote month of ringing or control, bracket around numbers for birds ringed as juveniles.

Abb. 7:
Kontrollen von Pfuhlschnepfen, die außerhalb des Sylt-Rømø Wattenmeeres beringt wurden (graue Punkte) und von Vögeln, die im Königshafen (Stern) beringt wurden und an anderen Orten kontrolliert wurden (schwarze Punkte). Zahlen geben den Monat der Beringung bzw. der Kontrolle an, Zahlen in Klammern kennzeichnen Vögel, die als Juvenile beringt wurden.

served for the first time in a rather short period in March. However, birds kept arriving until the beginning of May. They stayed in the area for 30 – 40 days until 3rd or 4th May (median day of last observation in 1992 and 1994; the days of the last observation in 1993 are not reliable since efforts to identify colour marked birds in April and May were too low). Marked birds started to leave the area already in the first half of April. Even though the total number of birds continued to increase or remained on a high through the end of April/early May, most of the marked individuals had already left the Königshafen, indicating a high turnover of individuals (Fig. 10).

With the data from spring 1994, it was possible to estimate the number of birds migrating through the Königshafen area. For the period from mid-February to end of May, a total of 140,345.23 bird days resulted from the phenology of fortnightly means. If each bird would stay for the mean stopover length of 37.8 days (Table 1), a total of 3,713 Bar-tailed Godwits would have used the Königshafen area as a stopover site during the spring migration of 1994. However, unmarked birds arriving late in the area stayed for a shorter time as phenology in relation to departure of marked individuals suggests, so that the total number of birds passing through must be higher. In fact, the maximum number of birds counted early May was 4020 individuals which might come close to the actual number of birds passing through.

In autumn, most individually marked birds returned before 14th August to the area (Fig. 11, 12, Table 1). Only a few birds were observed for the first time in September. Observations from 1992 were not as reliable as in 1993 or 1994 since the 44 days with attempts to read colour rings were scattered over a longer period than in the latter years. Unfortunately, the median day of last observation of marked individuals correlates with the end of the field season, so that no reliable estimate of the departure time can be made. However, some birds left the area already between late August and mid-September. Together with an increase in numbers from mid-September onwards, a higher turnover of individuals than at other times of autumn migration can be assumed in the first half of September (Fig. 12).

3.5. Return rates of Bar-tailed Godwits

To test for site fidelity of Bar-tailed Godwits, return rates of birds to the area around List were analysed (Table 2). Return rates depend on the efforts made to identify colour marked birds, since more Bar-tailed God-

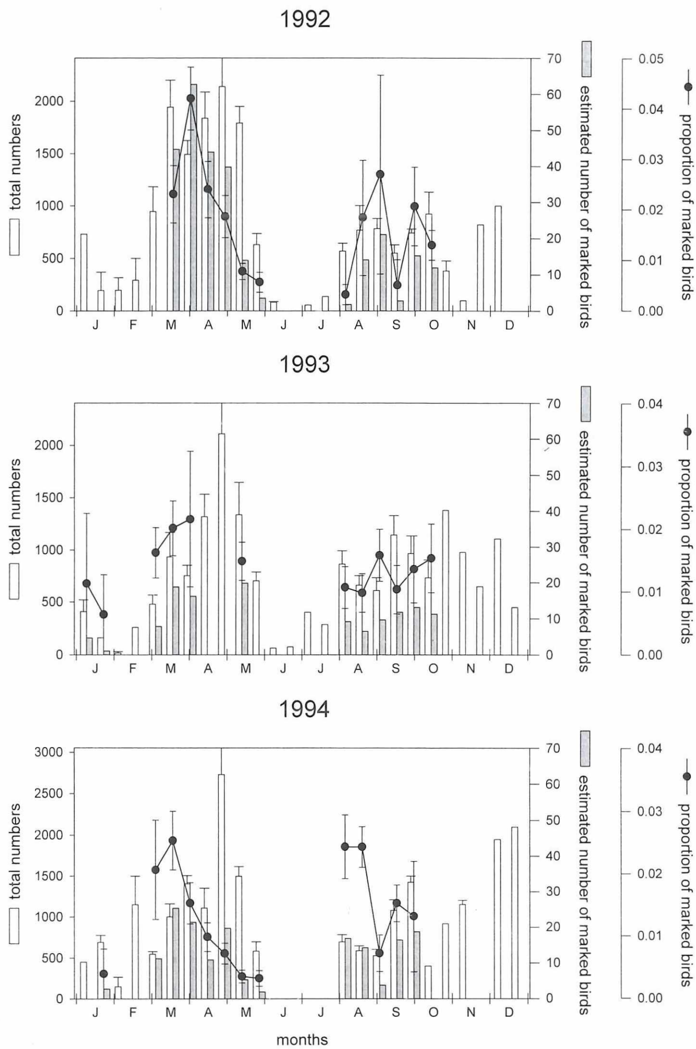

Fig. 8: Proportion of colour marked birds in the Königshafen area (± SE) and estimated number of colour marked birds (proportion of colour marked birds * total number of birds present).

Abb. 8: Anteil farbmarkierter Pfuhlschnepfen im Gebiet des Königshafens (± SE) und berechnete Absolutanzahl farbmarkierter Vögel (Anteil farbmarkierter * Gesamtanzahl anwesender Vögel).

wits ringed in spring 1992 were resighted in spring 1994 (68 %) than in spring 1993 (53 %) when flocks were searched for colour ringed birds on less days (35 %) as compared to spring 1994. Obviously, not all birds present in spring returned to the area in autumn, whereas return rates in spring are much higher. Considering only the return rates in spring 1994, the year with highest field efforts, and assuming 100 % site fidelity, annual adult mortality ranges between 17.4 % for the birds ringed in 1992 and 25.9 % for the birds ringed in 1993. If Bar-tailed Godwits are not 100 % site faithful, these rates would be even lower.

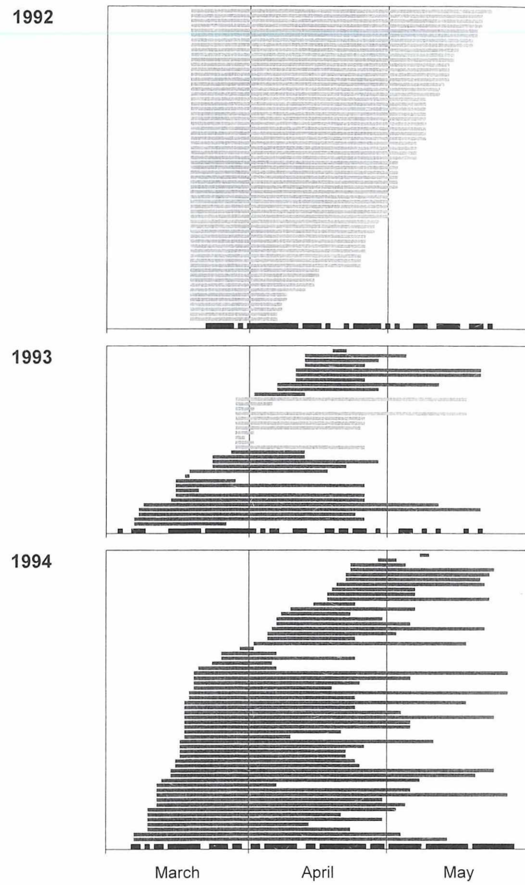

Fig. 9:
Length of stopover of individually colour ringed Bar-tailed Godwits in the Königshafen area in spring. Light grey bars denote birds caught in the respective season, dark grey bars in previous years, small black bars denote days when flocks were controlled for colour ringed birds.

Abb. 9:
Aufenthaltsdauer individuell markierter Pfuhlschnepfen im Bereich des Königshafens während des Frühjahrs. Hellgraue Balken kennzeichnen Vögel, die in der jeweiligen Saison gefangen wurden, dunkelgraue Balken kennzeichnen Vögel, die in vorherigen Jahren gefangen wurden, schwarze Balken markieren die Tage, an denen Trupps auf markierte Vögeln kontrolliert wurden.

4. Discussion

4.1. Mortality of European Bar-tailed Godwits

Boyd (1962) calculated an annual mortality of 39.5 % for adult Bar-tailed Godwits. For the similar sized Black-tailed Godwit (*Limosa limosa*) mortality rate estimates for adults range between 30.3 % (Boyd 1962) and 36.9 % (Glutz et al. 1977). Even the lower mortality estimate of 30.3 % for Black-tailed Godwits is higher than the estimated mortality in spring 1994 and matches exactly the number of birds resighted in 1997, when field effort was low and most probably some birds were missed. In conclusion, European Bar-tailed Godwits i) seem to be highly site faithful on spring migration and ii) most probably have lower mortality rates than estimated before.

4.2. Migration routes of European Bar-tailed Godwits

Bar-tailed Godwits of the European population are considered to breed in northern Fennoscandia and to winter mainly around the North Sea (Smit & Piersma 1989, Drent & Piersma 1990) whereas birds from the Afro-Siberian population winter in West Africa (Mauritania and Guinea-Bissau) and breed in Siberia (Taymyr and Yamal, Smit & Piersma 1989, Drent & Piersma 1990, Wymenga et al. 1990). Comparison of morphometric data from birds caught in the Königshafen with birds from the different breeding areas gives strong indication that the birds occurring in the

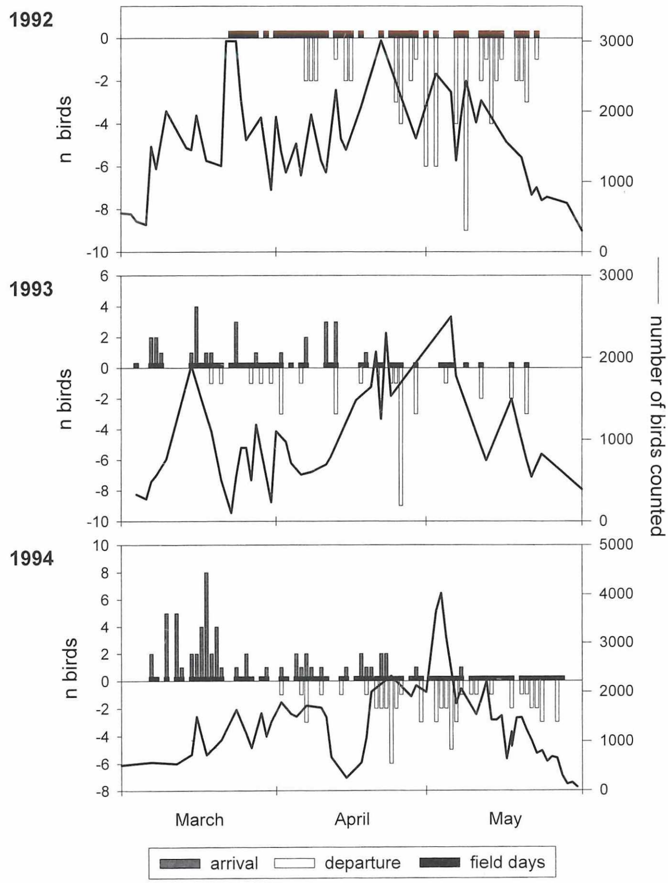

Fig. 10:
First ('arrival') and last ('departure') day of observation of individually colour ringed Bar-tailed Godwits in the Königshafen area in spring. Small black bars denote days when flocks were controlled for colour ringed birds, black line shows total number of Bar-tailed Godwits present at the high-tide roost in the Königshafen.

Abb. 10:
Erster ('arrival') und letzter ('departure') Tag, an dem markierte Individuen während des Frühjahrszuges im Königshafengebiet beobachtet wurden. Kleine schwarze Balken kennzeichnen Tage, an denen Trupps auf markierte Vögeln kontrolliert wurden, die schwarze Linie stellt die Gesamtzahl an Pfuhlschnepfen auf dem Hochwasserrastplatz im Königshafen dar.

Königshafen breed in northern Fennoscandia (Table 3): no difference was found in bill length and wing length (t-test for both measurements and sexes, $p > 0.05$). Additionally, birds breeding in central Siberia have shorter bills and wings than the Königshafen birds (t-test for both measurements and sexes, $p < 0.05$). As shown by ringed birds, wintering areas for Bar-tailed Godwits using the Königshafen as a stopover site are located in Great Britain and the Wadden Sea. Furthermore, morphometric data from birds wintering in West Africa indicated that these Bar-tailed Godwits were smaller and thus do not belong to the European population (WYMENGA et al. 1990). Thus Bar-tailed Godwits occurring in the Königshafen and most probably at other roosts with similar phenology on the island of Sylt, belong to the European population.

For European Bar-tailed Godwits the following migration pattern emerges (Fig. 13): birds winter around the North Sea with the Sylt-Rømø Wadden Sea as one of the northeasternmost wintering sites (SMIT & PIERSMA 1989, MELTOFTE et al. 1994). In late January or February, most Bar-tailed Godwits leave the northern part of the Wadden Sea. This decrease in numbers is paralleled by a slight increase in the western parts and a large increase on the Wash (MELTOFTE et al. 1994, ATKINSON 1996), so that birds move to these areas for a short period of time to escape high thermostatic costs (SCHEIFFARTH & NEHLS 1998). In March, birds return to the Wadden Sea; some of these birds fly directly to the northern part of the Wadden Sea whereas others seem to stopover for a brief pe-

Table 1: First and last day of observation and length of stay of Bar-tailed Godwits around List/Sylt in the northern part of the Wadden Sea. For length of stay and date of first observation per season, birds caught in the respective season and year were excluded. n_{birds}: number of individuals observed; $n_{readings}$: number of identifications; $n_{field\ days}$: number of days with reading attempts.

Tab. 1: Erster und letzter Beobachtungstag sowie Aufenthaltsdauer von Pfuhlschnepfen im Bereicht List/Sylt im nördlichen Wattenmeer. Zur Berechnung der Aufenthaltsdauer und des ersten Beobachtungstages wurden Vögel, die in der jeweiligen Saison gefangen wurden, ausgeschlossen. n_{birds}: Anzahl beobachteter Individuen; $n_{readings}$: Anzahl Ablesungen; $n_{field\ days}$: Anzahl Tage, an denen Kontrollen stattfanden.

	mean	SE	median	n_{birds}	$n_{readings}$	$n_{field\ days}$
spring						
first day of observation						
1992						
1993	26.3.	2.8	24.3.	26	151	43
1994	26.3.	2.1	19.3.	59	320	66
last day of observation						
1992	2.5.	1.6	2.5	64	325	44
1993	22.4.	2.8	26.4.	37	151	43
1994	2.5.	1.9	4.5.	59	320	66
length of stay						
1992						
1993	28.7	3.6	25	26	151	43
1994	37.8	2.4	36	59	320	66
autumn						
first day of observation						
1992	31.8.	5.7	29.8	15	82	44
1993	15.8.	3.5	10.8.	17	98	46
1994	14.8.	2.5	13.8.	21	170	44
last day of observation						
1992	12.10.	4.0	19.10	17	82	44
1993	24.9.	4.0	27.9.	18	98	46
1994	17.9.	3.1	20.9.	21	170	44
length of stay						
1992	40.1	6.5	42	15	82	44
1993	38.6	4.2	42	17	98	46
1994	32.7	3.7	36	21	170	44

riod in the western part (MELTOFTE et al. 1994). In late April, almost all Bar-tailed Godwits from the European population seem to gather in the Danish and northern German Wadden Sea, similar to the nearctic Knot (*Calidris canutus islandica*) which overwinters in western Europe (MELTOFTE et al. 1994, PIERSMA et al. 1994). In the first half of May, European Bar-tailed Godwits depart to their Fennoscandian breeding sites where they could be observed from mid May onwards (BYRKJEDAL et al. 1989). In autumn, migration seems to be more complex. Numbers of Bar-tailed Godwits in the Wadden Sea are lower than in spring (MELTOFTE et al. 1994) which can be caused by shorter stopover times and/or by birds not visiting the same stopover areas as in spring. In contrast to the high stopover site fidelity in spring, less than half of these birds used the Königshafen area in the northern Wadden Sea during autumn migration. Ringing controls, as well as the phenology on the Wash (ATKINSON 1996), indicate that some birds migrate directly from the breeding area to Great Britain. Others arrive in the northern Wadden Sea in August but move on to further sites in September, indicating that some European migrants may use shorter stopover times than in spring. Another group

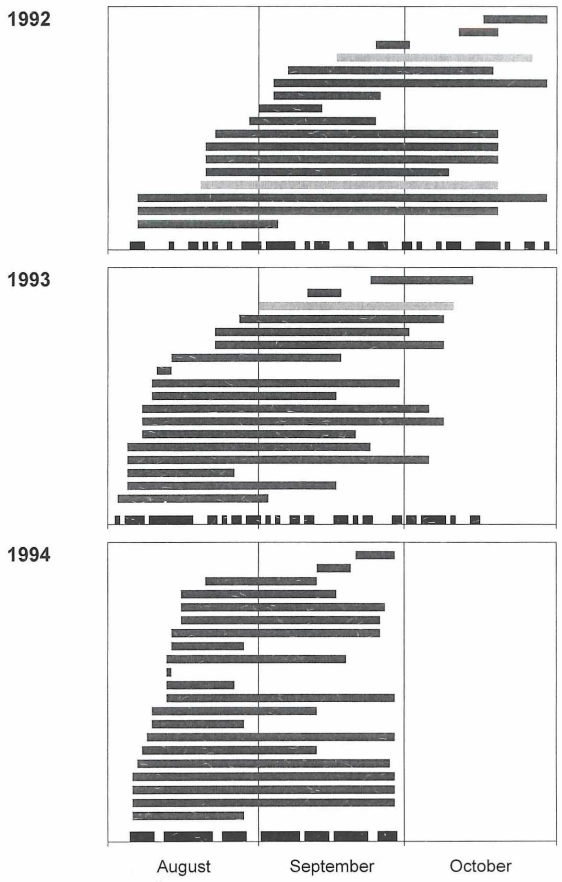

Fig. 11:
Length of stopover of individually colour ringed Bar-tailed Godwits in the Königshafen area in autumn; see Fig. 9.

Abb. 11:
Aufenthaltsdauer individuell farbmarkierter Pfuhlschnepfen im Königshafengebiet im Herbst; s. Abb. 9.

of birds arrives in August and September and stays in the northern Wadden Sea until late autumn, or even overwinters in the area.

4.3. Differential migration in European Bar-tailed Godwits?

Several authors state an excess of males in the Bar-tailed Godwit populations wintering along the East Atlantic flyway (Cramp & Simmons 1983, Piersma & Jukema 1990, 1993, Zwarts et al. 1990, Atkinson 1996). This is in contrast to what has been found in the northern Wadden Sea during spring migration, where equal numbers of males and females were observed (this study, cf. Table 4 in Prokosch 1988). There are two points to keep in mind when determining sex ratios in Bar-tailed Godwits. Males and females may use different habitats for foraging and roosting or occupy distinct positions within flocks (Smith & Evans 1973, Zwarts et al. 1990, own obs.), so that unequal sex ratios could be an effect of catching method or place as stated by Cramp & Simmons (1983). Furthermore, one has to distinguish between populations, since there is no reason to assume that the sex ratio is the same in all populations. In particular, this may be the case if different selection pressures act on these populations, as is evident for European and Afro-Siberian Bar-tailed Godwits (Drent & Piersma 1990).

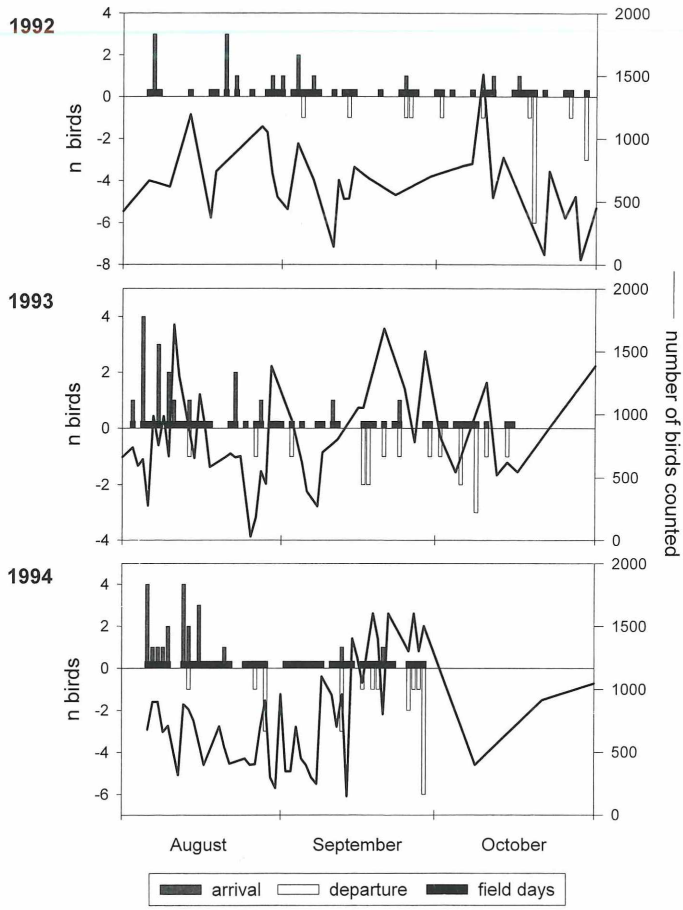

Fig. 12:
First ('arrival') and last ('departure') day of observation of individually colour ringed Bar-tailed Godwits in the Königshafen area in autumn, see Fig. 10.

Abb. 12:
Erster ('arrival') und letzter ('departure') Tag, an dem markierte Individuen während des Herbstzuges im Königshafengebiet beobachtet wurden, s. Abb. 10.

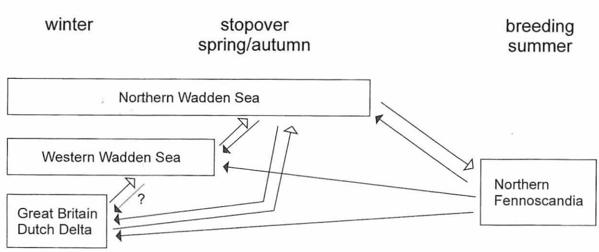

Fig. 13: Proposed migration patterns of European Bar-tailed Godwits. Open arrows represent spring migration, black arrows autumn migration.

Abb. 13: Schematische Darstellung der Wanderungsmuster Europäischer Pfuhlschnepfen. Offene Pfeile stellen den Frühjahrszug, geschlossene Pfeile den Herbstzug dar.

Table 2: Return rates of Bar-tailed Godwits in the area around List/Sylt. Given are the number of identified birds per season and the percentage of birds resighted from the number of ringed adult birds per season. Birds were caught in the Königshafen near List. Birds with unknown season of ringing were individuals with incomplete colouring combinations due to loss of rings. For effort to identify birds, number of days with reading attempts are given in the second row of the columnheads.

Tab. 2: Rückkehrraten von Pfuhlschnepfen im Bereich List/Sylt. Dargestellt sind die Anzahl identifizierter Individuen pro Saison und der prozentuale Anteil identifizierter Vögel an der Anzahl beringter Vögel pro Saison. Die Vögel wurden im Königshafen in der Nähe des Ortes List gefangen. Vögel mit unbekannter Beringungssaison sind Individuen mit unvollständigen Farbringkombinationen aufgrund des Verlustes einzelner Ringe. In der zweiten Kopfzeile ist die Anzahl an Tagen mit Kontrollen angegeben.

season of ringing	number of birds ringed	autumn 1992 44	spring 1993 43	autumn 1993 46	spring 1994 66	autumn 1994 44	spring 1997 7
spring 1992	88	23 (26.1 %)	47 (53.4 %)	22 (25 %)	60 (68.2 %)	33 (37.5 %)	14 (15.9 %)
autumn 1992	4		2 (50 %)	2 (50 %)	1 (25 %)	1 (25 %)	1 (25 %)
spring 1993	27			6 (22.2 %)	20 (74.1 %)	9 (33.3 %)	5 (18.5 %)
autumn 1993	1				1	1	1
unknown							5
sum	120	23 (26.1 %)	49 (53.3 %)	30 (25.2 %)	82 (63.3 %)	44 (36.7 %)	26 (21.7 %)

Table 3: Comparison of wing and bill length of birds caught in March in the Königshafen with measurements from potential breeding areas. Data for birds from Northern Fennoscandia including the White Sea and the Kanin peninsula (N. Fennoscandia) as well as Yamal and Taymyr (Taymyr) were taken from ENGELMOER & ROSELAAR (1998).

Tab. 3: Vergleich der Flügel- und Schnabellängen von Vögeln, die im März im Königshafenbereich gefangen wurden, mit den entsprechenden Maßen aus potentiellen Brutgebieten. Die Daten von Vögeln aus dem nördlichen Fenno-Skandinavien incl. Weißes Meer und Kanin Halbinsel (N. Fennoscandia) sowie von Yamal und Taimir (Taymyr) wurden ENGELMOER & ROSELAAR (1998) entnommen.

	wing	SD	n	bill	SD	n
males						
Königshafen	218.6	5.3	76	80.7	3.3	76
N. Fennoscandia	218.1	5.8	33	81.4	4.2	33
Taymyr	214.9	4.5	41	78.8	3.9	41
females						
Königshafen	231.8	6.3	42	99.3	5.9	43
Fennoscandia	230.8	6.1	23	101.6	5.3	23
Taymyr	227.0	4.4	29	96.0	4.4	29

For the Afro-Siberian population, most estimates of sex ratio resulted in an excess of males. In particular, in the main wintering area in Mauritania two different methods came up with similar results (PIERSMA & JUKEMA 1993). In Guinea-Bissau, another important wintering area along the African West coast, where 23 % of the Afro-Siberian population overwinters (SMIT & PIERSMA 1989), sex ratio equals 1 (ZWARTS 1988). Taking the numbers of both wintering areas together, there might be a real excess of males in the Afro-Siberian population. Thus, the equal sex ratio in Guinea-Bissau indicates differential use of wintering areas by males and females, with females migrating further south.

For European Bar-tailed Godwits in the northern Wadden Sea, no male bias could be established (PROKOSCH 1988, Fig. 4). In winter, even the opposite is the case, with an excess of females being present. In contrast, in the Wash in all months a male bias in catches exists with an increase in the proportion of males in January and February, which is not considered to be an artefact of the catching method (ATKINSON 1996). This complementary picture of sex ratios between European wintering sites suggests a differential migration of Bar-tailed Godwits, which is not unusual for a species with such a strong sexual dimorphism (KETTERSON & NOLAN 1983). Females, as the larger sex, may prefer to stay in the northern Wadden Sea as close to the breeding areas as possible, whereas males emigrate to milder wintering areas in Great Britain which might be related to the higher thermostatic costs of males compared to females (SCHEIFFARTH 1996).

5. Zusammenfassung

Das Sylt-Rømø Wattenmeer, ein Rückseitenwatt im nördlichen Wattenmeer, wird von zwei Pfuhlschnepfen-Populationen (*Limosa lapponica*) auf ihren Wanderungen zwischen Überwinterungs- und Brutgebieten als Zwischenrastplatz genutzt. Die in Westafrika überwinternde und in Sibirien brütende Population nutzt für jeweils einen Monat im Frühjahr und Herbst Hochwasserrastplätze an der Festlandsküste. Dagegen erscheint die in Fenno-Skandien brütende und in Westeuropa überwinternde europäische Population hauptsächlich für drei Monate im Frühjahr auf den Inseln. Einige dieser Vögel verbleiben im nördlichen Wattenmeer vom Herbst an bis Ende Januar. Die europäische Population wurde im Königshafen, am Nordende der Insel Sylt, näher untersucht. Sowohl morphologische, als auch Beringungsdaten bestätigten, daß diese Vögel zur europäischen Population gehören: 13 von 15 Beringungswiederfunden stammten aus Großbritannien.

Im Frühjahr mauserten die europäischen Pfuhlschnepfen innerhalb von 43 Tagen komplett vom Winter- ins Brutkleid. Während des Herbstzuges kamen die Pfuhlschnepfen bereits mit ¼ Winterkleid im Rastgebiet an. Um komplett ins Winterkleid zu mausern, benötigten die Vögel im Mittel 28 Tage. Das Geschlechterverhältnis betrug während des gesamten Jahres 1:1 bis auf i) die zweite Maihälfte, wenn die Männchen das Rastgebiet vor den Weibchen verlassen und ii) im Winter, wenn die meisten Männchen mildere Gebiete aufsuchen, wie das niederländische Wattenmeer oder Großbritannien. Jedoch unterschieden sich im Winter anwesende farbberingte Vögel nicht in der Größe von anderen im Untersuchungsgebiet farbberingten und dort nicht überwinternden Vögeln.

Im Frühjahr kamen die meisten farbberingten Vögel vor dem 24. März im Königshafen an und verließen das Gebiet wieder nach 30–40 Tagen am 3. oder 4. Mai. Im Mai wurde ein gegenüber März und April erhöhter Durchsatz an Vögeln beobachtet, wenn Pfuhlschnepfen aus anderen Gebieten sich im nördlichen Wattenmeer zu konzentrieren scheinen, bevor sie zu den fenno-skandischen Brutgebieten aufbrechen. Auf dem Wegzug kamen die meisten farbberingten Pfuhlschnepfen vor dem 14. August im Untersuchungsgebiet an. Allerdings ließen einige Vögel bis Anfang September auf sich warten. Zu dieser Zeit herrschte ein hoher Austausch an Pfuhlschnepfen, weil einige der früh angekommenen Vögel das Gebiet verließen, um andere Überwinterungsgebiete aufzusuchen. Auf dem Frühjahrszuges schienen Pfuhlschnepfen sehr ortstreu zu sein, während im Herbst weniger als 25 % der im Frühjahr beringten Vögel wieder im Untersuchungsgebiet auftraten. Geht man von 100 %iger Ortstreue im Frühjahr aus, so betrug die maximale jährliche Mortalitätsrate zwischen 17,4 und 26 % für adulte Pfuhlschnepfen, was weit unter den bislang publizierten Werten liegt.

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