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Wader Population Censuses in the Arctic: Getting the Timing Right

HANS MELTOFTE[1]

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ABSTRACT. There is increasing evidence that breeding wader censuses often have significantly underestimated densities in the Arctic and other areas. This evidence includes the recording of many more red knots *Calidris canutus* in the West Palearctic and African wintering areas than can be accounted for on the Arctic breeding grounds. The main causes of underestimated breeding numbers are that many species behave very inconspicuously during incubation, when most censuses have been performed, and that censuses taken later, during the chick-rearing period, record only successful breeding attempts. Records of four seasons at Zackenberg in central Northeast Greenland suggest that in the Arctic, the best population density data are obtained by mapping pairs and territorial individuals during the pair formation, territory establishment, and egg-laying periods, that is, when all birds are present and easiest to record. Revised summer population estimates for Old World wintering Nearctic waders are 20–200% higher than previous estimates.

Key words: behaviour, breeding phenology, census methodologies, eastern Canadian Arctic, Northeast Greenland, population densities, population sizes, shorebirds, waders, Zackenberg

RÉSUMÉ. On a de plus en plus de preuves que les recensements d'échassiers nicheurs ont souvent largement sous-estimé les densités dans l'Arctique et dans d'autres régions. Ces preuves comprennent le fait que l'on recense beaucoup plus de bécasseaux maubèches *Calidris canatus* dans les aires d'hivernage du paléarctique occidental et d'Afrique que l'on ne peut en compter sur les lieux de reproduction dans l'Arctique. Les principales raisons de cette sous-estimation sur les lieux de reproduction sont que bien des espèces ont un comportement peu visible pendant l'incubation, c'est-à-dire au moment où sont effectués la plupart des recensements, et que ceux faits plus tard, durant la période d'élevage des poussins, ne comptent que les tentatives de reproduction réussies. Les relevés effectués au cours de quatre saisons à Zackenberg, dans la région centrale du nord-est du Groenland, suggèrent que, dans l'Arctique, les meilleures données sur la densité de population sont obtenues en notant les paires et les individus territoriaux durant la formation des paires, l'établissement du territoire et la période de ponte, c'est-à-dire quand tous les oiseaux sont présents et le plus facile à compter. Les estimations révisées des populations estivales pour les échassiers néarctiques hivernant dans l'Ancien Monde sont de 20 à 200 p. cent plus élevées que les estimations précédentes.

Mots clés: comportement, phénologie de la reproduction, méthodologies de recensement, Arctique canadien oriental, nord-est du Groenland, densités de population, tailles de population, oiseaux de rivage, échassiers, Zackenberg

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INTRODUCTION

Pronounced discrepancies exist especially between the numbers of red knots *Calidris canutus islandica* and *C.c. canutus* recorded during mid-winter counts in Europe and West Africa and estimates of numbers breeding in High Arctic Greenland-Canada and Siberia, respectively. Many more birds have been found on the wintering grounds than can be accounted for in the breeding areas. Two explanations have been offered. Whitfield et al. (1996) argued that, since there appear to be so few knots on the Greenlandic-Canadian breeding grounds, about half the knots wintering in Europe may not be *C. c. islandica*, but *C. c. canutus*. Tomkovich and Soloviev (1996), on the other hand, argued that the huge discrepancy between population estimates derived from established densities within the known breeding range of *C. c. canutus* and the estimated mid-winter population of the species in West Africa may indicate the existence of unknown breeding areas somewhere in Siberia.

Something is obviously wrong. It is unlikely that the problem is with the counts in mid-winter, when the birds occur in large concentrations that are relatively easy to record. It is more likely that the summer population density estimates are incorrect (e.g., the estimates for the eastern Nearctic: Meltofte, 1985; Piersma, 1986). These estimates were based on traditional "territory" mapping during the (late) incubation and chick-rearing period, when the birds are supposed to be most localized and "safe" to record. Since the time of those estimates, I have been fortunate to spend five seasons at one site, the newly established Zackenberg Research Station in central North-

[1] National Environmental Research Institute, Department of Arctic Environment, Frederiksborgvej 399, DK-4000 Roskilde, Denmark; mel@dmu.dk

east Greenland. There I could follow the wader populations during the entire breeding season in a 19 km^2 study area (Meltofte, 1997, 1998, 1999, 2000). On the basis of these experiences, I will argue that most breeding wader censuses in the Arctic have probably significantly underestimated densities, not only of knots, but also of other wader species.

If this argument is correct, my conclusion is not much different from recent experiences from temperate regions. For example, intensive work on redshank *Tringa totanus* at the Dutch Wadden Sea has demonstrated that numbers of *individuals* recorded during one-time territory surveys should be multiplied by 2.4 to reach realistic *pair* numbers (Dallinga, 1993, cited by Thorup, 1998). Exactly the same ratio must be applied in censuses of breeding dotterel *Charadrius morinellus*, even during the optimal time period in Scotland (P. Whitfield, pers. comm. 2000). Similarly, work on dunlin *Calidris alpina* in Denmark has revealed that good population estimates (but still just 70–90% of the pairs) are obtained only if the highest number of pairs and single individuals (the latter counting as one pair each) obtained from 8 to 10 surveys is used (Thorup, 1998; see also Jackson and Percival, 1983). Hence, in his major analysis of 65 years of breeding bird censuses on the meadows of Tipperne in Denmark, Thorup (1998) had to add 50–100% to the earlier wader census results in order to obtain comparable and realistic figures.

The present paper applies to areas with moderate pair densities (<10–20 pairs/km^2) like those found in most of the Arctic, where one or a few researchers typically have to cover census areas of several square kilometres. In areas with high densities, such as those found in certain places in Alaska and northeastern Siberia, it may be possible to find virtually all nests in small sample areas, e.g., by rope-dragging in 10 ha plots (Troy, 1996; See, however, Soloviev et al., 1996 for examples of poor results even with this method). The present study mainly involves relatively monogamous and site-tenacious species, and more complicated situations may be encountered in areas dominated by species with more complex breeding systems.

MATERIAL AND METHODS

After initiating the establishment of the research station and surveying the area at Zackenberg in the summer of 1995, I staked out an 18.8 km^2 study area (for details of the study site see Meltofte, 1997). The area reaches from sea level to 600 m altitude on a gravel mountain slope, and it includes a wide variety of habitats, ranging from fertile fens with several ponds to dry and barren plateaux and slopes (Bay, 1998).

During 1996–99, the study area was surveyed regularly during the entire wader breeding season, from late May or early June to late July or August (Meltofte, 1996, 1997, 1998, 1999, 2000). After general surveys of snow-free, vegetated patches during late May and early June, the main survey had three phases: (1) an initial total survey of snow-free areas performed during mid/late June each year; (2) surveys during the rest of the breeding season that concentrated on the areas with most birds, in which the main effort was to find as many nests and broods as possible; (3) a final evaluation of the field maps made after the season to extract total numbers and distribution of the population.

Inside the 18.8 km^2 census area, a 3.39 km^2 intensive study area was established. In this intensive study area, I tried not only to find as many nests and young as possible, but also to scrutinize the entire area regularly throughout the breeding season.

During each survey, all records of birds were marked on field maps. These records included codes for behaviour, such as song, territory defence, mating displays, pair bonds, alarm calling, distraction displays, grouping, and flocking. The categories given are somewhat subjective. For example, two birds seen together did not necessarily make up a pair (even though the sexes were checked when possible), and aggressive and mating behaviour may be hard to distinguish. Also, alarm calls may be difficult to separate from other calls, and song is often provoked by the presence of the observer close to a nest or young. In general, pairs are best defined and thereby easiest to record in sanderling *Calidris alba*, followed in decreasing order by red knot, ruddy turnstone *Arenaria interpres*, common ringed plover *Charadrius hiaticula*, and dunlin. In the best habitats, dunlins are semicolonial, with concentrations of singing, displaying, alarm-calling, and feeding individuals. In all species, grouping and flocking depend on the time of the season and the situation. Loose aggregations of pre-breeders feeding on a snow-free patch were not considered groups or flocks, despite the fact that they will flock at the appearance of a skua or falcon. (True pre-breeding flocks may form during spells of inclement weather, but this did not occur during the study years.) Alarm-calling birds that gathered around the observer near a nest or young were considered a group, while only true flocks of post-breeders rambling over the tundra were considered flocks (see Meltofte, 1985). Post-breeding flocks were excluded from the present analysis; in any case, few such flocks were recorded at Zackenberg. Records of birds flying high were also excluded from the analyses. All censuses were performed during daytime (0900–1800), when the birds are most active, but no systematic studies are available on the diurnal rhythm of the species involved.

The efforts to find nests and young were concentrated on sanderling, dunlin, and ruddy turnstone. The breeding habitat of ringed plovers at Zackenberg (gravelly slopes and plateaux with little chance of finding elevated lookout posts) makes it very difficult to find these birds, and the knots are extremely difficult to find in any case.

The methods are described in a manual (Meltofte and Berg, 2000), which is available on the Internet (http://biobasis.dmu.dk). The number of census hours and hours used to search for nests and young per month and per year are given by Meltofte (1997, 1998, 1999, 2000). The total

TABLE 1. Total numbers of individuals recorded at the initial total census in the 18.8 km^2 census area during the territory establishment and egg-laying period by mid-summer, together with the results of the final evaluation of population size and number of breeding pairs confirmed by finds of nests and young.

	C. hiaticula	*C. canutus*	*C. alba*	*C. alpina*	*A. interpres*
1996					
Total individuals recorded 12–26 June	69	54	94	74	66
Final evaluation (pairs)	54–56	33–43	51–63	69–82	42–52
Percent individuals initially recorded	62–64	63–82	75–92	45–54	63–79
No. of nests and broods found	2	2–3	8	11	10
Percent of minimum population found	4	8	16	16	24
1997					
Total individuals recorded 12–24 June	61	60	103	102	87
Final evaluation (pairs)	41–49	35–44	55–70	75–91	49–58
Percent individuals initially recorded	62–74	68–86	74–94	56–68	75–89
No. of nests and broods found	5	2	9	16–17	17–18
Percent of minimum population found	12	6	16	21	35
1998					
Total individuals recorded 12–22 June	62	38	98	120	83
Final evaluation (pairs)	38–45	27–32	62–70	75–94	55–62
Percent individuals initially recorded	69–82	59–70	70–79	65–80	67–75
No. of nests and broods found	4	4	14	23	26
Percent of minimum population found	16	15	23	31	47
1999					
Total individuals recorded 17–26 June	104	44	109	100	69
Final evaluation (pairs)	53–67	25–33	60–67	75–89	43–48
Percent individuals initially recorded	78–98	67–88	81–91	56–67	72–80
No. of nests and broods found	4	2	18	23	13
Percent of minimum population found	8	8	30	31	30

number of census and search hours varied from 128 in 1996 to 185 in 1998. Time spent at the initial total census in mid to late June was 43 hours in both 1996 and 1997, 44 hours in 1998, and only 30 in 1999. In 1999, snow covered much more of the area for longer than in other years, allowing extensive use of skis and thus more rapid coverage of the study area.

In this paper, breeding pairs are defined as all pairs or individuals holding a territory or claiming a site, regardless of any definitive evidence of breeding (i.e., presence of eggs or young: see Discussion). Hence, when the field maps were evaluated for records of breeding pairs, all records of pairs, singing (or other territorial behaviours) and alarm-calling individuals were considered as representative of "territories." Records that did not fulfil these criteria, but still might have indicated the presence of a territory (e.g., stationary single but silent individuals), were plotted as additional territories, with a question mark. The same was done with possible double counts of the same individuals (Meltofte and Berg, 2000). The question-marked territories were added to the "safer" territories (minimum number) to provide a maximum figure.

The initial census in mid to late June was considered the basis for the final evaluation, but pairs found later in areas where no pairs were recorded nearby, or in areas that were poorly covered during the initial census, were added to these results. Similarly, territories were upgraded from question-mark status if more definitive records at the site were obtained later. Otherwise, later records of nests and small young together with stationary and clearly breeding pairs were counterbalanced by repositioning a nearby territory from the initial census.

For the red knot, even pairs and singing individuals recorded during early June were included in the evaluation, on the basis of Whitfield's (1996) results on song flight and territorial activity (see Discussion).

RESULTS

The final estimates of the number of territories within each sector of the study area have been published for each year, and so have data on breeding phenology and success (Meltofte, 1996, 1997, 1998, 1999, 2000). In total, about 250–300 pairs/territories of common ringed plover, red knot, sanderling, dunlin, and ruddy turnstone, as well as a few pairs of red-necked phalarope *Phalaropus lobatus*, were recorded in the census area (Table 1). Because of unprecedented amounts of snow and a very late snowmelt in 1999, ruddy turnstone figures were somewhat low that year, while common ringed plovers were found in higher numbers, since pre-breeders were present until mid-summer (Table 1; Meltofte, 2000).

Phenology of the Records

In Figure 1, the numbers of birds recorded per survey hour during the breeding seasons 1996–1998 are presented

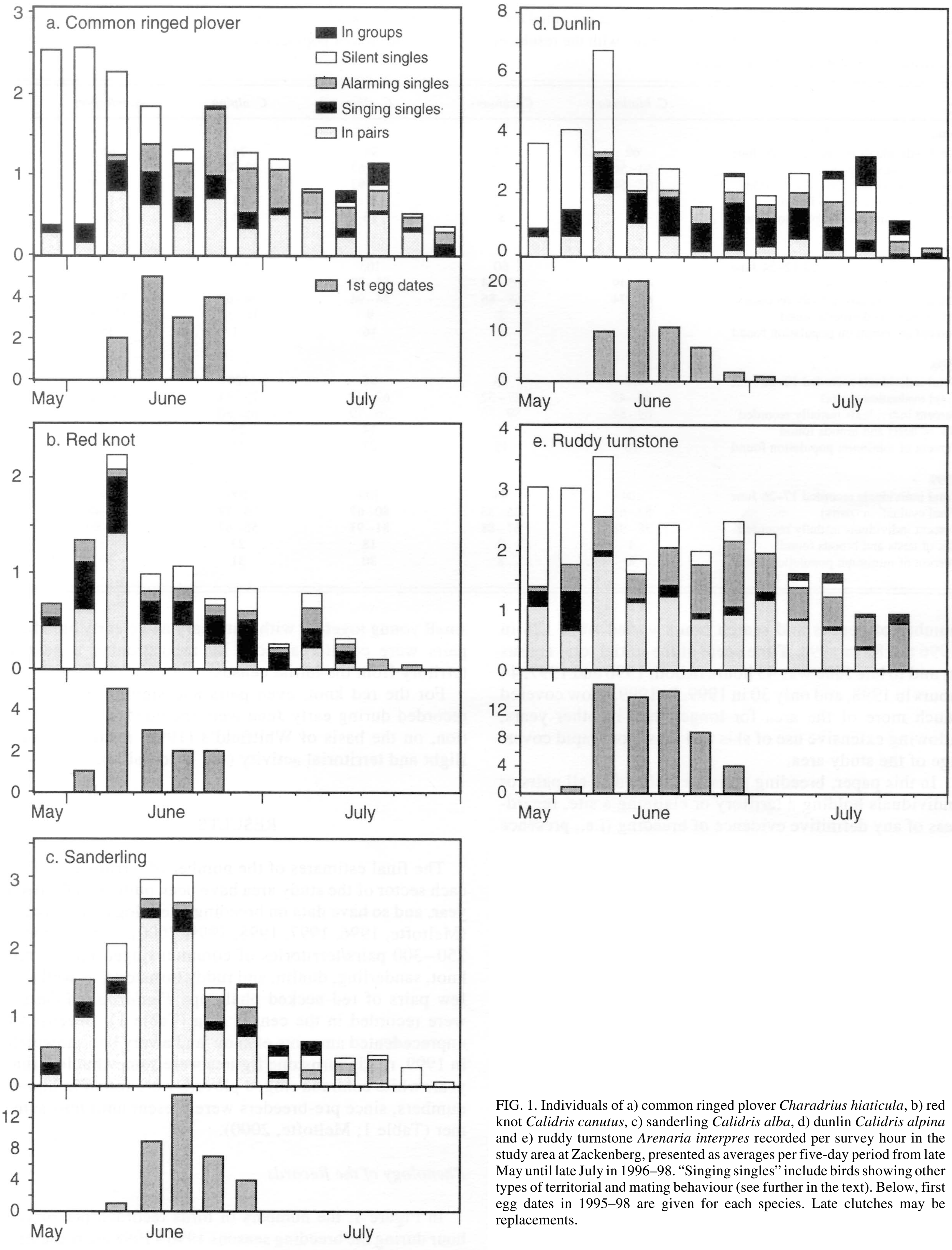

FIG. 1. Individuals of a) common ringed plover *Charadrius hiaticula*, b) red knot *Calidris canutus*, c) sanderling *Calidris alba*, d) dunlin *Calidris alpina* and e) ruddy turnstone *Arenaria interpres* recorded per survey hour in the study area at Zackenberg, presented as averages per five-day period from late May until late July in 1996–98. "Singing singles" include birds showing other types of territorial and mating behaviour (see further in the text). Below, first egg dates in 1995–98 are given for each species. Late clutches may be replacements.

(1999 data were omitted here because of the delayed phenology). It appears that in all species, the numbers of birds recorded declined to a smaller or greater extent from a peak in early to mid-June (see Discussion for possible reasons). However, there were striking differences between the species. For the ruddy turnstone, perhaps the least problematic species, the highest densities were found during late May and early June, when the birds were most concentrated on snow-free spots. Thereafter, densities stabilized at a relatively high level (though lower than the initial peak), where they remained from egg laying (around mid-June) until nonbreeders and failed breeders left in July (Fig. 1e). This is a very alarmist and aggressive species, but even turnstones may go unnoticed during incubation (Meltofte, 1979 and this study). The other end of the scale is represented by red knot and sanderling, which tended to "disappear" as soon as incubation began (Fig. 1b, c). The common ringed plover, like the turnstone, is a highly alarmist species. Many alarm-calling birds may gather around an observer who is close to a nest or young (I recorded up to 14 individuals at one site), and individuals may show distraction displays up to 250 m from their own nest or young (Meltofte, 1979).

Breaking the records down into categories shows that in common ringed plover and ruddy turnstone, both mates in a pair were recorded relatively often during the entire breeding season (Fig. 1a, e). However, pairs of red knots and sanderlings made up high proportions only in June (Fig. 1b, c), and dunlins, only in early and mid-June (Fig. 1d). Singing singles (and birds showing other kinds of territorial and mating behaviour) made up a large proportion of the records of red knot and dunlin even into July. But in common ringed plover and ruddy turnstone, alarm-calling singles made up larger proportions during the entire breeding season. Also recorded in all species were birds in pairs giving alarm calls, or pairs in which one bird was singing. Silent singles were recorded in large proportions only in common ringed plover, dunlin, and ruddy turnstone, and only during late May and early June, while birds in groups, as expected, were recorded mainly during the chick-rearing period in July. Of course, the individuals in these groups gave alarm calls as well.

Confirmed Breeders

In general, the number of individuals recorded during the mid-June census comprised about 60–90% of the final minimum estimate (see Discussion). The proportion of pairs/territories confirmed by finds of nests or young increased during the study years 1996–98, while the poor breeding season of 1999 is reflected in lower proportions found, especially in ruddy turnstone (Table 1). In the three species that were most intensively searched for, the proportions of pairs/territories confirmed in 1998 were 23% for sanderling, 31% for dunlin, and 47% for ruddy turnstone. These are relatively high proportions, considering that there were about 250–300 pairs of waders within 19 km^2, and that only half this area was searched intensively for nests and young. Moreover, an unknown proportion of the population did not breed or was depredated early in the season, and I had to take care of the monitoring of all other bird species as well. In sanderling, an unknown proportion of the breeding pairs may have laid double clutches (cf. Parmelee and Payne, 1973 *versus* Pienkowski and Green, 1976). If this was the case at Zackenberg, the percentage of territories on which breeding was confirmed should be reduced accordingly. This is particularly relevant for the 1999 season, when the number of nests and broods found in the intensive study area was higher than the minimum number of pairs estimated from the entire census (seven nests and one brood as compared to an estimated 6–8 pairs).

Comparison of Census Periods

Many censuses of breeding waders in the Arctic, including High Arctic Greenland, have been performed in July, during the incubation and chick-rearing period (cf. Meltofte, 1985; Boertmann et al., 1991; Mortensen, 2000). For this reason, I have tried to evaluate my census results for 1–20 July from the best-covered area, the 3.39 km^2 intensive study area. In accordance with the general practice of many breeding wader censuses in the Arctic, minimum numbers include only records of nests and young, records of birds showing clear distraction displays, or at least two records of singing or alarm-calling individuals or pairs on repeat visits at the same site.

A comparison of the final evaluation of the surveys in the intensive study area with the results obtained during 1–20 July (Table 2) indicates that for most species and years, highly reduced minimum numbers were found during the latter period: mostly only 40–70%. Even these figures are positively biased, because a number of nests were found before 1 July, so that the birds were easier to record and could not be excluded from the calculations. Some Arctic wader censuses have even been performed after 20 July, but these must be considered highly unrealistic (cf. Fig. 1).

As expected, the percentage of territories with confirmed breeding was somewhat higher in the more intensively surveyed area, with 50–83% of the minimum numbers of pairs confirmed in 1998 in all species except common ringed plover (Table 2). The maximum figures were generally closer to the final estimates in most species and years. These figures include all single records of singing and/or alarm-calling pairs or of individuals that were not allocated to any of the more safely recorded territories (= the minimum figures), but they do not include records of pairs and individuals that remained silent during my passage. The latter records were neglected. Even though this method is more liberal than that practised in many Arctic breeding bird censuses, it also produced significantly reduced maximum figures in several species and years (Table 2).

TABLE 2. Comparison of a retrospective evaluation of records made during 1 – 20 July in the 3.39 km² intensive study area with the original final evaluation of pairs/territories recorded within the same area, together with the number of breeding pairs confirmed by findings of nest or young. Counts do not cover the entire area each time, but varying and highly overlapping sections. See the text for further explanation.

	C. hiaticula	*C. canutus*	*C. alba*	*C. alpina*	*A. interpres*
1996 (5 counts during 1 – 20 July)					
Final evaluation (pairs)	10 – 11	3 – 4	10 – 12	24 – 27	6 – 7
Only 1 – 20 July evaluation (pairs)	5 – 9	2 – 4	2 – 4	10 – 26	3 – 6
Percent of final evaluation recorded in July	50 – 90	68 – 100	20 – 33	42 – 96	50 – 96
No. of nests and broods found	1	2 – 3	3	5	2
Percent of minimum population found	10	68	30	21	30
1997 (8 counts during 1 – 20 July)					
Final evaluation (pairs)	10	4 – 5	10	22 – 26	7 – 9
Only 1 – 20 July evaluation (pairs)	6 – 13	2	1	19 – 29	4
Percent of final evaluation recorded in July	60 – 130	50 – 40	10	86 – 112	57 – 44
No. of nests and broods found	3	2	3	6	3
Percent of minimum population found	30	50	30	27	43
1998 (9 counts during 1 – 20 July)					
Final evaluation (pairs)	9 – 11	3	12 – 13	20 – 25	6 – 9
Only July evaluation (pairs)	5 – 8	2	5 – 9	18 – 23	6 – 8
Percent of final evaluation recorded in July	56 – 73	68	42 – 69	90 – 92	100 – 89
No. of nests and broods found	2	2	6	11 – 12	5
Percent of minimum population found	22	68	50	55	83
1999 (7 counts during 1 – 20 July)					
Final evaluation (pairs)	6 – 11	1 – 3	12 – 13	24 – 27	4 – 5
Only July evaluation (pairs)	6 – 12	0	10 – 13	19 – 25	4
Percent of final evaluation recorded in July	100 – 109	0	83 – 100	79 – 93	100 – 80
No. of nests and broods found	2	0	8	10	3
Percent of minimum population found	33	0	67	42	75

DISCUSSION

There were several reasons for the progressively reduced numbers of birds recorded after the initial peak in early to mid-June. 1) In late May and early June, there were not many snow-free, vegetated areas to feed on, so the birds were highly concentrated and easy to record. For the common ringed plovers, this pattern was exaggerated because many pre-breeders fed in the lush fens in the lowland before some of them moved in mid-June up onto the gravelly slopes that were surveyed less regularly. In fact, there were probably fewer waders of all species present during this period than during the rest of June, since new birds apparently continued to arrive during early June. 2) From mid-June, all members of the local population must have been present, as few unsettled birds were seen after 10 – 12 June in "normal" years (Meltofte, 1985 and this study). At the same time, the birds were very active with all kinds of pair-formation and territorial behaviour, as most territories and clutches were initiated during this period (Fig. 1a – e, lower parts). 3) As soon as incubation began, most species behaved much more cryptically. 4) At the same time, most of the snow cover disappeared (most expanses of snow had melted by Midsummer Day in "normal" years), leaving a much larger area on which the birds could disperse. 5) From around 1 July, failed breeders, together with nonbreeders, left the breeding grounds and formed post-breeding flocks before departure (Meltofte, 1985). 6) When the young started to hatch in early July, the birds became much more alarmist, and groups of as many as 8 – 14 alarm-calling adults gathered around the observer when a brood had been found (Fig. 1 and Meltofte, 1979). But as more and more clutches and broods probably were lost, birds progressively left the breeding sites. 7) In late July, young started to fly, and most adults were gone by early August (Meltofte, 1985; this study). 8) Methodological biases were also involved. The switch from territory mapping in mid- and late June to nest and brood finding in late June and July meant that I spent longer periods at the same spot instead of walking all the time. This limited the area of ground covered per hour, but it also increased the likelihood of recording otherwise concealed birds.

Similarly, there are a number of likely reasons for the reduced numbers found in July in the intensive study area. 1) Minimum numbers included only records of nests and young or of birds showing clear distraction displays, or at least two records of singing and/or alarm-calling individuals or pairs on repeat visits to the same site. 2) Most nonbreeders and failed breeders had left the area by 1 July or left during the census period. 3) Incubating birds may behave very inconspicuously in some species or individuals, and the incubation period extended well into this latter census period in many pairs (cf. Fig. 1, where 25 days [28 days in common ringed plover] of egg-laying and incubation may be added to the first egg dates). 4) It is also possible that my final estimates are too high, but my study at Danmarkshavn in 1975 indicates this is not likely. In that study, I recorded no birds from late June to mid July at 14–31% of my visits to common ringed plover territories, 20–26% of visits to dunlin territories, 15–60% of visits to ruddy turnstone territories, and 42–55% of visits to sanderling territories (Meltofte, 1979).

In a few cases, the 1–20 July evaluation from the intensive study area gave higher maximum figures than the final evaluation. This result is likely due to double counts of individuals or pairs who sang or gave alarm calls far away from their own territories (recorded up to 1300 m away in common ringed plover; Meltofte, 1979). Likewise, it is possible that there were double counts of breeding attempts, in which a single attempt was recorded first as a nesting territory and later as a family with a brood. Broods may wander widely over the tundra soon after hatching (up to 1500 m recorded in dunlin during 10–11 days after hatching; this study), which at Zackenberg began in early July in "normal" years (cf. Fig. 1). (Double recording of breeding attempts within the brood-rearing period was avoided by ringing of the chicks.) Conversely, many of the "at least two records" (see paragraph above) of a single pair or territory were probably made up of different pairs or individuals that by chance sang or gave alarm calls close to previously recorded sites. The possibility also exists that the final estimates are too low, but I find this less likely than the other explanations.

Arctic Wader Censuses

During the last 40 years or so, many breeding wader censuses have been made in the Arctic. Methods and the timing of the counts in relation to breeding schedules have varied considerably between studies, but many have given a range of numbers, whose minimum and maximum are supposed to express something about the reliability of the counts. However, the reliability of any such figures has rarely been seriously studied, and so far, no standardized and commonly accepted methods are available. Few other studies of Arctic wader species have attempted to quantify census efficiency (Meltofte, 1979; Soloviev, 1995; Soloviev et al., 1996; Whitfield et al., 1996). The present study does not give definite answers either, but the data presented provide some background for discussing the kinds of biases that may be involved and make it possible to put forward some recommendations on how to proceed.

The first problem relates to the definition of a "breeding pair." To obtain realistic figures for population densities, we must refrain from demanding actual evidence of breeding as a criterion. Whether a pair or territorial individual is breeding or not belongs to a discussion about demography or breeding performance of the population. In other words, any site-claiming pair or individual belongs to the local population and counts in a population census. I can illustrate my point with the extreme situation of long-tailed skuas *Stercorarius longicaudus,* of which we have a population of about 20–25 pairs who establish territories every year in the census area. They remain and feed in the area from early June until late July, but the number of pairs that actually lay eggs in individual years varies between zero and 25. Now, how big is that population in nonbreeding years: zero pairs, or 20–25 pairs? My suggestion is that we should aim to produce total population estimates and then give data on breeding performance and related behaviour when available.

The second problem is a more psychological one. How sure should one be before accepting a pair as belonging to the local population? This problem may be illustrated by a few examples. The most conservative approach is presented by Schekkerman and van Roomen (1995), who give the combined number of nests and broods found as the minimum number of pairs present, adding other pairs that showed clear breeding behaviour to produce the maximum figure. This latter figure is used as the minimum figure in most other studies, while the maximum figure normally represents additional pairs or individuals that may possibly have bred in the area. The first approach is, of course, the safest one, but also the most likely to underestimate the population significantly. Both approaches—but especially the latter one—include a certain amount of subjectivity, which is rarely discussed but is nevertheless a significant source of bias. Scientists, in particular, do not like to run the risk of exaggeration. This means that, all other factors being equal, statements on population densities tend to be low. Pairs have often been neglected if the researchers did not feel confident about their presence or actual breeding. My study at Danmarkshavn in 1975 indicates the magnitude of this problem. Birds that were neglected during the late June to mid-July censuses because they could not be assigned to any finally accepted territory comprised 18–21% of the total population in common ringed plover, 21–33% in dunlin, 31–42% in ruddy turnstone and no less than 48–68% in sanderling (Meltofte, 1979).

The third problem is the timing of the counts. For the species involved, the results presented in this paper illustrate that recording the birds becomes more difficult as the breeding schedule progresses: the later after territory establishment and egg-laying that censuses are taken, the lower the chance of recording all the birds in the population. Even in the most alarmist species, individuals may behave very inconspicuously during incubation, and after around 1 July, increasing numbers of failed breeders leave the tundra. This means that breeding bird censuses in July record only successful pairs or individuals, and primarily those who are tending young. Hence, using line transects during the incubation period, Soloviev (1995) recorded only about one-quarter of the dunlins actually breeding, and he points out a number of other serious problems with applying this method to tundra birds. At the same time, censuses during the chick-rearing period are troubled by family groups' moving widely over the tundra or gathering at favourable feeding sites, and the chick-rearing period is the time when most alarm-calling individuals are attracted to the observer from far away. For these reasons, the line transect method, though recommended by both the Arctic

Monitoring and Assessment Programme and Conservation of Arctic Flora and Fauna (Olsen, 1995), has proved largely useless (Soloviev et al., 1996).

Standardization of Censuses

In the methods developed at Zackenberg, this sort of bias is minimized by building on standardized records of pairs, territorial individuals, and other birds seen during the time of the season when they are most observable and all local birds are present. This is the time between prebreeders' settling and incubation, when the birds become hard to record. During this period, the birds are not very alarmist, which means that records are not distorted by alarming birds attracted from larger areas. In most of the Arctic, this is also a time when parts of the tundra are covered in snow. The birds, concentrated on early snow-free areas, are therefore easier to record. At Zackenberg (and in most of central High Arctic Greenland; cf. Meltofte, 1985), where breeding is well synchronized, this optimum survey period ideally falls approximately at 12 – 20 June in "normal" years (see Results). Because of the size of the area and poor weather, in practice it has been between 12 and 26 June (Table 1). This optimum survey time is also before the failed breeders and nonbreeders form post-breeding flocks (from around 1 July) and the successful breeders start to ramble over the tundra with their young. In southern High Arctic Greenland, where heavier snow cover and later clearance of the tundra delay breeding, the ideal time may be a little later, i.e., around 20 – 30 June, but still before post-breeders start to gather around 1 July.

Even this method involves subjective assessments, as stated under Material and Methods. However, the subjectivity relates mainly to the separation of categories such as alarm calling or not, pair or just two individuals, etc. These judgements do not influence the evaluations significantly; most often, they simply move some birds between the minimum and maximum figure categories. A simple figure, the actual number of individuals recorded during the census period, can always be presented. Birds moving between snow-free areas during the census period present another bias that can be minimized only by timing the counts in adjacent areas as closely as possible and trying to avoid the most obvious mistakes.

The method also involves a certain bias introduced by pre-breeding birds that are still present during the census. This was clearly the case with common ringed plovers in the late season of 1999. This problem is particularly relevant for the red knots, since even pairs and singing individuals recorded in early June were accepted in the evaluations. But knots settle very early, and Whitfield et al. (1996) recorded song flight or other territorial activity in only 67% of the estimated population.

Birds supposed to have been missed during the initial total census were added from later surveys. This is also a weakness, because it adds another area of subjectivity and involves the risk of double recording. No doubt, however, some birds were actually missed during the initial census because they were already sitting tight on their nests, and this possibility had to be accounted for in the estimates. In practice, relatively few pairs/territories were added after the initial total census. However, several pairs/territories were repositioned following further dispersal and finding of nests or small young, while others were upgraded from uncertain pairs/territories after more "safe" records were added. Furthermore, the proportion of birds recorded already during the initial total count tended to increase over the years (Table 1) as I gained more experience with the area and its birds.

What we still do not know is the relation between the figures produced and the real numbers! Further studies are needed to produce the key for these results (see below).

Revised Population Totals

In my paper on wader populations and breeding phenologies in High Arctic Greenland (Meltofte, 1985), I ventured to present estimates for the total summer populations there and on Ellesmere Island and eastern Axel Heiberg Island in Canada, together with expected total autumn populations, including juveniles and immatures. These estimates showed vast discrepancies in comparison with mid-winter totals for the same populations, and this was especially true for the red knot, which is the only species/population for which we have relatively firm data on total winter numbers. In this population, the mid-winter total was much higher than the breeding population estimates, a discrepancy that is further pronounced because, as Whitfield et al. (1996) correctly pointed out, my estimate of the annual juvenile production was unrealistically high (two juveniles per pair).

I have now revised these estimates (Table 3) on the basis of the experiences presented here, the much larger number of census results obtained since 1985 (now a total of 34 census areas covering 425 km^2; Meltofte, 1985, 2000; Boertmann et al., 1991; Mortensen, 2000), and the same preconditions as in Meltofte (1985). For Canada, this involves the entire range of the populations in question, and not only Ellesmere and eastern Axel Heiberg Islands, as in my 1985 paper. For red knots in High Arctic Greenland, the increased estimates apply primarily to the southern half of Northeast Greenland, as low numbers in the central and northern parts were confirmed by Boertmann et al. (1991). For the red knot in Canada, I have used the estimate given by Whitfield et al. (1996). This means that the expected winter population is still significantly short of actual population counts in Europe, even though the population apparently experienced a low of around 350 000 birds in the mid 1980s (Davidson and Wilson, 1992), when a number of the summer population density censuses were made. This still means that the Canadian total should be more than doubled to obtain better accordance. It may be that such a doubling is not unrealistic, since *C. c. islandica* knots breed even on Prince of Wales Island

TABLE 3. Crude estimates of the sizes of Nearctic wader populations wintering in the Old World, based on summer population density censuses summarized by Meltofte (1985, 2000), Boertmann et al. (1991), and Mortensen (2000). The estimate for red knot in Canada is from Whitfield et al. (1996).

Species	Greenland Pairs	Canada Pairs	Total Pairs	Winter Population[1]	Winter Counts[2]
Common ringed plover	30 000 – 60 000	500 – 1 000	30 000 – 60 000	90 000 – 180 000	(187 000)
Red knot	15 000 – 30 000	41 000	55 000 – 70 000	200 000 – 250 000	450 000
Sanderling	25 000 – 50 000	0 ?[3]	25 000 – 50 000	75 000 – 150 000	(123 000)
Dunlin	7000 – 15 000	0	7000 – 15 000	20 000 – 45 000	8000 – 25 000
Ruddy turnstone	20 000 – 40 000	15 000 – 30 000	35 000 – 70 000	120 000 – 245 000	89 000

[1] Estimated mid-winter populations are based on the summer population estimates plus an average of one juvenile still alive per pair (and, in red knot and ruddy turnstone, a further 50% of these surviving as nonbreeding immatures until the next winter).

[2] "Winter counts" are the most recent estimates from the Wader Study Group (N. Davidson, pers. comm. 2000, Kirby et al., in press), except for dunlin (see text). Here, numbers in parentheses denote totals for both Nearctic and Palaearctic populations wintering in the same areas.

[3] The question mark for Canadian sanderling represents the possibility that some birds from northeastern Canada migrate to the Old World.

south of 75˚N in the Canadian Arctic Archipelago (Godfrey, 1992), and population densities have never been established for the western part of the range. Another major uncertainty is the proportion of juveniles and immatures in the winter population, but few appropriate data are available. Among red knots caught in September–May during 1963 – 98 by the Wash Wader Ringing Group in the United Kingdom, 18.8% were first winter birds (N = 37 189; Phil Ireland, pers. comm. 2000). Catches in cannon nets and mist nets involve certain biases, but compared to the 28% juveniles supposed to exist in the calculations presented above (Table 3), the data suggest that my estimates of winter population may even be too high. The alternative explanation, that wintering knots in Europe include Siberian *C. c. canutus* (Davidson and Wilson, 1992; Tomkovich and Soloviev, 1996), just makes the discrepancy between winter population counts and summer distribution and densities in Siberia even more dramatic.

The possibility also exists that significant numbers of nonbreeding immatures roam the breeding grounds and are missed at the population density censuses. My study at Danmarkshavn in 1975 (Meltofte, 1979) showed that relatively small numbers of immatures appear, but most of them apparently mate or occupy (marginal?) territories, or both. Hence, they should be covered at the breeding censuses (Meltofte, 1985). At least this is the case (and the intention) of the census method applied at Zackenberg (see above).

The new minimum estimates for the other species are in better accordance with the mid-winter counts. However, the maximum estimates for common ringed plover, sanderling, and ruddy turnstone are apparently too high, not leaving much room for Palearctic populations of ringed plover and sanderling. These high estimates may be due to overestimation of the maximum breeding populations, but they are more likely due to incomplete coverage of the non-estuary parts of their wintering grounds, so that the winter estimates for these species are too low. For the dunlin, we have only a tentative estimate of a proportion of 1 – 3% *C. alpina arctica* (the subspecies breeding exclusively in High Arctic Greenland) among the one million mainly Icelandic *C. a. schinzii* wintering in West Africa (Pienkowski and Dick, 1975; Kersten in Wymenga et al., 1990). This proportion is in reasonably good accordance with the breeding population estimate.

Future Research Needs

What we need now are some in-depth studies on the demography (e.g., proportion and performance of nonbreeders; see Meltofte, 1979, 1985), behaviour, and detectability of waders during different stages of the breeding cycle—not only in the Arctic, but in all relevant areas. There is growing evidence that most breeding wader censuses in the past (and present) have underestimated populations significantly (O. Thorup, pers. comm. 2000). Such studies should be performed not only in key areas, but over a range of habitats with varying densities, as the behaviour and demography of the birds is related to their density in the area in question. Not only do the birds' reactions vary with breeding stage and density, but behaviour is also highly individual. It may vary according to time of day or weather, and apparently depends from time to time on all kinds of circumstances, including the mode of the individual bird. However, it should be possible to recommend more secure ways of obtaining realistic figures. I hope that the present paper may at least provoke some more critical attitudes toward these problems.

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