Occurrence and habitat choice of waders in a high mountain sedimentation flat on Hardangervidda, South Norway

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Studies of the occurrence and nesting habitat choice of waders were conducted at Finsefetene (1200 m a.s.l.), a high mountain sedimentation flat on the Hardangervidda plateau, South Norway during 1967-1984. Eight species occurred in the study area during the period, either regularly such as *Calidris temminckii, Actitis hypoleucos, Charadrius hiaticula, Calidris alpina*, or occasionally, such as *Tringa totanus, Calidris maritima, Pluvialis apricaria* and *Phalaropus lobatus*. The densities of the whole wader community on the sedimentation flat were related to the proportion of snow-free areas at Finse around 10 July, and on the date when Finsefetene becomes totally snow-free (DFSF). Of the eight species, only *C. temminckii* and *P. lobatus* were found to be positively correlated with the extent of snow-free area, while *C. alpina* and *C. lobatus* were positively correlated with DFSF. In low density years the nests were usually placed in the same locations, these obviously being optimal sites. The majority of *C. temminckii* nests were located in the two intermediate fen vegetation associations, and according to its availability the Caricion canescentis-nigrae was clearly selected for. Two other preferred plant associations on drier ground, Lactucion alpinae and Arctostaphyleto-Cetrarion nivalis, were also selected for. Nest location preferences for vegetation associations are also indicated for the other wader species, but the data on these are limited. Changes in river flow causing varying water levels in the surroundings are a pronounced ecological trait on Finsefetene. In years with a heavy spring flood many nests would be submerged. The location of the nests in relation to a so-called «Zero point», varied from 34 cm below to 210 cm above. In high density years the nests of the most common species, *C. temminckii*, were spread over most of the flat. In years with a late spring flood, after the nesting had started, some low situated nests were flooded. To visualize the wader community pattern, the distribution of the variable number and scattered nest locations were plotted on maps. Details in nest locations of *C. temminckii* are given for each year; for the other recorded species the map covers all years. The Finsefetene sedimentation flat proved to be a valuable high mountain habitat for wader populations on Hardangervidda.

Key words: Habitat choice, waders, Hardangervidda

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INTRODUCTION

Waders are characteristic components of south Norwegian high mountain bird communities (Haftorn 1971, Østbye *et al*. 2007). They occur in most habitats, with wetlands as the preferred breeding ground for most of the species. Long-term studies have shown that there are great variations from year to year in population densities, synchronous with the variations in the densities of passerines and small rodents (Østbye *et al*. 2002, 2007). The variations in the wader community were related to the amount of snow-free area at the time when the birds arrive at their breeding grounds in the spring.

In an 18-year long study of the structure and dynamics of a wetland bird community (Østbye

et al. 2007), the occurrence and habitat choice of the wader species were studied with regard to nest recordings. Eight species of waders were recorded as territorial within the study area. Of these the Temminck's Stint *Calidris temminckii,* the Common Sandpiper *Actitis hypoleucos,* the Ringed Plover *Charadrius hiaticula* and the Dunlin *Calidris alpina* occurred «regularly» (i.e. occurring > half of the study period), while the Redshank *Tringa totanus,* the Purple Sandpiper *Calidris maritima,* the Golden Plover *Pluvialis apricaria* and the Red-necked Phalarope *Phalaropus lobatus* occurred less regularly.

This study describes their distribution and nesting habitats on a sedimentation flat with respect to preferred plant association, humidity and soil structure, height above the lowest point of the flat (Zero point; ZP), distance to water and wet bog, and to nests of members of own and other species as a measure of intra- and interspecific relations. How the different species coexist and use the different parts of this flat as breeding ground are also discussed, with emphasis on how the most numerous species, *C. temminckii*, used the area during the 18 years of study. Food and foraging is commented upon, also the recently detected wader foraging on microbial biofilms (see Kuwae *et al*. 2008). Such foraging might well have been of significance for the breeding waders in wetlands at the Finse sedimentation flat and its surroundings.

STUDY AREA

The study was conducted at Finse, in the northwestern part of the 10 000 km^2 large mountain plateau Hardangervidda, South Norway (60°36'N, 7°30'E). Bird censuses were carried out at Finsefetene, an approximately 1 km^2 large sedimentation flat, situated in the low alpine region at the bottom of the Finse valley, 1200 m a.s.l (Fig. 1). Water bodies, including a river, ponds and small lakes, cover 53% of the valley bottom, while the sedimentation flat constitutes 47%. Approximately 10 000 years ago this valley bottom was a lake, Fetavatn, which has since gradually been filled up with sediments. As recently as 150 years ago it was still characterised as lake, with only a smaller «dry» island in the central part (Østbye 2001).

This sedimentation flat is partly vegetated and is characterised as a wetland area (Fig. 2), dominated by intermediate fens and water bodies of variable size (see also photographs, maps over the area, vegetation maps and descriptions of vegetation types and their coverage of the total valley bottom in Lien *et al*. 1974, Østbye *et al*. 2002, 2007). When the water level is low, sand banks and stream beds are exposed along the river in the main channel, and part of the area is dotted with peaty «black holes» and other small water bodies. Pioneer ground without vegetation, river banks, silt and sandy dunes, where material is continuously deposited by the river, covers a considerable part (15%). The plant cover (Fig. 2) (vegetation units after Dahl 1956, Gjærevoll 1956 and Nordhagen 1936, 1943) of *the available breeding ground* is dominated by intermediate fens, Stygio-Caricion limosae Nordhagen 1943 (55%) and Caricion canescentis-nigrae Nordhagen 1936 (26%). Oligotrophic dry heath communities, including alpine ridge vegetation, Arctostaphyleto-Cetrarion nivalis Dahl 1956, early snow patch vegetation, Phyllodoco-Vaccinion myrtilli Nordhagen 1936, and late snow patch vegetation, Nardeto-Caricion bigelowii Nordhagen 1936, cover only a small part (2%). Dwarf willow snow patches, Cassiopeto-Salicion herbaceae Nordhagen 1936 including Polytrichion norvegicii Gjærevoll 1956, cover an even smaller part (1.5%). A eutrophic meadow community, Lactucion alpinae Nordhagen 1943, covers only a fraction of the area (0.5%).

MATERIAL AND METHODS

The material comprised data gathered over a period of 18 years (1967-84) on locations, descriptions and measurements from a total of 158 nests, of which 105 were of *C. temminckii* (Fig. 3), 16 of *A. hypoleucos*, 13 of *C. hiaticula*, 9 of *C. alpina*, 5 of *T. totanus*, 8 of *C. maritima*,

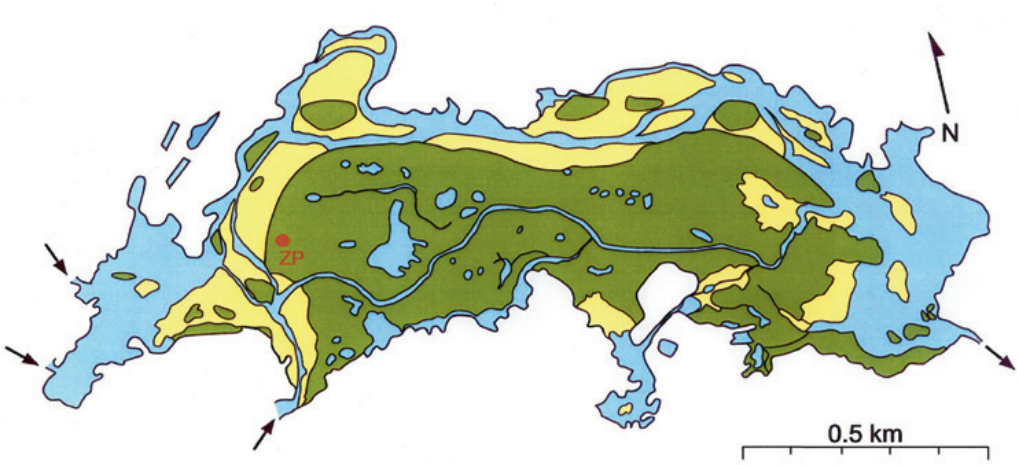


Figure 1. Physiographic map of the Finsefetene sedimentation flat on Hardangervidda, South Norway during summer, showing vegetated areas (green), the main river system and all the channels/smaller water bodies (blue) and details in the distribution of sanddunes and gravel bars (yellow); ZP – Zero Point (red). Arrows indicate in- and outflow of water. (From Østbye 2001).

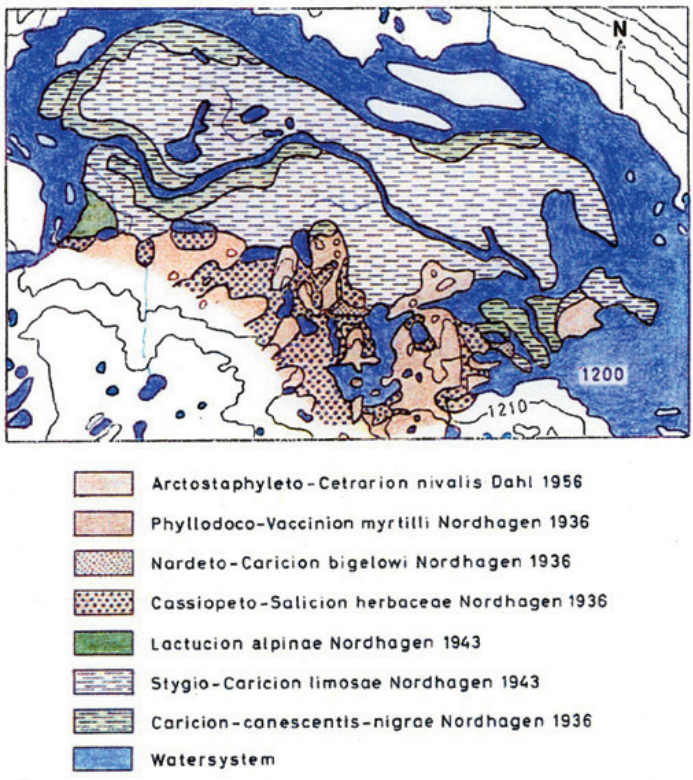


Figure 2. Map showing plant associations at the Finsefetene sedimentation flat on Hardangervidda, South Norway. Scale 1: 15 000. Contour intervals 10 m. (From Østbye et al. *1974).*

and one each of *P. apricaria* and *P. lobatus* (Fig. 4). The breeding population of wader species was surveyed at least 6 times each year from the last week of June until mid-July. The number of breeding birds was calculated from the number of nests found. Intensive searching during the census period resulted in successfully locating the number of nests matching the number of alarmed birds (for census methods; see Østbye *et al.* 2007). The very near surroundings of all recorded wader nests during this survey were described with regard to plant association, soil humidity and substrates. The whole sedimentation flat with the near surroundings was levelled with a precision of 1 cm (reference point hereafter referred to as Zero point, i.e. ZP). ZP is the lowest part of the flat on the western river bank, the site where flood water would flow in over the flat. With the help of this level map the height of the bottom of the nest cups over ZP could be calculated. The nearest distance to a water body, and to the dominating wet bog (Stygio-Caricion limosae) was measured. Furthermore intra- and interspecific relations were measured, on the basis of the distances to the nearest nest of own and other wader species. Clutch size and breeding success were also noted. In some years spring flooding could overflow and destroy many nests at the lowest parts of the flat, leaving only the higher located nests undisturbed. In a year with a late spring melt, larger areas of the flat could be covered with snow and ice when the birds started nesting. Only the higher situated parts were then available as nesting habitat. An index of snow-free habitat, based on the date for the total disappearance of snow from Finsefetene, was used to measure the breeding suitability of the area. A detailed study of production of invertebrate biomass of the study area was not undertaken, but occasional and short term samples are available and used for comments.

RESULTS

The species' preference for nest site plant association is shown in Table 1. Here the number and % of observed nests for each association, together with two indices of selectivity (see Alatalo 1981, Ivlev 1961) are given. In Alatalo's index a selection value equal to 1 indicates that the observed number of nests is equal to the expected value. This means that values larger than 1 indicate selection for, and values less than 1 no selection. Positive values in Ivlev's index indicate selection for the plant association, and negative values no selection. Zero value equals Alatalo's value of 1. As a rule both the indices gave the same result.

Table 2 shows the preferences for soil structures, given as number and % of nests found, as no values of availability could be given. The soil humidity was only subjectively judged, and this did not always allow an accurate description (depending on the weather conditions on preceding days) (Table 3).

The nest height (bottom of nest cup) above ZP is given in Table 4. There was great variation in nest height for most of the species. The most typical bog nesting species on average laid their nests about 50 cm above ZP. Minimum heights were often well under ZP, making nests vulnerable and exposed to «drowning» under flood situations. Maximum heights showed that several nests were laid well above the potential flood limit.

The distance from a nest to the nearest wet bog (Fetebog – Stygio-Caricion limosae) is given in Table 5, and to a water body in Table 6. Most species laid their nests relatively close to sites with bog conditions, some even in the bog. A few species nested on more highly situated areas on the border of the sedimentation flat. Usually all species nested within a relatively short distance from a water body, river, brook, or a smaller or larger pond or lake.

The distances to the nearest nest of own species is presented in Table 7, and to the nearest nest of other species in Table 8. Here there was a great variation from minimum to maximum distances, due to the yearly variations in population densities. In years with low densities we found long distances and shorter in years with high densities.

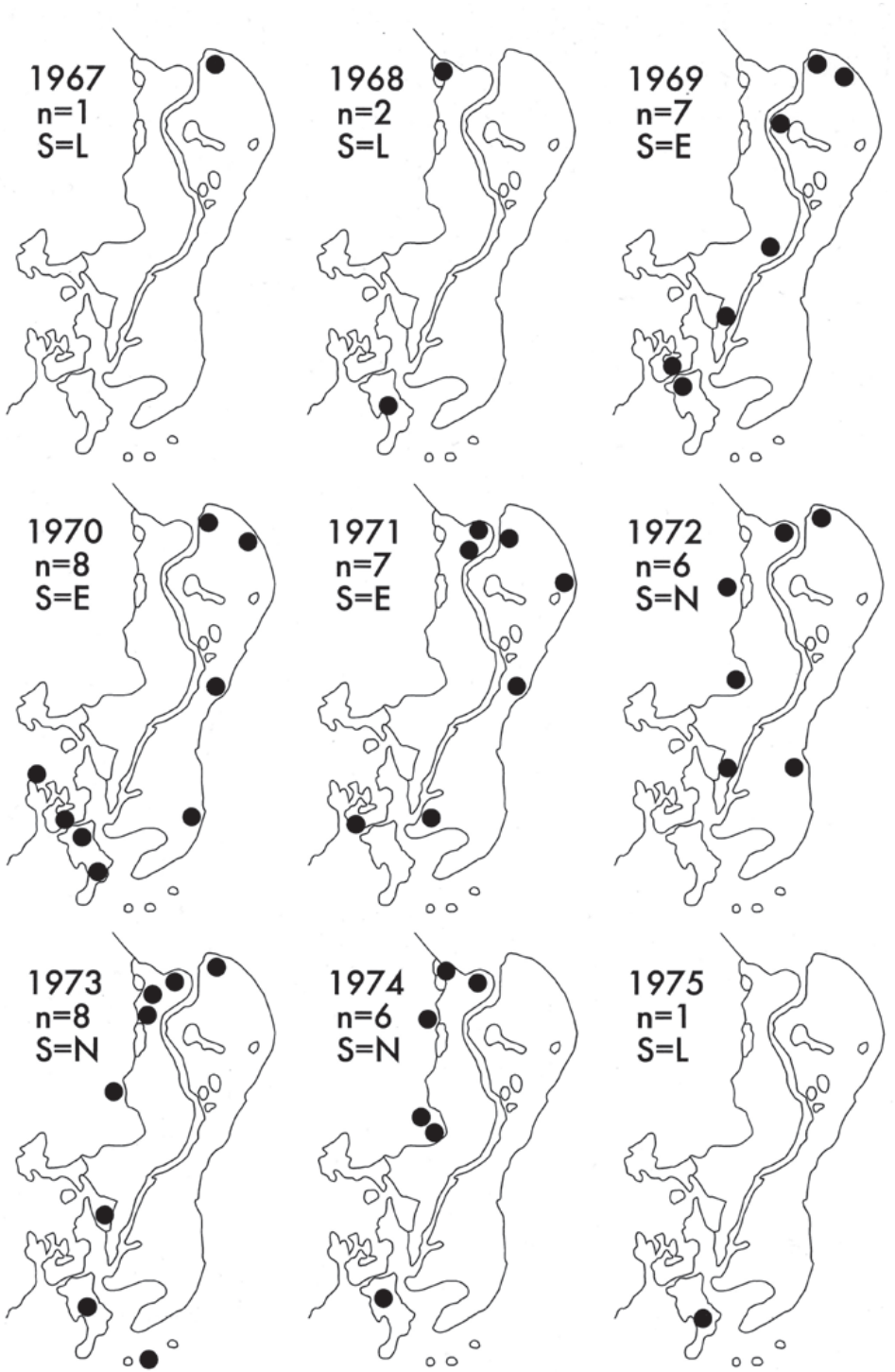
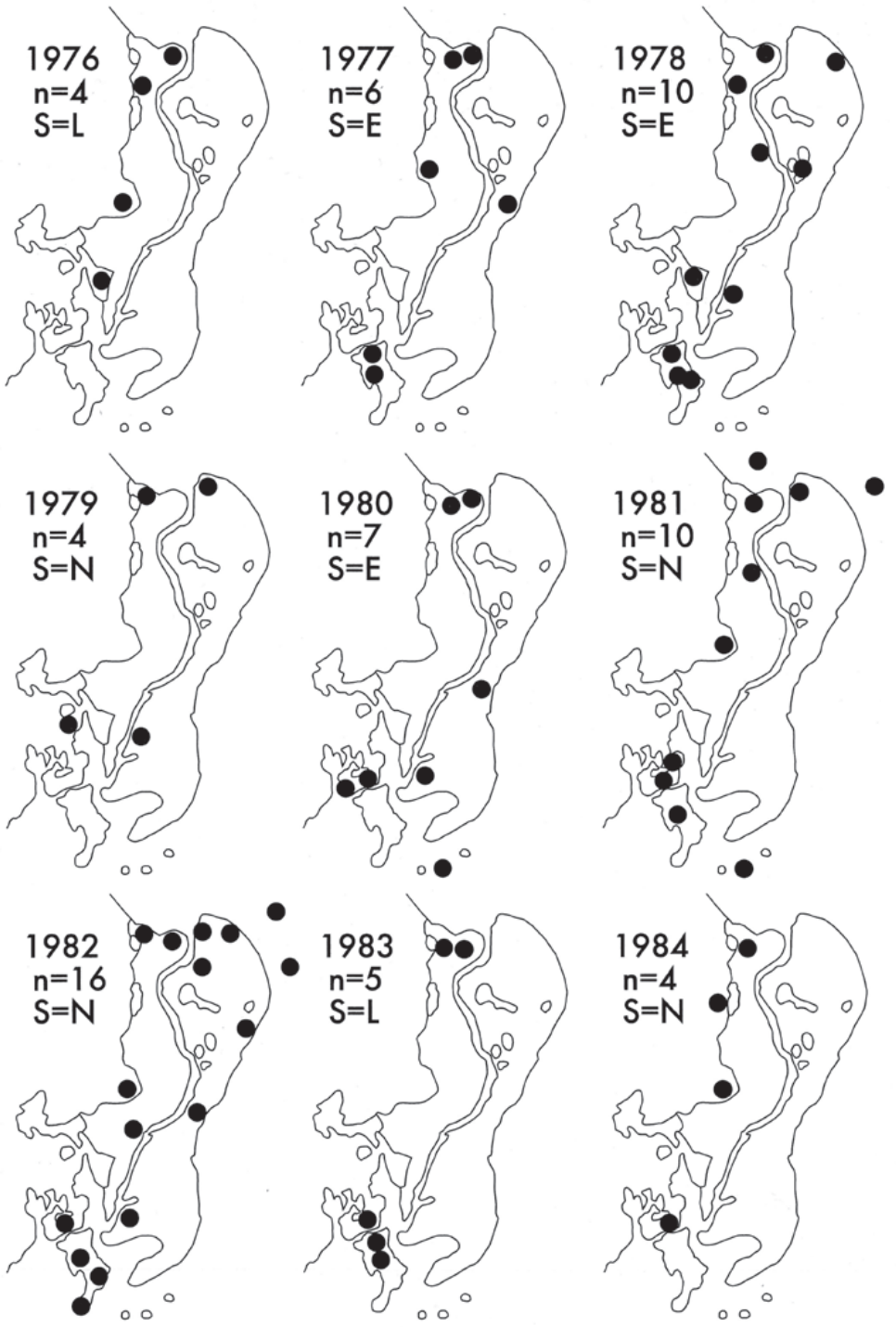


Figure 3. Yearly plots (solid circles) of the nests of C. temminckii during the study period 1967-1984; n = number of nests, S = snow melt, E = early, N = normal, L = late snowmelt.


1976
n=4
S=L
1977
n=6
S=E
1978
n=10
S=E
1979
n=4
S=N
1980
n=7
S=E
1981
n=10
S=N
1982
n=16
S=N
1983
n=5
S=L
1984
n=4
S=N

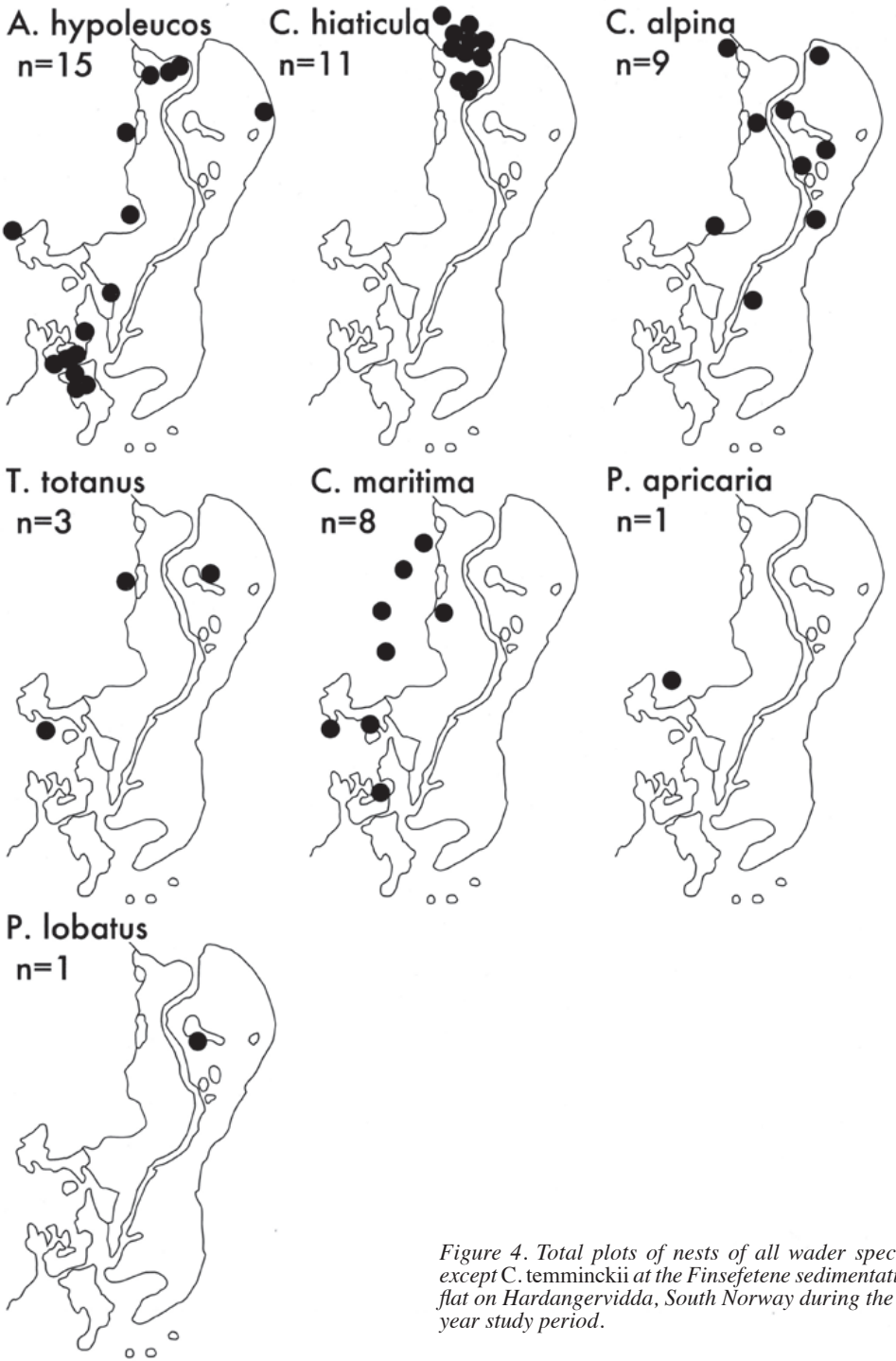


Figure 4. Total plots of nests of all wader species except C. temminckii *at the Finsefetene sedimentation flat on Hardangervidda, South Norway during the 18 year study period.*

Table 1. The species' preference for plant association. The coverage of the plant associations at Finsefetene is given in percent for each plant association. For each species, the total number of nests recorded in each association is presented, and the association's percent (in brackets) of the total number of nests recorded, as well as calculations of Alatalo's index (Alatalo 1981)/Ivlev's index (Ivlev 1961) of selectivity.

Species	Plant association					
	Caricion canescentis-nigrae	Stygio-Caricion limosae	Lactucion alpinae	Arctostaphyleto-Cetrarion nivalis	Cassiopeto-Salicion herbaceae	Pioneer ground without vegetation
	26%	55%	0.5%	2%	1.5%	15%
C. temminckii	40(45), 1.75/0.27	21(24), 0.48/-0.39	8(9), 9.09/0.89	19(22), 10.79/0.84	-	-
A. hypoleucos	11(69), 2.64/0.45	-	2(12), 12.50/0.92	3(19), 9.37/0.81	-	-
C. hiaticula	-	-	-	-	-	13(100), 6.67/0.74
C. alpina	4(44), 1.71/0.26	4(44), 0.81/-0.11	-	1(12), 5.55/0.086	-	-
T. totanus	-	-	-	5(100), 50.00/0.96	-	-
C. maritima	-	-	-	7(87), 43.75/0.95	1(13), 8.33/0.79	-
P. apricaria	-	-	-	-	1	-
P. lobatus	-	1	-	-	-	-

Table 2. The species' preference for soil (substratum) structure. For each species the total number of nests in each category with the occurrence in percent (in brackets) is presented.

Species	Substratum structure				
	Stony/hard (alluvial deposits)	Bare soil	Partly covered with vegetation	Covered with low vegetation	Covered with shrub
C. temminckii	-	-	-	26 (29)	62 (71)
A. hypoleucos	-	-	-	3 (19)	13 (81)
C. hiaticula	11 (85)	1 (8)	-	1 (8)	-
C. alpina	-	-	-	5 (56)	4 (44)
T. totanus	-	-	-	5 (100)	-
C. maritima	-	1 (12)	-	7 (88)	-
P. apricaria	-	-	-	1 (100)	-
P. lobatus	-	-	-	-	1 (100)

Table 3. The species' preference for soil humidity. For each species the total number of nests recorded in each category with the occurrence in percent (in brackets) is presented.

Species	Soil humidity			
	Dry	Semidry	Moist	Wet
C. temminckii	24 (27)	52 (59)	12 (14)	-
A. hypoleucos	4 (25)	12 (75)	-	-
C. hiaticula	13 (100)	-	-	-
C. alpina	-	3 (33)	6 (67)	-
T. totanus	-	1 (20)	4 (80)	-
C. maritima	4 (50)	4 (50)	-	-
P. apricaria	1 (100)	-	-	-
P. lobatus	-	-	-	1 (100)

Table 4. Height (cm) of nest above lowest part of Finsefetene (Zero point). SE = Standard error of the mean, n = number of nests.

Species	Mean height ± SE	Median height	Maximum height	Minimum height
C. temminckii	75 ± 8.011	53	400	-34
A. hypoleucos	86 ± 18.618	60	300	10
C. hiaticula	11 ± 8.737	30	55	-30
C. alpina	38 ± 10.773	35	100	-20
T. totanus	72 ± 35.972	50	200	-20
C. maritima	279 ± 82.168	220	800	100
P. apricaria	500 (n=1)	-	-	-
P. lobatus	-20 (n=1)	-	-	-

Table 5. Shortest distance (m) of nest to bog (Fetemyr – Stygio-Caricion limosae). SE = Standard error of the mean, n = number of nests.

Species	Mean distance ± SE	Median distance	Maximum distance	Minimum distance
C. temminckii	16 ± 1.730	10	80	0
A. hypoleucos	54 ± 20.863	30	300	0
C. hiaticula	18 ± 4.524	15	65	6
C. alpina	27 ± 13.085	10	100	0
T. totanus	24 ± 19.910 (n=3)		100	0
C. maritima	107 ± 22.892	135	175	15
P. apricaria	70 (n=1)	-	-	-
P. lobatus	0 (n=1)	-	-	-

Table 6. Shortest distance (m) of nest to water body. SE = Standard error of the mean, n = number of nests.

Species	Mean distance ± SE	Median distance	Maximum distance	Minimum distance
C. temminckii	14 ± 1.191	10	50	2
A. hypoleucos	13 ± 3.330	5	50	1
C. hiaticula	23 ± 5.099	15	60	9
C. alpina	17 ± 9.280	9	90	1
T. totanus	14 ± 4.848	10	30	5
C. maritima	19 ± 5.650	10	45	5
P. apricaria	18 (n=1)	-	-	-
P. lobatus	1 (n=1)	-	-	-

Table 7. Shortest distance (m) to nest of own species. SE = Standard error of the mean, n = number of nests.

Species	Mean distance ± SE	Median distance	Maximum distance	Minimum distance
C. temminckii	171 ± 18.105	150	1000	15
A. hypoleucos	638 ± 146.335	600	1250	70
C. alpina	675 ± 0 (n=2)	675	675	675
C. maritima	465 ± 77.942	465	600	330

Table 8. Shortest distance (m) to nest of other species. SE = Standard error of the mean, n = number of nests.

Species	Mean distance ± SE	Median distance	Maximum distance	Minimum distance
C. temminckii	268 ± 25.307	197	975	13
A. hypoleucos	125 ± 22.610	140	360	25
C. hiaticula	69 ± 14.532	50	180	15
C. alpina	98 ± 19.757	75	180	30
T. totanus	148 ± 24.290	150	200	80
C. maritima	278 ± 94.124	175	810	120
P. apricaria	345 (n=1)	-	-	-
P. lobatus	90 (n=1)	-	-	-

DISCUSSION

Wader reproductive strategies in harsh and variable high mountain habitats, must compromise adaptation to several environmental parameters, i.e. to 1) available food resources, 2) ground structure of a preferred nest habitat site and its physical availability during spring, and 3) habitat choice relevant to meet potential risk factors such as 3a) abrupt changes in physical habitat conditions (flooding, snow etc.) and 3b) occurrence of predators.

Food resources

As no direct food study was available, the potential of Finsefetene as feeding ground for high mountain waders could only be indirectly evaluated through occasional sampling. Wetlands like the Finsefetene sedimentation flat, with its high and variable stream flow and water level, and sediment influx and throughput, usually offer good areas for foraging to birds which choose to nest there. The flats are also much used as feeding ground by other groups of birds, such as passerines nesting in the vicinity. In this area *C. temminckii* very often lead their brood after hatching straight to the nearest pond or wet site rich in emerging chironomids, and stay there for several days (Breiehagen 1989). Incubating individuals were often seen foraging 50-600 m from their nest site (Breiehagen unpubl.). Observations and sampling show that a rich choice of many important forage items for waders occurred during the nesting season, both in the water bodies and the bog holes, as well as on the vegetated areas. We registered in the water bodies an abundance of Cladocera, Copepoda, and one very numerous population of Notostraca (*Lepidurus arcticus)*, *Pisidium*, Oligochaeta, Culicidae, Chironomidae, Ephemeroptera, Plecoptera, Trichoptera and Dytiscidae (Zoologisk feltstasjon 1967, Østbye 1969, 2001). In the vegetation communities on the drier ground we registered an abundance of Oligochaeta, Acari, Araneae, Opiliones, Collem-

bola, Orthoptera (only one species, *Melanoplus frigidus*), Homoptera, Hemiptera, Coleoptera, particularly Staphylinidae, Dytiscidae and Carabidae; Diptera, particularly Chironomidae, Culicidae and Tipulidae, Hymenoptera and Lepidoptera. Detailed studies of species and biomass during three successive seasons on a nearby tussock bog of the Oxycocco-Empetrion hermaphroditi Nordhagen 1936 association, showed a rich production of food objects during the nesting period of the wader species (Hågvar *et al*. 1978). Another recently detected potential general food resource available for wader consumption on the sedimentation flat, is biofilms (Kuwae *et al*. 2008), rich in proteins and carbohydrates. Alpine wetland areas have a considerable diversity of microorganisms organised in such biofilms («microbial mats») with extensive matrices of exopolysaccharides (EPS) or «slime», formed on suitable surfaces in and adjacent to water (Costerton *et al*. 1995). This is the case also in alpine oligotrophic brooks and streams in Norway (Mysterud & Laane 2008). Field surveys in Canada using video tape recordings have documented that a *Calidris* wader consumed superficial intertidal biofilms on marine sandbanks, and even possess anatomical tongue and beak adaptations for such consumption (Kuwae *et al*. 2008). During autumn the sedimentation flat was also used by pre-departure flocks of foraging young birds of up to 10 individuals. On August 3 1981, for instance, a foraging flock comprised individuals from six broods from two subplots (cf. Breiehagen 1989).

Nesting habitat availability

An environmental problem for waders breeding in high altitude mountains in the Scandes is habitat availability during early spring, as unpredictable seasonal flooding, snow melt and high and low temperatures fluctuate from year to year. The densities of the whole wader community in the sedimentation flat were related to the degree of snow-free area at Finse around 10 July, and to the date for Finsefetene 100% snow-free (DFSF) (Østbye *et al*. 2007). Of all the species, only *C. temminckii* and *P. lobatus* were found to be positively correlated with the degree of snow-free area and only *C. alpina* and *C. lobatus* were positively correlated with DFSF. This means that the species most inclined to place their nests in the lower parts of the sedimentation flat, require an almost snow-free breeding ground. Nests of most of the other species are usually placed at more elevated locations, which are snow-free earlier than the sedimentation flat.

Only for *C. temminckii* is there material enough to allow assessment of nest locations in space and time (Fig. 3). This plot of the yearly nest locations shows great variation from year to year, even though particular areas seem to be preferred most of the years. As referred to above, the number of nests of this species is related to the degree of absence of snow in the area. When compared with the «spring snow melt index» (SSMI) for the area (Østbye *et al*. 2007), it becomes obvious that in the years with a late snow melt (n=5) the number of nests was low, from one to five (mean 2.6). In years with a normal snowmelt (n=7) the highest densities were found, from four to 16 (mean 7.7). In two of these normal years the sex ratio of incubating birds was skewed towards excess of females (17 females vs. 6 males) in this subplot (cf. Breiehagen 1989). This support the view that females may utilize favourable feeding conditions locally by moving after the snow-melting zone before laying the last clutch themselves. However, if the snow melt is too late in one area in relation to the breeding phenology of the species (cf. Fig. 4; Breiehagen 1989), females laying their second clutches may already have moved to another nesting area with more favourable feeding conditions. In years with an early snowmelt (n=6), high densities between six and ten (mean 7.5), were found. In low density years the nests were usually placed in the same locations on the sedimentation flat; these obviously must be regarded as optimal sites.

Nesting habitat preference

A rough description of the nesting habitat preferences of different mountain wader species in Norway is given in Haftorn (1971). That material

embraces both his own observations as well as a summary from several other sources, such as Schaanning (1916), Collett (1921) and Løvenskiold (1947). In our discussion, only Haftorn (1971) will be referred to, if no other direct reference is given.

The majority of *C. temminckii* nests on the sedimentation flat were located in the two intermediate fen vegetation associations. When available the Caricion canescentis-nigrae was clearly selected for, rather than the Stygio-Caricion limosae. Two other preferred plant associations on drier ground were also selected for, namely Lactucion alpinae and Arctostaphyleto-Cetrarion nivalis. The nests were situated either on ground covered with low vegetation, mostly grass, sedges and heather species, or *Salix*-shrubs, the last mentioned being the most preferred. The soil humidity varied from dry to moist, with a preference for semidry condition. There was usually a short distance to the nearest water body and wet bog site. This is in accordance with information given in Haftorn (1971), who states that the species has a clear preference for low *Salix*-shrub habitat with variable degree of humidity, close to shallow water bodies.

A. hypoleucos too preferred the Caricion canescentis-nigrae association, but totally avoided the other fen type. Like *C. temminckii* it had a clear preference for the Lactucion alpinae and Arctostaphyleto-Cetrarion nivalis associations. The nests, very much like those seen in *C. temminckii*, were placed on vegetated soil sites, preferably in shrub associations and to a lesser degree soil covered with only short vegetation. The soil humidity at the nest locations was dry to semidry. Contrary to our observations, Haftorn (1971) claims that the species avoids bog habitats; otherwise our observations are in full agreement with his descriptions. The nests were as a rule situated at the same levels as those of *C. temminckii*, as were the distances to the nearest water body. The distance to the nearest bog was only slightly longer.

C. hiaticula had an exclusive preference for placing their nests on barren gravel banks or sand dunes only a very short distance away from the river. Dry ground, stony or hard alluvial deposits without vegetation were preferred; only one nest was found in a location with low vegetation. This is in accordance with Haftorn (1971), and although he states that nearness to water is no absolute condition, the nest could be situated a considerable distance from water, although water should always be visible from the nest. Our records show, however, that the nests were closer to water or to bogs.

C. alpina locations were quite similar to those of *A. hypoleucos* regarding preferences of vegetation associations for nesting. It too, like *C. temminckii* and *A. hypoleucos*, preferred ground covered either with low vegetation or shrub, in semidry or wet conditions. In wet conditions, the nest was situated on the top of a small tussock, i.e. in practically dry condition. As a rule it was situated close to a bog or a water body; the habitat preference of the species on the flat was in accordance with information in Haftorn (1971).

Of *T. totanus* only a few nests were recorded, all of them on the Arctostaphyleto-Cetrarion nivalis association, on semidry or wet soil covered with low vegetation, very close to a bog or water body, and with descriptions almost identical to those given by Haftorn (1971).

C. maritima had the strongest preference for the Arctostaphyleto-Cetrarion nivalis association, and a weaker preference for the Cassiopeto-Salicion herbaceae, on dry or semidry ground, mostly covered with low vegetation, or even on bare soil. The nests were usually not placed close to bogs or water bodies. In contrast, Haftorn (1971), states that it prefers to breed close to water; otherwise his descriptions on habitat preferences are in accordance with ours.

Only one nest of *P. apricaria* was recorded on the study plot, being located on a dry ridge in the Cassiopeto-Salicion herbacea association,

on higher ground covered with low vegetation, at a moderate distance to both water and bog. Many other nests of this species found during this survey in areas outside the study plot confirm the habitat description, as do information in Haftorn (1971).

Only one nest of *P. lobatus* was recorded during the years of study. This was placed on a tussock in completely wet surroundings in a small lake, in the Stygio-Caricion limosae association. The nest location is in accordance with Haftorn's (1971) descriptions, and with what we have found for other nests on the Hardangervidda.

Intra- and interspecific relations

Although the material is rather scanty, several observations were made indicating dynamic relations to pairs of own species as well as to pairs of other waders.

C. temminckii seems to tolerate nests of its own species even at a rather short distance. Collett (1921) even says it actually breeds in *colonies*; this is also well documented in population studies at several sites in the Finnish Bothnian Bay (Rönkä 1996). Short distances to nearest nest of own species is typical for years with high populations (cf. Breiehagen 1989). In years with a low density the distance between nesting pairs can be substantial, up to one km. Distances to the nearest nest of another wader species are usually longer. However, in some years such distances may be very short, indicating a certain degree of interspecific tolerance of a neighbour. It is however, unclear whether any form of «species packing» occurs among these species during years when 1) available nesting habitat space is severely restricted owing to late snowmelt or 2) there is an overabundance of food resources. In *A. hypoleucos* there was a considerable distance to the nearest nest of own species, which might just be a consequence of the yearly low breeding population of this species. Nests of other species seem to be moderately tolerated in their neighbourhood. Of *C. hiaticula* we found only one breeding pair per year, which means that nothing could be said about the distance to the nearest nest of own species. Nests of other species, however, were tolerated at a rather short distance. Because of low yearly breeding populations in *C. alpina*, little could be said about the shortest distance to nest of own species. The few years two pairs bred at the sedimentation flat, the distance between the nests were considerable, as was the distance to the nearest nest of other species. However, in some years *C. alpina* could tolerate a near neighbour. The distance to nearest nest of other species in *T. totanus* was considerable. As only one pair was recorded as breeding in a single year, no intraspecific nest relations were recorded. The distances to the nearest nest of own and other species in *C. maritima* were rather long on the flat; however, Collett (1921) once found three nests of *C. maritima* over a distance of 350 m indicating a certain intraspecific tolerance. The single nest found for *P. apricaria* was located a considerable distance away from the nearest nest of other species. The same holds for *P. lobatus*: only one nest, located at a considerable distance to the nearest nest of another species, was observed in the flat.

Flooding and late snowfall

Water-level changes in the river are a pronounced environmental trait of the Finse sedimentation flat, and the short distance from the Hardangerjøkulen glacier makes the stream fluctuations even more marked. The height of the nest in relation to ZP varied from 34 cm below to 210 cm above. In years with a heavy spring flood many nests situated on the sedimentation flat would then be «drowned» and only those on higher levels or on surrounding borders would escape being flooded. In high density years the nests of *C. temminckii* were spread over most of the flat. In years with a late spring flood, after the nesting had started, only the very low situated nests were at risk being «drowned». Altogether, during a three year study (1980-1982) of the nesting biology of *C. temminckii* in two additional plots in the same area, the main cause of nesting failure was flooding (12.2%) (Breiehagen 1989). In addition, in 1982, a year with a high density of nesting birds, it was mostly female-attended clutches

laid late in the nesting season that were flooded. Unfortunately we have no continuous records of floods or numbers of flooded nests, so the risk of being «drowned» at the different nesting places on the sedimentation flat could not be calculated. The nests of *C. hiaticula* were found at levels very close to ZP, or even lower. During the years we recorded that several of them were destroyed during moderate flooding in spring. Most nests of *C. alpina* were situated at a height just slightly above or below ZP, with high risk of destruction by flooding. The nest height of *T. totanus* was just a little above or below ZP, again risking being flooded. As all the nests recorded for *C. maritima* were situated on higher ground surrounding the core sedimentation flat, the height of the nests above ZP was considerable. A single nest for *P. lobatus* was located well below ZP. During one year all nests of *C. temminckii*, and even the nests of passerines breeding in areas surrounding the sedimentation flat, were abandoned owing to late and heavy snowfall.

Predation

Ground microvariation and vegetation structure (height, density) of surroundings close to nests may be crucial for survival in these wide open mountain habitats, strongly affecting the risk of predation. Adaptations for ground nesting birds must «balance» the sighting of predator and sentinel birds early enough to allow escape, and at the same time have cover enough for optimal concealment of nest, egg clutch and the breeding bird. Having a sentinel bird is the case for all species except *C. temminckii*, where the female leaves the nesting locality when the clutch is laid, and the male takes over brooding and is left to himself. The female always changes mates between the laying of successive clutches and invariably incubates the second clutch herself in another area, but sometimes quite nearby her last mate (cf. Fig. 3; Breiehagen 1989). Although high-mountain wader eggs as a rule are brilliantly camouflaged, and nests most often well concealed, habitat structure close to nests is certainly of importance in wader defensive strategies, because loss to predation is often considerable in wader populations (Koivula & Rönkä 1998). Both avian and mammalian predators regularly visit the sedimentation flat, especially during rodent highs. Species of corvids, i.e. Raven *Corvus corax*, Hooded Crow *Corvus corone*, birds of prey such as the Rough-legged Buzzard *Buteo lagopus*, Kestrel *Falco tinnunculus* and others, and carnivores such as the Red fox *Vulpes vulpes*, Arctic fox *Alopex lagopus*, American mink *Mustela vison* and smaller mustelids are observed in the area. The Common Gull *Larus canus* is also resident in the area during the summer season, well known as an important nest predator from studies in Finland (Rönkä *et al*. 2006).

In a 19-year study of nesting habitat changes in *C. temminckii* along the Baltic coasts of Finland (Koivula & Rönkä 1998), the factors affecting breeding success and ultimate population dynamics were investigated. The authors concluded that nesting habitat characteristics such as visibility from the nest and sentinel birds influence the effectiveness of the nest defence strategy of this species. Therefore, it is essential that there is at least some space with moderate visibility around the nest. This might also explain the species preference for the two intermediate fen vegetation associations at the edges of Finsefetene, as both have a certain density of *Salix* shrub. Compared with the alpine breeding population at Finse, the predation rate was very high in the Baltic sites, being 10.4% (Breiehagen 1989) vs. 87.7%, with an increase in predation rate from 48.9 % during the 19-years period. However, in the Baltic area this was mainly due to habitat deterioration (Rönkä *et al*. 2006), several species are vulnerable to changes in habitat structure, among others regrowth of earlier open habitat.

Concluding comments

The Finsefetene sedimentation flat proved well suited to surveying wader populations, although most of the species occurred in scattered distribution and was very variable in number. For comparison, the total numbers of nest locations of *C. temminckii* (see Fig. 3) and the other recorded species (see Fig. 4) covering all years, have been

presented. Even if the number of nests for each species is low, some of the birds show a tendency to use the same locations (and same type of terrain) for nesting most of the years. *A. hypoleucos* used more highly situated areas near running water. *C. hiaticula* nested exclusively on barren sand dunes and gravel banks, either close to the river or a little distance away, but then usually close to a small brook. *C. alpina* choose lower locations on the main wet bog, usually close to running water. *C. maritima* were normally found on more elevated dry land at the border of the flat, while *T. totanus* were found both there and on the lower wet part of the flat. *P. lobatus* was, as expected, found nesting only on the wettest part of the flat, on a tuft of grass in a small lake, the only year it was recorded. *P. apricaria* is only represented with one nest in this survey, on drier land situated at the border of the flat. For most of the years it was recorded as territorial in the near surroundings of the sedimentation flat, but with territories stretching away from the border of Finsefetene up to higher altitudes. Wader food ecology information from high mountain habitats in Norway is scattered and incomplete. The recently detected biofilm consumption could also have been an important source of foraging in the study area. The food ecology of waders during breeding in high altitude habitats is in need of further study.

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SAMMENDRAG

Forekomst og habitatvalg hos vadere på en sedimentasjonsflate i høyfjellet på Hardangervidda, Sør Norge.
Studier av forekomst og valg av reirhabitat ble gjennomført på Finsefetene (1200 m o.h.), en sedimentasjonsflate på Hardangerviddaplatået, Sør-Norge, i perioden 1967-1984. Åtte arter opptrådte i studieområdet i undersøkelsesperioden, enten med regelmessig forekomst slik som *Calidris temminckii, Actitis hypoleucos, Charadrius hiaticula* og *Calidris alpina*, eller med mer tilfeldig forekomst slik som *Tringa totanus, Calidris maritima, Pluvialis apricaria* og *Phalaropus lobatus*. Undersøkelser over tilgjengelige næringsressurser ble utført ved tilfeldige, korte stikkprøver, som viste at en lang og variert liste over grupper av invertebrater utgjorde tilgjengelig biomasse for vadere. Våtmark som Finsefetene med sin skiftende vannstrøm og store tilførsler av sedimenter, utgjør vanligvis gode furasjeringsområder for vadere, men tilgjengelig areal av reirhabitat om våren er høyst variabelt fra år til år. Tettheten av hele vadersamfunnet på sedimentasjonsflaten var relatert til graden av snøfritt areal på Finse ca. 10. juli, og datoen når Finsefetene ble 100% snøfritt (DSFS). Blant artene var det bare *C. temminckii* og *P. lobatus* som var positivt korrelert med graden av snøfritt areal; *C. alpina* og *C. lobatus* var positivt korrelert med DSFS. I år med lav tetthet var reirene vanligvis plassert på de samme lokalitetene; disse var tydeligvis optimale. Reproduktive strategier hos vadere i ugjestmilde og variable leveområder i høyfjellet må utgjøre kompromisser med tilpasning til flere miljøvariable samtidig. Tilgjengelige næringsressurser, optimal topografisk plassering (økt høyde reduserer risiko for «drukning»), mikrovariasjon i marksjikt og vegetasjonsstruktur (høyde, tetthet) i reirets umiddelbare nærhet, kan være kritisk for gjennomføring av optimal flukt- og forsvarsatferd, og dermed for overlevingen i disse åpne fjellområdene. Bakkehekkere er generelt svært sårbare for predasjon.

De fleste av reirene til *C. temminckii* var plassert i to intermediære myrsamfunn, og i forhold til forekomsten var typen Caricion canescentis-nigrae klart selektert. To andre plantesamfunn på tørrere mark, Lactucion alpinae og Arctostaphyleto-Cetrarion nivalis, ble også foretrukket. Reirene var enten plassert på mark med lavvokst vegetasjon, for det meste gras, starr og lyngarter, eller i vierkratt, det sistnevnte var klart foretrukket. *A. hypoleucos* foretrakk også Caricion canescentis-nigrae samfunn, og hadde en klar preferanse for de to samfunnene Lactucion alpinae and Arctostaphyleto-Cetrarion nivalis. *C. hiaticula* foretrakk ensidig å plassere reirene på nakne grus- eller sandbanker i kort avstand fra elva. *C. alpina*-lokalitetene var ganske like de som ble påvist hos *A. hypoleucos*, når det gjaldt foretrukne vegetasjonssamfunn. De få reirene til *T. totanus* ble alle funnet i Arctostaphyleto-Cetrarion nivalis samfunn. *C. maritima* hadde også størst preferanse for Arctostaphyleto-Cetrarion nivalis samfunn, og en litt svakere preferanse for Cassiopeto-Salicion herbaceae. Alle lå på lokaliteter som for det meste var dekket av lavvokst vegetasjon, eller til og med direkte på bart jordsmonn. Bare ett reir til *P. apricaria* ble påvist i studieområdet, dette lå på en tørr rygg i Cassiopeto-Salicion herbacea samfunn. Det eneste reiret av *P. lobatus* ble lokalisert på en tue i Stygio-Caricion limosae samfunn i fullstendig våte omgivelser i en liten sjø.

Intra- and interspesifikk toleranse kan være viktig for arter som lever i områder hvor arealet av reirhabitat er begrenset; for å beskrive dette målte vi avstanden til nærmeste reir av samme art og til andre arter. For de fleste artene var det stor variasjon mellom minimums- og maksimumsavstander, noe som hadde sin årsak i den årlige variasjonen i bestandstetthet.

Raske endringer i vannstrømmen i elva som forårsaker varierende vann-nivå i omgivelsene, er et markert økologisk trekk ved Finsefetene. Høyden i beliggenheten av reirene over et såkalt Nullpunkt (ZP) varierte fra 34 cm under, til 210 cm over. Under stor vårflom kan mange reir være utsatt. I år med stor tetthet av den vanligste arten, *C. temminckii*, forekom den spredt over nesten hele området. I år med sein vårflom, etter at reirene var etablert, ble flere av de som lå lavest oversvømt. Bakkehekkende vadere er også sårbare for tap til predasjon. Tilpasningene forbundet med valg av reirsted må «balansere» muligheten til å få øye på predatoren og se vaktfuglen tidlig nok til å unnslippe, og samtidig ha nok skjul for optimal kamuflasje av reir, eggkull og hekkefuglen. Dette gjelder for alle artene bortsett fra *C. temminckii*, hvor hunnen forlater reirlokaliteten da første kull er fullagt og hannen overtar rugingen og blir overlatt til seg selv.

For å synliggjøre mønsteret i fordelingen av vadersamfunnet, ble fordelingen og det varierende antall reirsteder plottet på oversiktskarter. Detaljer i fordeling hos *C. temminckii* er vist for hvert enkelt år, for de andre artene dekker plottingen alle årene. Finsefetene utgjør ved sin mangfoldighet av arter et verdifullt leveområde for bestander av vadere på Hardangervidda.

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