Structure and dynamics of a high mountain wetland bird community in southern Norway: An 18-year study of waders and gulls

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Østbye, E., Hogstad, O., Østbye, K., Lien, L., Framstad, E. & Breiehagen, T. 2007. Structure and dynamics of a high mountain wetland bird community in southern Norway: An 18-year study of waders and gulls. - Ornis Norvegica 30: 4-20.

We studied the breeding bird density of wader and gull species for 18 years (1967-1984) at a study plot at Finse (1200 m a.s.l.) in the northwestern part of the 10 000 km^2 high mountain plateau Hardangervidda, South Norway (60°36'N, 7°30'E). The study plot was a 1 km^2 large sedimentation flat in the bottom of the Finse Valley.

Eight species of waders were recorded as territorial, and their combined densities varied from 2 to 19 (mean 10) territories/km^2. Four species, the Temminck's Stint, *Calidris temminckii*, the Common Sandpiper, *Actitis hypoleucos*, the Ringed Plover, *Charadrius hiaticula* and the Dunlin, *Calidris alpina*, occurred regularly (>half of the study period) and constituted about 87% of the annual community densities in the study plot. One species, *C. temminckii*, was the dominant species, and held on average 60% of the territories. Four species, the Redshank, *Tringa totanus*, the Purple Sandpiper, *Calidris maritima*, the Golden Plover, *Pluvialis apricaria*, and the Red-necked Phalarope, *Phalaropus lobatus*, occurred only irregularly, with a low number of territories, and did not breed every year. Only one gull species was recorded as territorial, the Common Gull, *Larus canus*, and the density varied from 1 to 5 (mean 2.4) territories/km^2.

The variations in density of the wader community was correlated positively with the mean temperature in June, and negatively with the NAO index for June, the date of snow-melt and the percentage of snow cover in the area, showing that an early snow-melt was important for the establishing of territories.

Both the wader community, the combined wader and gull community, each of the species *C. temminckii*, *C. alpina* and *P. lobatus* fluctuated in synchrony with the populations in the passerine community of the area. The wader community, the combined wader and gull community and the species *C. temminckii* and *L. canus* also varied with the fluctuations of the small rodent populations in the area.

The densities of territories of the different wader species are compared with literature data from other parts of their distributional area.

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INTRODUCTION

The great variation from year to year in population densities of small mammals and several bird species is a characteristic feature of boreal high mountain ecosystems. Our long-term studies in the high mountain ecosystem of Hardangervidda, South Norway, have generally confirmed the synchronous variation in the densities of passerines and small rodents (Lien *et al*. 1974, Stenseth *et al*. 1979, Østbye & Mysterud 1984, Østbye *et al*. 2002). This study reports a 18-year (1967-1984) long study of the structure and dynamics of a wader and gull bird community in a high mountain area of South Norway. The structure and dynamics of the passerine bird communities in the same area have earlier been reported (Østbye *et al*. 2002). In this mountain region there is a pronounced inter-annual variation in the amount of snow-free area at the time when the birds arrive at their nesting grounds in the spring. During the nesting season the weather and the continued snowmelt are also highly variable. One aim of this study has been to examine whether climatic factors prior to and during the nesting period have any influence on the population density of the waders. Furthermore, we have investigated the structure and stability of the bird population over time. Finally, we have tested if variations in the wader and gull populations coincide with the variations in other vertebrate populations in the area, here the passerines and the small rodents.

STUDY AREA

Habitats

The study was conducted at Finse, in the north-western part of the 10 000 km^2 large high mountain plateau Hardangervidda, South Norway (60°36'N, 7°30'E). Bird censuses were carried out in a 1 km^2 large sedimentation flat, Finsefetene, in the bottom of the Finse valley, 1200 m a.s.l. (Figure 1). The plot forms a component of an ecosystem model for the Finse area, based on a landscape transect of the Finse valley and the coverage of the different vegetation units of the area (mapped in 1972) (see photographs, map and descriptions of vegetation types and their coverage in Østbye *et al*. 2002). It is characterised as

Figure 1. The Finsefetene sedimentation flat, in a year with normal snow melt, 01 July 1991. Photo: E. Leslie.

a wet area, dominated by intermediate fens and water bodies, a large river, the Ustekveikja, and various ponds and small lakes (Figure 2). Water bodies are covering 53%. The plant cover (vegetation units after Dahl 1956, Gjærevoll 1956, Nordhagen 1936, 1943) is dominated by intermediate fens, Stygio-Caricion limosae Nordhagen 1943 and Caricion canescentis-nigrae Nordhagen 1936, covering approximately 38%. 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 approximately one percent. Part of the sedimentation flat is unvegetated sand and silt dunes, being continuously deposited by the river, covering approximately 8%. Due to this material transport from the nearby glacier Hardangerjøkulen, 73 km^2 in area, the sedimentation flat is increasing in size and amount of «dry» land every year. Approximately 10 000 years ago this valley bottom was a lake, Fetavatn, which has since gradually filled up with glacial sediments. Nearly 150 years ago it was still characterised as a lake, with only a smaller «dry» island in the middle part (Østbye 2001). Finsefetene is situated in the low alpine region.

Climate

Alpine areas are characterised by very variable weather conditions. Hardangervidda owes its variable weather conditions and its relatively mild climate to the prevailing warm, moisture-bearing westerlies and southwesterlies of the North Atlantic. Because of an orographic upglide forced upon these air currents at the western slopes and the leeward effects of the mountains at the eastern side of the mountain chain, a pronounced gradient in climate is experienced from west to east across Hardangervidda. The heaviest precipitation, the greatest amount of cloud cover and the most oceanic temperatures are therefore found in western parts of the area.

Weather records for June and July from the Finse meteorological station showing the yearly variation in mean temperature and precipitation during the study period are presented in Figure 3. The birds arrive in the Finse area in the beginning of June. The hatching of young takes place from the last half of June into the first half of July. The date for the total disappearance of snow from Finsefetene was used as a measure for the suitability of breeding conditions. An index of snow-free habitat covering the Finse area, based on the percentage of snow-free areas of the valley sides mapped around 10 June and 10 July, respectively, has been useful for estimating if the spring is early or late, and also for estimating the habitat availability (Figure 4).

METHODS

The Finsefetene sedimentation flat was surveyed by two to six observers walking 10-30 m apart. A marked trail was not used because of great variation in water level of the meander system. The flat was surveyed at least 6 times each year from the last week of June until mid-July. The number of territorial waders and gulls was estimated according to the number of nests found (territory=nest). Flight observations of alarmed birds indicated where nests could be searched for. Intensive searching during the census period resulted in successfully finding the number of nests matching the number of alarmed birds. *C. temminckii* normally has two nests per pair (see later in discussion), and it is therefore a question if the recorded number of nests should be divided by two to give the correct number of territories. Since our study plot is of relatively restricted size, we have chosen here to calculate the number of territories as equivalent to the number of nests found. In table 6, however, we have divided our number of recorded nests by two when comparing our data with other published data on the density of territories of the different species.

In order to study the effect of climatic factors on the population variation, we tested possible relationships (Spearman's rank correlation) to the local weather records of temperature and precipitation for the months of June and July (Det Norske Meteorologiske Institutt). The population variation was similarly tested against the NAO index (North Atlantic Oscillation; Hurrel 1995) for the same months. Finally, population variation was tested with our records for the date at which the snow cover had totally disappeared from the study plot, and against the amount of snow-free area in the nearby transect Blåisen during the breeding period (see Østbye *et al*. 2002). The snow-free date at Finsefetene very closely follows the general snow-melt in the surrounding north-facing and south-facing hillsides (r=0.64, P<0.005).

A relationship of fairly synchronous variation in number of passerine birds with the density of small rodents in the Finse area has been demonstrated (Østbye & Mysterud 1984, Østbye *et al*. 2002). The fluctuations in the relative density of the small rodents and passerine birds show a cyclic pattern with peak densities about every 3-4 years. We therefore tested if the population variation in waders and gulls was synchronous with the fluctuations of small rodents and passerine birds.

The time series of both climate and population variables may exhibit an autocorrelation structure, where observations of a given variable are correlated at specific time lags. Strong autocorrelation would invalidate the assumption of statistical independence of the observations and hence the inferences that can be made from simple correlations. However, the relatively short length of these time series makes it difficult to apply standard methods of time series analysis and verification of the autocorrelation structure (Box & Jenkins 1976). We have therefore limited our analysis to a cursory inspection of the sample autocorrelations for the first few time lags of the series, and have used these results as a background for interpretation of the biological significance of the simple correlations between variables.

RESULTS

Structure of the community

Eight species of waders were recorded as territorial within the sedimentation flat (Table 1). Their combined density varied from 2 to 19 territories/km^2, with a mean of 10.4 (Tables 1 & 2). The species richness varied from 2 to 6, with a mean of 4.3 species per year. The species diversity (Shannon's index H, cf. Magurran (1988)) varied from 0.88 to 2.28, with a mean of 1.57 (Table 1 & 2). Four species, *Calidris temminckii, Actitis hypoleucos, Charadrius hiaticula* and *Calidris alpina*, were regulars (occurring > half of the study period) and together constituted 67-100% (mean 93%) of the wader community. The irregulars, the other four species, *Tringa totanus, Calidris maritima, Pluvialis apricaria* and *Phalaropus lobatus*, occurred in only 8, 7, 4 and 3 years, respectively (Table 1). Only one species, *C. temminckii*, bred every year during the 18 year long study period. One gull species occurred, *Larus canus*, and the density varied from 1 to 5 territories/km^2, with a mean of 2.4. It had a regular appearance, breeding every year (Table 1).

The wader community varied considerably in density (CV about 43,5%; Table 2). Except for *C. temminckii* that was found to have territories every year, the other regular species and the four irregular species were present at low densities, and did not breed every year. *A. hypoleucos* occurred with a maximum of four territories in two years, whereas the others normally occurred with only one territory per year, very seldom with two or three (only *C. alpina* and *C. maritima*).

The relative species turnover rate in the community (for calculation see Østbye *et al*. 2002) varied during the study period from 0 to 1.5 (min. - max.) for any two consecutive years. The mean relative species turnover rate was rather high, 0.70 (Table 2).

C. temminckii had the highest yearly density except for three years, where it had about the

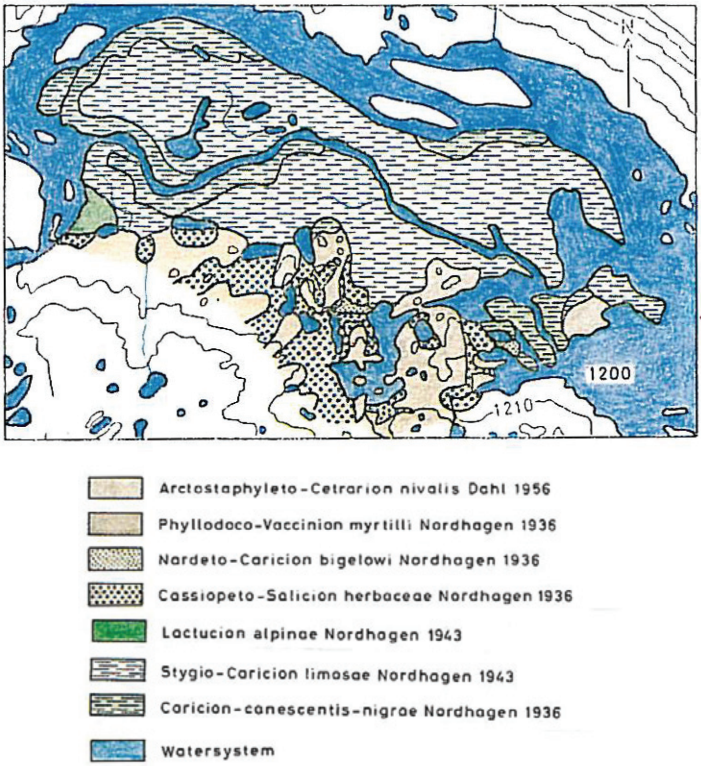

Figure 2. Vegetation map of the Finsefetene sedimentation flat. Scale 1: 15 000. Contour intervals 10 m. From Østbye et al. *(1974).*

same density as the next species. Apart from *C. temminckii*, only *A. hypoleucos* for six years occurred in a number slightly above the other regular and irregular species, which normally occurred with only one territory per breeding year.

Fluctuation patterns

The one dominant species and the most numerous of the incident wader species, *C. temminckii* and *A. hypoleucos*, respectively, as a rule showed rather similar fluctuation patterns, with high densities in the same years. All the other species of incidents and subdominants occurred in most cases with only one territory in some of the years (Figure 5).

Of the regular wader species, the population density of *C. temminckii* was the more stable (CV=58%). The other three regular species in comparison varied from 55 to 139%, whereas the four irregular species varied from 115 to 230% (Table 3).

To test the covariation between the species fluctuations, correlation matrices for all the wader species and the gull have been calculated (Table 4). Only two significant correlations were found, between *A. hypoleucos* and *C. alpina*, and *P. lobatus* and *L. canus*. *P. lobatus* only occurred in three years in which *L. canus* occurred in their highest numbers.

The densities of each of the species *C. temminckii, P. lobatus* and *L. canus,* together with the densities for waders, and wader and gull community, were found to be related to the percentage of snow-free area around 10 July (taken from the nearby situated Blåisen transect) (Table 5). When

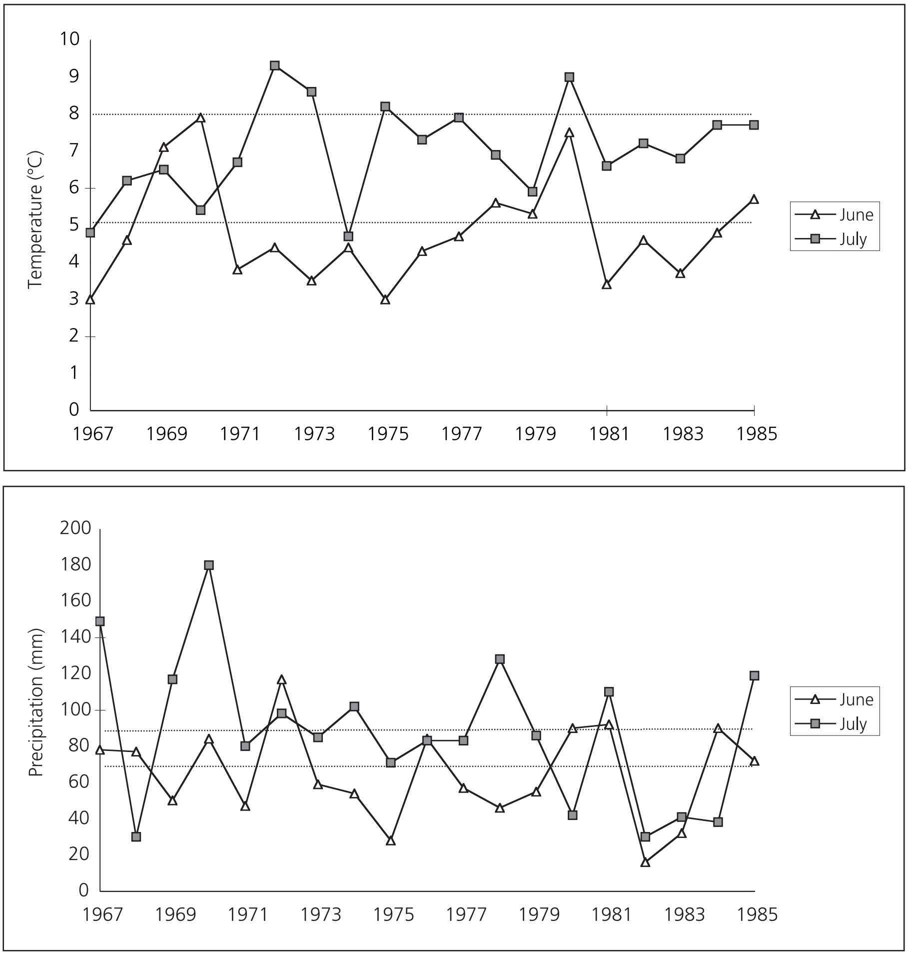

Figure 3. Mean monthly temperatures (°C) and precipitation (mm) for June and July 1967-1985 from the Finse meteorological station. Standard normals for 1961-1990 are indicated by dotted lines (temperatures: 5°C in June, 8°C in July; precipitation 69 mm in June and 88 mm in July). Data from the Norwegian Meteorological Institute.

using the date for Finsefetene 100% snow-free, only *C. alpina* and *P. lobatus*, together with the total wader, and wader/gull community were found to be related to the snow situation.

When correlating the mean temperatures and total precipitation for June and July with the total wader, and the total wader and gull density, only June temperatures were positively correlated. Of the different wader species *A. hypoleucos* was negatively correlated with the temperature for July. *C. temminckii* and *L. canus* were negatively correlated with the NAO index for June, as were the total wader and wader/gull community.

The total wader community and the combined wader and gull community co-varied with the fluctuations of the passerines in the Finse area (the Blåisen transect) (Table 4). Of the wader species, *C. temminckii*, *C. alpina* and *P. lobatus* showed a significant positive co-variation with the passerines.

The population densities of *C. temmincki,* and *L. canus*, as well as the wader and wader/gull community showed a positive co-variation with

Table 1. The Finsefetene sedimentation flat, 1967 - 1984. Annual number of territories/km² of the equitability, and the number of territories/km² of gulls.

Species	1967	1968	1969	1970	1971	1972	1973	1974	1975
C. temminckii	1	2	7	8	7	6	8	6	1
A. hypoleucos	2	1	4	4	1	1	-	3	-
C. hiaticula	1	1	-	1	1	1	1	1	-
C. alpina	-	-	-	1	1	1	-	2	-
T. totanus	-	-	1	-	1	-	1	-	-
C. maritima	2	2	1	-	-	-	-	1	1
P. apricaria	-	-	-	-	-	1	-	-	-
P. lobatus	-	-	1	1	1	-	-	-	-
No. of territories	6	6	14	15	12	10	10	13	2
No. of species	4	4	5	5	6	5	3	5	2
Diversity, H'	1.92	1.92	1.83	1.77	1.95	1.77	0.92	1.99	1.00
Equitability, E	0.96	0.96	0.79	0.76	0.75	0.76	0.58	0.86	1.00
L. canus	2	1	4	3	5	2	2	3	2

Table 2. Community parameters of the wader guild at the Finsefetene sedimentation flat, 1967 - 1984: Mean values ± SD of total density, species richness, species diversity index (H'), relative species turnover rate (RT, based on comparisons between successive years), coefficient of variation (CV). Snow free date is the mean date for Finsefetene 100% snow free at about 10. July.

Parameters	Estimates
Mean snow free date	20. June
Years	18
Mean density	10.44 ± 4.44
CV (density)	42.53
Species richness (mean number of species)	4.28 ± 1.18
CV (species richness)	27.57
Diversity (H')	1.57±0.44
CV (H')	28.02
Turnover rate (RT)	0.70
CV (RT)	49
Equitability (E)	0.77 ± 0.14

different wader species, with total number of wader territories, number of species, species diversity and

1976	1977	1978	1979	1980	1981	1982	1983	1984
4	6	10	4	7	10	16	5	4
1	1	2	1	2	2	1	1	-
-	-	1	1	1	1	1	1	1
-	-	1	1	3	1	-	-	-
-	-	-	1	1	-	1	1	1
-	-	1	-	1	-	-	-	-
1	1	-	1	-	-	-	-	-
-	-	-	-	-	-	-	-	-
6	8	15	9	15	14	19	8	6
3	3	5	6	6	4	4	4	3
1.25	1.06	1.56	2.28	2.15	1.29	0.88	1.55	1.25
0.79	0.67	0.67	0.88	0.83	0.65	0.44	0.77	0.79
2	3	2	2	2	2	3	2	2

Table 3. Mean density (territories/km²) and range (min. - max.) with standard deviation (SD), coefficient of variation of the mean (CV, in percent), mean relative density (density as percent of the total bird density), mean relative density as proportion of the total community (waders alone for the waders, waders and gulls combined for the gulls) (Dominants D>25%, Incidents I=5-25%, Subdominants S<5%), and frequency of yearly occurrence (%).

Species	Mean density	Min.-max. density	SD	CV	Relative density	Rel.dens. proportion	Frequency
C. temminckii	6.22	1 - 16	3.61	57.98	59.6	D	100
A. hypoleucos	1.50	0 - 4	1.20	80.03	14.4	I	83
C. hiaticula	0.78	0 - 1	0.43	55.00	14.4	I	78
C. alpina	0.61	0 - 3	0.85	139.06	5.8	I	44
T. totanus	0.44	0 - 1	0.51	115.04	4.2	S	44
C. maritima	0.50	0 - 2	0.71	141.42	4.8	S	39
P. apricaria	0.22	0 - 1	0.43	192.51	2.2	S	22
P. lobatus	0.17	0 - 1	0.38	230.09	1.6	S	17
Total	10.44	2 - 19	4.44	42.53	-	-	-
L. canus	2.39	1 - 5	0.92	260.67	18.6	I	100

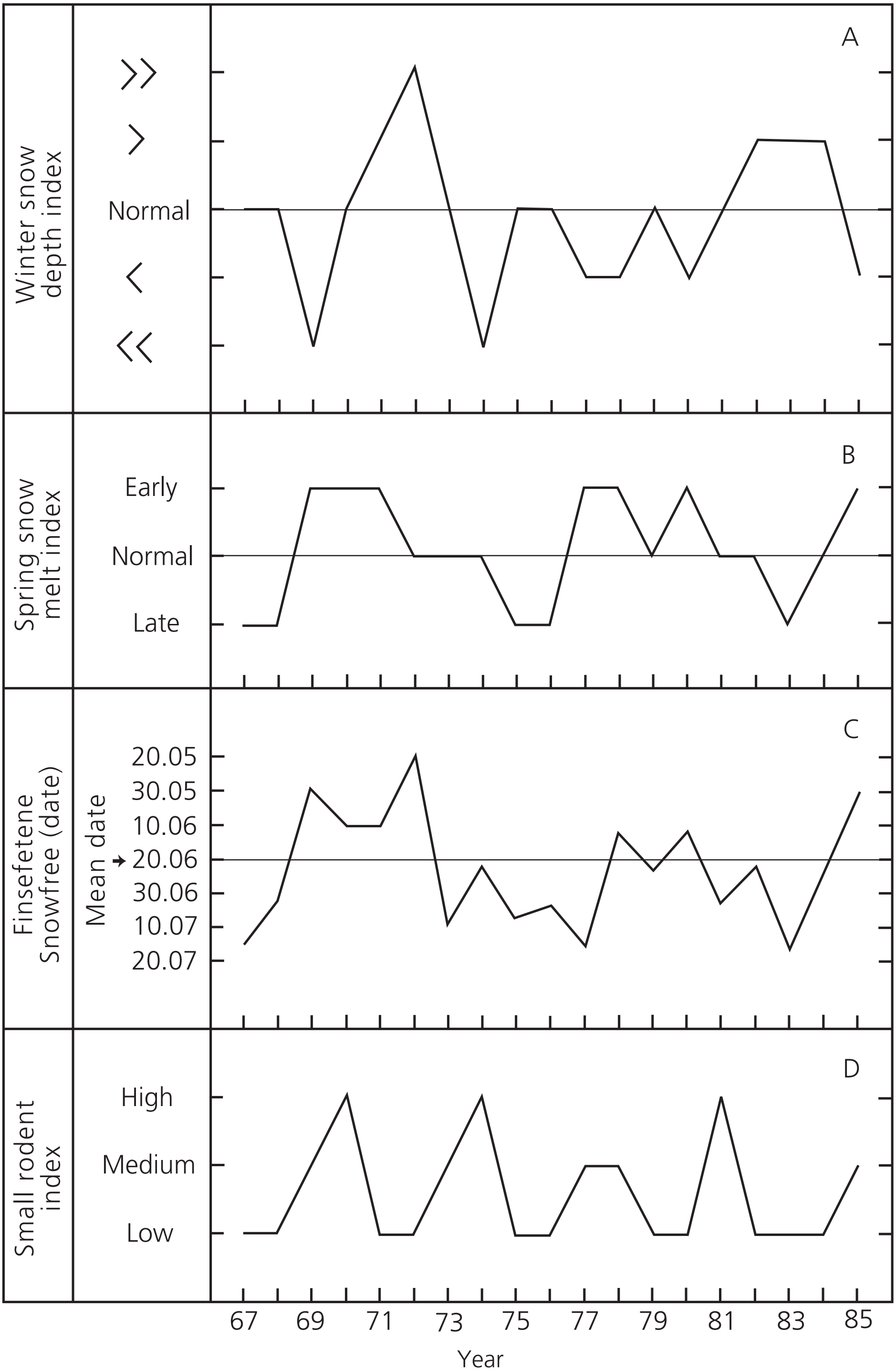

Figure 4. Index for depth of winter snow cover (A) and progression of spring snow melt (B) in the Finse area, as well as the date for Finsefetene being snow free (C), with variations in population level of small rodents (D). From Østbye et al. *(1989).*

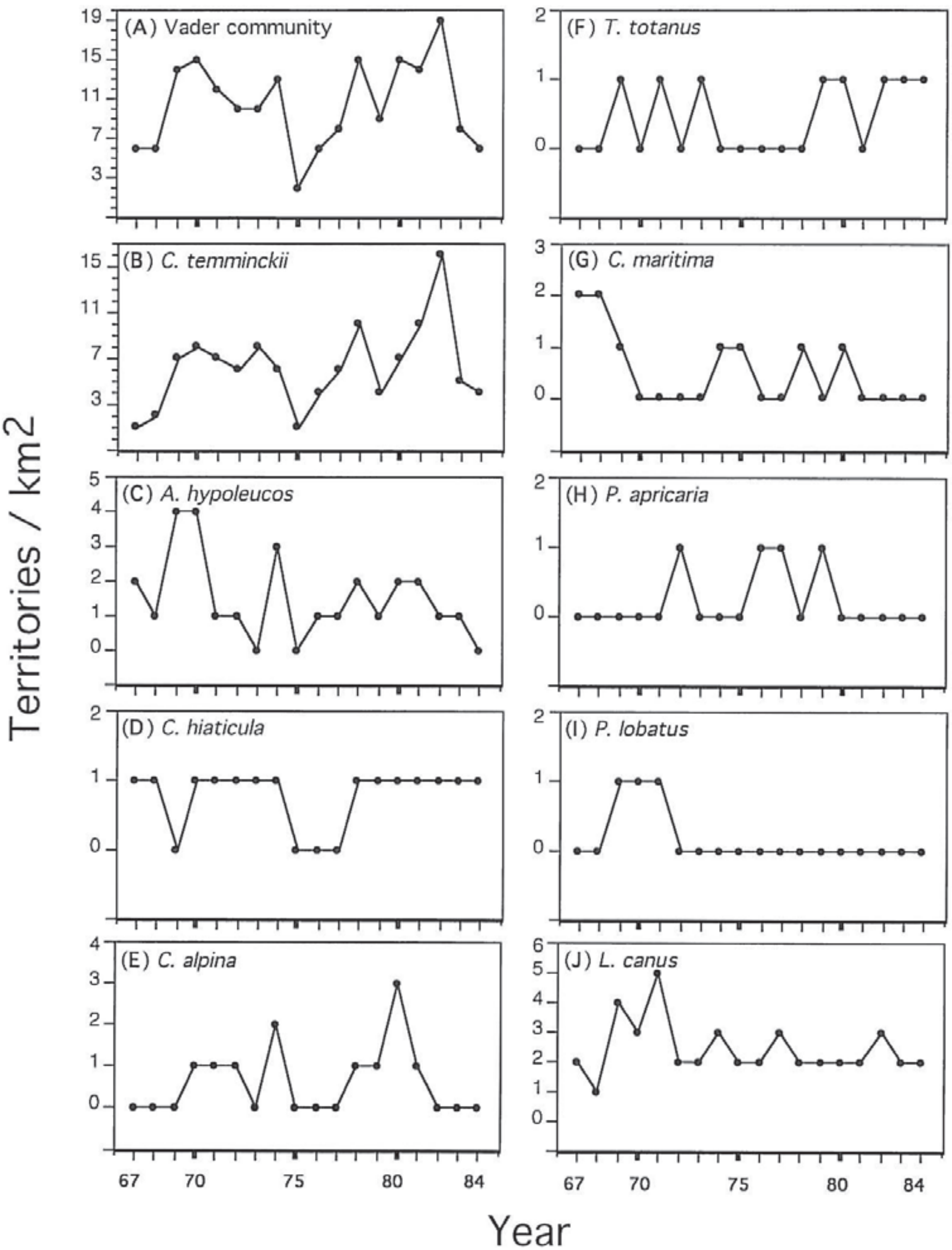

Figure 5. Fluctuations in density of the wader community (A), and the occurring species C. temminckii *(B),* A. hypoleucos *(C),* C. hiaticula *(D),* C. alpina *(E),* T. totanus *(F),* C. maritima *(G),* P. apricaria *(H),* P. lobatus *(I) and* L. canus *(J).*

the populations of small rodents that fluctuated regularly with peak densities about every 3-4 years (Table 4).

The time series 1967-1984

Although the time series of bird populations in this study span a considerable number of years, they still fall short of the requirements for standard time series analysis (Box & Jenkins 1976), where at least 50 observations are recommended. We therefore limit our assessment to the sample autocorrelations for the first few time lags of the relevant variables. For most of the climate variables, there were no significant autocorrelations for any of the time lags less than 10. The July NAO index exhibited significant autocorrelations at lags 1 (-0.46) and 5 (+0.46), but after fitting an autoregressive model to this index, there were still no significant relationships to any of the bird population series. The date of snow melt also exhibited significant autocorrelation at lag 5 (-0.50), but no suitable autoregressive model could be fitted. The relative density fluctuations for rodents did not show any significant autocorrelations. The passerines exhibited significant autocorrelation at lag 5 (-0.39), although no suitable autoregressive model could be fitted to this series. With one exception, none of the wader or gull species showed any significant autocorrelations. *P. lobatus* had a significant autocorrelation (0.59) at lag 1, a rather spurious result due to the occurrence of one territory in three consecutive years. The combined wader and wader/gull community showed significant autocorrelations at lag 6 (-0.40 and -0.41, respectively). No suitable autoregressive models could be fitted to these series. The lack of fit for autoregressive models for most of these series is mainly due to the shortness of the time series, combined with significant autocorrelations mainly at rather extended lags (5 and 6). Overall, it therefore seems reasonable to interpret the non-parametric correlations of tables 4 and 5 as expressions of co-variation between the relevant variables, although care should be taken in emphasising particular significance levels, especially for series with few non-zero observations.

Charadriiformes occurring in other parts of the Finse Valley

In the hill sides of the Finse valley, *P. apricaria* is common and regular on drier ridges and meadows, especially on the south-exposed side. *A. hypoleucos* is common and regular along rivers, brooks and water bodies. *C. temminckii*, *C. alpina* and *C. maritima* appear sparsely and irregularly in connection with small bogs. *Eudromias morinellus* is regular but occurring in low numbers in the upper part of the hillsides. *Gallinago gallinago* has been found more irregularly in occurrence, on small bogs in the valley sides. *Stercorarius longicaudus* is rare, only recorded breeding in south-facing hillsides in a few years with a very high peak in the lemming population.

DISCUSSION

The number of species of waders and gulls is low in the alpine region at Finse, with the number of breeding species varying from year to year. Eight species of waders and one gull species were recorded as breeders in the wetlands at the bottom of the Finsedalen valley. Four wader species were regulars, breeding at least half of the years of the study period, *C. temminckii, A. hypoleucos, C. hiaticula* and *C. alpina*. The other four species, *T. totanus, C. maritima, P. apricaria* and *P. lobatus*, were recorded as irregulars, being recorded as territorial less than half of the study period. The only gull species, *L. canus,* was regular, breeding every year, although in low numbers. All recorded species are typical alpine species, where *C. temminckii, A. hypoleucos, C. hiaticula, C. alpina, T. totanus, P. lobatus* and *L. canus* belong to a group of birds typical for both alpine areas and areas below the forest line, mainly open lands such as bogs and grasslands etc. (Svensson *et al*. 1984). Two species belong to a group of birds confined to alpine habitats, *C. maritima* and *P. apricaria*.

C. temminckii was the dominant wader species of the wetlands in the valley bottom at Finse, occurring regularly and breeding every year. The number of territories varied from year to year, from 1 at the lowest density to 16 at the highest. One has to bear in mind that the number of territories in this species does not necessarily account for the number of breeding pairs, due to its special breeding biology. Usually the female leaves the nest and breeding responsibilities over to the male when she has finished egg laying. Then, as a rule, she mates with another male, lays another clutch of eggs, which she always incubates herself (Hildén 1979, Breiehagen 1989). However, during a three year study (1980-82) of the nesting biology of *C. temminckii* in two additional plots in the same area, the size of the nesting population varied considerable from one year to the next, but the number of nesting birds varied only between 26 and 31 breeding individuals in the whole study area which included three sub-plots altogether (Breiehagen 1989). This indicates that the whole population was quite stable, but the females may utilize favourable feeding conditions locally by moving after the snow-melting zone before laying the last clutch for herself. This was supported by a skewed sex ratio of breeding birds towards an excess of females in late-melting plots within the study area. In this alpine population more nesting females were found altogether due to immigration of late-arriving females, which probably had laid their first clutch in another part of the mountain plateau Hardangervidda, which was available earlier. This was in contrast to Hildén's Finnish coast-breeding population, where an excess of nesting males was found. This supports the view that feeding conditions and mating strategies are important factors which may affect the density of breeding birds in this species.

All other wader species occurred only in low numbers, not breeding every year. *A. hypoleucos* was the most regular breeder of these. Most of the years only one territory was found for each of these species.

The highest number of wader territories occurred in years when the breeding grounds were available early in the spring. This is the result of an early snow-melt, usually caused by high June temperatures when the winter snow depth was high, or a normal or low winter snow depth combined with normal June temperatures. The local temperature conditions in June, together with the NAO index for June were correlated with the breeding wader and gull population when regarding the population as a whole. Only a few of the species were significantly correlated to the climate variables when calculated individually. Overall, precipitation did not seem to play any influential role. The snow-free date at Finsefetene very closely follows the general snow-melt in the surrounding hillsides, north-faced as well as south-faced. Both the wader community, and the combined wader and gull community were positively correlated with the snow-melt (measured both by percentage of snow-free area and date of snow melt). Of the various species, *C. temminckii, C. alpina, P. lobatus* and *L. canus* responded very clearly to the snow conditions in the spring. The years with a late snow-melt and reduced area of available breeding grounds when the birds arrive in the spring had the lowest number of breeding birds. Years with extensive available breeding grounds early in the spring normally had the highest number of breeding birds, but not always.

The fluctuations in the wader community showed great variations from year to year, in considerable synchrony with the fluctuations in the passerine communities in the surrounding hillsides. The passerine community at Finsefetene was poor in both species and individuals, but tended to fluctuate in the same pattern. The passerines in the Finse area were found to fluctuate in synchrony with the small rodent populations in the same area (Østbye *et al*. 2002). The wader and gull community fluctuations showed similar correlations with the small rodents. Both *C. temminckii* and *L. canus* showed significant correlations with the rodents and *A. hypoleucos* also appeared with the highest number of breeding pairs in years with peaks in the rodent density.

The densities of the wader species at Finse show considerable variation when compared to the

*Table 4. Correlation coefficients (Spearman's rho) for pairwise combinations of the wader and gull species, are also shown for relationships with the variation in the density of passerines in the nearby Blåisen transect, *=P<0.05, **=P<0.01, ***=P<0.001.*

Species	*A.hypoleucos*	*C.hiaticula*	*C.alpina*	*T.totanus*
C. temminckii	0.36	0.27	0.37	0.21
A. hypoleucos	-	0.09	**0.50***	-0.25
C. hiaticula		-	0.46	0.21
C. alpina			-	-0.08
T. totanus				-
C. maritima				
P. apricaria				
P. lobatus				
L. canus				
Wader community				
Wader/gull community				

densities of these species in other habitats, both locally and regionally (Table 6). These variations may be caused by differences in geographical location, the local variation in censused habitats, size of investigated area and the duration of the study. As our longtime study shows, a study period of one or a very few years will never capture the great variations in density. A realistic comparison of the densities of the different species is therefore not always possible. Most of our density estimates are within the range found for the same species investigated in similar habitats in other parts of Hardangervidda, and to some degree in similar habitats in Scandinavia, and for some species in similar habitats even in Iceland, Svalbard and Greenland (see Table 3 in addition to Table 6). Finsefetene is a locality dominated by bogs and mires, with a richness in water bodies ranging from small brooks to larger rivers, from small ponds to smaller lakes. Thus, birds with preferences for such a habitat type normally will occur in a higher density than on less preferred habitat types. *C. temminckii* may serve as an example of that. It occurs more scattered and seldom in the drier valley sides. *P. apricaria*, on the other hand, seems to prefer more oligotrophic dry heaths, and the densities are higher in the valley sides, thus a low density on wetlands like Finsefetene is reasonable. It is almost impossible to find a study locality of a size practicable to investigate, that will satisfy the optimal habitat preferences for all the occurring wader species in a given area.

The density of *L. canus* was low at Finsefetene as it is in the Finse area. High mountain habitats do not seem to be optimal for this species compared with lowland and coastal ones.

According to our own experience from other parts of the mountain plateau Hardangervidda, we believe our data give a realistic picture of the densities of most wader species and gulls in wetlands in valley bottom habitats in South Norwegian alpine areas.

the wader community, and the combined wader and gull community density. Correlation coefficients and the variation in small rodent density. Bold symbols denote statistically significant relationships:

C.maritima	*P.apricaria*	*P.lobatus*	*L.canus*	Passerines	Rodents
-0.33	-0.26	0.29	0.44	**0.64****	**0.61****
0.36	-0.22	0.42	0.37	0.36	0.43
-0.06	-0.36	-0.12	-0.22	0.33	0.00
0.01	0.00	0.13	0.14	**0.52***	0.18
-0.30	-0.21	0.20	0.21	0.14	-0.18
-	-0.42	-0.08	-0.24	-0.32	-0.20
	-	-0.24	-0.07	-0.19	-0.13
		-	**0.69****	**0.47***	0.21
			-	0.42	**0.49***
				0.60**	**0.53***
				0.63**	**0.54***

*Table 5. Correlation coefficients (Spearman's rho) for pairwise combinations of the wader and gull species, the wader community, and the combined wader and gull community, and the climate parameters monthly mean temperature (°C), total monthly precipitation (mm), the NAO index, the percentage snow-free area around 10. July for the Blåisen transect (% snow), and the date for Finsefetene study plot snow-free (snow-free date). Bold symbols denote significant relationships: *=P<0.05, **=P<0.01, ***=P<0.001.*

	Mean temperature		Precipitation		NAO index		% snow free area	Snow-free date
	June	July	June	July	June	July		
C. temminckii	0.33	0.08	-0.24	0.23	**-0.67****	-0.13	**0.62****	-0.45
A. hypoleucos	0.41	**-0.61****	0.06	**0.65****	-0.32	0.40	0.45	-0.42
C. hiaticula	0.01	-0.19	0.14	0.00	0.05	-0.08	-0.08	-0.19
C. alpina	0.31	-0.15	0.10	0.33	-0.30	0.21	0.42	**-0.60****
T. totanus	0.19	0.25	-0.39	-0.42	0.26	-0.09	0.17	-0.16
C. maritima	-0.02	-0.33	-0.06	0.12	0.16	0.13	-0.13	0.04
P. apricaria	0.13	0.23	0.31	0.04	0.31	0.03	0.00	0.00
P. lobatus	0.32	-0.29	-0.09	0.33	-0.39	0.10	**0.58***	**-0.56***
L. canus	0.24	-0.20	-0.37	0.23	**-0.68****	0.14	**0.68****	-0.40
Wader community	**0.51***	-0.09	-0.23	0.28	**-0.66****	0.05	**0.70****	**-0.64****
Wader/gull community	**0.51***	-0.10	-0.27	0.31	**-0.70****	0.07	**0.78*****	**-0.69****

Table 6. Breeding densities (territories/km²) of waders in different localities.

Species	Location	Density - mean	Area surveyed (km²)	Source	Duration of study (years)
C. temminckii	Finse	3.1	1	This study	18
	Finse	7.9	1.8	Breiehagen (1989)	3
	S & N Norway	0.2	-	Kålås & Byrkjedal (1981)	-
	Swedish Lapland	0.05 - 0.35	1	Svensson *et al*. (1984)	20
A. hypoleucos	Finse	1.5	1	This study	18
	S & N Norway	0.5	-	Kålås & Byrkjedal (1981)	-
C. hiaticula	Finse	0.8	1	This study	18
	S & N Norway	0.1	-	Kålås & Byrkjedal (1981)	-
	Swedish Lapland	0.05	1	Svensson *et al*. (1984)	20
	Svalbard	0.2 - 1.1	7.7	Bengtson (1975)	2
	Svalbard	0.5 - 1.4	3.7	Meltofte *et al*. (1983)	2
	Svalbard	0.3 - 0.5	6.3	Meltofte *et al*. (1983)	1
C. alpina	Finse	0.6	1	This study	18
	Hardangervidda	0.8 - 1.2	-	Kålås & Byrkjedal (1984)	1
	S & N Norway	0.5	-	Kålås & Byrkjedal (1981)	-
	Swedish Lapland	1.1 - 3.5	1	Svensson *et al*. (1984)	20
	Svalbard	0.3 - 0.5	3.7	Meltofte *et al*. (1983)	2
	Svalbard	0.3	6.3	Meltofte *et al*. (1983)	1
T. totanus	Finse	0.4	1	This study	18
	S & N Norway	2.0	-	Kålås & Byrkjedal (1981)	-
C. maritima	Finse	0.5	1	This study	18
	Hardangervidda	2 - 3	-	Cane (1979)	1
	Hardangervidda	1.2 - 1.5	-	Kålås & Byrkjedal (1984)	1
	S & N Norway	0.2	-	Kålås & Byrkjedal (1981)	-
	Swedish Lapland	0.05	1	Svensson *et al*. (1984)	20
	Svalbard	3.8	3.2 - 9	Summers & Nicoll (2004)	1
	Svalbard	3.2 - 4.7	6.3	Meltofte *et al*. (1983)	1
	Svalbard	0.6 - 1.5	-	Alendal *et al*. (1982)	1
	Svalbard	0.3	-	Kålås & Byrkjedal (1981)	1
	Svalbard	1.7 - 2.3	4.7	Bengtson (1975)	2
	Iceland	0.7	1.5 - 3.9	Summers & Nicoll (2004)	1
	Iceland	-	-	Petersen (1973)	-
	Greenland	5	-	Joensen & Preuss (1972)	1
	Greenland	1.25	16	Longstaff (1932)	1
P. apricaria	Finse	0.2	1	This study	18
	Hardangervidda	4.0 - 4.2	-	Kålås & Byrkjedal (1984)	1
	S & N Norway	1.0	-	Kålås & Byrkjedal (1981)	-
	Swedish Lapland	2.7 - 2.95	1	Svensson *et al*. (1984)	20
P. lobatus	Finse	0.2	1	This study	18
	S Norway	0.5	-	Kålås & Byrkjedal (1981)	-
	N Norway	1.0	-	Kålås & Byrkjedal (1981)	-
	Svalbard	0.3 - 0.5	3.7	Meltofte *et al*. (1983)	2
	Svalbard	0.3	6.3	Meltofte *et al*. (1983)	1

ACKNOWLEDGEMENTS

We wish to express our gratitude to a great number of colleagues who have participated in the field work during the years. The investigations have been supported by grants from the Norwegian Research Council for Science and the Humanities (NAVF), the Norwegian International Biological Programme (IBP) and the University of Oslo.

SAMMENDRAG

Struktur og dynamikk i et fuglesamfunn av vadere og måker i høyfjellet; Finse, Hardangervidda. En 18-årig undersøkelse.

Fennoskandiske høyfjellsøkosystemer er kjent for å ha store årlige variasjoner i populasjonstetthet hos smågnagere og flere fuglearter. Denne undersøkelsen beskriver et fuglesamfunn av vadere og en måkeart i et høyfjellsområde på Hardangervidda i årene 1967-1984. Strukturen og populasjonsdynamikken i et spurvefuglesamfunn i samme område og tidsrom er beskrevet tidligere (Ornis Norvegica hefte 1, 2002).

Det undersøkte feltet, Finsefetene, er en 1 km^2 stor sedimenteringsflate i dalbunnen av Finsedalen og tilhører den lavalpine regionen (Fig. 1 og 2). Området er karakterisert ved variable værforhold (Fig. 3), og stor årlig variasjon i snøfrie arealer hvor fuglene kan hekke (Fig. 4).

Antall territorielle fugler ble basert på reirfunn (reir = territorium). Åtte arter vadefugler ble registrert som territorielle og deres samlete tetthet varierte fra 2 til 19 territorier/km^2 med et gjennomsnitt på 10.4 (Tabell 1 og 2). Antall arter varierte fra 2 til 6 med et gjennomsnitt på 4.3 arter per år. Temmincksnipe, strandsnipe, sandlo og myrsnipe var regulære arter, dvs. territorielle i feltet minst halve studieperioden. Disse artene utgjorde til sammen 67-100% (gj.sn. 93%) av den samlete tettheten. Bare temmincksnipe forekom hvert år. Fire arter var irregulære, dvs. territorielle i mindre enn halve studieperioden: rødstilk (forekom i 8 år), fjæreplytt (7 år), heilo (4 år) og svømmesnipe (3 år). Bare en måkeart, fiskemåke, hekket i feltet – tettheten varierte årlig fra 1 til 5 par med et gjennomsnitt på 2.4 territorier/km^2.

Artenes tetthet varierte betraktelig fra år til år (Tabell 3). Strandsnipe og myrsnipe samt svømmesnipe og fiskemåke fluktuerte relativt synkront (positiv korrelasjon; Tabell 4). Den årlige tettheten av hver av artene temmincksnipe, svømmesnipe og fiskemåke samt den totale tettheten av vaderne, og vadere + fiskemåke, var relatert til det prosentvise arealet som var snøbart rundt 10. juli (Tabell 5). Den samlete tettheten av vaderne og den kombinerte tettheten av vadere og fiskemåke varierte i takt med tettheten av spurvefuglsamfunnet, så vel som med fluktuasjonen av smågnagere i området.

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Temminck's Stint female (colur-ringed) at Finsefetene 9. June 1982, she completed her first clutch (male-attended) of 4 eggs on 13. June, cf. Breiehagen (1989). Photo: Torgrim Breiehagen.