

Habitat Use and Resource Overlap by Breeding Golden Plovers and Dotterels (*Pluvialis apricaria*, *Charadrius morinellus*)

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Over much of their breeding range Dotterels *Charadrius morinellus* live sympatrically with Golden Plovers *Pluvialis apricaria* (CRAMP & SIMMONS 1983). Although Golden Plovers extend their breeding distribution lower down than do Dotterels in montane parts of their range (HAFTORN 1971) they are still numerous at the high elevations inhabited by Dotterels. Due to their morphological similarities (Tab. 1) the two species may be expected to compete for resources in places where both of them occur (RATCLIFFE 1976; see HUTCHINSON 1959, and MACARTHUR 1972 for supposed relationship between morphology and competition, and ROTH 1981, WIENS 1982, SIMBERLOFF 1982 for critical remarks). In fact, the two species have a fairly similar diet during the breeding season (BYRKJEDAL 1980, 1989). Potentially this could cause differential habitat use, interspecific aggression, and a negative correlation between population densities of the two species.

This study describes their habitat use and resource overlap in an area of co-occurrence in southern Norway, and analyzes their population densities, and aggression in relation to predictions from the competitive exclusion principle.

Material and methods

The study was performed in 1977—81, and some supplementary data were collected in 1984 and 1985. The field work was carried out in a 16.7 km² area in Steinbuheii, Hardangervidda (60°23'N 07°38'E), about 1200—1350 m a.s.l.

Habitat use was sampled opportunistically whenever feeding birds were exactly located before they had moved due to the presence of the observer. Such data were collected through the summer season and in all parts of the study area. Habitat was classified into 8 different

Tab. 1. Golden Plover (GP)/Dotterel (D) size ratios. — Größenverhältnisse zwischen Goldregenpfeifer (GP) und Mornellregenpfeifer (D).

Dimension	GP ♂ (n=52)		GP ♀ (n=12)	
	D ♂ (n=19)	D ♀ (n=7)	D ♂	D ♀
Bill length	1.36	1.36	1.38	1.38
Bill depth at base	1.23	1.19	1.13	1.09
Wing length	1.22	1.19	1.22	1.20
Tarsus	1.11	1.12	1.11	1.11
Weight	1.58	1.45	1.68	1.54

plant communities (NORDHAGEN 1943), and the habitat on the exact spot where a bird was observed, was assigned to one of the 8 habitat types. Nest habitat was recorded in the same way. No samplings were repeated for the same individual in the same stage of the nesting cycle. Many of the Dotterels and several Golden Plovers were individually colour marked.

Habitat availability was sampled in parallel transects 150 m apart (mid July 1981): at each 150th footstep the plant community was recorded, giving a total of 570 sampled points.

The occurrence of the prey taxa utilized by the two species was studied from (a) soil samples, and (b) pitfall traps on the 6 most important habitat types. The soil samples gave data on the subterranean prey. Totally 4 squares, each $\frac{1}{16}$ m² and 10 cm deep, were cut, sealed in plastic bags, put in a deep freeze within 24 h to prevent any development, and then sorted manually. The above-ground prey were sparsely represented in these samples, hence pitfall traps were operated in the same 6 habitats in 1979–81, comprising from 1005 to 2180 trapdays per season.

The food and feeding of the two species have been described elsewhere (BYRKJEDAL 1980, 1985, 1989). Stomach samples from 101 Golden Plovers and 5 Dotterels, and faecal samples from 111 Dotterels were examined, and observations of feeding behaviour were carried out for both species.

Resource overlaps were measured by the equation

$$C = 1 - 0.5 \sum / p_{ij} - p_{ik} /,$$

where p_i is the proportion of the i^{th} resource category for species j and k (COLWELL & FUTUYMA 1971).

In both species resource use changed from one stage of the breeding cycle to another (e. g. from pre-laying to incubation). The overlap of the various stages in time is therefore an important aspect of resource partitioning. Such time overlaps were calculated from breeding schedules given by BYRKJEDAL (1978) and KÅLÅS & BYRKJEDAL (1984a), supplemented by data from subsequent years. Censuses were carried out in late May, i. e., after the Golden Plovers were on territories but had not yet laid eggs. In this period both mates are together on small snowfree patches in their territories and can easily be seen. A census was also carried out after hatching (mid July), when Golden Plovers are conspicuous at considerable distances (up to 800 m). In spite of high nest predation (BYRKJEDAL 1987) the post-hatching figures were nearly identical to the pre-laying figures; re-nesting and/or sequential nesting (PARR 1978) may have been frequent. In the present analysis only the pre-laying figures are used. Dotterels were more cryptic than Golden Plovers, did not defend territories, and were polyandrous (KÅLÅS & BYRKJEDAL 1984a). They were therefore difficult to census, and the number of breeding pairs (i. e., in which the males were different) had to be established from the number of nests and broods found throughout the whole season and from observed pairs (see KÅLÅS & BYRKJEDAL 1984b for details on census methods). Censuses were done all years except 1985.

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Results

Habitat use

In both species lichen heath is highly utilized (Tab. 2), strongly disproportionately so by both species in the pre-laying phase ($\chi^2 = 15.45 - 32.75$, $p < 0.001$) and as nest

Tab. 2. Occurrence (%) of plant communities in the study area and their use by Golden Plovers and Dotterels. — Pflanzengesellschaften (% des Untersuchungsgebietes und ihre Nutzung durch Gold- und Mornellregenfeifer.

	N	<i>Salix herbacea</i> bed	<i>Carex bigelowii</i> heath	<i>Cladonia</i> heath	<i>Vaccinium myrtillus</i> heath	Grass meadow	<i>Nardus stricta</i> bed	Bog	Prostrate <i>Betula nana</i>
Occurrence	570	20.4	19.6	20.5	7.7	10.0	7.4	10.9	3.7
Golden Plovers:									
Pre-laying ♂	35		2.9	94.3					2.9
Pre-laying ♀	35		5.7	91.4					2.9
Nests	49		24.5	53.1	8.2	8.2	4.1		2.0
Off-duty ♂	7	14.3		57.1			28.6		
Off-duty ♀	26	30.8	19.2		7.7	11.5	19.2	11.5	
♂ w/chicks	56	7.1	14.3	19.6	12.5	16.1	8.9	7.1	14.3
♀ w/chicks	56	7.1	14.3	7.1	12.5	19.6	8.9	16.1	14.3
Postbreeding flocks*)	233	47.6	1.7		1.3	28.8	8.6	12.0	
Dotterels:									
Pre-laying ♂	19		10.5	84.2					5.3
Pre-laying ♀	20		1.0	85.0					5.0
Nests	51	19.6	31.4	35.3	5.9	2.0	3.9	2.0	
Off-duty ♂	6		33.3	66.7					
Displaying ♀	10	20.0	10.0	60.0	14.3	10.0	4.8	4.8	
♂ w/chicks	21	19.0	4.8	28.6	9.3	23.8			
Postbreeding ♀	118	83.1	5.1			2.5			

Terminology used by NORDHAGEN (1943), from left to right: *Salicetum herbaceae boreale*, *Caricetum rigidae-Lachenalii*, *Juncetum trifidi scandinavicum*, *Phylodoco-Vaccinetum myrtilli*, *Anthoxantho-Deschampsietum flexuosae*, *Nardetum chinophilum*, *Stygio-Eriophoretum polystachyi*, *Empetrum-Betulum nanae*

*) Probably including an uncertain number of off-duty ♀ still in the incubation phase.

habitat for Golden Plovers ($\chi^2 = 11.24$, $p < 0.001$). Also off-duty (feeding) males in the incubation period and mate-seeking ("displaying") Dotterel females seemed to utilize this habitat type to a large extent, but the sample sizes were small. Off-duty Golden Plover females used a wide spectrum of habitats, but *Salix herbacea* beds were positively selected ($\chi^2 = 12.43$, $p < 0.001$), and lichen heath negatively selected ($\chi^2 = 5.95$, $p < 0.02$). Likewise, female Dotterel flocks showed a strong positive selection for *Salix herbacea* beds ($\chi^2 = 92.67$, $p < 0.001$); in fact, nearly all the females in postbreeding flocks were found on this type of habitat. Parents with chicks utilized the whole array of habitats in the study area, and only Golden Plovers showed any significant deviations from the frequencies of habitat availability: *Salix herbacea* beds were avoided ($\chi^2 = 4.12$, $p < 0.05$) and *Betula nana* shrub positively selected ($\chi^2 = 3.95$, $p < 0.05$). The post-breeding Golden Plover flocks resembled Dotterel flocks in a strong positive selection for *Salix herbacea* ($\chi^2 = 38.55$, $p < 0.001$), and negative selection of *Carex bigelowii* ($\chi^2 = 45.44$, $p < 0.001$), *Cladonia* ($\chi^2 = 53.26$, $p < 0.001$), and *Betula nana* ($\chi^2 = 8.35$, $p < 0.005$). But they showed a positive selection of grass meadows ($\chi^2 = 26.23$, $p < 0.001$).

Six of the habitats were sampled for invertebrates. Series of 10 (in some habitats 5) pitfall traps were run in each of these habitats from mid June through July in 1979–1981, using the same sites each year. Due to small variation between the years in food availability ranks of the sampled habitats (only shift of 1 rank by 2 habitats between 2 years), the average values are used for simplicity (Tab. 3). Grass meadow, *Nardus stricta* beds, and *Carex bigelowii* heaths ranked as the three highest, while *Vaccinium myrtillus* heath, *Salix herbacea* beds, and lichen heath ranked lowest early in the season ("early", 12 June–2 July, corresponding roughly to the incubation season, and the period in which female Dotterels search for new mates). In the late part of the season the most conspicuous change occurred with the *Salix herbacea* beds, increasing in rank from 5 to 1; and in *Nardus stricta* beds, decreasing from 2 to 4.

Tab. 3. Occurrence of invertebrate prey on the 6 most important habitats, based on (a) pitfall traps for above-surface prey (985 trap days 1979, 2180 trap days 1980, 1645 trap days 1981), and (b) soil samples for subterranean prey (24 samples, a $\frac{1}{4}$ m², 10 cm deep; July 1979). — Beutetiere in den 6 wichtigsten Habitaten, ermittelt nach Fallenfängen für Oberflächentiere und nach Bodenpunkten für bodenlebende Arten.

Plant community	Adult insects and arachnids per 30 d and 5 traps (average for 3 years)				Larvae of Diptera + Coleoptera, oligochaets per 0.25 m ²	
	11 June–12 July		12 July–11 August		N	Rank
	N	Rank	N	Rank		
<i>Salix herbacea</i> bed	206.8	5	455.1	1	10	5
<i>Carex bigelowii</i> heath	293.3	3	289.3	3	18	3
<i>Cladonia</i> heath	124.3	6	229.3	6	1	6
<i>Vaccinium myrtillus</i> heath	253.3	4	237.7	5	12	4
Grass meadow	388.0	1	306.9	2	38	2
<i>Nardus stricta</i> bed	360.0	2	261.9	4	64	1

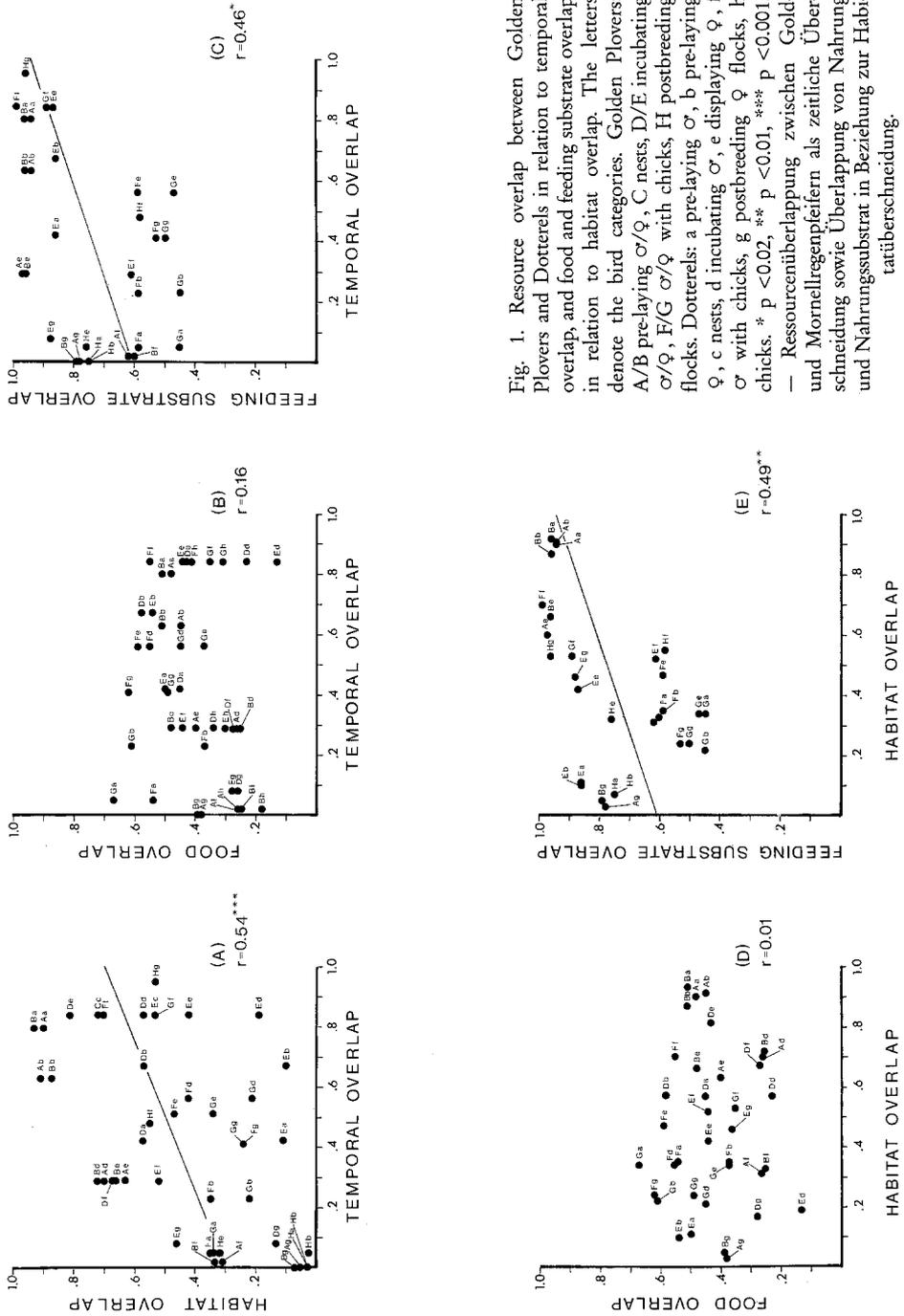


Fig. 1. Resource overlap between Golden Plovers and Dotterels in relation to temporal overlap, and food and feeding substrate overlap in relation to habitat overlap. The letters denote the bird categories. Golden Plovers: A/B pre-laying σ/\varnothing , C nests, D/E incubating σ/\varnothing , F/G σ/\varnothing with chicks, H postbreeding \varnothing , c nests, d incubating σ , e displaying \varnothing , f σ with chicks, g postbreeding \varnothing flocks, h chicks. * $p < 0.02$, ** $p < 0.01$, *** $p < 0.001$.
— Ressourcenüberlappung zwischen Golden und Mornellregenpfeifern als zeitliche Überschneidung sowie Überlappung von Nahrung und Nahrungssubstrat in Beziehung zur Habitatüberschneidung.

Subterranean prey were extracted from soil samples, and the rank between habitats was almost identical to the early season ranks of above-ground prey (Tab. 2).

There were no significant correlations (SPEARMAN'S) between the birds' habitat use and the food abundance, except in off-duty Golden Plover females and postbreeding Golden Plover flocks, both showing a positive correlation with above-ground prey ($r_s = 0.99$, $p < 0.01$; $r_s = 0.86$, $p < 0.05$).

Resource overlap

Due to differences between the sexes and seasonal variations in the use of habitat, food, and feeding substrate, males and females were treated separately in the different stages of the breeding season. Interspecific resource overlap showed a wide spectrum, from 0 to 99%. Overlaps in habitat, food, and feeding substrate were plotted against time overlaps, and the food and feeding substrate overlaps against habitat overlaps (Fig. 1). Competition theory would predict niche complementarity (e.g. SCHOENER 1974), whereby an increasing temporal overlap should lead to an increasing resource use segregation, and an increased habitat overlap to an increased segregation in food and feeding substrate. No negative relationships were found between any of the resource parameters; in fact, habitat overlap and feeding substrate overlap showed a positive correlation with temporal overlap, as did feeding substrate overlap with habitat overlap (Fig. 1A, C and E).

Fluctuations in breeding pairs

The population sizes of the two species within a 6 km² part of the study area were censused in 6 seasons. There was no significant correlation between the number of pre-laying territorial Golden Plover pairs and the number of Dotterel pairs (based on estimates from number of nests, broods, and observed pairs through the season) over these 6 years (Fig. 2).

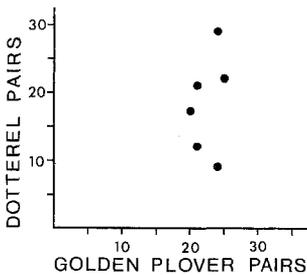


Fig. 2. Relationship between the number of Dotterel and Golden Plover pairs in a 6 km² part of the study area in 6 breeding seasons ($r = 0.27$, n.s.) — Zahlenverhältnisse der Brutpaare beider Regenpfeifer auf 6 km² in 6 Jahren.

Interspecific aggression

Six cases of aggressiveness by Golden Plovers (males in 5 cases, female in 1 case) towards Dotterels were seen. The Golden Plovers attacked the Dotterels by running with head low, bill pointing straight forward, and back feathers ruffled. The Dotterels

Tab. 4. Aggression between Golden Plovers (GP) and Dotterels (D) in different parts of the breeding season. — Aggressive Auseinandersetzung zwischen Gold- (GP) und Mornellregenpfeifer (D) während verschiedener Phasen der Brutzeit.

Breeding phase of GP	GP chasing D	Totals of GP/D encounters (≤ 30 m apart)
Pre-territorial	2	7
Pre-laying territorial	4	10
Incubation	0	4
Chick period	0	5
Postbreeding flocks	0	1

let themselves be chased along the ground for about 10–30 m in 4 of the 6 cases before the chase stopped; in the other 2 cases they took flight and disappeared.

The longest distance from which Golden Plovers released attacks on Dotterels was 30 m. All attacks were recorded in the Golden Plovers' pre-laying period, although Dotterels were seen <30 m from Golden Plovers also later in the season (Tab. 4). In order to compare attack rates, the birds were kept under observation for 15 minutes whenever they were seen with an interspecific distance of 50 m or less. The attack rate in the pre-laying period was significantly higher than later on (FISCHER's exact test, $p = 0.003$, two tailed).

Discussion

From this study it appears that in the Scandinavian lower alpine zone both Golden Plovers and Dotterels are birds of lichen heath and *Salix herbacea* beds, the former being particularly prominent early in the season and the latter after breeding. The strong selection of the former early in the season is dictated by the snow-melt patterns. Lichen heath is found on top of morains and ridges. Very little snow accumulates there during winter, and these ridge-tops are the first to get free from snow in spring. The figures for availability of plant communities are therefore not representative for the pre-laying and most of the egg-laying season, when the snow covers about 95–50 % of the study area (BYRKJEDAL 1978, KALÅS & BYRKJEDAL 1984a). The *Salix herbacea* beds are in places (depressions) with very persistent snow banks; the earliest ones emerging around mid June, the latest ones in mid July. Thus, the use of this habitat is also to some extent affected by snow cover. On the other hand, the *Salix herbacea* beds are attractive to the birds by holding relatively high densities of adult insects and arachnids in the latter part of the season, whereas the lichen heaths were comparatively poor feeding habitats throughout the season as far as invertebrate prey is concerned. Nearly all the *Empetrum* grows on lichen heath, however, and *Empetrum* berries are important in the diet at least for the Golden Plovers (BYRKJEDAL 1980).

Provided prey abundance measurements were representative, the lack of relationship between food availability ranks and habitat use in all but the off-duty Golden Plover

females (incubation period), suggests that other factors than invertebrate availability may have strong effect upon the habitat choice of Golden Plovers and Dotterels. Apart from the effects of snow cover, vegetative cover for the chicks and unimpeded view from the nests may be such factors. The study indicates that interspecific competition for habitat and food is of little importance in the coexistence of these species. A high temporal overlap did not appear to cause any resource segregation, and a high habitat overlap led to no food segregation in the different categories of birds; in fact, the tendency was towards the opposite.

The lowest possibility for any resource segregation is during the period from arrival until the first pairs start egg-laying. Snow covers usually more than 75 %, often more than 95 %, of the ground. Only small snowfree patches of lichen heath are available, upon which the birds disperse (BYRKJEDAL 1978, KÅLÅS & BYRKJEDAL 1984a). The aggressiveness of Golden Plovers (the larger of the two species) toward Dotterels in this period is in accordance with a competitive situation, but the aggression is much milder than between Golden Plovers trespassing each other's territories. When the available bare ground rapidly increases in early and mid June Dotterels are tolerated by the Golden Plovers. In fact, 3 Dotterel nests have been found less than 30 m from simultaneously active Golden Plover nests, in one case as close as 15 m, without any problems.

As the snow melts away, not only available area, but also invertebrate availability increases (e. g. BYRKJEDAL 1980, HOFVANG 1973). The fact that resource segregation is not practiced in this part of the season, when the potential for such segregation should be greatest, and that interspecific aggression is lacking, suggests that the population densities are below the carrying capacity relative to the food situation. The average breeding density in the study area is about the same for the two species (3.4 pairs per km² for Dotterel, 3.8 for Golden Plover; somewhat more variable in the former than the latter). Golden Plovers are highly (intraspecifically) territorial (e. g. D. & C. NETHERSOLE-THOMPSON 1961, RATCLIFFE 1976, BYRKJEDAL 1985, PARR 1980), while in Dotterel a low population density appears to be achieved without any territoriality (KÅLÅS & BYRKJEDAL 1984a). The two species do not appear to influence each other's breeding density. The spacing may more likely be gauged to density dependent nest predation (cf. TINBERGEN 1967, GÖRANSSON et al. 1975, PAGE et al. 1983) than to food resources or habitat. In fact, data from the study area suggest that a density dependent nest predation may exist in these two species (unpubl.).

In conclusion, these two morphologically similar species seem to coexist on montane breeding grounds without any notable competitive effect on each other, in spite of a high degree of resource use overlap. This situation is in agreement with what has been found in breeding arctic shorebirds (HOLMES et al. 1986, BAKER & BAKER 1973, BAKER 1977). The competitive exclusion principle has been considered an important mechanism in natural selection, but an increasing number of studies have failed to demonstrate competitive exclusion (reviews e. g., by DEN BOER 1986, WIENS & ROTENBERRY 1981, SIMBERLOFF 1982, WIENS 1982). The present study adds itself to that list.

Summary

Golden Plovers and Dotterels breeding in sympatry fed and nested on *Cladonia* heath, especially in the early part of the season. An increasing number of habitats were used as they became available, and *Salix herbacea* beds were used disproportionately frequently by post-breeding flocks of both species and off-duty (incubating) Golden Plover females, apparently due to good insect and arachnid availability late in the season. The species overlapped considerably in resource use and showed no signs of resource partitioning under circumstances where it could be expected from the competitive exclusion principle. Aggression from Golden Plovers towards Dotterels indicated some competitive interaction early in the season, when snow cover reduced the feeding grounds to 5–25%. There was, however, no evidence for interspecific effects on breeding densities. It is concluded that competition between the two species is of little importance; their spacing patterns are probably usually governed by other factors than food.

Zusammenfassung

Gold- und Mornellregenpfeifer benutzten bei sympatrischen Vorkommen in S-Norwegen in hohem Maß flache Hügelketten mit *Cladonia* sowohl als Nesthabitat als auch zur Nahrungssuche, besonders zu Beginn der Brutsaison. Diese flachen Hügelketten waren arm an Invertebraten, doch reich an *Empetrum*-Beeren, und bildeten fast das einzige zugängliche Habitat vor dem vollen Eintritt der Schneeschmelze. Später wurden mehrere Habitats besetzt. Flächen mit *Salix herbacea* wurden sowohl von Vögeln, die das Brutgeschäft beendet hatten (Trupps beider Arten), als auch von Weibchen des Goldregenpfeifers in der Brutzeit vorzugsweise aufgesucht. Wahrscheinlich hing dies mit dem Angebot an Insekten und Spinnen in der zweiten Hälfte der Brutzeit zusammen. Die Ressourcennutzung beider Arten war sehr ähnlich; Anzeichen für Ressourcenaufteilung gemäß dem Konkurrenz-Ausschlußsprinzip wurden nicht gefunden. Aggression von Goldregenpfeifern gegen Mornellregenpfeifer am Anfang der Saison deutet auf Konkurrenz zu dieser Zeit hin, als nur 5–25% der Fläche vom Schnee frei waren. Eine Auswirkung auf die Siedlungsdichte ließ sich nicht erkennen. Konkurrenz zwischen beiden Arten dürfte also nur einen geringen Einfluß auf die Dispersionsmuster haben, das wahrscheinlich von anderen Faktoren als der Nahrung bestimmt wird.

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