Plover's Page turns into Plover's Parasite: a look at the Dunlin/Golden Plover association

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The association between Golden Plovers and Dunlins was studied on a middle alpine breeding ground at Hardangervidda, S Norway. Associations were most common in the pre-laying period. Dunlins had greater flushing distances and fewer, and less distinct, alert pauses when feeding in such associations. Golden Plovers in the associations had a lower feeding rate and males spent more time resting than those not in association with Dunlin. Food overlap (α) between the two species was 0.64. It is suggested that the association benefits the Dunlins by decreasing the risk of predation and allowing more efficient feeding, whereas it weakens the Golden Plovers' antipredator strategy and decreases their food supply.

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Introduction

The Dunlin *Calidris alpina* is well-known for its association with the Golden Plover *Pluvialis apricaria* on breeding grounds where both species occur (Ingram 1942, Oakes 1948). The two species may walk within a few feet of each other, and as the Golden Plover takes flight and settles again, the Dunlin follows closely. So striking is this behaviour that in parts of England the Dunlin is called "Plover's Page" (Oakes 1948) and in Iceland *Lòuþrœll* ("Plover's Slave").

We have frequently seen this behaviour on breeding grounds of the two species in Norway (e.g. Fig. 1), and our curiosity has been aroused about its adaptive value. During studies of Golden Plover and Dotterel *Charadrius morinellus,* we have collected data on the Golden Plover/Dunlin association as opportunities arose.

We expected that one reason why the Dunlin associates with Golden Plovers would be to take advantage of the extreme wariness of the plovers, thus achieving more efficient feeding. Due to their extreme proximity during feeding, the Dunlins might be expected to compete with the Golden Plover for food, either directly or through interference. This paper investigates these possibilities.

Material and methods

The data were collected at Steinbuheii, Hardangervidda, S Norway, in 1977—81. The study area covered 16.5 km^2, between altitudes of 1170 and 1356 m in the middle alpine zone. The vegetation is short, and dominated by snow-bed communities *(Salix herbacea* and *Nardus stricta* fields), grass meadows and *Carex bigelowii* fields, *Vaccinium myrtillus* heath, and *Cladonia* heath with rich *Juncus trifidus* stands. There are small patches of *Betula nana,* and short-growing *Salix* spp. are abundant locally. The area contains about 40—60 pairs of Golden Plover, about 25 pairs of Dunlin, 8—10 pairs of Purple Sandpiper *Calidris maritima,* and more than 30 nests of Dotterel. Other shorebirds breed there only occasionally.

Data on the relative occurrence of the Dunlin/Golden Plover association early and late in the season were obtained from pre-laying and post-hatching Golden Plover censuses. Dunlins also associate with shorebirds other than the Golden Plover. The 21 associations between Dunlins and other shorebirds seen on the pre-laying censuses were compared with the frequency distributions expected between the various species of these Dunlin associations, to see if the Dunlin preferred any of the species.

Data on feeding Dunlin and Golden Plover were recorded in the pre-laying period in 1981. Observations were made of individuals of both species feeding (a) together and (b) with conspecifics only. These data were obtained on 23 May from one particular Golden Plover pair and 2—4 Dunlins. The Golden Plover pair held a territory covering 3—4 patches of snow-free ground, the vegetation of which was primarily composed of *Juncus trifidus/Cladonia,* the plant community which is most available to the birds early in the season. The observations were made through 20x spotting scopes from a vantage point at a distance of about 200 m from the birds, which were thus unaffected by our presence. We recorded (a) the number of pecks made per minute by male and female Golden Plovers (i) into the substrate (presumably for insect larvae, earthworms) (ii) on the ground surface (for adult insects), and (iii) in the vegetation (for adult insects, berries), both in association with, and not in association with Dunlin; (b) the number of alert halts per minute made by feeding Dunlin in, and not in, association with Golden Plover. Alert halts were short pauses when the bird assumed an alert posture and scanned its surroundings. This was used as an indication of the Dunlin feeding rate, as recording the proper feeding rate (pecks per minute) would require a cine-

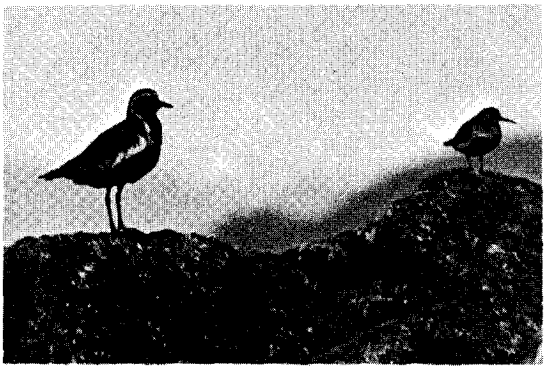

Fig. 1. Association between Dunlin and Golden Plover, Jæren, SW Norway, June 1973.

camera, which was not practical to use under the circumstances. Dunlin in association with Golden Plovers were less than 10 m, usually 1—2 m, from the plovers, whilst those not in association were more than 100 m away from them.

A total of 1462 minutes' pre-laying observations of Golden Plovers were analysed to see if the presence of Dunlin affected Golden Plover behaviour other than feeding. All the behaviour data were recorded on a portable tape recorder. On our various trips in the study area during the pre-laying period, we recorded the flushing distances of Dunlins in, and not in, association with Golden Plovers, as we approached the birds at a normal walking (skiing) speed.

The food of the Golden Plover on the breeding grounds had been studied earlier (Byrkjedal 1980). A comparison was made between these results and the stomach contents of 18 Dunlins collected in the same area on 6—13 June 1974 for the purpose of skinning. The processing of the Dunlin stomach contents followed that of Byrkjedal (1980). Food overlap was calculated according to Pianka (1973):

$$\alpha = \Sigma p_1 p_2 / (\Sigma p_1^2 p_2^2)^{1/2},$$

where summation is over all foods and p_1 and p_2 are the proportions of each type of food in the diet of the first and second species.

Results

The occurrence of the association. The frequencies of associations between Dunlin and Golden Plover and between Dunlin and Purple Sandpiper are not significantly different from the frequencies expected from the numbers of these species seen on censuses. However, Dunlins do not seem to associate with Dotterel (Table 1).

As Dunlins together with Golden Plovers are more likely to be detected on the Golden Plover censuses than Dunlins not with Golden Plovers, the frequency of Golden Plovers associated with Dunlins on the pre-laying and post-hatching censuses is used to illustrate the occurrence early and late in the season. There are more such associations before egg-laying than after hatching (χ^2 = 7.619, $P<0.01$, Table 2). The same tendency seems to be found in the frequency of associations between Purple Sandpiper and Golden Plover, though the numbers involved are very small. Associations between the last two species seem to be looser than those between Golden Plover and Dunlin, as Purple Sandpipers often do not rise together with the Golden Plovers when flushed.

Table 1. Affinities of Dunlin with other shorebird species.[1)]

		Accompanying species: Golden Plover	Dotterel	Purple Sandpiper
Dunlin units[2)]	observed	18	0	3
	expected	15.9	2.9	2.3

[1)] Shorebirds seen feeding on pre-laying censuses (1977—81)
[2)] Single individuals, pairs, flocks

Table 2. Number of feeding Golden Plovers in association with Dunlins and Purple Sandpipers on censuses in 1977—81 (percentages given in parentheses).

	Total no. Golden Plover units[1)] censused	No. of occasions when Golden Plovers associated with: Dunlin	Purple Sandpiper
Pre-laying	146 (100)	18 (12.3)	9 (6.2)
Post-hatching	56 (100)	2 (3.6)	1 (1.8)

[1)] Single individuals, pairs, flocks

Feeding alertness of the Dunlin. Dunlins associated with Golden Plovers flush at a much greater distance than those not associated with Golden Plovers ($t = 8.5$, $P<0.001$, Table 3). However, Dunlins feeding in association with Golden Plovers have fewer alert pauses during feeding than other Dunlins ($t = 11.7$, $P<0.001$, Table 4). The postures assumed during alert pauses also differ (Fig. 2). When Dunlins feed with conspecifics only, they make these halts much more distinctly and the posture is much more erect than when they feed with Golden Plovers.

The effect of Dunlins on the behaviour of the Golden Plovers. The Golden Plover female fed with fewer pecks per minute when there were

Table 3. Flushing distances of Dunlins feeding with Golden Plovers, and with conspecifics only.

	Flushing distance m±SD	Number of records
With Golden Plovers[1)]	81.3±31.6	12
With conspecifics[2)]	13.1± 4.4	8

[1)] 1 pair of Golden Plover, 1—4 Dunlins (different Golden Plovers and Dunlins on each occasion)
[2)] 2—4 Dunlins

Table 4. Alertness of Dunlins during feeding with Golden Plovers and with conspecifics only.

	Number of alert halts[1] per minute ± SD	Observation period (minutes)
With Golden Plovers[2]	7.5±3.0	33
With conspecifics[3]	19.2±3.1	13

[1] Short pauses between pecks, bird scanning surroundings
[2] 1 pair of Golden Plover, 2—4 Dunlins
[3] 2—4 Dunlins

Dunlins nearby than when there were no Dunlins around ($t = 9.4$, $P<0.001$, Table 5). The same tendency, though not statistically significant, was found with the Golden Plover male. There were no significant differences for male or female Golden Plover in the frequency of pecks in different parts of the feeding substrate in the two situations.

During a total of 1462 min of time-budget recording on Golden Plovers in the pre-laying period, Dunlins were associated with the plovers for 39.8 % of the time. In the presence of Dunlins, Golden Plover males, but not females, spent significantly more time resting ($\chi^2 = 6.1$, $P<0.02$) than in their absence. The Dunlins' presence did not affect the time spent in any of the following behavioural categories by Golden Plovers (males and females analysed separately): feeding, preening, inter- and intraspecific chasing, standing or running alert, copulation and courtship, and flights between feeding patches.

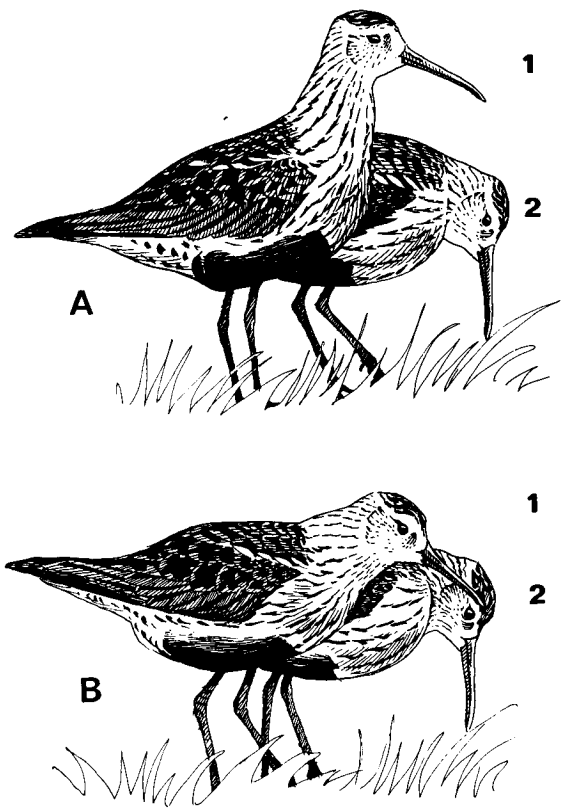

Fig. 2. Alert (1) and feeding (2) postures of Dunlin feeding (A) only with conspecifics and (B) with Golden Plovers.

Aggression towards Dunlins. During the time-budget observations of Golden Plovers, a total of 6 cases of aggressiveness by Golden Plovers towards Dunlins were seen. Only Golden Plover males were involved. They made attacks on Dunlins from distances of 0.5 to 2 m. The attacked Dunlins ran and fluttered as they readily let themselves be chased away over a few metres by the Golden Plover. The Golden Plovers soon gave up the chase, as they found themselves closely followed by other Dunlin members of the association. The chased Dunlin immediately resumed feeding after the chase.

The diets of Golden Plovers and Dunlins. The total contents of 18 Dunlin stomachs (6 males and 12 females) are given in Appendix 1. The food categories are, by and large, the same as those eaten by Golden Plovers in the same area (cf. Byrkjedal 1980). The food overlap (α) shown by these Dunlins and Golden Plovers for the period before and around egg-laying is 0.64 (37 Golden Plover stomachs, 2027 food items, mid May — mid June).

Discussion

Although our data on the frequency of association between Dunlin and other shorebird species are weak, we are sure from our daily field work in the area that associations with Dotterel are avoided, in favour of those with Golden Plover and Purple Sandpiper. Whether one of the latter two is preferred to the other is uncertain. Association is most likely to occur with Golden Plovers as they are the most numerous.

It is also quite in accordance with our general impression that the association is most common early in the season, especially before laying. Later, the various shorebird species are more confined to specific nesting and feeding habitats. In the incubation period, we have seen Dunlins feeding in flocks of off-duty female Golden Plovers. Presumably these Dunlins were off-duty individuals as well.

Our observations that Dunlins associating with Golden Plovers flush at a greater distance, and have fewer alert pauses when feeding than those that are not associating, support the idea that Dunlins use the Golden Plover as a "watch-dog".

Table 5. Feeding rate of Golden Plovers[1] with and without Dunlin in association.

	Number of pecks (percentage in parentheses): In ground	On ground	In vegetation	Total no. pecks	Pecks per min±SD	No. of minutes
Golden Plover male						
Dunlin present	13 (32.5)	25 (62.5)	2 (5.0)	40	4.0±2.70	10
Dunlin absent	29 (33.0)	56 (63.6)	3 (3.4)	88	4.6±2.97	19
Golden Plover female						
Dunlin present	54 (41.1)	70 (51.5)	10 (7.4)	136	2.6±1.37	52
Dunlin absent	39 (34.8)	56 (50.0)	17 (15.2)	112	3.3±1.70	34

[1]) 1 pair of Golden Plover, 23 May 1981

The wariness of the Golden Plover contrasts strikingly with the "tameness" of the Dotterel. The most likely predators on adult Dunlins in the area are falcons *Falco* ssp. and Red Foxes *Vulpes vulpes*. Few falcons are observed through the summer, but foxes occur daily in the study area. The Dunlins may be easier to detect when associated with the plovers, yet will be far more difficult to approach. Thus the association may give the Dunlins a direct antipredator advantage. What is likely to be more important, however, is increased feeding efficiency. Not only will the Dunlins gain feeding time by not having to pay so much attention to the surroundings, but as they can concentrate more on feeding, the feeding *per se* may become more efficient. From the alert halts during feeding with Golden Plowers we gained the impression that the Dunlins were mainly looking up to observe the movements of the Golden Plovers, and did not even stop walking in most instances. When with conspecifics only, they seemed to be making the halts in order to scan the surroundings. Thus Dunlins seem to gain from the association with Golden Plover by decreasing predation risk and increasing feeding efficiency.

With the Dunlins' relaxed attitude towards potential dangers, it is difficult to see that Golden Plovers could have any benefit from the association. On the contrary, several negative effects can be pointed out, some of which are supported by our data.

By increasing the number of birds walking together, the Dunlins make the Golden Plovers (and themselves) more visible. Increased alertness and decreased feeding rate in Golden Plovers would be expected as a consequence. A decreased feeding rate was indeed found, but the Golden Plovers did not seem to become more alert, unless some of the time recorded as spent resting by Golden Plover males was, in fact, spent keeping guard as well. It is rather more likely that the reduced feeding rate was due to the Dunlins affecting the food availability for the Golden Plovers, either by directly competing with Golden Plovers for food, or by causing prey animals to hide or to lie still, thereby making them less detectable. The food overlap between the species is great, especially considering that the Dunlins examined for stomach contents were probably not associated with Golden Plovers when shot, as that would have required special effort to get within shooting range. In fact, as the Dunlins often feed less than 1 metre from the Golden Plovers, they could be competing for the same prey items. Goss-Custard (1970) has shown that, on mudflats, *Corophium* withdraws into the substrate when a Redshank *Tringa totanus* is walking close by. Similar avoidance mechanisms could be used by the prey animals available to the shorebirds on Hardangervidda (mainly Tipulidae larvae and adult Coleoptera early in the season). The presence of Dunlins should greatly increase the chances of eliciting such behaviour in potential prey animals, as the Dunlins constantly walk around when searching for food by touch. In contrast, the Golden Plovers find their food by a quieter "stand and watch" method.

As the number of birds in a flock increases, the likelihood of one particular bird being taken by a predator diminishes. Admittedly, Golden Plovers could benefit from this, just as much as the Dunlins. However, the effect could easily be counteracted by the increased detectability, and, being the larger, the Golden Plover should be the more attractive prey for foxes and large falcons.

Thus, there is reason to suppose that Dunlins might weaken the Golden Plovers' antipredator strategy and feeding efficiency by their association.

The fact that so few aggressive interactions have been seen is probably a result of the Dunlins' reactions to chasing by Golden Plovers. It seems a hopeless task for the Golden Plovers to chase away the Dunlins, for as soon as the chase is over and the Golden Plover turns its back on the "victim", the latter returns to continue following close behind. Moreover, when two or more Dunlins operate together, there is always a persistent Dunlin

trailing the Golden Plover, even when it is chasing another Dunlin. Under such circumstances, the costs in time and energy for the Golden Plovers to chase away the competitors probably exceed those of having them around.

The old English name "Plover's Page" and the Icelandic *Lòuþræll* imply that the Golden Plover is exploiting the Dunlin. Paradoxically, it turns out that the opposite seems to be true.

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Selostus: **Suosirrin ja kapustarinnan yhteiselo: suosirri pikemminkin loinen kuin apuri.**

Suosirrit seuraavat usein pesimäalueillaan varsin tiiviisti kapustarintoja. Tämä liitto on niin läheinen (ks. kuva 1), että Englannissa suosirriä kutsutaan "kapustarinnan hovipojaksi" ja Islannissa "kapustarinnan orjaksi". Kansanomaisten nimitysten antama käsitys tästä assosiaatiosta ei ole kuitenkaan oikea.

Tutkimus tehtiin Hardangerviddalla, Etelä-Norjassa. Suosirri/kapustarinta-assosiaatio oli yleisimmillään munintaa edeltävänä kautena, jolloin kapustarinnan käyttäytymistä joko yksin tai suosirrin kanssa seurattiin yhteensä 1462 minuuttia, suosirrin vaikutuksen selvittämiseksi.

Suosirri/kapustarinta- ja suosirri/merisirri-assosiaatioiden esiintymisfrekvenssit eivät poikenneet merkitsevästi odotettavissa olevasta frekvenssistä, joka laskettiin lajien runsaussuhteista. Keräkurmitsaan suosirrillä ei näytä olevan läheistä suhdetta (taul. 1). Suosirri/kapustarinta-assosiaatio on tiiviimpi munintaa edeltävänä aikana kuin kuoriutumisen jälkeen (taul. 2). Sama muutos havaitaan myös suosirri/merisirri-liitossa, mutta niiden välinen suhde on ylipäätään löyhempi.

Kapustarintojen seurassa olevat suosirrit pakenevat merkitsevästi kauempaa (taul. 3) ja ne tähyilevät harvemmin ravinnonhaun aikana (taul. 4) kuin lajikumppaniensa seurassa olevat sirrit. Tähyilyasentokin näyttää olevan valppaampi lajikumppanien (kuva 2B) kuin kapustarintojen (kuva 2A) joukossa.

Suosirrien läsnäolo vaikutti kapustarinnan ruokailuintensiteettiin (nokkaisua/minuutti) alentavasti. Ruokailuparven koon kasvaessa suosirrit aiheuttavat kapustarintojen (ja itsensä) havaittavuuden kasvavan. Tästä johtuen voisi olettaa, että kapustarintojen ravinnonhakuintensiteetti vähenisi ja varuillaanolo lisääntyisi. Ensimmäinen olettamus osoittautui todeksi, mutta toisen tueksi ilmaantui ainoastaan se seikka, että kapustarintakoiraat käyttivät enemmän aikaa lepoon ja samanaikaiseen vartiontiin.

Verrattaessa 18 suosirrin ja 37 kapustarinnan mahanäytteitä voitiin todeta ravintokohteissa voimakasta päällekkäisyyttä (food overlap). Päällekkäisyysindeksi (α) on 0.64. Suosirrin maha-analyysitulokset on esitetty liitteessä 1.

Suosirrit hyötyvät "loisimisestaan" kapustarintojen seurassa, sillä niiden predaatioriski pienenee ja ravinnonhakutehokkuus kasvaa. Liiton vaikutus kapustarintaan on sitävastoin negatiivinen sekä antipredaattoristrategian että ravinnon tarjollaolon osalta.

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Appendix 1. Stomach contents of 18 Dunlins shot at Hardangervidda, S Norway, in the period 6—13 June 1974 (6 males, 12 females).

Food category		Number of items (161)	Percentage of total items	Number of stomachs	Percentage of stomachs
Coleoptera, adults					
Carabidae	*Notiophilus aquaticus*	11	6.8	7	38.9
	Patrobus sp.	7	4.3	6	33.3
	Amara alpina	1	0.6	1	5.6
	Nebria sp.	6	3.7	3	16.7
Staphylinidae		4	2.5	3	16.7
Byrrhidae	*Byrrhulus pilula*	11	6.8	9	50.0
Curculionidae	*Otiorrhynchus dubius*	16	9.9	10	55.6
Coleoptera, larvae					
Carabidae		1	0.6	1	5.6
Byrrhidae		25	15.5	3	16.7
Diptera, larvae					
Tipulidae	*Tipula* sp.[1)]	57	35.4	10	55.6
	Prionocera sp.	4	2.5	1	5.6
Muscidae		4	2.5	2	11.1
Araneae		2	1.2	2	11.1
Opiliones	*Mitopus morio*	2	1.2	2	11.1
Lumbricidae		1	0.6	1	5.6
Berries	*Empetrum hermaphroditum*	5	3.1	5	27.8
Seed	*Carex* sp.	4	2.5	4	22.2

[1)] Probably *T. excisa*