The phenomenon of brood aggregations and their structure in waders in northern Taimyr

M.Y. Soloviev & P.S. Tomkovich

Observations of the spatial distribution of the broods of five wader species Grey Plover *Pluvialis squatarola*, Curlew Sandpiper *Calidris ferruginea*, Turnstone *Arenaria interpres*, Knot *Calidris canutus*, and Sanderling *Calidris alba* were carried out in 1991 in the northern Central Taimyr, near Knipovich Bay. These species were found to form loose aggregations in which the adults were never out of earshot of each other. Statistical analysis demonstrated associations between Grey Plover and Knot, Grey Plover and Curlew Sandpiper, and Curlew Sandpiper and Turnstone. This attraction of broods to each other can be explained by the protection provided by the aggressive and vocal Grey Plovers and Turnstones to the weaker Knot and Curlew Sandpiper against avian predators. The former are usually found alone and rarely, if ever, join conspecifics. Of the "weak" species, Curlew Sandpiper is the most gregarious: 85.1% of its broods were recorded in aggregations, 75.4% of broods were associated with broods of other species and only 14.9% of broods were found to wander solitarily. Therefore inter- and intra-specific aggregations are equally important for Curlew Sandpipers. Broods of Knot and Sanderling are found significantly less often in associations. Sanderling showed no inclination to aggregate with any other species. The probability of encountering a solitary brood was highest (52.8%) and can be explained by the comparatively small scale of brood movements in this species. The probability of finding at least two broods in an aggregation decreased in the order Curlew Sandpiper, Turnstone, Grey Plover, Knot, Sanderling. Chick exchange between broods in aggregations is briefly discussed as a probable negative consequence of the formation of aggregations. The phenomenon described is probably a result of complex interactions between species, each adopting brood-rearing strategies which will increase their reproductive success.

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Наблюдения за пространственным размещением выводков пяти видов куликов (тулес *Pluvialis squatarola*, краснозобик *Calidris ferruginea*, камнешарка *Arenaria interpres*, исландский песочник *Calidris canutus* и песчанка *Calidris alba*) проводились в 1991 году на севере Среднего Таймыра, в районе бухты Книпович. У этих видов было отмечено образование рыхлых агрегаций, в которых взрослые птицы никогда не находились за пределами слышимости друг друга. Используя статистический анализ, было продемонстрировано наличие ассоциаций между тулесом и исландским песочником, тулесом и краснозобиком, и между краснозобиком и камнешаркой. Такое тяготение выводков друг к другу может быть объяснено защитой от пернатых хищников, обеспечиваемой агрессивными и крикливыми тулесами и камнешарками в пользу более слабых исландских песочников и краснозобиков. Первые два вида обычно встречаются одиночными и только изредка присоединяются к другим особям своего вида. Среди "слабых" видов, самым стадным является краснозобик: 85,1% его выводков были встречены в ассоциациях, 75,4% были в ассоциациях с выводками других видов, и только 14,9% обнаружены в одиночных кочующих выводках. Следовательно, меж- и внутривидовые агрегации для краснозобиков имеют равное значение. Выводки исландского песочника и песчанки встречаются значительно реже в ассоциациях. Не было продемонстрировано никакой склонности песчанки к агрегации с каким-либо другим видом. Вероятность встречи с одиночным выводком была самой высокой (52,8%), что объясняется относительно небольшим масштабом перемещений выводков у этого вида. Вероятность встречи по крайней мере двух выводков в агрегации уменьшалась в следующем нисходящем порядке: краснозобик, камнешарка, тулес, исландский песочник, песчанка. Обсуждается вкратце обмен слетками между выводками, как вероятное негативное следствие образования агрегаций. Описанное явление следует, наверное, из сложных межвидовых взаимодействий, при которых каждый вид заимствует стратегии выведнения потомства с целью повышения успех размножения.

Introduction

The existence of nesting aggregations is well known for different bird species, including waders (Mayo 1974; Dyrcz *et al.* 1981; Paulson & Erckmann 1985; Newman 1992), the usual explanation for which has been the relative safety of the nests of small "weak" species in the vicinity of larger "strong" species, which actively chase predators which come near their nests. The attraction of certain species to others can be considered to have evolved as a way of increasing reproductive success. One would therefore also expect that there would be similar interspecific aggregations later in the brood-rearing period. However, we know of only one reference to interspecific associations, where broods of Buff-

Study Area

breasted Sandpipers *Tryngites subruficollis* were seen to associate with Grey Plovers *Pluvialis squatarola* (Paulson & Erckmann 1985), the only other reference to grouping of broods being intraspecific, in Bristle-thighed Curlew *Numenius tahitiensis* (Gill *et al.* 1991). During our studies in the Northern Taimyr, we noticed that the occurrence of the broods of certain species was highly clumped. Moreover, in one case, resightings of colour-marked birds in 1990 showed that Curlew Sandpipers *Calidris ferruginea* alarming near broods associated for at least six to seven days with a pair of Turnstones *Arenaria interpres* and that the two species moved several kilometres together. In order to study the composition of these aggregations and to find possible reasons for their formation, we undertook research in 1991 in the vicinities of Knipovich Bay (76°N; 98°30'E) in the northern Central Taimyr. This paper presents the results of the study.

Methods

Within the study area, five species of waders were regularly recorded in brood aggregations: Grey Plover, Turnstone, Knot *Calidris canutus*, Curlew Sandpiper, and Sanderling *Calidris alba*. Only these were included in the analysis. Among other breeding wader species in the region, Pacific Golden

Plover *Pluvialis fulva* and Grey Phalarope *Phalaropus fulicarius* were uncommon. They and the very common Little Stint *Calidris minuta* inhabited tundra marshes during the brood-rearing period, areas which were rarely visited by other waders with broods.

Mono- or polyspecific concentrations of adult waders displaying the alarm behaviour typical during the brood-rearing period (in our case mostly a reaction to the appearance of an observer) were considered as brood aggregations. We included all actively alarming adult waders that could be heard in normal wind conditions in a single aggregation. Large-scale individual colour-marking of adult waders on nests and with broods (except Curlew Sandpiper and Turnstone) has enabled us to a) exclude birds with nests, and b) confirm the existence of a brood, as indicated by the behaviour of the adult birds.

We treated each encounter with an aggregation as a separate record, regardless of whether it was: a) a group of broods recorded on different days, or in different places; b) an identifiably different group of broods; or c) all records of solitary broods.

The year of this study (1991) was favourable with a combination of an absence of Arctic Foxes *Alopex lagopus* and an average number of lemmings which resulted in high nesting success for tundra birds. As a result, in the second half of July, the study area contained a relatively high number of waders with broods. In total, we obtained data on the occurrence and composition of 66 aggregations and 86 solitary broods.

The term "monospecific" is here used for aggregations formed by birds belonging to the same species. There were two categories of "polyspecific" aggregations (*i.e.* including broods of more than one species): interspecific and combined. The former was used when a species in an aggregation was represented by a single brood, the latter when there was more than one brood of a particular species. From the statistical point of view, brood aggregations can be regarded as observations characterised by a set of variables corresponding to the species recorded within them. These variables have a limited range of values (presence or absence of species in an aggregation, or number of broods in it) and thus they are categorical. The data set can be represented as a contigency table, with the number of factors equal to the number of variables (species), and a number of categories equal to the number of observed values. To study the interactions in such tables, we decided to apply the method of log-linear models (Upton 1978). The amount of available data determined the choice of table, with no more than two categories for each species, allowing easier interpretation of the results. The simplest table had two categories for each species: 1 - if a species was present in an aggregation; 2 - if it was absent. The information in this table was used to model the communal occurence of species (model-0).

The presence of more than one brood of Curlew Sandpipers, Knots and Sanderlings in many aggregations is of special interest when compared with Grey Plover or Turnstone, where more than one brood in an aggregation was recorded less than five times. To study this phenomenon, we added three more variables to the model. In each of them, the species categories of Curlew Sandpiper (model-1), Knot (model-2) and Sanderling (model-3) were given the value 2 when one brood was present in an aggregation and the value 1 when there was more than one brood (we recorded up to 10 broods of Curlew Sandpiper in one aggregation). Categories 1 and 2 of another four variables in each of these models reflected the presence or absence of other species in an aggregation, in a similar way to model-0.

The table for model-0 was incomplete because the cell 2 x 2 x 2 x 2 x 2, corresponding to an absence of broods of any species in an aggregation, cannot contain frequencies other than zero. The significance of any interaction between variables, but not its value, was calculated using the statistical package Systat 3.0. Other models were fitted using the statistical package Statgraphics 3.0, with a subsequent estimate of the degree of interaction and standard error in each model. In all cases only hierarchical models were fitted. A small frequency (0.5) was added to all cells of the tables, as suggested by Upton (1978). The adequacy of a model after the removal of one of the variables was checked by estimating the difference between the maximum likelihood chi-square values for models with and without the variable being considered. If this difference exceeded the critical level of chi-square distribution for one degree of freedom and 95% significance level (equal to 3.84), then an exclusion of the variable was considered to be unjustified. All log-linear models included no more than two variables, which allowed an illustration of the results by diagrams.

In order to give a better graphical presentation of the results, correspondence analysis was used on the table, in which each of five columns represented a different wader species, rows - aggregations, cells - number of broods observed in each aggregation. The algorithm for the analysis was taken from Davis (1986), and appropriate programs were written and run in BASIC, apart from the estimate of eigen-values and eigenvectors of the chi-square distance matrix, which was calculated in the Systat 3.0 package.

Results

The general model of communal occurrence (model-0), demonstrates pairwise mutual attraction of broods of Grey Plover and Knot, Grey Plover and Curlew Sandpiper, Curlew Sandpiper and Turnstone (Figure 1a). Sanderling shows no relationship with broods of other species, neither in respect of attraction or avoidance.

1a. Model-0

1b. Model-1

1c. Model-2

1d. Model-3
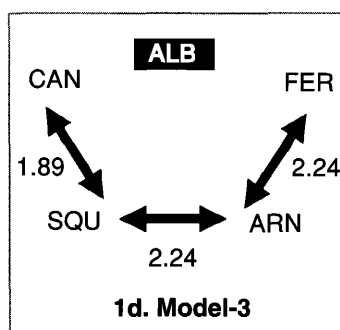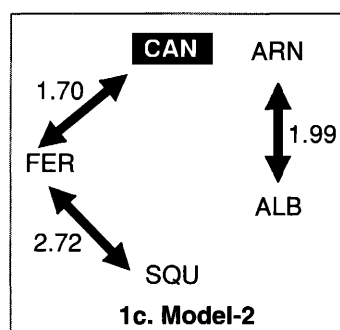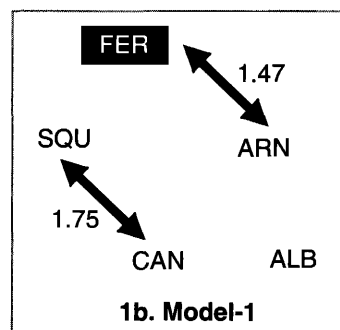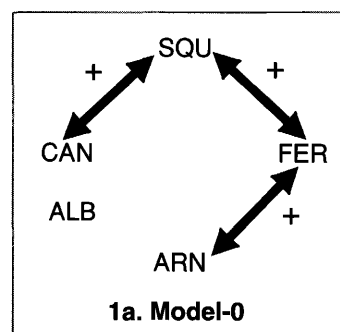
ALB	Sanderling
CAN	Knot
ARN	Turnstone
FER	Curlew Sandpiper
SQU	Grey Plover

FER Dependence of number of broods on presence of other broods analysed

◄──► Significant interactions

+ tendency to occur together in aggregations

1.75 Normalized effect coefficient If value >1.96 then p< 0.05

Figure 1. Path diagrams for the models of species interactions in wader brood aggregations.

Model-1 (in which Curlew Sandpiper is represented by categories with one and more than one brood in an aggregation) shows that the number of Curlew Sandpiper broods is higher in the presence of Turnstone broods (Figure 1b). The presence of any number of Curlew Sandpiper broods in an aggregation makes the presence or absence of both Grey Plover and Knot more probable than if they occur alone.

Model-2 (in which Knot is represented by categories with one and more than one brood in an aggregation) shows a positive interaction between the presence of Curlew Sandpiper and the number of Knot broods. It also demonstrates mutual pairwise attraction of both Curlew Sandpiper with Grey Plover, and Sanderling with Turnstone, in the presence of Knot broods (Figure 1c). However, in the case of Sanderling and Turnstone, an analysis of

2. Broods of Grey Plover and Curlew Sandpiper have a tendency to occur in aggregations together, as well as in the presence of broods of Knot.

3. Broods of Knot and Grey Plover are attracted to each other, as well as occurring in aggregations with Curlew Sandpiper or Sanderling.

4. The number of broods of Knot is larger in aggregations with Curlew Sandpiper (or, put another way, broods of Curlew Sandpiper prefer to associate with two or more broods of Knot - statistical methods cannot distinguish between the two).

5. The presence and number of broods of Sanderling are unrelated to the presence of broods of other species.

Table 1. Distribution of broods in different types of aggregations.

| Species | % Solitary | % in aggregations | | | No. of broods total |
		monospecific species*	interspecific species**	combined***	
Calidris alba	52.8	18.9	20.8	7.6	47.2	53
Calidris canutus	38.8	13.4	22.4	25.4	61.2	67
Calidris ferruginea	4.9	9.7	16.7	58.8	85.1	114
Arenaria interpres	17.4	21.7	43.5	17.4	82.6	23
Pluvialis squatarola	28.2	0.0	71.8	0.0	71.8	39

* aggregation is represented by broods of one species
** aggregation is represented by one brood of considered species and one or more broods of other species
*** aggregation is represented by more than one brood of considered species and one or more broods of other species

cross-tabulation tables suggests that their apparent association is in fact due to the absence of both in aggregations with Knot.

Model-3 (in which Sanderling is represented by categories with one and more than one brood in an aggregation) shows that the presence of broods of any other species do not influence the number of Sanderling broods (Figure 1d). Nevertheless, there are some pairwise interactions between other species participating in aggregations with Sanderling. These are between Knot and Grey Plover, Turnstone and Curlew Sandpiper, and Grey Plover and Turnstone. The interactions between the two first pairs correspond well with the results of the general model (model-0), but the attraction of Turnstone and Grey Plover appears in the model due to the almost complete absence of both from aggregations with Sanderling.

These results can be summarised as the following key points:

1. Broods of Curlew Sandpiper are attracted by broods of Turnstone, up to the point at which the number of broods of each species become equal.

An analysis of the composition of brood aggregations shows that the probability of encountering a solitary brood decreases in the

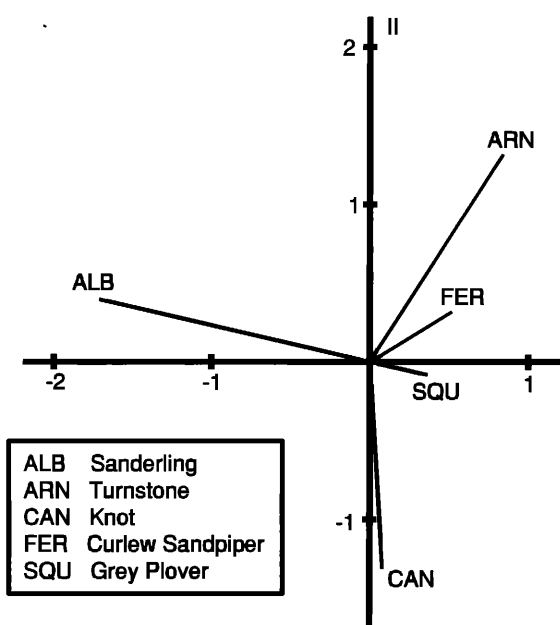| ALB | Sanderling |
ARN	Turnstone
CAN	Knot
FER	Curlew Sandpiper
SQU	Grey Plover

Figure 2. The position of each wader species on the first and second correspondence axes.

following sequence: Sanderling - Knot - Grey Plover - Turnstone - Curlew Sandpiper (Table 1). In other words, broods of Sanderling show the least tendency, and broods of Curlew Sandpiper show the greatest tendency to aggregate.

As to participation in different types of aggregation, the absence of Grey Plover brood aggregations with conspecifics and the relative rarity (only 9.7%) of records of monospecific groups of Curlew Sandpiper broods were of particular note.
The results of the correspondence analysis are presented in Figure 2. The first two correspondence axes are responsible for 60.7% of the total variance.

These results were extracted from the table containing all the information on the number of broods participating in certain aggregations, and they seem to confirm pretty well the conclusions drawn concerning species interactions listed above. In particular, the large separation of Sanderling from the other species on the first axis demonstrates its relative lack of association with them.
The data we have at our disposal are not sufficient to identify the reasons for the changes in structure of individual aggregations. It is only possible to say that, according to records of colour-marked birds, the structure of some aggregations hardly varies at all over a period of several days, while others are more variable.

Discussion

Of the wader species inhabiting the Northern Taimyr, only Grey Plover and Turnstone are "bold" species as defined by Dyrcz et al. (1981) i.e. they are able actively to protect their nests and broods by attacking approaching avian predators with alarm calls (Cramp & Simmons 1983; our observations). Knot also, on rare occasions, attack skuas Stercorarius spp. which get too close to a brood (Whitfield & Brade 1991; our observations). Other waders are "timid" and react to avian predators either by adopting a motionless, crouching posture preceded by an alarm call, initiating the same reaction in chicks, or by mobbing the predator with alarm calls produced in flight or from the ground, whilst keeping themselves aloof. In this respect, our results fit well the concept of a "protective umbrella" provided by large species of waders that will chase predators to smaller ones (Paulson & Erckmann 1985), however there are probably also other reasons.

The interspecific wader brood aggregations that we observed have little in common with the "creche-type" brood associations recorded in Bristle-thighed Curlew (Gill et al. 1991). The former are loose associations which move around together, which are formed and maintained by the greater antagonistic tendencies of one species over another, the mutual aggression of adult birds in the brood-rearing period, and the apparent desire of at least some of them to be close to other birds with broods.

The results show that there is an association of "timid" Knot and Curlew Sandpiper broods with "bold" Grey Plover and Turnstone. There can be little doubt about the role of "bold" waders as the focus of aggregations, because some early broods of Curlew Sandpiper and Knot were even attracted by pairs of Grey Plover which were still at the incubation stage (these aggregations were not included in the analysis).

The increase in the probability of the appearance of Curlew Sandpiper broods in aggregations with more than one brood of Knot may be a result of complex interactions between broods of Grey Plover, Knot and Curlew Sandpiper, which were not shown statistically because of the general shortage of data. However, Green et al. (1990) suggested that communal nest defence is recorded more often in birds of intermediate size, because they are less successful at it, than large birds. In our case, Grey Plovers did not permit conspecifics to remain in the vicinity of their broods. Aggregations of up to four broods of Knot probably have some ability to protect their broods and may be attractive to Curlew Sandpipers in the absence of Grey Plovers or Turnstones. The rarity of monospecific aggregations of Curlew Sandpiper broods can be explained in the same way, because even the communal efforts of several Curlew Sandpiper females would hardly be sufficient to stop a predator.

The lack of any relationship between Sanderling and other species can be explained by the noticeably smaller-scale movements of its broods in comparison with other wader species. It may therefore be difficult for a Sanderling brood to follow an aggregation composed of more mobile wader species. The fact that Sanderlings are more "settled" than other species may be due to the fact that Sanderling broods do not need to move very far to meet their food requirements.

Aggregations exist until the fledging period or even a bit later, in other words, until the moment that the ties between adult birds and juveniles are lost and the brood disperses. Later, the aggregations form flock-like groups from which adult birds disappear because they leave the breeding grounds earlier, while juveniles in many cases accompany late-hatched broods of conspecifics, or broods of Grey Plovers and Turnstones, which stay together longer. This phenomenon needs further study.

Some negative consequences are also possible for at least some of the species that form aggregations. It is possible, for example, that there may be intense competition for food in associations of Golden Plovers Pluvialis apricaria with Dunlins Calidris alpina (Byrkjedal & Kålås 1983), but this is unlikely in the Siberian tundra which is so rich in food resources (Ryabitsev 1992). Moreover, the Golden Plover and Dunlin observed in the earlier study were separated from each other by short distances of up to about 10 metres. The broods in the wader

aggregations we observed on the Taimyr, on the other hand, were distributed over quite a large area of tundra, often several hectares.

Chick exchange between broods in aggregations as a result of chick dispersal when a predator appears is likely to be a more serious problem. When a brood consists of chicks of significantly different ages, one might expect that the smaller chicks would get left behind and die. We recorded an exchange of chicks between several broods of Knot, the most commonly observed species, in monospecific and combined aggregations (Table 1). This could only have happened as a result of chick dispersal.

Formation of polyspecific brood aggregations in waders is probably a result of a complex interaction of species, optimising their brood-rearing strategies. Features of aggregation participants such as size, aggressiveness, territoriality, fidelity and chick mobility, as well as, probably, synchronisation of reproduction and a degree of overlap in the broods' habitats, may influence the structure of an aggregation. In this study, we found Curlew Sandpiper to be the most social species, for which participation in aggregations seems to be an important reproductive strategy. Further studies of the phenomenon of brood aggregation would provide a deeper understanding of the behavioural adaptations of waders for increasing their reproductive success.

Acknowledgements

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