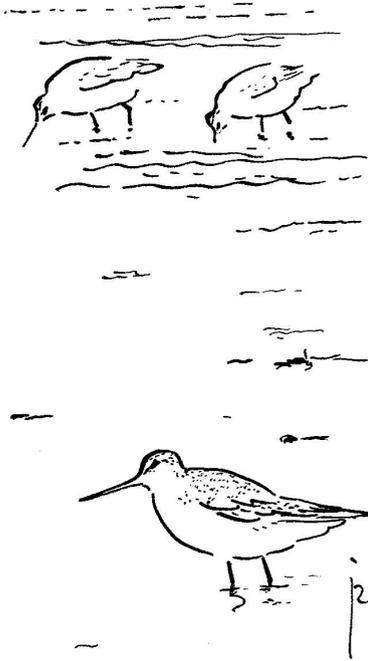


# INTERFERENCE BETWEEN THE SEXES IN FORAGING BAR-TAILED GODWITS *LIMOSA LAPPONICA*

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Sexual size dimorphism is common in many bird species. A consequence of sexual size dimorphism is that the larger sex has larger food requirements, and also that it might be dominant over the smaller sex. We studied the foraging behaviour of Bar-tailed Godwits *Limosa lapponica*, a highly sexually size dimorphic species. Our interest is in intersexual competition and its consequences for habitat use. Male and female Bar-tailed Godwits were distributed non-randomly over the intertidal foraging areas. Males were concentrated on exposed mud flats, while females occurred more along the waterline. Also within these habitat types, the sexes associated with same-sex individuals. Males were more susceptible to intraspecific kleptoparasitism than females, which we suggest is the cause of the unequal spatial distribution of male and female Bar-tailed Godwits. Females seem to monopolise the better quality foraging areas, leaving males the rest.

Key words: *Limosa lapponica* – foraging behaviour – interference – kleptoparasitism – dominance - sex

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A foraging individual deciding where to forage should take into account not only differences in food density between patches, but also the density of (conspecific) competitors the food has to be shared with. The decrease in food intake with increasing competitor density is the underlying mechanism why foraging individuals often have similar food intake rates across patches with highly variable food densities (Fretwell & Lucas 1969; Sutherland 1996). If individuals differ in their sensitivity to competition, the best competitors are expected to forage in the better patches than the sub-ordinates (Fretwell & Lucas 1969). Variation in competitive strength is often related to the size of individuals. One of the main sources of size variation in birds is due to sex, and sexual differences in competitive ability are often reported in which the larger sex is dominant over the smaller sex (Carpenter *et al.* 1993; Peters & Grubb 1983; Hepp & Hair 1984; Choudhury & Black 1991; Benkman 1997). Also on larger geographical scales intersexual competition might be the cause of the smaller sex migrating further southwards (Gauthreaux 1982; Perdeck & Clason 1983; Hepp & Hair 1984; Owen & Dix 1986; Choudhury & Black 1991). The aim of this study is to examine the foraging behaviour, competition and distribution among patches of a highly sexually dimorphic bird species, the Bar-tailed Godwit *Limosa lapponica*, with females being bigger than males (Prokosch 1988; Piersma & Jukema 1993). The sexes have been shown to select different foraging areas (Smith 1975; Cramp & Simmons 1983). Males seem to outnumber females in most wintering areas from which data are available (Piersma & Jukema 1993). Data were collected at an autumn stop-over site in the Dutch Wadden Sea. In this area Bar-tailed Godwits mainly forage during low tide on the mudflats. The most important prey items are worms from the genus *Arenicola* and *Nereis* (Scheiffart 2001). We examined differences between the sexes in habitat selection, and the likelihood of being kleptoparasitised.

Data were collected between 2-8 Sep 1996 on the mudflats south of Terschelling (Dutch Wadden Sea island). Observations were made

from the dike during low tide. The sexes of Bar-tailed Godwits were determined using a field estimate of general body size and bill length, the latter being highly sexually dimorphic: male bill length ranges from 68 to 90 mm, while female bill ranges from 86 to 110 mm (Piersma & Jukema 1990; Prokosch 1988). In situations where the sex of a bird was doubtful, the bill length was compared with nearby Godwits and also plumage coloration was used (most males still had some red feathers from their summer plumage). Sexing of the birds was consistent among the two observers.

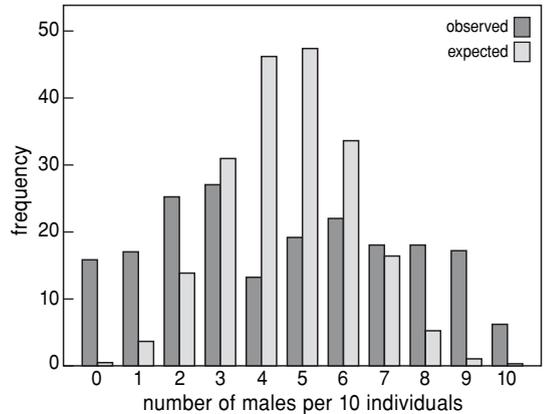
The spatial variation in distribution of both sexes was measured by counting the number of males per ten foraging individuals, for all the foraging Godwits within about 500 m from the observers. Scans of the mudflats were made on three different days. Data are analysed within days and pooled for all three days. Foraging habitat was subdivided into waterline (mudflat covered with shallow water) and mudflat (exposed mudflat). If Godwits distribute themselves randomly with respect to sex over the area, the frequency distribution of the number of males per ten individuals would follow a binomial distribution. The binomial distribution was calculated with the observed sex ratio of 46% males on the high tide roost ( $n = 1500$ ). This sex ratio was equal to the average sex ratio during all scans (46% males;  $n = 1980$ ). The observed distribution is compared with the binomial distribution using a  $\chi^2$ -test. Because expected numbers in the tails of the distribution do not exceed five, we have combined some of the categories to perform a  $\chi^2$ -test (the categories 0-2 and 8-10 males per ten individuals are combined).

Foraging behaviour was observed for two minutes per individual. During this period each prey was recorded. We hardly saw focal birds eating prey types other than worms (species unknown; but probably mainly *Nereis* spp.). Kleptoparasitic actions were defined as all instances of interference where a prey was or might have been involved, i.e. a prey that has been stolen or a foraging individual that was displaced by a competitor while trying to extract a prey. To increase the number of observed kleptoparasitic

actions, we made scans of foraging groups, from which as many kleptoparasitic actions as possible were registered. From these interactions the sex of both opponents was recorded, as well as which bird won, and the number of males and females in a radius of approximately five meters. For each kleptoparasitic interaction, we calculated the encounter probability between the attacked individual with an individual of either sex, using the number of males and females in a radius of five meters around the focal individual. This serves as the expected random interaction probability. The observed frequencies are compared with the expected frequencies using a  $\chi^2$  test. Contrary to normal 2x2 contingency tables, this test uses three degrees of freedom, because the cell frequencies do not follow automatically from the frequencies of rows and columns. Data analysis has been performed on average values per two-minute protocols. Most analyses are performed non-parametrically. In a single case we used ANCOVA, although the data were not normally distributed. This was done in order to test interaction terms, and we also present the non-parametric univariate statistics.

Local sex ratios were obtained from 198 groups of ten foraging individuals. The distribution of foraging Bar-tailed Godwits deviated strongly from a random distribution according to sex (Fig. 1). Also within days local sex ratios deviated significantly from a binomial distribution (day 1:  $\chi^2_5 = 87.1$ ,  $P < 0.001$ ,  $n = 89$ ; day 2:  $\chi^2_4 = 56.8$ ,  $P < 0.001$ ,  $n = 42$ ; day 3:  $\chi^2_5 = 41.8$ ,  $P < 0.001$ ,  $n = 67$ , categories combined in the way that the expected values were larger than 5). This unequal distribution was also reflected in foraging microhabitat: on the exposed mudflats there were on average 5.5 males per ten individuals, while in the waterline this was 2.6 (comparison of frequencies:  $\chi^2_6 = 143$ ,  $P < 0.001$ ). Given the sex-ratios in the two habitat-types, the distribution of the sexes was non-random within each habitat type (exposed mudflats:  $\chi^2_5 = 182.7$ ,  $P < 0.001$ ; waterline:  $\chi^2_4 = 17.56$ ,  $P = 0.0015$ , categories combined in the way that the expected values were larger than 5).

Males took more prey per two minute period



**Fig. 1.** Frequency distribution of number of males in groups of ten foraging Bar-tailed Godwits. Observed and expected frequencies differed:  $\chi^2_6 = 330$ ,  $P < 0.001$ .

than females, while the habitat difference in prey number approached significance, with more prey being taken in the waterline (sex:  $F_{1,86} = 4.75$ ,  $P = 0.03$ , habitat:  $F_{1,86} = 3.42$ ,  $P = 0.07$ , interaction  $F_{1,85} = 0.07$ ,  $P = 0.79$ ). In a non-parametric test sexes differed in prey number (Mann-Whitney  $U = 1109$ ,  $P = 0.035$ ,  $n = 84$ ), but no statistical differences were found between habitats (Mann-Whitney  $U = 927$ ,  $P = 0.28$ ,  $n = 84$ ). Intraspecific kleptoparasitic actions were in 89% successful to the extent that the focal bird displaced the conspecific from its foraging site. In the two-minute protocols 3.2% of the prey were lost by intra- and interspecific kleptoparasitic actions together, while 1.5% of the prey were gained by kleptoparasitism.

To investigate whether males are more vulnerable to kleptoparasitism we took the different distribution of the sexes into account. Males and females differed in the likelihood of being kleptoparasitized by either sex (Table 1). This is mostly because females overall initiated kleptoparasitic interactions more frequently than expected ( $\chi^2_1 = 7.77$ ,  $P = 0.005$ ,  $n = 89$ ).

Foraging male and female Bar-tailed Godwits were distributed non-randomly with respect to sex. This non-random distribution reflects differences in microhabitat: males and females used

**Table 1.** Frequency of kleptoparasitic actions in relation to sex. Horizontally the sex of the winner, and vertically the sex of the victim is given. The first numeral in each cell represents the observed kleptoparasitic actions. The second number in each cell is the expected number of kleptoparasitic actions taking into account the local differences in distribution of the sexes. Observed and expected frequencies differed significantly ( $\chi^2_3 = 8.51, n = 89, P = 0.037$ ).

Victim	Winner	
	Females	Males
Males	24 / 17.6	13 / 20.4
Females	50 / 44.3	2 / 6.7

the same area, but females mostly foraged in the waterline, while males used the mudflats after they were exposed (Smith & Evans 1973; Zwarts 1988). Which has not been shown before, is that also within these two habitat types the sexes were distributed non-randomly with respect to sex. Males were more vulnerable to kleptoparasitism from females than the other way round, which may explain the sexual niche differentiation. Kleptoparasitism is a general problem in prey choice in species foraging at high densities and on prey with long handling time (Brockmann & Barnard 1979). The proportion of prey gained and lost from kleptoparasitism in this study is rather small, suggesting that the problem to the Bar-tailed Godwits of prey being stolen is trivial. However, because especially the larger prey were stolen (pers. obs.), the amount of food lost in terms of energy is larger than this proportion suggests. Moreover, selection of lower quality foraging habitats to avoid heavy kleptoparasitism could bear a cost in terms of lost feeding opportunities (i.e. lower prey encounter rate and smaller size on mudflats). These costs are obscured by the birds' solution. The sexual differences in spatial distribution and prey size preference of waders are normally explained by differences in bill length (see Ens *et al.* 1990; Zwarts & Wanink 1993). In the case of Bar-tailed Godwits, males have shorter bills, which might prevent them from eating deeper buried larger prey (Zwarts & Wanink 1993;

Pierre 1994). According to this idea, the partial spatial separation of the sexes results from spatial differences in availability of different sized prey. As alternative we suggest that males forage in lower quality habitat, because the high food density habitat is less profitable for them due to competition from females. The observation that sexes were more segregated than expected within habitats suggests that competition between the sexes instead of habitat preference caused the differential distribution. This suggestion should however be confirmed by experimental removal of females to see whether males then switch to foraging in the water line. Experiments in other sexually dimorphic bird species showed that the smaller sex generally shifts to the niche previously occupied by the larger sex (Peters & Grubb 1983; Marra *et al.* 1993; Aho *et al.* 1997; Ardia & Bildstein 1997), as would be expected if intersexual competition is the cause of the niche difference between sexes.

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## SAMENVATTING

Bij veel vogelsoorten verschillen de mannetjes en vrouwtjes in lichaamsgrootte. Dit verschil moet belangrijke ecologische consequenties hebben. De kleine sekse heeft bijvoorbeeld minder voedsel nodig, maar zal ook de strijd om beperkende voedselbronnen makkelijker verliezen. Bij Rosse Grutto's *Limosa lapponica* zijn mannetjes duidelijk kleiner dan vrouwtjes. In de onderhavige studie is onderzocht of dit consequenties heeft voor de wijze waarop beide seksen het wad onder Terschelling gebruiken. Foeragerende mannetjes en vrouwtjes kwamen niet willekeurig door elkaar voor. Mannetjes foerageerden vaker bij andere mannetjes in de buurt, terwijl ook vrouwtjes vooral met hun seksegenoten foerageerden. Dit verschil is deels te verklaren uit het feit dat de vrouwtjes hun voedsel meer bij de waterlijn zochten, terwijl mannetjes dit vaker op de drooggevallen wadplaten deden. Ook binnen deze habitattypen waren de seksen echter meer gescheiden dan je per toeval zou verwachten. De waterlijn lijkt een betere plek om voedsel te zoeken, omdat hier meer prooien per tijdseenheid werden gegeten. Het lijkt daarom verbazingwekkend dat de mannetjes juist vooral op de drooggevallen platen foerageerden. De mannetjes hadden echter te lijden van de nabijheid van foeragerende vrouwtjes, omdat deze geregeld de door hun gevonden prooien stalen. Het lijkt er dus op dat vrouwtjes van de Rosse Grutto de beste voedselplekken voor mannetjes minder interessant maken en hen daardoor dwingen om met slechtere voedselgebieden genoegen te nemen. Hoewel wij hier alleen beschrijvende gegevens hebben verzameld, is het consistent met experimenteel onderzoek aan andere soorten waarbij de kleinere sekse de foerageerniche verschoof nadat de grotere sekse hieruit verwijderd was. (CB)

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