TIME BUDGETS, FEEDING EFFICIENCY AND FLOCK DYNAMICS IN MIXED SPECIES FLOCKS OF LAPWINGS, GOLDEN PLOVERS AND GULLS

by

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INTRODUCTION

In recent years, an enormous amount of work has been done on the relationships between flocking behaviour and feeding efficiency in birds. Among the most revealing studies are those which have examined the effects of flocking on individual time budgets (the way time is allocated to different behaviours) (*e.g.* KREBS, 1974; PULLIAM *et al.*, 1974; POWELL, 1974; LAZARUS, 1979; CARACO, 1979a, b; BARNARD, 1980a). Some studies have also quantified the relationship between flock size effects on feeding efficiency and flock size dynamics (*e.g.* CARACO, 1979, a, b, c; BARNARD, 1980b, c). However, the best quantitative studies have been with single species flocks. Although there is a wealth of information in the literature concerning interspecific interactions in mixed flocks (*e.g.* MORSE, 1970, 1978; KREBS, 1973; RUBENSTEIN *et al.*, 1977; KUSHLAN, 1977, 1978; BALPH & BALPH, 1979; BROCKMANN & BARNARD, 1979; CALDWELL, 1981), little attention has been paid to the effects of species composition within flocks on time budgeting and flocking dynamics of component species. In a recent paper, BARNARD & STEPHENS (1981) examined the effects of flock size, and the addition to the flock of kleptoparasitic gulls (*Larus ridibundus*) (see KÄLLANDER, 1977, 1979; BROCKMANN & BARNARD, 1979), on feeding efficiency in lapwings (*Vanellus vanellus*). These authors found that gulls depressed the feeding benefits of large flocks of lapwings through changes in the amount of time lapwings

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devoted to selecting prey items. In this paper, we investigate the effect of flock size and species mixtures on two component species of a 3-species mixed association. We examined winter associations between lapwings, black-headed gulls and golden plovers (*Pluvialis apricaria*) feeding on agricultural pasture. The aims of the study were to quantify the relationship between species sub-flock size (the number of birds of a given species within the flock) and overall flock composition and both the time budgets and feeding efficiency of lapwings and golden plovers. In addition, we made and tested some predictions about species sub-flock sizes based on the time budget and feeding efficiency results we obtained.

METHODS

Observations were made during the winters of 1979/1980 and 1980/1981. Single and mixed species flocks were located opportunistically in pastures around the villages of Wysall, Keyworth and Rempstone, about 10 miles southeast of Nottingham. The pastures were similar in type and quality to those described by BARNARD & STEPHENS (1981) and, as in the earlier study, almost the only prey taken by birds and found in the turf were species of oligochaete worm (between 97.5% and 99% of invertebrate species taken from the turf by observers were oligochaetes). Observational techniques for recording time budgets were also similar to those in Barnard and Stephens' study. Arbitrarily chosen lapwings or golden plovers were observed through a x15-x60 HT8 telescope mounted on a tripod and their sequences of behaviour dictated into a Uher 4000 report C tape recorder. Recorded sequences were then transcribed on the computer to obtain frequencies and durations of each activity. Birds were observed until they left the flock or were obscured from view by grass, undulations in the ground or other birds (mean duration of observation for lapwings = 112.1 ± 17.7 s, range: 24.1-344.0 s; for golden plovers = 91.7 ± 2.9 s, range: 40.1-157.0 s). Activities were categorized as *stepping* (rapid stepping actions with the head held erect and each step measuring about 3.5 cm in lapwings and 5.0 cm in golden plovers), *pecking* (all actions associated with catching and handling prey once the bird first pecked at the ground), *crouching* (body orientation with head pointing down and tail up and the long axis of the body held at about 20° to the ground (crouching usually occurred immediately before a peck and was shown by BARNARD & STEPHENS to be associated with increased selectivity in the range of prey sizes taken by lapwings) and *scanning* (assumed to occur when birds stopped after bursts of rapid stepping and the head was held in an extreme erect position). Scanning was assumed to reflect vigilance for approaching predators, the most serious of which, judging by the alarm responses of flocks, were kestrels (*Falco tinnunculus*), carrion crows (*Corvus corone*) and rooks (*C. frugilegus*). Although only one attack (unsuccessful) was witnessed, there is evidence that kestrels may take lapwings and even black-headed gulls (KIRKMAN & JOURDAIN, 1966; YALDEN, 1980) and corvids are at least known nest predators of lapwings and golden plovers (PARR, 1979). Both kestrels and corvids sometimes swooped on feeding charadriiform flocks. We also recorded the length of each worm caught by birds during observation (estimated relative to bill length (tip of the bill to the end of the gape)). Where access to fields permitted, surface-dwelling oligochaetes were sampled along the approximate search paths of observed golden plovers in the same way as in BARNARD & STEPHENS (1981). Where possible, time budgets for lapwings and golden plovers were taken from the same flocks. In all cases the number of individuals of each species present in the flock was noted. Additional protracted observations (mean duration = 2,383 ± 520.6 s, range: 913-5,322 s) of arrivals, departures and birds passing over were taken for single and mixed species flocks. Protracted observations with and without gulls were periodically interrupted for time budget recordings. In this way detailed simultaneous recordings of individual feeding behaviour and overall flock dynamics were obtained. Additional data for flock density and species interneighbour distances were obtained by measuring the maximum length and breadth of flocks and sub-flocks using a Ranging 1200 distance finder (calibrated for measurements between 46 and 1000 m) and mapping the position of birds on duplicated scale maps of fields. Inter-neighbour distance (D) within a flock was calculated as:

$D = \sqrt{}^{1}/[\pi(ml.mb/N]$ .... (1)

where ml is the radius at the maximum length of the flock, mb the radius at the maximum breadth, N the number of birds present and the flock was assumed to be elliptical in shape.

RESULTS

FLOCK COMPOSITION AND LAPWING FEEDING EFFICIENCY

Barnard & Stephens (1981) showed that increased flock size in lapwings (in the absence of gulls) correlated with an increased individual net rate of energy intake. However, their conclusions were limited because the scarcity of large flocks without gulls necessitated a broad lumping of worm and flock size classes. The analysis we report here makes use of much more extensive data. Instead of lumping size classes, we have calculated net rates of energy intake for individual time budgets on a continuous scale of flock size and species composition.

For the purposes of analysis we distinguished 22 different lenghts of worm taken by lapwings (ranging in size from $< {}^{1}/_{2}$ to 6 bill lengths). Bill lengths were converted to mm by multiplying by a bill length constant. A corrected calorific value of each sized worm was then calculated to allow for the fact that a proportion of the worms observed being taken were likely to be broken pieces of larger worms (see Barnard & Stephens, 1981, and Burton, 1974). A 16 mm worm, say, which was really part of a 60 mm worm would be fatter and contain more calories than a complete 16 mm worm. From estimates of the risk of worms of given observed length really being broken pieces of larger worms and the approximate length of worm which was lost in the ground (Barnard & Stephens, 1981), we calculated the calorific value of each worm taken as:

$C_{i.corr.} = {}^{1}i/l_{r}.\ C_{r}$ .... (2)

where $C_{i.corr.}$ is the corrected calorific value (cals.) of taken worm i, l; is the observed length of worm 1, l_r is the estimated original length of the worm and C_r is the calorific value of the original length worm. C_r and $C_{i.corr.}$ were calculated from the polynomial regression equation for the relationship between worm length and calorific value (see Barnard &

Stephens (1981), for details of calorimetry and calculation of the regression equation). Although this correction spreads the breakage risk over all worms taken, it is probably a more accurate reflection of what birds actually obtain for two reasons. Firstly, Burton (1974) and S-A. Bengtson (pers. comm.) found that a large proportion of earthworms in golden plover guts were broken anterior ends of larger worms. This is supported by our own observations that an average of between 17 and 24% (and, in some samples, as high as 38%) of worms found in the turf where charadriiform flocks had recently been feeding were broken posterior ends. Secondly, the correction makes very little difference to the calorific value until observed worm size taken reaches 55-60 mm. This reflects the observed situation in the field where it is larger worms which are more liable to break and leave a large proportion still in the ground.

The net rate of energy intake during each recorded sequence for lapwings in flocks without gulls (but with or without golden plovers) was then calculated in two ways:

$$\mathrm{NetC_f} = \frac{\Sigma(nC_1 + nC_2 + \ldots\ldots\ldots\ldots\ nC_{22})}{t_s + t_c + \Sigma(nt_{h1} + nt_{h2} + \ldots\ldots\ldots\ldots\ nt_{h22})} \quad \ldots\ldots\ldots\ldots \tag{3a}$$

$$\mathrm{NetC_b} = \frac{\Sigma(nC_1 + nC_2 + \ldots\ldots\ldots\ldots\ nC_{22})}{T} \quad \ldots\ldots\ldots\ldots \tag{3b}$$

where $C_{1\text{-}22}$ are the corrected calorific values for worm sizes 1 to 22, n is the number of worms of each size taken during an observed behaviour sequence, t_s is the total time spent stepping during the sequence, $t_{h1\text{-}22}$ is the handling time for each worm taken calculated from the polynomial regression equation for the relationship between handling time and worm length, t_c is the total time spent crouching during the sequence and T is the duration of the whole sequence. $\mathrm{NetC_f}$ thus represents the net energetic returns based on *foraging* time (stepping, crouching and handling) only and $\mathrm{NetC_b}$ represents the net energetic returns for the whole sequence (which therefore includes scanning).

Equation 3a, b, was also used to calculate net rate of energy intake for lapwings in flocks containing gulls. Here, however, $\mathrm{NetC_f}$ and $\mathrm{NetC_b}$ were calculated using shorter handling times (lapwings handled given sized worms more quickly when gulls were present (Barnard & Stephens, 1981)). These handling times were calculated from a separate regression equation for the relationship between handling time and worm length in the presence of gulls.

Computed values for $\mathrm{NetC_f}$ and $\mathrm{NetC_b}$ were then entered with a number of other variables into a stepwise partial regression analysis. Separate analyses were carried out for flocks with and without gulls. The independent variables entered into the analysis were those which intuitively or from previous analyses might be expected to influence lapwing feeding efficiency. We used a forward stepwise inclusion technique which entered independent variables in single steps from best to worst in terms of explaining observed variance in the chosen dependent variable. The variable that explained the greatest amount of the variance was entered first, the variable which in conjunction with the first explained the greatest amount of variance was entered second and so on. Thus the variable that explained the greatest amount of variance unexplained by the variables already in the equation entered the equation at each step. Variables were not entered if the variance in the dependent variable remaining unexplained by the independent variables already included in the equation did not result in an F-ratio greater than 1.5. In this way we were able to arrive at the best set of predictors for each chosen dependent variable. The relationships between lapwing $\mathrm{NetC_f}$ and $\mathrm{NetC_b}$ and independent variables included in the regression equation are shown as F-ratios in Table 1a, b.

Table 1a shows results for flocks without gulls. The most striking trends are those between lapwing flock or subflock size and the proportion of time spent crouching in a sequence and capture rate and $\mathrm{NetC_b}$. The net rate of energy intake (Net $\mathrm{C_b}$) per bird was much higher when more lapwings were present. Similarly, both $\mathrm{NetC_b}$ and capture rate increased with the proportion of time birds spent crouching. This is also reflected in the (non-significant) tendency for worm length taken to increase with the proportion of time spent crouching. Finally, the number of golden plovers present in the flock significantly increased lapwing capture rate but not $\mathrm{NetC_f}$ or $\mathrm{NetC_b}$. Lapwings thus did not do any better in terms of their net rate of energy intake when plovers were present.

Very different trends emerge, however, from Table 1b which shows F-ratios for flocks with gulls. Most obvious are the apparently paradoxical positive relationships between the number of gulls present and lapwing $\mathrm{NetC_f}$ and $\mathrm{NetC_b}$. The number of gulls also correlated positively with the mean length of worm taken by lapwings. Other striking results are the lack of any relationship between lapwing subflock size and lapwing feeding efficiency and the significant *negative* effect of the presence of golden plovers on lapwing $\mathrm{NetC_f}$, $\mathrm{NetC_b}$ and capture rate (c.f. Table 1a, and see Discussion). It is interesting, in view of the negative effects of golden plovers, that lapwing capture rate but not net energy intake increased as a function of the number of gulls per golden plover in the flock. We shall return to these points later.

At first sight, the positive relationship between lapwing feeding efficiency and the number of gulls in the flock appears to contradict BARNARD & STEPHENS' (1981) finding that net rate of energy intake in lapwings *decreased* when gulls were present. However, it is likely that the relationship arises because gulls tended to associate only with lapwing flocks in which birds were doing well. BARNARD and STEPHENS found that although lapwings in large flocks tended to take a large proportion of very small worms, they also took some very large (65-310 mm) worms which gulls were more effective at stealing. It may be that the number of gulls depended on the rate at which lapwing flocks made large worms available while lapwing subflock size depended on the rate at which lapwings

TABLE 1a

F-ratios from stepwise partial regression analysis of the relationship between feeding efficiency and flock composition variables for lapwings in the absence of gulls

	No. Lapwings	No. Golden plovers	Gol:Lap ratio	% time crouching
$NetC_f$	—	—	—	—
$NetC_b$	4.40*	—	—	9.15**
Mean worm length	—	—	—	2.83
Capture rate	24.52**	3.99*	—	16.22**

Data for 186 flocks. — indicates that an independent variable was not included in regression equation because it yielded an F-ratio of less than 1.5. * = $p < .05$, ** = $p < .01$.

TABLE 1b

Same as a) but for flocks in which gulls were also present

	No. Lapwings	No. Gol plovers	No. Gulls	Gol:Lap ratio	Gull:Lap ratio	Gull:Gol ratio	% time crouching
$NetC_f$	—	-3.74*	24.88**	—	—	—	—
$NetC_b$	—	-4.37**	28.73**	—	—	—	3.99*
Mean worm length	—	—	11.37**	—	—	—	—
Capture rate	—	-5.49**	31.45**	—	—	6.45**	7.82**

Data for 217 flocks. Minus sign indicates negative partial regression coefficient. Significance levels as in Table 1a.

found more profitable (for lapwings) intermediate (17-48 mm) sized worms.

The rate of finding large worms is likely to correlate with the rate of finding intermediate sized worms and hence with NetC$_f$ and NetC$_b$. This does not mean, however, that lapwings in large flocks with gulls could not have done better in the absence of gulls. To see whether lapwing and gull numbers depended on the rate at which lapwings found different sized worms, we examined data for lapwings with and without gulls and divided worm sizes taken into the size classes used in the earlier study. We then calculated the rates at which lapwings were finding different size classes and hence making them available to gulls. Since gulls could potentially monitor all birds in the flock, we estimated 'flock productivity' (FP) for each worm size class as:

$$FP_i = \left[\frac{\Sigma(I_{1i} + I_{2i} + \dots\dots\dots\dots I_{ni})}{n}\right] N \quad \dots\dots\dots\dots \quad (4)$$

where $I_{1i\text{-}ni}$ is the rate at which focal lapwings 1-n found worms of size class i, n is the number of focal lapwings recorded in the flock and N is the total number of lapwings in the flock. Stepwise partial regression analysis was then carried out relating the numbers of lapwings and gulls in a flock to FP for different size classes of worm.

The results in Table 2 show that, whether or not gulls were present, the number of lapwings in a flock was best predicted by the rate at which birds were catching worms of size classes 2 and 3 although there was also a significant positive relationship with total capture rate in flocks without gulls. The number of lapwings in flocks with gulls correlated negatively with FP for size classes greater than 3. The number of gulls, on the other hand, showed a strong *negative* relationship with FP 2 + 3 but strong positive relationships with the number of lapwings and FP > 3 (the significance of the 'spacing' category will become clear later). As expected on the basis of previous analyses, therefore, the numbers of lapwings and gulls in a flock correlated well with the size ranges of worm birds of each species were most efficient at taking. There were more gulls in larger flocks of lapwings and larger flocks were those in which lapwings were achieving high net rates of energy intake.

However, if lapwings in any given flock size tended to do better without gulls than with gulls, we might expect this to show up in samples taken from flocks before and after the arrival of a gull. On the basis of our previous results, we would expect lapwings to have lower NetC$_f$ and NetC$_b$ values after the arrival of a gull than before. Despite taking samples from over 400 flocks, however, instances in which we were able to record 'before and after' samples were very rare. This was mainly because gulls seldom arrived in small flocks of lapwings, while large flocks usually had one or more gulls permanently in attendance. Even when flocks were disturbed and moved to another field, any attendant gulls usually moved with them. Nevertheless, those cases which we were able to record bore out our expectations. Both $NetC_f$ and $NetC_b$ were significantly lower for lapwings after the arrival of a gull (mean $NetC_f$ before arrival = 20.55 ± 6.12 cals/s., mean $NetC_f$ after = 6.57 ± 1.28 cals/s., $t = 2.85$, d.f. = 11, $p < .02$; mean $NetC_b$ before arrival = 5.12 ± 1.16 cals/s., mean $NetC_b$ after = 1.99 ± .40 calls/s., $t = 2.94$, d.f. = 11, $p < .02$).

TABLE 2

F-ratios from stepwise partial regression analysis relating the number of lapwings and gulls in a flock to the rate at which lapwings found worms of different sizes

	No. Lapwings	No. Gulls	Total capt. rate	Capt. rate for size classes 2+3	Capt. rate for size classes >3	Spacing
No. Gulls	15.57**	—	1.25	-19.56**	19.99**	1.23
No. Lapwings (with gulls)	—	15.57**	0.086	2.98*	-2.63*	-5.20**
No. Lapwings (no gulls)	—	—	2.84*	27.51**	-0.89	—

Data for 67 flocks. Symbols and significance levels as in Table 1, except that a 0.1% variance contribution was used as the criterion for including an independent variable.

FLOCK COMPOSITION AND EQUILIBRIUM SUBFLOCK SIZE IN LAPWINGS

Since net rate of energy intake for lapwings in any given flock size appears to be depressed by the presence of gulls, we might expect gulls to lower the utility of a given feeding site. If so, we would expect the site to attract and support fewer lapwings than in the absence of gulls. To test this, we analysed data from protracted observations of flocks (see Methods) during which all arrivals, departures and passers-by at the flock were recorded. Because it is difficult to distinguish short term changes in flock size in relation to an event from random fluctuations which are due to factors unrelated to that event, we sought changes in lapwing equilibrium subflock size (E.F.S.) E.F.S. was defined by Krebs (1974) as the flock size at which arrival rate equals departure rate. It is thus the size at which the flock reaches a *dynamic* equilibrium. The emphasis on 'dynamic' is important. As BARNARD (1980b) points out, a dynamically stable flock suggests that more birds are attempting to feed at a site than can be accommodated at one time. A statically stable flock (where there are no arrivals or departures) may simply indicate that the maximum number of birds which could be accommodated at a site was not attempting to feed at the time. The E.F.S. is thus a useful measure of the utility of a feeding site. Because an E.F.S. can be measured only over a long period, it helps to guard against misinterpreting random fluctuations in flock size.

For the same reasons as before, we were limited in the number of 'before and after' observations we could make. We were further limited by the fact that not all flocks we observed reached an E.F.S., either before or after the arrival of gulls. As in BARNARD (1980b), we calculated subflock E.F.S. as the mean number of birds present during periods of approximately equal arrival and departure rates. Although we were able to record only 15 cases in which lapwing subflocks reached an E.F.S. before and after the arrival of gulls, there was in each case except one a drop in the mean and range of lapwing numbers after gulls arrived (Fig. 1a).

Since lapwing feeding efficiency in flocks with gulls was apparently negatively affected by increased golden plover numbers, we also examined the effect of large numbers of plovers arriving on lapwing subflock E.F.S.

Data were taken from flocks where plover numbers changed by different numbers of birds but the number of gulls remained constant. Fig. 1b shows an overall negative correlation between lapwing E.F.S. and the number of plovers arriving. However, the trend was not a simple one. Lapwing E.F.S. tended to increase when only a few plovers arrived. When gulls were present, therefore, plovers had a negative effect on lapwing feeding efficiency and change in subflock size. When gulls were not present and plovers had no effect on lapwing feeding efficiency, there was no directional effect of plover arrival on changes in lapwing E.F.S. (Fig. 1c), although arrivals generally correlated with a decrease in lapwing E.F.S.

FLOCK COMPOSITION AND GOLDEN PLOVER FEEDING EFFICIENCY

To see how golden plovers fared when flock composition changed, we carried out a similar series of analyses that described for lapwings here and by BARNARD & STEPHENS (1981). 99% (of 1,725 flocks) of golden plovers were recorded in association with lapwings, and all golden plover data here refer to subflocks within mixed lapwing/golden plover flocks.

To begin with we examined the range of worm sizes taken in relation to those available in the turf to see whether plovers selected certain worm

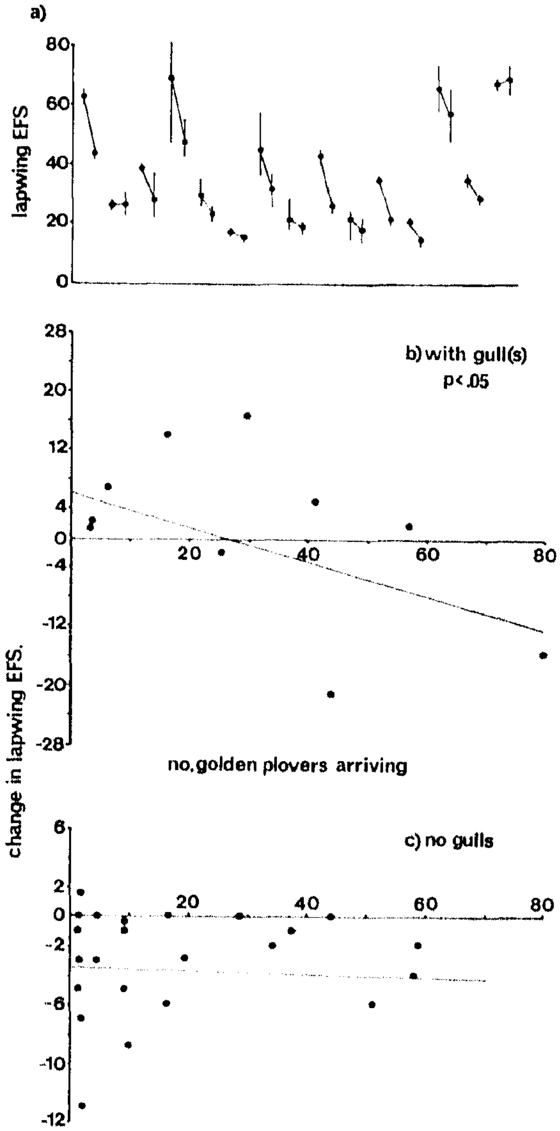

Fig. 1. a) Changes in lapwing E.F.S. with the arrival of one or more gulls and when golden plover number remained relatively constant. Each pair of joined points represents one flock. The point nearest the y-axis of each pair represents the E.F.S. before gulls arrived, the other point the E.F.S. after gulls had arrived. E.F.S. showed a significant decrease ($\chi^2 = 14.2$, $p < .001$) after gulls arrived. Data for 15 flocks observed for 15 minute periods when flocks had reached an E.F.S. before and after gull arrival. Bars represent ranges of flock size. b) Changes in lapwing E.F.S. with the arrival of different numbers of golden plovers. Data for 10 flocks in which gulls were present. $r = -.64$, $p < .05$. c) Same as b) but for flocks in which there were no gulls. Data for 24 flocks. $r = .15$ n.s.

sizes and whether plover subflock size and the presence of gulls influenced the range of worm sizes taken. Fig. 2a-d provides a direct comparison with the data presented for lapwings by BARNARD & STEPHENS (1981). Like lapwings, golden plovers tended to take disproportionately more of the smaller size classes of worm available. Plovers in large flocks also tended to take more worms of size classes 2 and 3 and fewer of size class 1 and this tendency was suppressed in the presence of gulls. BENGTSON *et al.* (1978) also found that golden plovers concentrated on worms equivalent in size to our classes 2 and 3, though their birds took more very large worms than those in this study. To see whether the apparent worm size selection shown by the plovers reflected their expected net rate of energy intake from each size class, we used BARNARD & STEPHENS' equation 2 (with the risk of worm breakage already taken into account). As in the earlier study, expected net rate of energy intake in flocks with gulls was corrected for the probability of loss of different worm

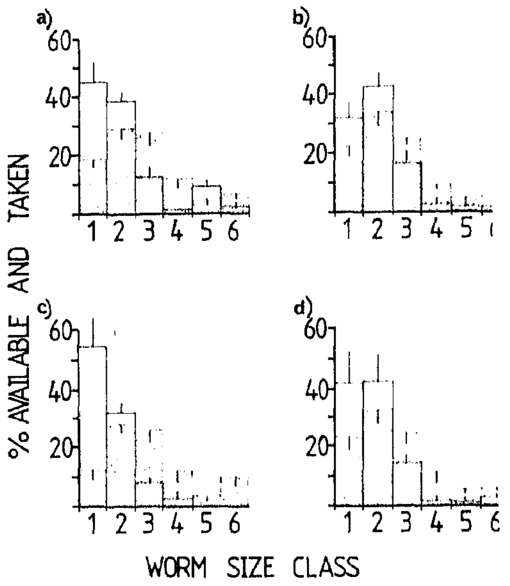

Fig. 2. a) The range of worm sizes taken by golden plovers in small flocks (< 13 plovers) without gulls expressed as the mean percentage number of worms taken per recorded sequence (☐) falling into each of six size classes and plotted with the percentage total number of worms obtained from turf samples which fell into each size class (▨). D_{max} (worm size class distribution (W.C.D.) taken *vs* W.C.D. in the turf): = .37, p< .01. Data for 9 sequences. b) Same as a) but for large flocks (> 13 plovers). D_{max} (W.C.D. taken *vs* W.C.D. in turf) = .21, p< .01. Data for 15 sequences. c) Same as a) but with gulls present. D_{max} (W.C.D. taken *vs* W.C.D. in turf) = .39, p< .01). Data for 7 sequences. d) Same as b) but with gulls present. D_{max} (W.C.D. taken *vs* W.C.D. in turf) = .29, p< .01. Data for 11 sequences. Bars represent standard errors.

sizes to gulls. In addition we had to correct for loss to lapwings. During field observation it became clear that a number of worms caught by plovers were being stolen by lapwings. Fig. 3a shows that food-stealing by lapwings occurred most when plovers found worms of size class 3 and above. This may explain the occasional discarding of large worms by golden plovers even when kleptoparasitic gulls were not present. Fig. 3b, c shows the expected net rate of energy intake per second handling and travelling time for each size class taking into account the probability of loss to lapwings (Fig. 3b) and to both lapwings and gulls (Fig. 3c). Travel

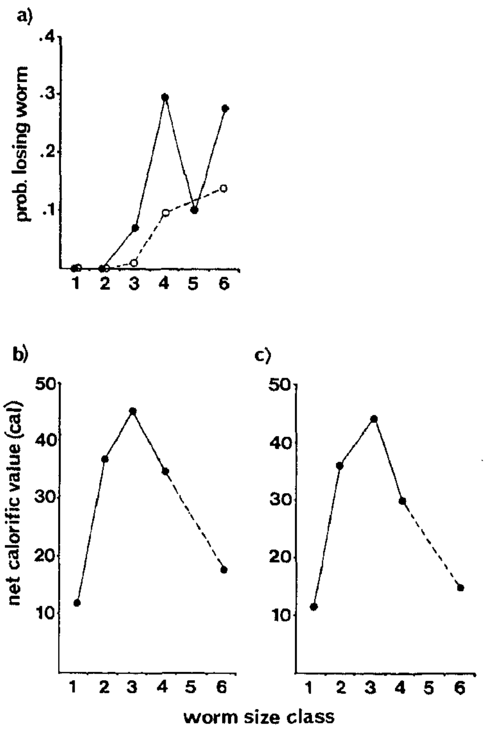

Fig. 3. a) The probability that a plover will lose a worm of given size class to lapwings (•——•) and gulls (o-----o). b) Net calorific value of the average sized worm in each class taking into account the probability of loss to lapwings. c) Same as b) but taking into account the probability of loss to both lapwings and gulls.

time was calculated on the basis of the density of each size class in turf samples using BARNARD & STEPHENS' equation 1 modified for plover step length and rate. Values in Fig. 3c were also calculated using a different regression equation for the relationship between worm length and handling time to that used in Fig. 3b. This was because, like lapwings, golden plovers handled given sized worms more quickly in the presence of gulls (mean handling time (s./mm) without gulls = 0.069 ± 0.007 s;

mean with gulls = 0.054 ± 0.002 s, t = 2.05, $p < .05$). As in lapwings, size classes 2 and 3 emerged as the most profitable when taken in isolation. It is notable, however, that the net calorific value for each class is much (roughly 5x) higher for golden plovers than for lapwings (c.f. BARNARD & STEPHENS, 1981. Fig. 5a, b). Two factors account for this. Firstly, handling times for any given sized worm were approximately 25% shorter in plovers (compare the s/mm figures above with those in BARNARD & STEPHENS, 1981, p. 12) and secondly plovers took longer (5.0 cm *vs* 3.5 cm) and more rapid (mean step rate = 2.34 ± 0.07 steps/s *vs* 0.65 ± .068 steps/s) steps than lapwings and so had much reduced expected travel times. One shortcoming with this comparison, however, is that it does not take into account the possible increased energy costs of moving and handling more quickly.

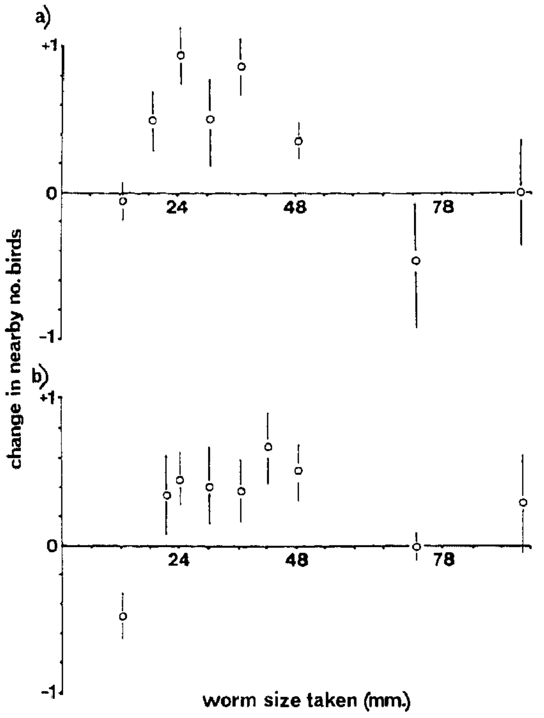

Fig. 4. a) Changes in the number of lapwings within 8 plover lengths of a golden plover after the plover found worms of different length. b) Changes in the number of plovers within 8 plover lengths of a lapwing after the lapwing found worms of different length.

The loss of worms to lapwings was very infrequent, mainly because it occurred on the relatively rare occasions when plovers took large worms and also when the species ratio was skewed towards lapwings (see later). Food stealing was never detected in the focal lapwings used here and in the earlier study, even though 24.7% of them were recorded in association with golden plovers. However, there is a possibility that some of the worms taken by lapwings were found by area-copying (BARNARD & SIBLY, 1981) plovers. Fig. 4a, b shows that both lapwings and golden plovers tended to approach individuals of the other species when they found worms. Moreover the tendency was most pronounced for worm sizes between 18 and 48 mm, the size range which yielded the highest net rate of energy intake for the two species. Interactions initiated by plovers against lapwings will be discussed later. The nature of area-copying and other interspecific feeding interactions is currently being studied in more detail.

NetC_f and NetC_b values for each recorded sequence were then calculated using equation 3a, b and again separate calculations were made for flocks with and without gulls. The relationship between NetC_f and NetC_b and a similar range of independent variables to that used in the lapwing analysis was then analysed using stepwise partial regression.

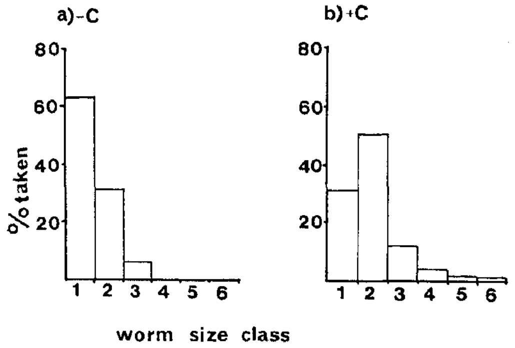

Fig. 5. a) the percentage number of worms taken by golden plovers without crouching which fell into each size class. n = 16 worms. b) Same as a) but for pecks preceded by crouching. n = 167 worms. C = crouching.

Table 3a shows the results for plover subflocks without gulls. The best predictors of plover feeding efficiency were the number of lapwings in the flock and the proportion of time plovers spent crouching during a recorded sequence. Both NetC_f and NetC_b increased with the amount of crouching in a sequence, reflecting the tendency for crouching to result in more profitable worms being taken (Fig. 5). NetC_f, NetC_b and mean worm length taken were all negatively influenced by the number of lapwings, but capture rate increased with lapwing number. Capture rate was therefore not a good predictor of the net rate of energy intake. The number of conspecifics in the flock had no effect on plover energy intake, although capture rate increased with the number of plovers per lapwing.

When gulls were present (Table 3b), the influence of lapwing number on NetC$_f$, NetC$_b$ and mean worm length disappeared and there was now a significant negative relationship between plover capture rate and lapwing number. Also apparent was a significant positive effect of the number of conspecifics on NetC$_b$ (c.f. Table 3a) and the proportion of time spent crouching on NetC$_f$. As with lapwings (Table 1b), the presence of gulls (here the ratio of gulls to plovers) correlated with an increase in NetC$_b$. However, in plovers, this *did* reflect increased individual net energy intake in response to gulls. Analysis of plover net rate of energy intake before and after the arrival of one or more gulls (when lapwing number remained constant to within 3 birds) showed an increase in both NetC$_f$ (mean NetC$_f$ before gull arrival = 3.85 ± .69 cals/s, mean after = 14.75 ± 3.97 cals/s, t = 2.72, d.f. 12, $p < .05$) and NetC$_b$ (mean NetC$_b$ before = 1.53 ± .23 cals/s, mean after = 3.82 ± .73, t = 2.88, d.f. 12, $p < 0.5$) with gull arrival.

TABLE 3a

F-ratios from stepwise partial regression analysis of the relationship between feeding efficiency and flock composition variables for golden plovers in the absence of gulls

	No. Lapwings	No. Golden plovers	Gol:Lap ratio	% time crouching
NetC$_f$	-8.35**	—	—	10.32**
NetC$_b$	-8.21**	—	—	12.99**
Mean worm length	-3.55*	—	—	5.80**
Capture rate	3.75*	—	4.97**	18.06**

Data for 67 flocks.

TABLE 3b

Same as a) but for flocks in which gulls were also present

	No. Lapwings	No. Gol plovers	No. Gulls	Gol:Lap ratio	Gull:Lap ratio	Gull:Gol ratio	% time crouching
NetC$_f$	—	—	—	—	—	—	3.34*
NetC$_b$	—	2.89*	—	—	—	5.51**	2.21
Mean worm length	—	2.13	—	—	—	—	8.40**
Capture rate	-4.87	2.12	—	—	—	—	—

Data for 63 flocks. Symbols and significance levels as in Table 1.

Changes in lapwing feeding efficiency with flock composition are explicable in terms of differences in individuals' time budgets (particularly crouching behaviour) within lapwing subflocks (BARNARD & STEPHENS, 1981). To see whether the plover feeding efficiency trends in Table 3a, b could be explained in the same way we performed another stepwise partial regression analysis relating the frequency and/or durations (BARNARD & STEPHENS discuss the rationale for using frequency or duration in analyses) of each of the recorded behaviours (see Methods) and flock composition variables.

Table 4a shows the results for plover subflocks without gulls. Here, all frequencies and durations of behaviours included in the analysis except stepping rate correlate significantly with lapwing number. The results

TABLE 4a

F-ratios from stepwise partial regression analysis of the relationship between time spent by golden plovers in various activities and flock composition variables in the absence of gulls

	No. Lapwings	No. Golden plovers	Gol:Lap ratio
% time scanning	-5.00**	4.12*	—
Scan rate	-12.39**	-3.31	—
Step rate	-2.35	-7.26**	—
% time crouching	48.24**	—	1.80
% pecks + crouch	12.02**	—	9.94**
Crouch rate	12.74**	3.91*	—
Peck rate	6.21**	—	—

Data for 67 flocks.

TABLE 4b

Same as a) but for flocks in which gulls were present

	No. Lapwings	No. Golden plovers	No. Gulls	Gull:Gol ratio	Gol:Lap ratio	Gull:Lap ratio
% time scanning	6.08**	1.63	—	3.41*	—	13.18**
Scan rate	—	—	3.81*	1.97	13.70**	-8.66**
Step rate	—	—	—	—	—	-3.40**
% time crouching	-3.78*	-2.37	—	-6.84**	-4.64**	—
% pecks + crouch	—	—	—	-7.54**	7.29**	—
Crouch rate	-2.71	—	—	-11.38**	—	—
Peck rate	—	—	—	—	—	—

Data for 63 flocks. Symbols and significance levels as in Table 1.

suggest that plovers do better when there are more lapwings because they spend more time crouching and less time scanning. However, Table 3a showed that lapwing number had an independent *negative* effect on plover $NetC_f$ and $NetC_b$. One possibility is that crouching was related to worm density rather than lapwing number (see BARNARD & STEPHENS, 1981). However, stepwise partial regression analysis taking worm density into account showed that while the proportion of pecks preceded by crouching correlated best with worm density, crouching rate, $NetC_f$ and $NetC_b$ correlated best with lapwing number (Table 5). Note the positive relationship between feeding efficiency and lapwing number when crouching is not partialled out. The most likely explanation for the negative effect of lapwing number on feeding efficiency in Table 3 is some kind of interference effect with large numbers of lapwings (see Fig. 4).

TABLE 5

F-ratios from stepwise partial regression analysis of the relationship between feeding efficiency and time budget variables in golden plovers and both the numbers of lapwings and plovers in the flock and worm density in the turf

	No. Lapwings	No. Golden plovers	Worm density
$NetC_f$	7.45*	—	—
$NetC_b$	10.77**	—	—
% pecks + crouch	—	11.2**	13.70**
Crouch rate	6.53*	—	—
% time crouching	—	—	—
Peck rate	4.53*		

Data for 27 flocks without gulls.

One way of testing for this is to look at changes in plover energy intake with changes in lapwing number in flocks already containing large numbers (> 20) of lapwings. We therefore compared $NetC_f$ and $NetC_b$ values for plover recordings for periods when large lapwing subflocks changed by 12 or more birds but the number of plovers did not change by more than 3 birds. Again, sample sizes were small because few flocks with a large number of lapwings were free of gulls and large changes in lapwings number were often accompanied by larger than 3 bird changes in plover number. Nevertheless, in those cases where suitable changes had been recorded, both $NetC_f$ and $NetC_b$ for plovers dropped significantly when lapwing number increased (mean $NetC_f$ before change = $4.36 \pm .64$ cals/s, mean $NetC_f$ after = $1.11 \pm .19$ cals/s, $t = 5.27$, d.f. 8, $p < .001$; mean $NetC_b$ before change = 1.93 ± .32 cals/s, mean $NetC_b$ after = .59 ± .12 cals/s, $t = 3.92$, d.f. 8, $p < .01$).

Lapwing number also correlated negatively with plover scanning rate and proportion of time spent scanning. For both crouching and scanning behaviour, the effects of lapwing number were more marked than those of plover number. Moreover, opposing effects of plover number were found for the two scanning variables. Plovers tended to scan less often but for longer overall when the number of conspecifics was high. In addition, plovers stepped more quickly when more conspecifics were present.

When gulls were present (Table 4b), the effect of lapwing number was reduced to positive and negative relationships with the proportions of time spent scanning and crouching respectively and there was now no significant effect of plover number on behaviour. Scanning rate and the proportion of time spent scanning increased with the number of gulls and the gull:plover ratio respectively, and the gull:plover ratio correlated with a decrease in the frequency and duration of crouching. Interestingly, therefore, plovers did better in high gull:plover ratios despite crouching less (see Discussion). The number of gulls per lapwing was negatively related to scanning and stepping rate but positively related to the proportion of time spent scanning, while the ratio of plovers to lapwings correlated positively with scanning rate and the proportion of pecks preceded by a crouch but negatively with the proportion of time spent crouching. The presence of gulls therefore depressed crouching and worm size selection by plovers but did not correlate with a decrease in feeding efficiency (Table 3b).

FLOCK COMPOSITION AND SUBFLOCK SIZE IN GOLDEN PLOVERS

To see whether the effects of flock composition on plover feeding efficiency were reflected by changes in plover subflock size, we carried out a similar analysis to that performed for lapwing subflocks. Here, however, it was not feasible to monitor changes in *equilibrium* subflock size. Plovers tend to arrive at and depart from flocks in large and variable numbers (often in groups of 50 or more) and seldom move between flocks singly. Changes in subflock size are therefore characterized by sudden large increases or decreases rather than the smaller oscillations characteristic of lapwing subflocks. Nevertheless, we might still except changes in mean plover subflock size to reflect changes in plover net energy intake. In this case we might expect gull arrival to correlate with an *increase* in plover subflock size since focal plovers tended to do better after a gull arrived.

Analyses of changes in plover subflock size after a gull arrived, however, showed no consistent trend, although 40% of the flocks showed an increase in plover number (Fig. 6a).

Since plover feeding efficiency in flocks without gulls was negatively affected by lapwing number, we also examined changes in plover subflock

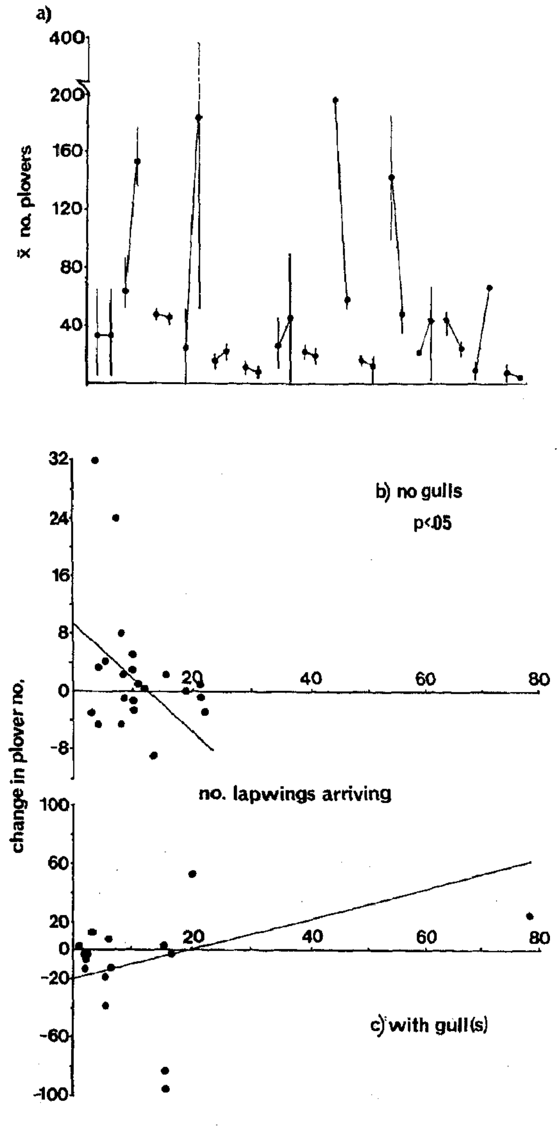

Fig. 6. a) Changes in the mean number of golden plovers present after the arrival of one or more gulls. Symbols identical to those in Fig. 1a except that points represent mean subflock sizes not E.F.S.s. Data for 15 flocks observed for 15 minute periods before and after gull arrival. b) Changes in the mean number of golden plovers present after the arrival of different numbers of lapwings. Data for 22 flocks in which no gulls were present. r = -.43, p < .05. c) Same as b) for 16 flocks with gulls. r = .22, n.s.

size when more lapwings arrived. Fig. 6b shows the relationship between the number of lapwings arriving and subsequent changes in plover subflock size. The change in plover number showed an overall negative correlation with the number of lapwings arriving but, as with lapwing E.F.S. in Fig. 1b, there was an *increase* in plover number when only a few lapwings arrived. Since lapwings did not affect plover feeding efficiency when gulls were present, we might expect no directional change in plover number when more lapwings arrive. Fig. 6c shows that this was the case.

DISCUSSION

In this paper we have examined net rate of energy intake by lapwings and golden plovers in single and mixed species flocks and the relationships between individual feeding efficiency, flock composition and flock dynamics.

The results show two important points: a) the effect of conspecifics and heterospecifics on individual net rate of energy intake varies with flock composition and b) heterospecific effects on individual net rate of energy intake are reflected in changes in the number of conspecifics in the flock. In the absence of gulls, lapwing net rate of energy intake per recorded sequence was most closely related to lapwing number with no significant effect of golden plovers. When gulls arrived, intake rate was reduced and once gulls were present, it was also negatively correlated with plover number. Net rate of energy intake in golden plovers, however, was influenced more by the number of lapwings in the flock than the number of conspecifics when no gulls were present. When gulls arrived, lapwings ceased to have an effect and conspecific number became more important.

The negative effect of gulls on lapwing feeding efficiency arose because, as kleptoparasites, gulls caused reductions in crouching (prey assessment) behaviour and consequently feeding selectively in lapwings. However, gull number correlated positively with lapwing feeding efficiency because gulls tended to join flocks in which lapwings were catching a lot of large worms. These tended to be the flocks in which lapwings were also capturing a lot of the most profitable intermediate sized worms. Analysis showed that gull and lapwing numbers correlated independently with the rate at which the worm sizes most profitable to each species were being found by lapwings.

Worm size selection by golden plovers followed a similar trend to that in lapwings. The same size classes of worm were the most profitable and plovers tended to take proportionally more of these when large numbers of conspecifics were present. The presence of gulls depressed selection so that more small worms were taken in large flocks. Crouching appeared to facilitate prey assessment prior to pecking but lapwing rather than conspecific number was the most pronounced positive influence on crouching tendency. Lapwing number also correlated with a reduction in plover scanning rate. A major reason for plovers joining lapwings, therefore, may be a reduction in scanning commitment and consequent increase in time available for prey assessment. Lapwings are marginally taller birds with perhaps a larger field of view. Furthermore, in 93.3% of recorded cases, it was lapwings which took off before plovers after a disturbance. Lapwings, however, also interfere with plovers through food-stealing and other interactions. When crouching was held constant, lapwings had an independent negative effect on plover net energy intake.

When gulls were present, crouching by plovers was depressed in relation to the number of gulls per plover, and birds tended to take smaller worms. Despite these changes, however, gulls did not have the significant negative effect on plover net rate of energy intake that they had on lapwings. Instead feeding efficiency increased. The reasons may have been a) the much shorter handling and inter-capture travel times shown by plovers, and b) the concentration of gull kleptoparasitism on lapwings (see later). In the presence of gulls, lapwings had no significant effect on plover energy intake while energy intake increased with the number of conspecifics present.

Why did the effect of plovers on lapwings and *vice versa* change when gulls were present? One possibility is that the infrequently recorded food-stealing and area-copying by plovers interfered with lapwings in mixed flocks. The incidence of food-stealing between lapwings and golden plovers was frequency-dependent. When there were more lapwings than plovers, the incidence of lapwings stealing from plovers was higher (mean no. interactions/lapwing/plover/min. = 0.0058 ± .0034) than the incidence of plovers stealing from lapwings (mean no. interactions/plover/lapwing/min. = 0.00085 ± .00004). When there were more plovers than lapwings, the reverse was true (mean no. interactions/lapwing/plover/min. = 0.00020 ± .00003, mean no./plover/lapwing/min. = .00093 ± .00018) (data for 30 flocks). While the low level of interference by plovers may not have been sufficient to reduce lapwing feeding efficiency when no gulls were present, it may have had more effect when lapwings were under additional pressure from kleptoparasitic gulls.

In plovers, however, the relationship was the other way round. Lapwings had a negative effect on plover feeding efficiency when no gulls were present but no effect when there were gulls. This may also be explicable in terms of kleptoparasite pressure on lapwings. In mixed flocks, gulls showed a two-fold preference for attacking lapwings (mean attack rate against lapwings = 0.012 ± 0.002 attacks/lapwing/gull/min; mean against plovers = 0.006 ± 0.002 attacks/plover/gull/min; $t = 3.09$, $p < 0.01$). This correlated with a higher success rate against lapwings (74% success with lapwings *versus* 36% success with plovers). (Almost identical relative success rates have been recorded in Scandinavian birds

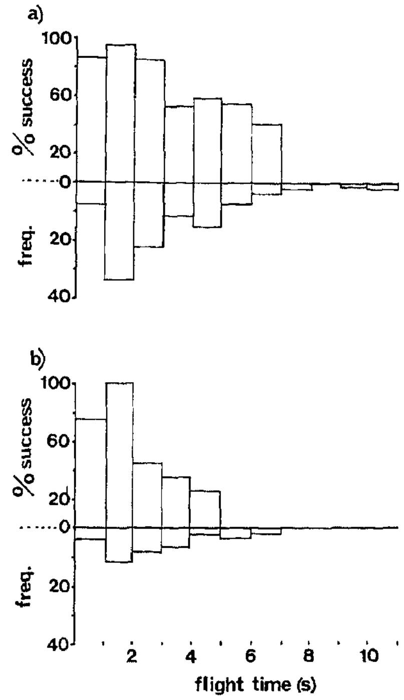

Fig. 7. a) The relationship between distance of attack initiation by gulls and attack success against lapwings. Data for 108 observations. b) The frequency of attacks initiated by gulls at different distances against lapwings. c) Same as a) but against golden plovers. Data for 46 observations. d) Same as b) but against golden plovers.

-H. Källander, pers. comm.). Gulls were less successful against plovers because more attacks resulted in protracted aerial chases during which plovers were likely to escape (golden plovers fly faster than lapwings (Hale, 1980)). Most attacks on lapwings resulted in target birds dropping worms without taking off or very shortly after taking off. A critical factor in attacks success, therefore, was the distance of the gull from its target at the time of attack initiation. Fig. 7a, c shows the success rate of attacks launched at different distances (expressed as gull flight time) from target lapwings and plowers. For both species, attack success drops with increasing distance, as does the frequency of attack (Fig. 7b, d), but the effect was much greater for plovers. Interestingly, lapwing interneighbour distance correlated negatively with flock size when gulls were present (see equation 1 and Table 2 'spacing' column). When there were gulls, therefore, lapwings tended to clump together more, suggesting a 'selfish herd' effect to avoid detection by gulls. A full analysis of gull feeding behaviour and victim reaction in mixed flocks is provided elsewhere (BARNARD, in prep.). Interference of plover feeding behaviour by lapwings may therefore have been less pronounced when lapwings were being preferentially kleptoparasitized by gulls, hence the increase in plover energy intake after the arrival of gulls.

We predicted that species' subflock size within any given flock would reflect species' net rate of energy intake. Where the presence of species A reduces the feeding efficiency of species B, we predicted that B's subflock size would decrease because the utility of the feeding site to its individuals is reduced.

This prediction is partly borne out by limited data for the arrival of gulls in a flock. Lapwing subflock size generally went down when a gull arrived but there was no consistent increase in golden plover subflocks. The change in lapwing subflock size after plovers arrived showed a negative relationship with increasing numbers of additional plovers. When only a few more plovers arrived, however, lapwing subflock size increased. A possible reason for this is that arriving plovers tend to land in the centre of a flock. Characteristically, lapwings fed on the periphery of plover subflocks. If only a few additional plovers arrive in a flock, there may be little displacement of lapwings. Instead there is a bigger flock to attract more birds (THOMPSON, in prep.) and a dilution of gull kleptoparasitism (there is more likely to be a plover near enough to a gull to make an attack worthwhile).

When a lot of plovers arrive, however, displacement of lapwings and higher rates of plover/lapwing interactions in higher plover:lapwing ratios may be sufficient to cause some lapwings to leave. Although there was no linear correlation between lapwing subflock change and the number of additional plovers arriving when there were no gulls in the flock, the number of lapwings almost always decreased. Since no dilution benefit accrued to lapwings, the displacement cost of a few extra plovers may have been sufficient to cause more birds to leave. Large numbers of additional plovers would have increased the plover:lapwing ratio and thus the relative frequency of feeding interactions initiated by golden plovers.

Changes in plover subflock size in response to lapwing arrivals can be explained in the same way. In the absence of gulls, *changes in* plover subflock size when lapwings arrived correlated negatively with the number of lapwings arriving. However, plover number tended to increase when only a few lapwings arrived. Again, the reason may be that a few additional lapwings did little to change the lapwing: plover ratio and thus the frequency of feeding interactions initiated against plovers by lapwings. Small increases in lapwing number, however, may have allowed plovers to crouch more and scan less and hence do better than by leaving. When gulls were present, there was no significant trend in the relationship between the number of lapwings arriving and subsequent changes in plover subflock size. However, the tendency for plover number to increase slightly with the number of additional lapwings may have been due to the greater reduction in kleptoparasitic attacks on plovers when more lapwings were present.

SUMMARY

1. In mixed species flocks of lapwings and golden plovers, lapwing net rate of energy intake was positively related to the number of conspecifics and the amount of time individuals spent crouching during feeding, but was unaffected by the presence of golden plovers. Plover net rate of energy intake, however, was positively related to crouching tendency, negatively related to the number of lapwings present but unaffected by the number of conspecifics.

2. Golden plovers appeared to join lapwing flocks because they could then crouch more and scan less. The independent negative effect of lapwing number may have been due to feeding interference when there were large numbers of lapwings relative to plovers.

3. When black-headed gulls joined a flock, both lapwings and plovers tended to crouch less and take smaller worms. However, in lapwings these changes appeared to reduce feeding efficiency but plover net rate of energy intake increased as a function of the gull: plover ratio.

4. When gulls were present, the effect of conspecifics on lapwing feeding efficiency disappeared and the presence of plovers had a negative effect. Conversely, in plovers the presence of conspecifics enhanced feeding efficiency and the negative effect of lapwing number disappeared.

5. The arrival of gulls resulted in a decrease in equilibrium lapwing number but no consistent, directional change in plover number. When gulls were present, lapwing number tended to decrease when large numbers of plovers arrived, but increase when small numbers arrived. Increased lapwing number had no significant directional effect on plover number. Changes in lapwing and plover energy intake and species numbers are interpreted in terms of feeding interference and 'dilution' of gull kleptoparasitism.

6. In the absence of gulls, there was no significant directional relationship between increased plover number and lapwing number, but the presence of plovers generally correlated with a reduction in lapwing number. Plover number, however, decreased when large numbers of additional lapwings arrived but increased with small numbers of arrivals. Changes in species energy intake and numbers here are interpreted in terms of feeding interference and time budget changes.

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ZUSAMMENFASSUNG

1. In gemischten Flügen von Kiebitzen und Goldregenpfeifern stand die Rate der netto Energieaufnahme für die Kiebitze in positiver Beziehung zur Zahl der anwesenden Artgenossen und positiv zu der Zeitsumme, in der diese sich bei der Nahrungssuche bückten, während die Anwesenheit der Goldregenpfeifer keine Auswirkung hatte. Dagegen bezog sich die Energieaufnahmerate der Goldregenpfeifer positiv auf die Neigung, sich zu bücken, negativ auf die anwesende Zahl der Kiebitze und war von der Zahl der Artgenossenen unbeeinflusst.

2. Es scheint, dass sich die Goldregenpfeifer mit dem Flug der Kiebitze vereinigten, weil sie auf diese Weise weniger um sich zu sehen brauchten und mehr Zeit mit Bücken verbringen konnten. Der unabhängige negative Einfluss der Anzahl der Kiebitze könnte einer Störung bei der Nahrungssuche zuzuschreiben sein, sobald die Kiebitze im Verhältnis zu den Regenpfeifern sehr zahlreich waren.

3. Wenn Lachmöwen sich zu einem Flug gesellten, nahmen Kiebitze und Goldregenpfeifer kleinere Würmer und bückten sich weniger. Das führte bei den Kiebitzen anscheinend zu einer weniger ökonomischen Nahrungsaufnahme, während die netto Narungsaufnahme der Goldregenpfeifer proportional zum Verhältnis Möwen:Goldregenpfeifern stieg.

4. Wenn Lachmöwen da waren, verschwand der positive Einfluss der Zahl der Artgenossen auf die Nahrungsaufnahme der Kiebitze und hatte die Anwesenheit von Goldregenpfeifer einen negativen Effekt. Dagegen erhöhte die Anwesenheit von Artgenossen bei den Goldregenpfeifern die Wirksamkeit der Nahrungssuche und verschwand der negative Einfluss der Kiebitze.

5. Bei der Ankunft von Lachmöwen verminderte die relative Zahl der Kiebitze, indess die Zahl der Goldregenpfeifer keine konsequente Veränderung aufwies. In Anwesenheit von Lachmöwen verringerte sich die Zahl der Kiebitze, sobald grosse Zahlen von Regenpfeifern ankamen, vergrösserte sich aber, wenn nur wenige Goldregenpfeifer kamen. Eine erhöhte Zahl der Kiebitze hatte keinen konsequenten Einfluss auf die Zahl der Goldregenpfeifer. Die auftretenden Veränderungen in der Energieaufnahme der Tiere beider Arten verstehen wir als Störungseffekte bei der Nahrungssuche und "Verdünnung" des Futterangebotes durch die Möwen als Kleptoparasiten.

6. Ohne die Anwesenheit von Lachmöwen gab es keine Korrelation zwischen grossen Zahlen von Goldregenpfeifern und Kiebitzen, aber im allgemeinen nahm die Zahl der Kiebitze in der Gegenwart von Regenpfeifer ab. Wenn sich aber grosse Flüge Kiebitze niederliessen, nahm die Zahl der Goldregenpfeifer ab; bei kleineren Flügen nahm sie zu. In diesen Fällen verstehen wir die Veränderungen in der Energieaufnahme der Arten und ihre relative Anwesenheit als eine Folge von Störung bei der Nahrungsaufnahme und Änderungen im Zeitbudget.

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