

Behaviour 51 99-134
1974

Behaviour, LI 1-2

COLONIAL NESTING AND SOCIAL FEEDING AS STRATEGIES FOR EXPLOITING FOOD RESOURCES IN THE GREAT BLUE HERON (*ARDEA HERODIAS*)

by

JOHN R. KREBS^{1) 2) 3)}

(Institute of Animal Resource Ecology, University of British Columbia,
Vancouver, B. C., Canada)

(With 14 Figures)
(Rec. 10-IX-1973)

INTRODUCTION

In the last few years several workers have suggested that sociality in birds and other vertebrates has evolved as a strategy for exploiting food resources (e.g. FISHER, 1954; CROOK, 1965, 1970; LACK, 1968; EMLEN, 1971; MURTON, 1971a, b; WARD, 1965, 1972; ZAHAVI, 1971a, b; WARD & ZAHAVI, 1973; SCHALLER, 1972; VERMEER, 1973). In birds, this hypothesis has been applied to winter flocks of non-breeders (MURTON, 1971a, b; MURTON *et al.*, 1971; KREBS *et al.*, 1972; KREBS, 1973; CODY, 1971; MORSE, 1970), communal roosts (ZAHAVI, 1971a, MURTON *et al.*, 1972; FRENCH, 1967; SIEGFRIED, 1971; WARD, 1965), and nesting colonies (LACK, 1968; FISHER, 1954; CROOK, 1965; HORN, 1968; EMLEN, 1971). In spite of all this discussion in the literature, there is virtually no concrete evidence to show that sociality acts as a strategy for exploiting food resources. It was my aim in this study to collect field data which would test this hypothesis as directly as possible.⁴

WARD & ZAHAVI (1973) have recently discussed the hypothesis that nesting colonies of birds act as 'information centres', the argument being that if food

1) Present address: Department of Zoology, University College of North Wales, Bangor, Caerns, U.K.

2) I thank the following people who made crucial contributions to this study: Steve BORDEN for building the computer interface for the event recorder and for writing various programs; Brian PARTRIDGE, Joe PAINE, Carl WHITNEY, Mike MORRELL, Karen UL-DALI-EXMANN and Ursula BLUMENTHAL for help in collecting field data; Rudi DRENT and Wayne CAMPBELL for helping to build the observation hide; and Jamie SMITH, Eric CHARNOV, and Mike CULLEN for discussing some points with me.

The work was financed by grants from the National Research Council of Canada and the University of British Columbia.

3) From December 31, 1974, address will be: Department of Zoology, South Parks Rd, Oxford OX1 3PS, England.

occurs in large but ephemeral clumps that are unpredictable in time, then the ability of any one individual to find a clump will be enhanced if it can take advantage of the searching power of a whole group of individuals (see also FISHER, 1954; Horn, 1968). The suggestion is that individuals that have been unsuccessful in searching for food follow successful individuals out of the colony on foraging trips. Thus the advantage to an individual of being in the colony is that there is more opportunity to observe other birds and if necessary to follow them to good feeding areas. The same sort of argument has been applied to communal roosts by ZAHAVI (1971), WARD (1965) and SERGFRIED (1971), and the phenomenon of unsuccessful birds 'copying' successful individuals has been shown to occur on a finer scale in winter flocks of tits (KREBS *et al.*, 1972) and pigeons (MURKON, 1971a, b).

Evidence for the 'information centre' hypothesis is either anecdotal or indirect. WARD (1965), and SERGFRIED (1971) have observed that when birds leave the colony in the morning, some individuals hang back and wait until other, more 'purposeful' individuals fly out, and then they follow these individuals. HORN (1968) found that the one of the major food times of nesting Brewer's Blackbirds, newly emerged damselflies, were spatially unpredictable in their distribution (depending on where the wind carried them) and that the blackbirds were highly efficient at capitalising on temporary local concentrations of food. He interpreted this as being a consequence of the birds following each other to food sources, and observed directly instances of following in the field. Less direct evidence for the hypothesis comes from comparing the ability of birds in the center and at the edge of a colony to raise young, the argument being that center birds have more possibilities for following neighbours to feeding grounds and should therefore be able to collect more food for the young (similar arguments could be applied to colonies of different sizes). HORN (1968) found that young of central nests grew faster than young from peripheral nests, and EMLEN (1971) showed that in Bank Swallows central nesters had a higher reproductive success than edge birds. In these instances differential predation did not seem to be an important factor (cf. PATTERSON, 1965 and TENAZA, 1971). However, simply showing a difference between edge and centre birds may not tell us anything about the use of the colony as an information centre, since the differences may reflect differences in the age or quality of birds (COURSON, 1971; TENAZA, 1971; BALDA & BATEMAN, 1972). HORN (1968) discusses this point and argues that since the clutch sizes are the same for edge and centre birds, only the growth rate of young being different, there are no differences in quality between the birds.

In order to demonstrate convincingly that the colony acts as an information

centre and that necessary to show and that differ-
 dependently of
 foraging in grow
 individuals, bec
 feeding area. In
 these two aspect

The species I
 the Pacific Nor
dinus farmini) (I
 less a complete s
 (*e.g.* Cattle Egr
 European Bitter
 The Great Blue
 partly social. It
 common, and in
 feeding in flock
 1960; PALMER,
cinnerea) obvious
 LINDAHL, 1970
 SOUTHERN, 1939

Several autho
 it has generally
 an adaptation f
 since this could r
 in which the dif
 herons are socia
 has argued that
 Cattle Egret ac
 MEYERREICHERS (1
 that social feedi
 advantage to the
 rendering them

As a final poi
 of colonial nesti
 present study. F
 is clumped and
 for birds collect
 of all potential p

centre and that colony members benefit as a result of this, I consider it necessary to show (a) that the birds are exploiting a shifting food supply and that different individuals in the colony are not behaving independently of one another in their foraging trips and (b) that individuals foraging in groups have on average a higher rate of food intake than solitary individuals, because being in a group means that the bird has located a good feeding area. In this paper I present the results of a study designed to test these two aspects of the hypothesis.

The species I studied is the Great Blue Heron (*Ardea herodias*) which in the Pacific Northwest occurs in the form of a separate subspecies (*A. herodias farrisi*) (PALMER, 1962). Members of the heron family show more or less a complete gradation from highly social colonial nesters that feed in flocks (e.g. Cattle Egret *Bubulcus ibis*), to completely solitary species such as the European Bittern (*Botaurus stellaris*) (MEYERREICKS, 1960a; JENNI, 1969). The Great Blue Heron falls about half way along this continuum, being partly social. It usually nests in colonies although single nests are not uncommon, and in its foraging it ranges from solitary and territorial to social feeding in flocks of as many as 50 individuals (BENT, 1926; MEYERREICKS, 1960; PALMER, 1962; pers. obs.). The European Grey Heron (*Ardea cinerea*) obviously is very closely related to the Great Blue Heron (CURRY-LINDAHL, 1970) and it shows a similar range of sociality (OWEN, 1960; SOUTHERN, 1939; WHITERBY *et al.*, 1939).

Several authors have discussed the significance of sociality in herons, and it has generally been concluded that colonial nesting in these species is not an adaptation for exploiting food resources (LACK, 1968; JENNI, 1969), since this could not account for the fact that herons often form mixed colonies in which the different species feed in different places, and also because some herons are social nesters and solitary feeders. SIEGFRIED (1971), however, has argued that communal roosts (and presumably nesting colonies) in the Cattle Egret act as information centres in the manner discussed above. MEYERREICKS (1960b), RAND (1954) and HEATWOLE (1965) have argued that social feeding in some types of herons (mainly the Cattle Egret) is of advantage to the participants because it results in 'beating' of insect prey, rendering them easier to catch.

As a final point, I should discuss briefly some of the other major theories of colonial nesting and explain why I do not consider them applicable to the present study. HORN (1968) developed a model which showed that if food is clumped and unpredictable, the strategy which minimises travel distance for birds collecting food for the young is to nest in the geometrical centre of all potential patches, or as near as available nesting sites permit. Thus the

model predicts colonial nesting in a species which exploits ephemeral, clumped food, even without the considerations of an information centre, just because it minimises travel distance. Whilst I agree with HORN's theoretical analysis, I did not try to collect data to test his hypothesis, firstly because it is difficult to devise a simple empirical test, and secondly because the colony that I studied was clearly not in the centre of the utilised foraging patches (Fig. 1), an assumption of HORN's model: of course it can be argued that the colony was at some stage in the past in the centre of the utilised foraging areas. LACK (1968) among others, has argued that colonial nesting in many species may be primarily an antipredator device, KRUTIK (1964) and PATTERSON

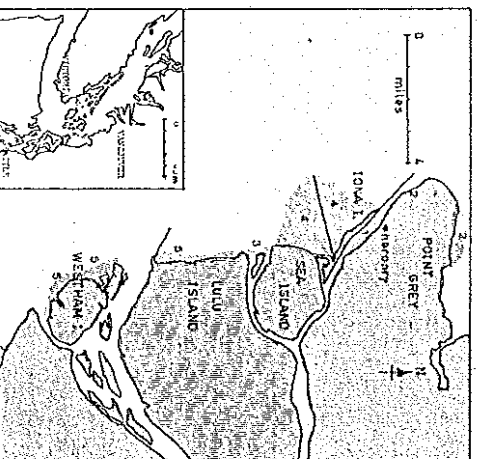


Fig. 1. A map showing the relationship between the colony and the main feeding grounds. The feeding areas, shown cross-hatched, are numbered according to the divisions used in Tables 1 and 2. The feeding areas shown on the map are not the only ones used by the herons, but are the most important ones, at least in the breeding season.

(1965) have shown how in the Blackheaded Gull (*Larus ridibundus*) the communal mobbing of aerial predators by the parents gives protection to the young. As a result, nests in the middle of the colony have a lower rate of predation than nests at the edge. Even in species which do not have communal antipredator displays, colonial nesting could reduce predation of any individual due to a swarming effect. Further, if safe nesting sites are in short supply, densely packed colonies may arise in the few highly protected places which are available (CROOK, 1964). Although heron colonies do suffer considerable nest predation (e.g. JENNY, 1969), the striking feature of this is that the adults have virtually no antipredator behaviour (MILSTEIN *et al.*, 1970 review this extensively). In several instances of egg predation by

Ravens (*Corvus*) to chase away the of these instance herons causing ti 1970). In one ins the colony, and that colonial nest difficult to visita nest in colonies acres of similar I In summary, t been much discu to collect critical two types of dat the colony and w in separate sectio

The observations sity of British Coli has been followed : were 120 nesting i pairs, and the colou satellite' area abou completely and the sharp decline are t severe winters in th have been observed colony over short di *et al.*, 1970). Both *ribrus*) surrounded i *mercurii*), Westerr *cata*), Sika Spruce *A. grandis*). The n trees contained one of about 200 m (F other colonies near and Sika Spruce. I colony was that the protected from the house in a Douglas vations were made an observer to look platform to permit collected for the r The main feeding the areas are either the mouth of the F

Ravens (*Corvus corax*) that I observed, the parent herons made no attempt to chase away the Ravens even when their own eggs were being eaten. Most of these instances of predation occurred after an observer had disturbed the herons causing them to stand up or leave the nest (see also MILSTEIN *et al.*, 1970). In one instance a Bald Eagle (*Haliaeetus leucocephalus*) flew through the colony, and all the incubating parents panicked and left. Thus it seems that colonial nesting is not obviously an antipredator adaptation. It is also difficult to visualise that shortage of safe nesting sites forces the herons to nest in colonies when the nesting area is surrounded by many hundreds of acres of similar habitat, as was the case in the present study.

In summary, the idea that nesting colonies act as information centres has been much discussed but there is little evidence for it. In this study I tried to collect critical data to test the idea as applied to Great Blue Herons. The two types of data, concerned with analysis of flight paths of birds leaving the colony and with success of birds on the feeding grounds, are presented in separate sections.

STUDY AREA

The observations were made on a colony of Great Blue Herons nesting on the University of British Columbia Endowment Lands in Vancouver, B. C. (Figure 1). The colony has been followed since 1970, and seems to be decreasing rapidly in size. In 1970 there were 120 nesting pairs (W. CAMPBELL, pers. comm.), in 1971 there were 78 nesting pairs, and the colony had split in two, with 55 nests in the main area, 23 nests in a new 'satellite' area about 400 m away. In 1972, the old main colony had been abandoned completely and the satellite colony contained about 30 active nests. The reasons for this sharp decline are totally unknown, but the decline did coincide with two exceptionally severe winters in the Vancouver area and similar declines associated with severe winters have been observed in England (LACK, 1954; MILSTEIN *et al.*, 1970). Movement of a colony over short distances has also been recorded frequently in the literature (MILSTEIN *et al.*, 1970). Both parts of the colony were located in groves of Red Alders (*Alnus rubra*) surrounded by a mixture of coniferous trees, mainly Douglas fir (*Pseudotsuga menziesii*), Western Hemlock (*Tsuga heterophylla*), Western Red Cedar (*Thuja plicata*), Sitka Spruce (*Picea sitchensis*) and two species of fir (*Abies amabilis* and *A. grandis*). The nests were all between 60 and 100 feet from the ground, and most trees contained one or two nests. The main colony was roughly circular with a diameter of about 200 m (Fig. 2). Although in this colony the birds only nested in alders, in other colonies near Vancouver, herons were seen to nest in Douglas Firs, Red Cedars and Sitka Spruce. I suspect that the main advantage of the alder trees in this particular colony was that they were somewhat lower than the surrounding conifers, and therefore protected from the wind. Observations of birds in the colony were made from a tree house in a Douglas fir tree in the alder grove of the main colony (no colony observations were made in 1972). The platform was about 100' off the ground and allowed an observer to look down onto the nests. Nine nests were close enough to the observation platform to permit detailed observations (PAINE, 1971) and less detailed data were collected for the rest of the colony (see later).

The main feeding areas of birds from the study colony are shown in Figure 1. All the areas are either intertidal mud and sandflats, intertidal reedbeds, or reed beds around the mouth of the Fraser River. As mentioned later, most of the data on feeding rates

eral, clumped
just because
tical analysis,
it is difficult
colony that I
shes (Fig. 1),
at the colony
raging areas.
many species
PATTERSON

feeding grounds.
re divisions used
ones used by the
s season.

idibundus) the
tection to the
lower rate of
not have com-
edation of any
ug sites are in
ighly protected
onies do suffer
feature of this
MILSTEIN *et al.*,
predation by

were collected at Iona Island (Fig. 3) from a man-made stone jetty some 2.5 miles long. The intertidal area to the north of this jetty is largely sandy, and to the south extremely soft mud. The outfall channel of the Iona Island Sewage Treatment Plant is immediately to the south of the jetty.

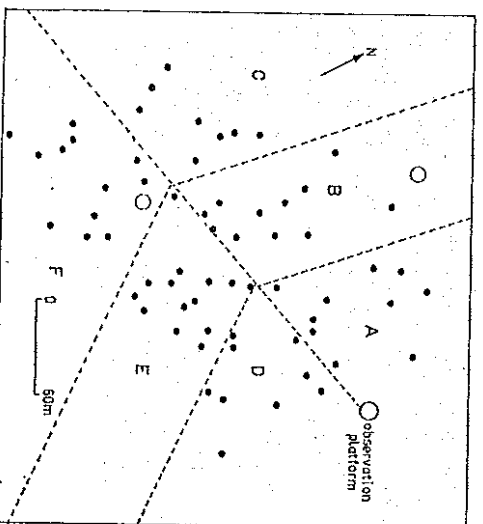


Fig. 2. A map of the colony showing the position of the observation hide and the division of the colony into different nest areas for the analyses in Tables 2 and 3. Nests are shown by black circles; open circles represent tall trees used as land marks.

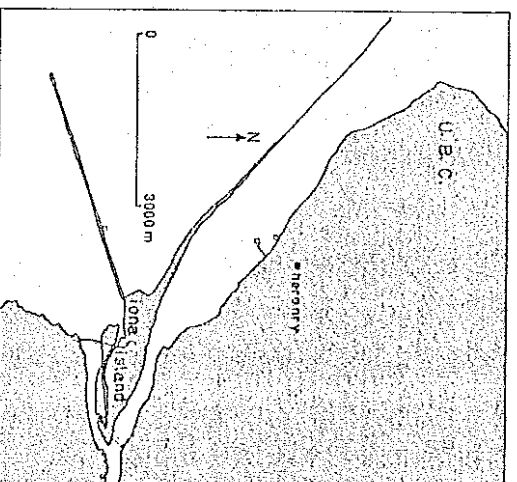


Fig. 3. A map of Point Grey and Iona Island to show the positions of the observers who were recording flights from the heronry to the feeding grounds. The positions of the observers are shown by open squares. The long jetty on which the third observer stood was also the place where most of the feeding data were collected.

If the birds each other to get about the direct an information predictable food to another. If information ce from one feeding individual indej birds should uti as a whole show second predictic the pattern of c tendency for de

Two more pr is more likely t colony. We can be especially like at random from bouring nests sh on foraging trip

In the summer in the peak of the r at the same tide h one day spanned t observers, two of w stationed in the ob observer on the sho between them, to ; which direction it revealed that birds fly to. The third ob birds flying 'south' flying on to Lulu ; accurate time recor according to sector compass readings o on the other. The o compass or noted t

THE ANALYSIS OF FLIGHT PATHS OF BIRDS LEAVING THE HERONRY

INTRODUCTION

If the birds are using the colony as an information centre and following each other to good feeding areas, we should be able to make several predictions about the direction and timing of food gathering flights. Firstly, in order for an information centre to be of value, the birds must be utilising an unpredictable food supply which shifts on a short term basis from one area to another. If the birds are following this shifting food supply through an information centre, then the members of the colony should tend to shift from one feeding area to another in unison rather than in succession as each individual independently discovers it. Thus the first prediction is that the birds should utilise different food areas on different days and that the colony as a whole should show a tendency to shift from one area to another. A second prediction is that if birds are following one another from the colony, the pattern of departures in time should be non-random. There should be a tendency for departures to fall into 'clumps'.

Two more predictions can be made if we make the assumption that a bird is more likely to follow its near neighbours than other individuals in the colony. We can predict firstly that birds from neighbouring nests should be especially likely to go to the same feeding areas (more so than birds taken at random from the colony as a whole), and secondly, that birds from neighbouring nests should show an even stronger tendency than average to leave on foraging trips at the same time.

METHODS

In the summer of 1971, I collected data on feeding flights during June and July, in the peak of the nesting period. As far as possible, data on different days were collected at the same tide heights to eliminate the effects of this variable (usually the data for one day spanned the whole low tide period). The observations were made by three observers, two of whom communicated with a portable transceiver set. One observer was stationed in the observation hide in the colony and was in radio contact with a second observer on the shore line close to the heronry (Fig. 3). These two observers were able, between them, to record which part of the colony each heron departed from, and in which direction it flew off after passing over the shore. Preliminary observations had revealed that birds almost invariably flew to the shoreline before 'deciding' where to fly to. The third observer was situated on Iona Island (Fig. 3) and his job was to separate birds flying 'south' into those which landed at Iona Island (north or south) and those flying on to Lulu Island or further. These records were correlated with the others by accurate time records. The colony observer divided departures by birds into six groups according to section of the colony (nest area) (Fig. 2). These divisions were based on compass readings on one axis and distance with reference to landmarks (e.g. tall trees) on the other. The other two observers recorded disappearance directions with a sighting compass or noted the exact spot in which the heron landed. The complete analysis of

by some 2.5 miles
and to the south
Treatment Plant

de and the division
e and 3. Nests are
land marks.

s of the observers
3. The positions of
the third observer
a collected.

these data is presented in PAINE (1971); here I only deal with departures from the colony and not arrivals. In total the data were successfully correlated for 10 days giving a total of over 400 flights. Observations were made throughout the nesting period of about 50 days, but only on 10 of these days were the observations considered good enough to warrant detailed analysis. The days were not all successive.

RESULTS

A. Treating the colony as a whole:

(i) Utilisation of different feeding areas:

Table 1 shows that the birds do utilise different feeding areas on different days, and that there is a tendency for the colony to switch from one area to another in unison on different days. For example, on days 3 and 4, area 3 was the most popular, and on days 5 and 7, area 5 was used most. On some days, several areas seemed to be equally popular. One possible interpretation

TABLE 1

Data showing that the herons tended to use different feeding areas on different days

Feeding Areas	Days									
	1	2	3	4	5	6	7	8	9	10
1	2	2	1	2	7	3	3	6	10	1
2	1	1	4	3	8	1	0	1	7	1
3	1	1	20	24	8	4	3	1	12	2
4	9	7	2	5	9	5	6	17	13	5
5	2	3	11	5	27	8	15	11	20	4

$\chi^2_{\text{sest}} = 112.01$ ($p < 0.001$).

The numbers in the matrix of the Table refer to the numbers of departures to different feeding areas observed on various days. A chi-square analysis of the Table shows that days are heterogeneous with respect to feeding areas.

of these data is that the birds are showing a seasonal trend to move from one area to another, and that they are behaving quite independently of one another but all responding to some environmental cue. Table 1 does not suggest an obvious systematic trend with time, and the data on timing of departures which I present below suggests that the birds are not behaving independently.

(ii) Intervals between successive departures:

The analysis of clumping of departure times was complicated by the fact that the birds show a tidal rhythm of departure frequency (Fig. 4), which would in itself introduce an element of clumping if one analysed the data for a whole day. To get around this, I analysed just the departures occurring during the peak of activity at low tide. The cut-off points for this analysis are shown in Figure 4. To analyse for clumping, I compared the distribution

of inter-departures to the equation:

where $Nt = N$

number of inter-departures in times interval t . The results (Fig. 4) show that the distribution within the low tide is more than expected on the colony in general, and that departures were not departures

Fig. 4. The frequency of departures from the colony when the tide is at low tide. Only points where the tide is at low tide are shown.

Fig. 5. The observed distribution of inter-departures by adults in the colony. The observed distribution is compared with the expected distribution. 1

3) An alternative distribution is shown with one alternative more or less than the observed distribution throughout the day.

atures from the
or 10 days giving
resting period of
ced good enough

as on different
om one area to
3 and 4, area 3
most. On some
e interpretation

feeding areas

8	9	10
6	10	1
1	7	1
1	12	2
17	13	5
11	20	4

atures to different
the Table shows

1 to move from
ndently of one
able 1 does not
ta on timing of
re not behaving

ated by the fact
(Fig. 4), which
nalsed the data
atures occurring
for this analysis
the distribution

of inter-departure intervals with a random expectation generated according to the equation:

$$Nt = N_0(e^{-P_0t})$$

where Nt = Number of cases of intervals longer than time t , N_0 = total number of intervals, $P_0 = 1/t_0$, $t_0 = \bar{N}t(t + 0.5)$, $\bar{N}t$ = Number of departures in times interval t (ANDRZEJEWSKI & WIERZBOWSKA, 1961).

The results (Fig. 5) show that the distribution of inter-departure intervals within the low tide peak is non-random. There are more very short intervals than expected on the random model; in other words the birds tend to leave the colony in groups: I interpret this as suggestive evidence that the birds were not departing independently of one another δ).

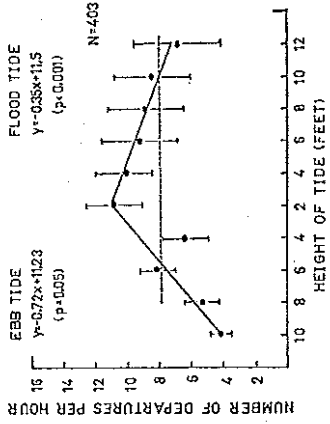


Fig. 4. The frequency of foraging trips by adult herons plotted against height of the tide. When the tide is above 10', most of the feeding grounds are inaccessible to the birds. Only points above the horizontal broken line were used in Fig. 5.

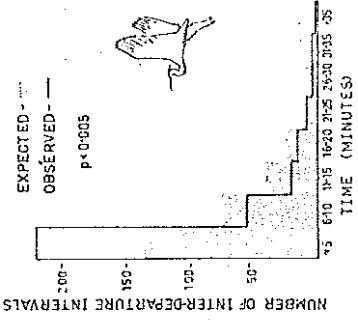


Fig. 5. The observed distribution of intervals between successive departures from the colony by adults making foraging trips (open histogram). The shaded histogram represents an expected distribution generated according to a negative exponential distribution. The observed distribution shows that departures are 'clumped'.

3) An alternative possible interpretation is that the birds are forced into synchrony with one another at the beginning of each low tide period, and that they each spend more or less the same time on a foraging trip and therefore remain in synchrony throughout the day.

Summarising, these two bits of evidence suggest that the birds follow one another out of the colony and that they switch from one feeding area to another on different days.

B. Subdividing the colony into different nest areas:

(i) The use of different feeding areas:

To test whether birds from neighbouring nests tended to use the same feeding areas, I divided the data according to the nest areas described above. I then calculated for each area separately the proportion of birds using the feeding grounds most favoured by that nest area described. For example if from nest area A, more birds went to feeding ground 3 than to any other, and 8 out of 16 observed flights were to this area, the proportion going to the most favoured feeding ground would be 50%. I compared this proportion with a similar percentage calculated by treating the colony as a whole: the proportion of birds going to the feeding area most used by the colony for each day. The rationale of this is that if within a nest area, birds have a stronger tendency to use the same feeding ground than does the colony as a whole, the within area proportion should be larger than the proportion calculated for the colony as a group. Because the number of observations for any one day was quite small, I had to combine days for the analysis. This

TABLE 2

A test to see whether or not birds from within one nesting area show a stronger tendency to go to some feeding area than do birds from the colony as a whole

Nest Area	Number of birds going to:		Percent going to "best" area
	"best" 1) feeding area for that day	Other feeding areas	
A	35	45	43
B	31	39	44
C	25	21	54
D	24	18	57
E	38	38	50
F	43	41	51
Combined 2) "within areas"	188	202	48%**
Colony total	160	230	41%**

** $\chi^2 = 4.07$, $p < 0.05$.

1) The "best" feeding area for a day is defined as the area to which most birds departed from a nest area (or from the colony as a whole in the last row of the Table).

2) Heterogeneity $\chi^2_{sat} = 5.23$ ($p > 0.30$).

Data for the separate nest areas and for areas combined are shown. When the data for different nest areas are combined there is a significant effect ($p < 0.05$), different areas all show the same trend.

assumes that the case from a trend towards heterogeneity of the effects is the combined data. Thus the results nests should be colony as a whole Herring Gulls breeding in nesting

(ii) The interval To test whether foraging trips in random basis, from that area the number of (D). If the bird value of S for areas from area As in the previous the assumption

The analysis of whether or not a by another

Nest area	Obs.	Number of departures followed
A	1	1
B	1	1
C	1	1
D	1	1
E	1	1
F	1	1

Combined*

Notes: Data from departures were not
* Heterogeneity χ^2_{sat}
For method of calc

birds follow one feeding area to

best areas:

o use the same described above. birds using the For example if in to any other, portion going to i this proportion as a whole; the colony for a, birds have a the colony as a the proportion observations for e analysis. This

g area show a birds from the

Percent going to "best" area

43
44
54
57
50
51
48% **
41% **

which most birds row of the Table).

wn. When the data $p < 0.05$, different

assumes that there is no heterogeneity between days, which appeared to be the case from scanning the data. Table 2 shows that all 6 nest areas show a trend towards greater uniformity than the colony as a whole, however, none of the effects is significant. Since the areas all show the same trend and the heterogeneity X^2 is not significant, it is reasonable to combine them, and the combined data do show a significant effect in the predicted direction. Thus the results seem to bear out the prediction that birds from neighbouring nests should be more unanimous in their choice of feeding areas than the colony as a whole. DAVIS (1973) similarly found that individual parent Herring Gulls (*Larus argentatus*) using one particular feeding area were breeding in neighbouring nests in the colony.

(ii) The intervals between successive departures:

To test whether or not birds from the same nest area tended to leave on foraging trips immediately after one another more often than expected on a random basis, I calculated for each area the number of times a departure from that area was followed by a departure from the same area (S) and the number of times a departure was followed by one from a different area (D). If the birds are leaving at random with respect to area, the expected value of S for area i is $N_i (N_i/N_c)$, where N_i is the total number of departures from area i and N_c is the total number of departures from the colony. As in the previous analysis, data for all ten days are combined, which makes the assumption of no heterogeneity. Again, there was no apparent hetero-

TABLE 3

The analysis of departures from the heronry by foraging parents, to test whether or not a departure from one nest area is more likely to be followed by another departure from the same area than expected by chance.

Nest area	Number of times a departure from area i followed by another departure from i		Number of times departure from area i followed by departure from another area		N ²	P	
	Observed	Expected	Observed	Expected			
A	15	7.6	31	38.4	46	8.64	< 0.01
B	15	9.4	34	39.6	49	4.16	< 0.05
C	10	4.3	25	30.7	35	8.71	< 0.01
D	5	3.1	23	24.9	28	1.32	> 0.10
E	13	9.2	39	42.8	52	1.91	> 0.10
F	32	16.8	40	55.2	72	17.9	< 0.001
Combined*	90	50.4	192	231.6	282	37.88	< 0.001

Notes: Data from different days were combined; only days in which more than 20 departures were recorded are included in this analysis.

* Heterogeneity $X^2_{\text{test}} = 475$ ($p > 0.30$).

For method of calculation of expected frequencies see text.

generity from scanning the data, but the number of observations on each day was not large enough to test this statistically. The results (Table 3) show that four of the six areas show a significant tendency for departures to occur in groups (*i.e.* there is a greater likelihood of two departures from the same area following one another than expected). If the data for the six areas are combined (heterogeneity X^2 not significant), the effect is highly significant.

Thus the analysis of departures from different parts of the colony supports the idea that birds tend to follow their near neighbours. Birds from neighbouring nests show both a stronger tendency to use the same feeding areas, and to leave the colony at the same time, than expected by chance. As I mentioned in the introduction, the information centre hypothesis postulates that successful birds are followed by unsuccessful birds. I have only shown that birds respond to their neighbours, and have no information on the roles of move and less successful individuals. These data could in theory be collected by weighing the food regurgitated to chicks and noting the actual sequence of departures of individuals. Some birds left the colony immediately after delivering food to the chicks while others flew to the edge of the colony and waited for a few minutes. It is tempting to speculate that the latter were unsuccessful birds.

In addition to following neighbours, the herons used at least two other methods of selecting feeding places. One was to fly over the feeding grounds and search for flocks (see below) and the other was to return to places where success had been high on previous trips. The advantage of following neighbours as opposed to seeking out feeding flocks is presumably that it saves searching time.

THE BEHAVIOUR OF BIRDS ON THE FEEDING GROUNDS

The analysis of the flight paths of the parents on foraging trips from the colony demonstrated that birds follow each other, presumably unsuccessful individuals following successful ones. In this section I describe the behaviour of the birds on the feeding grounds, and in particular I examine whether or not the rate of food intake of a bird in a flock is higher than that of a solitary individual, which would be predicted by the hypothesis.

1. THE ATTRACTION OF HERONS TO FEEDING FLOCKS

INTRODUCTION

Not all aggregations of individuals are social groups, sometimes the members of a group are responding independently to some outside stimulus. I thought it necessary to test therefore, whether groups of feeding herons are true social aggregations in the sense that birds are attracted to one another

and not to another individual. The tests were designed to measure the tendency of birds to aggregate and without a

The tests were per day at a station. A test of by 30 m, for 15 m the models and control periods (or within 50 m of stay of each the second series were run on alternate days).

The models were placed in the middle of the feeding area, and appeared to be a hunting posture, when the models

The tests showed that the proportion of birds that aggregated around the models (Table 1) was significantly higher than the single pool and the control. The proportion of birds that aggregated around the models was significantly higher than the single pool and the control.

Results of

Control
One model
Five models

Notes: Control: $p < 0.001$. On the figures are Control data for

and not to another stimulus. I further wanted to test, whether the birds would be more attracted to a larger group of birds. The experiment consisted simply of measuring the attractiveness of a particular piece of foraging ground with and without a group of model herons on it.

METHOD

The tests were carried out in June, 1972 during the nestling period. One test was done per day at a standard tide height and, by a quirk of fate, under standard weather conditions. A test consisted of watching a particular tidepool, which measured about 100 m by 30 m, for 15 minutes, then putting out the models for 30 minutes and finally removing the models and watching for a further 15 minutes. During both the experimental and control periods an observer recorded (a) the number of herons flying over the pool (or within 50 m on either side) (b) the number landing in the pool and (c) the length of stay of each individual. One series of tests compared controls with one model, and the second series compared controls with a group of five models. The two types of test were run on alternate days. Each type of test was repeated seven times.

The models were made by pouring liquid styrofoam chemicals into a fibreglass mould. The mould was built around a carved styrofoam original, and each model contained a central wooden support and a steel leg for mounting it in the mud. They were painted with matt-finish colours to match a museum specimen. During a test the models were placed in the middle of the pool, and in the case of the group of five, arranged in what appeared to be a realistic spatial pattern. The model herons were in a typical "upright" hunting posture, with the neck outstretched. If any birds were feeding in the pool at the time of transition between experimental and control periods, they were frightened away when the models were put out or taken away.

RESULTS

The tests showed that the attractiveness of an area as measured by the proportion of birds flying over that landed is related to the presence of models (Table 4). Further, the group of five models was more attractive than the single bird, both in terms of the number of birds flying near the pool and the proportion landing. The birds that landed usually landed very close to the models and started to forage near them. On many occasions, a bird that subsequently landed by the models altered its flight path by 90°

TABLE 4

Results of experiments in which model herons were put in a tidepool

	Number of birds that flew over model	Number landing in pool	Percent landing
Control	18	8	30.8
One model	6	11	64.7
Five models	4	31	88.6

Notes: Control vs One Model, $X^2 = 4.8$ ($p < 0.05$), Control vs Five Models, $X^2 = 21.6$ ($p < 0.001$), One Model vs Five Models, $X^2 = 4.19$ ($p < 0.05$). The figures are totals for 14 experiments, 7 with one model, and 7 with 5 models. Control data for the two groups did not differ significantly and are combined.

when it apparently "saw" the models. In other words it was quite obvious that birds were actually cueing in to the models. Sometimes a bird that had been attracted into the area caught a fish, and this presumably affected its length of stay. This is why I did not use the length-of-stay data in my analysis. Usually the birds stayed a matter of one or two minutes.

The fact that more birds flew over the pool with five models than with the single model may be a function of greater conspicuousness of the group. However, the proportion of birds landing was probably not related to conspicuousness of the models, as all birds flying over were very close to the models. The tests contain an inherent weakness in that once one bird has landed in the area, the stimulus properties of the pool automatically change. Since most birds left the area soon after landing, this type of bias only occurred during a small proportion of the total observation time, and I ignored it in the analysis. I did not try to investigate how accurate the resemblance of the models to a real bird has to be in order to draw in birds. I did note from casual observations, that herons were never attracted in an obvious way to land near logs, sticks pointing out of the mud or cormorants roosting on logs in the mud, all of which were common stimuli, and ones which confused human observers. It did seem on occasions that herons cued in to gulls, which often fed on the same types of fish, and it was very clear that gulls cued in to both real herons and our models. I did try some preliminary tests using models of herons in different postures. The results indicated that a model in a "hunched neck" roosting posture was less attractive than an "upright" model.

2. FEEDING BEHAVIOUR, ESPECIALLY IN RELATION TO FLOCK SIZE

INTRODUCTION

In the following paragraphs, I describe how I measured the rate of food intake of foraging adults in groups of different sizes in order to see if feeding rate is a function of group size, and if so, why. As mentioned in the Introduction, if the colony acts as an information centre helping individuals to locate good food sources, the prediction is that birds feeding in flocks will have a higher rate of food intake than solitary individuals.

METHODS

The data were virtually all collected at Iona Island (Fig. 3). This area was chosen because it was one of the most often used feeding areas; there was a 2.5 mile long jetty leading out to sea so that it was easy to follow the birds as they moved in and out with the tide, and finally because as the tide retreated, it left large pools of water on the mudflats which were convenient for sampling fish. Usually two observers at a time collected feeding rate data, each watching a particular heron through a telescope for a standard observation period of about 15 minutes (mean length 13.56 mins). The

analysis I present about 100 observations (Krebs, in prep.), techniques in 1971. Organ (DAWKINS, portable tape recorder (PDP 8, occurred. The behaviour (i) Fish capture estimated their length small (less than 1 than or equal to larger than 1½ from data in the means, 67% of *arvachis*) and the were recorded on (of a particular scope. The common *gregata* and *Perypteryx* small flounders assigned weights of regurgitated prey which we had (ii) Handling (iii) Aggressor attacked another.

Proportion

Number
Percentage
* Including *Cymatogaster*
with infringement
beak at another.
(iv) Changes in
This enabled me
period and (b) w
(v) Strike: A 1
(vi) Drop: a b
total catch for th
(vii) Orientation
in the water (pr
orientation.
(viii) Look: A 1
around. Usually 1
disturbance near.

analysis I present here is based on 381 such standard observations. In addition we made about 100 observations of juveniles, the data from which are presented elsewhere (Kees, in prep.). Two months were spent standardizing and developing the observation techniques in 1971. The observers recorded their observations on a Dawkins Behaviour Organ (DAWKINS, 1972), a small electronic organ which codes events as tones on a portable tape recorder (Uher 4000 L in this case). The tape later is decoded by the computer (PDP 8) to give a punched record of events and the time at which they occurred. The behaviours recorded were as follows:

(i) Fish capture: We identified fish as they were caught, usually to species, and also estimated their length in relation to the heron's bill. We used three size categories: small (less than $\frac{2}{3}$ beak length), medium about $\frac{1}{2}$ beak length) and large (greater than or equal to one beak length). Herons rarely succeeded in swallowing prey much larger than $1\frac{1}{3}$ beak lengths. I converted the length estimated into weights either from data in the literature (WEISS, 1969; O'CURR, 1950) or from my own measurements. 67% of all prey belonged to two species: the Staghorn Sculpin (*Leptocottus armatus*) and the Starry Flounder (*Platichthys stellatus*) (Table 5). These two species were recorded on the organ separately. The other captures were classed as 'unidentified' (of a particular size), although in fact we often did recognize them through the telescope. The commonest 'unidentified prey' were Shiner Sea Perch (*Cymatogaster aggregata* and Penpoint Gunnels (*Apodichthys flavidus*) and shrimp. Probably also many small flounders were classified as small unidentified. The unidentified fish were assigned weights on the basis of an average of values for several species. A collection of regurgitated fish from nests revealed that the birds were not taking any important prey which we had not identified during the feeding observations.

(ii) Handling time: The time between capture and swallowing each prey.

(iii) Aggression: Any interaction in which one bird in a group under observation attacked another. Usually these attacks were associated with attempts to steal fish, or

TABLE 5
Proportions of various types of fish in the diet of herons feeding
at Iona Island

Number	<i>Leptocottus armatus</i>		<i>Platichthys stellatus</i>			Other*		
	Small	Medium	Large	Small	Medium	Large	Small	Medium
681	186	54	2.2	367	199	129	754	87
Percentage	27.8	7.6	0.3	53.6	28.8	18.9	10.9	12.6

* Including *Cymatogaster aggregata*, *Apodichthys flavidus*.

with infringements of individual distances. An attack consisted of one bird lunging its beak at another, and often included 'dancing' with outstretched wings or loud cries.

(iv) Changes in group size: Whenever a bird left or joined a group this was recorded. This enabled me to calculate (a) the average group size for a 15 minute observation period and (b) whether the group size was increasing or decreasing over the period.

(v) Strike: A bird lunged at the water but did not catch a fish.

(vi) Drop: a bird dropped a fish. The weight of the fish was subtracted from the total catch for that observation period.

(vii) Orientation: A bird suddenly moved its head and neck to look at something in the water (presumably a fish). Usually a strike or capture was preceded by an orientation.

(viii) Look: A bird lifted its head so that the beak was above the horizontal and looked around. Usually looks were given in response to another heron flying over or to a disturbance nearby.

(ix) Short flight: A bird flew a short distance but without leaving the area or group in which it was feeding. A short flight is by definition less than 100 m.

(x): Long flight: a flight of more than 100 m, in which a bird left the area or group in which it was feeding.

We tested the inter-observer reliability of these behaviours by having two observers watch the same bird and record independently on the organs. Agreement between observers was good, the only points of confusion being occasionally between 'orient' and 'look', 'small' and 'medium' fish of all types, and 'small flatfish' and 'small unidentified' fish. It was usually straightforward to define a flock, since the birds in a group mostly fed within 3-10 m of each other. Under some conditions, however, the flock spread out so that the birds were 50-100 m from their nearest neighbour, but still clumped in relation to the total feeding area of about 8 square miles. For the sake of consistency, we decided that if a bird was less than 100 m from its nearest neighbour, the two individuals were in the same flock.

For each 15 minute observation, the observers noted down the time, tide, wind speed, cloud cover, precipitation (if any), depth of water in which the birds were feeding, date and initial group size. These environmental factors were incorporated as independent dummy variates in the multiple regression analyses discussed below.

In August 1972, I took standard seine samples to try and estimate the abundance of fish in relation to feeding rate. The seine samples were taken by hauling a two man 30' beach seine (1/2" mesh, 6' deep) through 20 m of water in a pool in which herons had just been feeding. The catch was weighed on a beam balance and the fish returned to the pool. Care was taken never to seine in water too deep for herons to feed in.

Water turbidity was measured by taking a sample of water from in a glass vial and measuring the absorbance relative to distilled water in a spectrophotometer. Absorbance was measured at four different wavelengths, showing little or no variation. In Figure 2 measurements are expressed as absorbance at 500 millimicrons.

RESULTS

(i) Social structure of the flocks:

Only juvenile birds were colour banded, so I cannot give detailed data on the social structure of flocks of adults. However, even casual observations show that the flock does not have a rigid social hierarchy, no birds tended to win or loose encounters systematically during an observation period. There was also no tendency for some birds to feed at the edge and others at the centre of flocks (in contrast to Woodpigeons — MURRON *et al.*, 1971, 1972). The data on marked juveniles show that flock composition is not stable from day to day, although in the short term (over a few hours) the members of a group do move around together. If, say, three individuals from a flock of 10 moved, the other seven were highly likely to follow. The average group size observed was 6.41 ± 0.37 (S.E.), with a maximum of 46 and minimum of one. Although there was apparently no hierarchy amongst adults, juveniles were on the whole subordinate to adults.

(ii) Feeding tactics:

The basic methods of feeding in Great Blue Herons have been thoroughly described by MEYERRECKS (1960, 1962). My data add little that is new. The

commonest form 'slow-wade', used catching', a terr to capture fish duck-like fashion saw birds picki outgoing tide. I did see birds ch to what MEYER Sometimes her observations of mandibulation before swallowi for the differ

F
Sms
Med
Larg
Sms
Med
Lar
Sms
Med

(iii) The re
s u c c e s s :

In order to b
per minute) is
aging, I carried
size and all the
mentioned earl
food intake: fi
Figure 6 shows
and flock size.
beyond this an
rate. Figure 7
strikes/total nu
ship was also ar

commonest hunting tactic amongst the birds in my study was MEYERREICKS' 'slow-wade', usually in water about 6"-12" deep. Two variations were 'hover catching', a tern-like hovering over deep water punctuated by occasional swoops to capture fish near the surface, and "swimming" in which the birds swam in duck-like fashion striking at fish under water (BENT, 1926). I occasionally saw birds picking up dead fish which had been stranded on the mud by the outgoing tide. I did not see wing flicking as described by MEYERREICKS, but did see birds chasing fish through shallow water in a wildly erratic fashion akin to what MEYERREICKS calls 'disturb and chase' feeding in the Reddish Egret. Sometimes herons mandibulated the prey extensively before swallowing and observations of a captive heron revealed that the bird apparently may use this mandibulation to break the sharp protruding spines of the staghorn sculpin before swallowing it. As reported by SALT & WILLARD (1971), handling time for the different prey was a function of size (Table 6).

TABLE 6

Handling times of prey of different sizes and standard errors

Prey	Handling time (mins) (= catch-swallow time)	S.E.
Small sculpin	0.009	0.004
Medium sculpin	0.02	0.005
Large sculpin	0.05	0.01
Small flatfish	0.004	0.001
Medium flatfish	1.36	1.35
Large flatfish	2.07	0.05
Small other	0.003	0.002
Medium other	0.02	0.01

(iii) The relationship between flock size and feeding success:

In order to test whether or not the rate of food intake of a bird (in grams per minute) is a function of the size of flock in which the individual is foraging, I carried out a stepwise multiple regression of feeding rate on group size and all the physical variables, such as tide and water depth, which were mentioned earlier. Only two factors were significant predictors of rate of food intake: flock size and date. Of these, flock size was the more important. Figure 6 shows the relationship between the rate of feeding of an individual and flock size. The curve reaches an asymptote at flock size of about 20 birds, beyond this an increase in flock size does not result in any increase in feeding rate. Figure 7 shows that percent success in hunting (number of successful strikes/total number of strikes) is also a function of a flock size (this relationship was also analysed in a stepwise multiple regression). Interestingly enough

ing the area or
an 100 m.
left the area or

two observers
ment between
between 'orient'
and 'small un-
e the birds in a
ns, however, the
t neighbour, but
es. For the sake
arest neighbour,
tide, wind speed,
ere feeding, date
as independent

he abundance of
ing a two man
in which herons
the fish returned
ns to feed in.
in a glass vial
photometer. Ab-
or no variation.
herons.

detailed data on
al observations
to birds tended
rvation period.
dge and others
ON *et al.*, 1971,
osition is not
few hours) the
individuals from
w. The average
num of 46 and
archy amongst

been thoroughly
that is new. The

the success of birds appears to decrease in very large flocks, perhaps as a result of interference between individuals (Goss-Crusard, 1970). This increase in percent success of flocking birds is difficult to explain; it seems to imply that either the fish are less wary when being hunted by a flock (because the flock stirs up fish — see below) or that herons strike in response to less appropriate stimuli when their feeding rate is low.

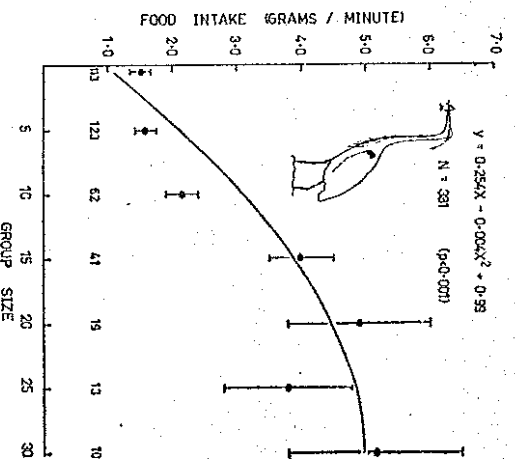


Fig. 6. Rate of food intake of adult herons as a function of flock size. The regression equation describing the relationship was arrived at by step-wise multiple regression. The data are grouped into blocks according to flock size purely to make the figure look neater; the analysis was done on the original points. The vertical bars represent standard errors of the means of grouped data.

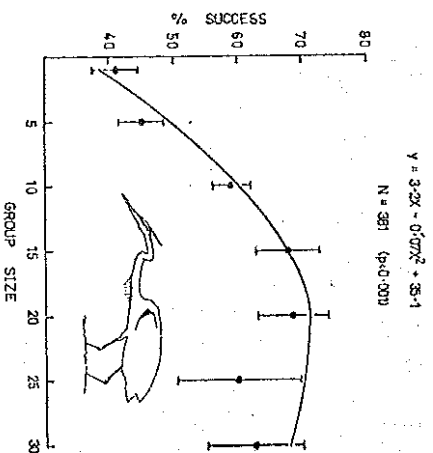


Fig. 7. Percentage of strikes which were successful as a function of flock size. Analysis and grouping of data as in Figure 6.

Figure 8 shows that the success of a bird doing an important activity, because time may result simply from the result of chickadees as a function of TINSKY & KATZ (1973). It has argued that "resilience" is a relatively simple variable to put relative to put relative. In the multivariate analysis, only the birds were Presumably (1973).

The obvious do better? See

Fig. 8. The coefficient of variation of flock size flocks. Age

hunt more in around for pr would not exp (b) Birds in a by 'herding' c advantage of

Figure 8 shows that the coefficient of variation of feeding rate goes down with increasing flock size. Thus apparently flocking may decrease the risk of a bird doing very badly in the short term (and perhaps also the chances of doing exceptionally well). This decrease in risk may in fact be a more important advantage of flocking than the increase in average rate of food intake, because leaving the nestlings without food for longer than a critical time may result in death, while delivering food to them at a slower rate may simply result in slower growth. A recent simulation study of winter flocks of chickadees has also suggested that minimising risk might be as important a function of flocking as maximising rate of food intake (THOMPSON, VER-TINSKY & KREBS, 1974). In an analogous fashion, HOLLING (in press) has argued that ecological systems in general might be geared to maximising "resilience", rather than maximising short term efficiency.

Summarizing, birds in flocks catch more grams of food per minute, suffer a relatively smaller amount of variation in the rate of food intake, and have to put relatively less effort into catching fish.

In the multiple regression of percent success on the various independent variables, only cloud cover was a significant predictor other than group size; the birds were less successful in sunny weather than in cloud or rain. Presumably this is an effect of glare from the sun (KREES & PARTRIDGE, 1973).

The obvious question arising from these results is why do birds in a flock do better? Several explanations seem possible: (a) Perhaps birds in flocks

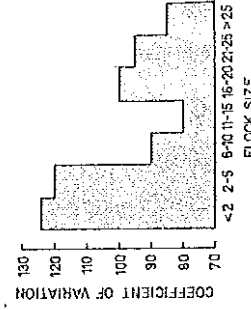


Fig. 8. The coefficient of variation (S.D./ \bar{X}) of rate of food intake of birds in different size flocks. Again the data are grouped according to flock size as in Figure 6. The relationship is significant at the 5% level.

hunt more intensively, for example because they spend less time looking around for predators (MURTON & ISAACSON, 1962; PULLIAM, 1973). This would not explain, however, why flock birds have a higher percent success. (b) Birds in a flock might increase the availability of fish for one another by 'herding' or disturbing them in some way. It is well known that the advantage of flocking in some types of birds results from disturbance of prey,

s, perhaps as a (1970). This in- plain; it seems ted by a flock -like in response

ze. The regression ide regression. The figure look neater; int standard errors

flock size. Analysis

rendering them easier to catch (RAND, 1954; SWYNNERTON, 1915, BROSSER, 1968) and this explanation has been proposed to account for flocking in some herons (see Introduction). In some cases, this disturbance of the prey has evolved into complex flock herding maneuvers to prevent prey from escaping (*e.g.* BARTHOLOMEW, 1942). The best quantitative data on hunting success of groups and single individuals in cases involving this type of cooperation comes from the studies of KRUVK (1972) and SCHALLER (1972) on mammalian predators. (c) A final possibility is that flock birds do better because flocks only occur in places where the feeding conditions are good (*e.g.* MURTON *et al.*, 1966).

Figure 9 shows that flock birds do not orient to prey significantly more

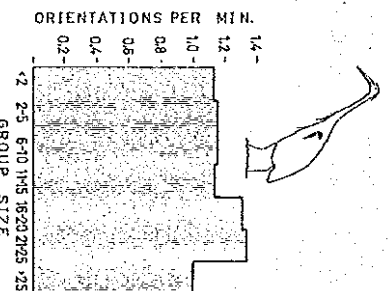


Fig. 9. The number of orientation movements made per minute per bird in flocks of different sizes.

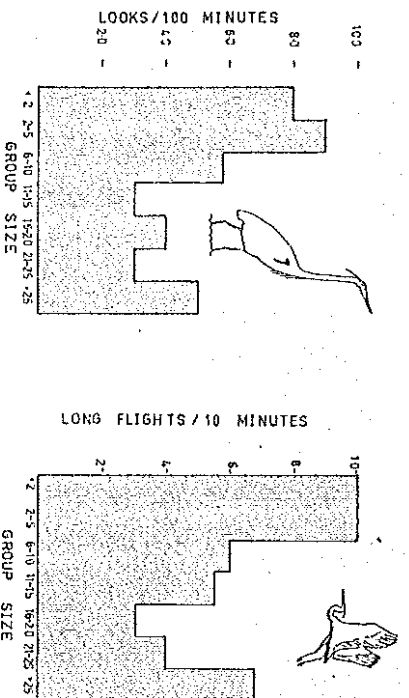


Fig. 10. The frequency (per individual) with which birds in flocks of different sizes (a) looked up and (b) flew further than 100 m. Both these behaviours are significantly negatively correlated with flock size, but a partial regression shows that the true correlation is with feeding rate and not flock size.

often than single searching more and change feed. Both of these behaviors more 'nervous' (that the only possible quite intensively moving from on antipredator response 'long flight' feeding rate is. Thus both behaviors As mentioned earlier flying over, and it watches other 1971 reached a tries in another exceeded (see below long flights. Sun 'nervous' about 1

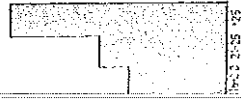
In order to find somehow stir up feeding rate and for flock members single birds. If increased as a result feeding rate and bird for two 15 diately sampled above (Methods the turbidity (s were feeding in escaping, and so 11 and 12 show dance and feeding there must even negative relation significant). This that turbidity an together to influ

1915, BROSSER, for flocking in presence of the prey prevent prey from being this type of HALLER (1972) birds do better conditions are good significantly more

often than single birds, in other words flock birds do not appear to be searching more intensively than singles. However, single birds both 'look' and change feeding places more often than birds in a flock (Figure 10). Both of these behaviours could be taken to indicate that single birds are more 'nervous' of potential predator attack (PULLIAM, 1973). (I presume that the only potential predator of adult herons is man, who does hunt herons quite intensively in the Vancouver area). However, I feel that looking and moving from one area to another are food searching behaviours rather than antipredator responses. A partial regression of both 'look' frequency and 'long flight' frequency on group size and feeding rate revealed that when feeding rate is 'held constant', neither behaviour is related to group size. Thus both behaviour patterns seem to be a response to low feeding success. As mentioned earlier, a 'look' is usually given in response to another heron flying over, and I suggest that when a bird is having a low feeding success, it watches other herons to see where they are going to feed (MURTON *et al.*, 1971 reached a similar conclusion for pigeons). A bird leaves an area and tries in another place when its 'giving up time' (CROZE, 1970) has been exceeded (see below), which is why birds with a low feeding rate make more long flights. Summarising, flock birds do not do better because they are less 'nervous' about predators.

In order to find out whether flock birds do better than singles because they somehow stir up fish for each other, I determined the relationship between feeding rate and prey abundance for single birds, and then collected data for flock members to see if for a given prey abundance, they did better than single birds. If they did, it would suggest that *availability* of food is increased as a result of being in a flock. To establish a relationship between feeding rate and prey abundance, I recorded the feeding rate of a single bird for two 15 minute periods (sometimes less than this) and then immediately sampled the fish in the area with a standard seine haul as described above (Methods). At the same time, water samples were taken to determine the turbidity (see Methods). These data were only collected when herons were feeding in isolated tidal pools, so that there was no possibility of fish escaping, and so that the area to be sampled was clearly delineated. Figures 11 and 12 show (a) that there is a positive relationship between prey abundance and feeding rate (over the range studied there is no asymptote, but there must eventually be one (HOLLING, 1965)), and (b) that there is a negative relationship between turbidity and feeding rate (which is not quite significant). This suggests, if Figures 11 and 12 are internally consistent, that turbidity and fish abundance are correlated and that the two are acting together to influence feeding rate. When turbidity is partialled out, feeding

ed by birds in flocks



SIZE
s of different sizes
birds are significantly
shows that the true
e.

rate is no longer significantly dependent on prey abundance. One possible explanation of why fish should be more abundant in clearer water is that the fish are themselves visual predators, and need clear water to feed successfully.

The important conclusion from the point of view of the present study is that in Figure 11 the few data points for flock birds do not tend to fall above the regression line for single individuals. In other words, flock birds are not doing any better for a given abundance of food than single birds. Since this conclusion is based on a small sample, it should certainly be tested further. However, other observations suggest that it is probably correct to conclude that flocks do not stir up the fish and increase prey availability. Firstly, members of a flock tend to feed rather far apart (at

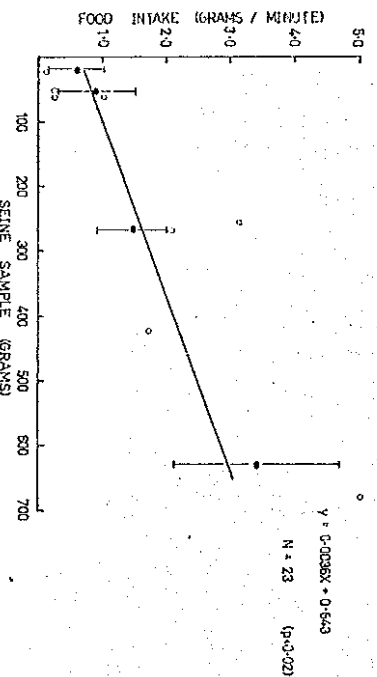


Fig. 11. The relationship between feeding rate and weight of fish caught in a standard seine haul. The solid circles represent data for single birds only, grouped into four blocks, each point being based on about five observations. The vertical bars are standard errors. The open circles are points for flock birds. Of the eight open circles, 4 fall above the line for single birds and four below; thus there is no trend apparent in this small sample for flock birds to do better for a given abundance of fish.

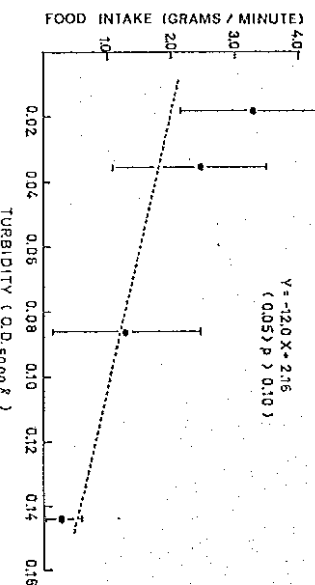


Fig. 12. The relationship between rate of food intake and turbidity of the water. When turbidity is partialled out, the relationship in Figure 11 is no longer significant.

least 3 m), so minimizing disturbance to the prey. Water to defecate and walk upstream increase in percentage that the prey are the vulnerable. The remaining only build up where the water feeding conditions bird arriving indicators of birds are attributed to as extremely widespread *et al.*, 1955: N

The results in Great Blue predictable food follows: (i) V switch from c that the food s in unison. (ii) tendency to go from the color foraging excursions more likely to parts of the c other from the bours tend to looking for flo they have prev centre, as disc grounds, birds is a function (minute) of a

least 3 m), secondly herons have several adaptations apparently aimed at minimising disturbance to the prey and the water; they always leave the water to defecate (RECHER & RECHER, 1972; pers. obs.) and they usually walk upstream into a tidal current (pers. obs.). As I mentioned earlier, the increase in percent success with flock size (Fig. 7) could be taken to indicate that the prey are more vulnerable when being hunted by a flock of herons. However, most of the evidence seems to be that flocking does not increase the vulnerability of prey.

The remaining explanation of why flock birds do better is that flocks only build up in areas where the feeding conditions are good, in other words where the water is clear and fish density is high. If flocks only occur where feeding conditions are good, then it will be a profitable strategy for a new bird arriving in the area to join a flock, thus the birds can use flocks as indicators of good feeding conditions. The model experiment shows that birds are attracted to flocks. This type of local enhancement (which is referred to as "type one" social learning in KREBS *et al.*, 1972) is extremely widespread in animals, ranging from birds (RAND, 1954; FRINGS *et al.*, 1955; MURTON *et al.*, 1966) to honey bees (WENNER, 1971).

GENERAL DISCUSSION

The results of this study support the hypothesis that colonial nesting in Great Blue Herons acts as a strategy for exploiting patchy and unpredictable food resources. The most important results can be summarized as follows: (i) When foraging to collect food for the young, birds tend to switch from one feeding area to another on successive days, suggesting that the food supply is ephemeral. The colony shows a tendency to switch in unison. (ii) Birds from neighbouring nests in the colony have a greater tendency to go to the same feeding area on a particular day than do birds from the colony as a whole. (iii) Departures from the colony by birds on foraging excursions occur in clumps, and birds from neighbouring nests are more likely to leave shortly after one another than are birds from different parts of the colony. These three results all suggest that birds follow each other from the colony to the feeding grounds, and particularly that neighbours tend to follow each other. Birds also locate good feeding places by looking for flocks on the feeding grounds and by returning to places where they have previously been successful. Thus the colony acts as an information centre, as discussed by ZAHAVI & WARD (1973). (iv) On the feeding grounds, birds are attracted to other feeding individuals, and attractiveness is a function of flock size. (v) Both the rate of food capture (grams per minute) of a bird and the percent success increase with increasing flock

One possible
ater is that the
ed successfully.
present study
ot tend to fall
ds, flock birds
in single birds.
ld certainly be
it is probably
increase prey
r far apart (at

ght in a standard
grouped into four
l bars are standard
pen circles, 4 fall
nd apparent in this
ce of fish.

of the water. When
ager significant.

size up to flock size of about 20 birds. Beyond this, capture rate appears to remain constant, while success goes down slightly. The coefficient of variation of feeding rate goes down with increasing flock size. (vi) The flock birds do better because flocks only occur when food is abundant and the water is clear, two factors which enhance feeding efficiency. There is no evidence that flock birds search harder, spend less time looking around for predators or benefit from stirring up of fish by the group.

The mechanism underlying the advantage of flocking:

Several workers have shown that flocking enhances feeding efficiency, the most direct field evidence with birds coming from the work of MURRON (1971) who showed that pigeons in a flock peck at a greater rate than solitary birds (he did not have direct data on grams of food eaten per minute). KRUVK (1972) and SCHALLER (1972) have good field evidence for predatory mammals that groups are more effective in prey catching than single individuals. KREBS *et al.*, (1972) and KREBS (1973) demonstrated in aviary experiments that flocking enhances feeding efficiency in Great tits and chickadees. In herons, I have argued that the advantage of flocking is purely because a flock signals a good feeding area, and not because of interactions between the birds once they are in the flock.

The explanation of why flocks only occur in areas of good feeding can be best understood by means of a simple graphical model (Fig. 13). The flock size at any instant in time in an area is a result of the rate at which birds join a flock, and the rate at which they leave. These two functions are shown in Figure 13, and the point at which they intersect is the equilibrium flock size (E). We know that the rate of joining a flock is a function

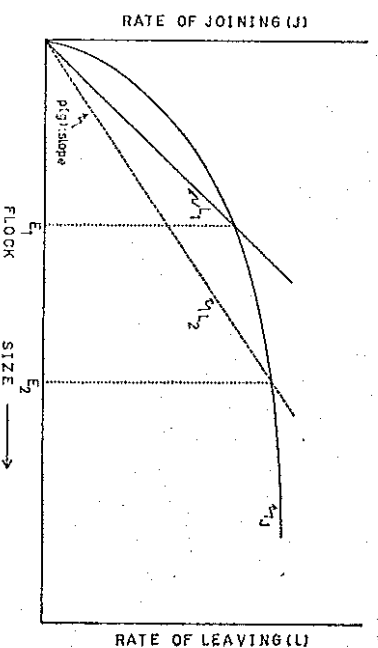


Fig. 13. A simple graphical model to show how flock size is adjusted to the feeding conditions, for explanation see text.

of flock size (the rate of joining is shown as a negative

Fig. 14. The rate at of curve used in the

the flock depends its giving up time up time' — the in Croze, 1970; See Table shows that

Mean intercatch

Catch-ca
Catch-to

the average intercatch without catching a on feeding rate a has any value in be treated as a α the giving up time simple linear increase the more likely it The equilibrium

intersect, and this is a function of the slope of the line representing the rate of leaving the flock: when the slope is steep, the flock will be small, if the slope is shallow, the flock will be large. Now the slope of the line is directly related to $p(g)$ — the probability that a bird will exceed its giving up time — and $p(g)$ increases as the catching rate goes down. Thus when the catching rate is low, $p(g)$ is large and the flock size is small (E_1). The steepest line is when the bird catches nothing and stays in the area only for g minutes (the giving up time); if g were very short in relation to the rate of joining, then flocks will virtually never build up in places where there is no food. In fact g is long enough in relation to the rate of joining, for flocks to build up sometimes in areas where the feeding is not good. When catching rate is high, $p(g)$ is low and the slope is shallow, giving a large equilibrium flock size (E_2). These two possibilities are shown in Figure 13.

Colonial nesting as a foraging adaptation and the evolution of coloniality.

I have presented evidence to show that in the colony of herons that I studied, the nesting colony acts as an information centre as proposed by WARD & ZAHAVI (1973) among others, and that individuals do benefit in terms of a higher rate of food intake by joining other birds on the feeding grounds. SIEGFRIED (1971) has proposed a similar explanation of communal roosts and breeding colonies in another ardeid, the cattle egret and a variety of studies in other animals seem to show that the social structure of a species is closely related to feeding behaviour and food distribution. So far, however, I have not discussed the question of whether or not the information centre hypothesis can provide a sufficient explanation for the evolution of colonial nesting in herons. In addition to demonstrating that colonial nesting has survival value in terms of food exploitation, it is necessary to consider whether the hypothesis can account for (a) intraspecific variations in sociality and (b) interspecific differences in sociality. Since more information is available on the former question, I will deal with it in more detail.

The Great Blue Heron shows variations in sociality both in feeding behaviour and in nesting, giving rise to two questions: firstly, whether the variations in feeding are related to variations in the distribution of food and secondly whether the variations in nesting are related to variations in feeding.

It has been shown in a variety of descriptive field studies that the social organization of a species is not rigidly fixed, but can be adapted to local conditions of, for example, food supply and predators (CROOK, 1970;

WALTERS, 1977 experimentally the *alba*) can be at food supply. V packets, the bird large clumps, has argued that of resources, it modifications o Variations in explained with widely scattered territorial, where herons forage streams and the shoreline in are foraging in the breeding supply shifts are aggressive CUSTARD (197 with large individuals in these species other by flight between selection is an antipredator catching prey. flocking herons to prevent disturbance to locate patches. In the winter severely reduce the birds have (unpubl.). At feeding, to hunt. However, some the few dayling March, 1972, of territorial behaviour of 30 heron birds

WALTHER, 1972; KRUK, 1972). ZAHAVI (1971a) has demonstrated experimentally that the social organisation of wintering wagtails (*Motacilla alba*) can be altered in the field simply by altering the distribution of the food supply. Where food is distributed in conveniently defendable small packets, the birds are territorial, where food is irregularly distributed in large clumps, the birds flock. Thus in the same way that BROWN (1964) has argued that the evolution of territoriality depends on the defendability of resources, it is apparent that higher vertebrates are capable of phenotypic modifications of social structure according to the defendability of resources. Variations in the social organisation of foraging herons can readily be explained within this framework. When the food resources are either widely scattered and/or easily defendable, foraging herons are solitary and territorial, when food occurs in large undefendable, unpredictable clumps, herons forage in flocks. In the Vancouver area, herons feeding in small streams and ditches in pasture land (where they catch mice) or along the shoreline in small inlets are territorial (pers. obs.). However, when they are foraging in large intertidal mudflats (the main foraging grounds during the breeding season), territorial defence is not feasible because the food supply shifts rapidly with time, and the birds flock. They still, however, are aggressive to one another, maintaining large individual distances. GOSS-CUSTARD (1970) has pointed out that some types of waders form flocks with large individual distances, and he presents evidence to suggest that in these species, if the birds forage too close together, they hamper each other by frightening the prey. The widely spaced flocks are a compromise between selection for flocking (in GOSS-CUSTARD's case he argues flocking is an antipredator adaptation), and selection for spacing which helps catching prey. I suggest that the large individual distances maintained by flocking herons represent a compromise between the need for spacing out to prevent disturbing the prey, and the advantage of flocking which helps to locate patches of prey.

In the winter around Vancouver, low tides are always at night, which severely reduces the profitability of the intertidal as a foraging area, since the birds have a very low success rate at catching fish in the dark (KREBS, unpubl.). At this time of year the birds tend to switch from intertidal foraging, to hunting for mice in fields and fish in shallow streams and ditches. However, some birds continue to use the intertidal, foraging mainly during the few daylight hours in which the tide is low enough to hunt. During March, 1972, I made a short term comparison of the rate of food intake of territorial birds in fields and flocking birds in the intertidal. The results of 30 heron hours of observation in each habitat showed that flocking birds

in the intertidal catch about 3 times as much food per minute as the territorial field birds. However, the available daylight foraging time for field birds is about 3 times that of the intertidal birds. Thus the two strategies are (at least from this brief study) equally profitable alternatives, further suggesting that territorial and flocking behaviour are adaptations to the local food conditions. (No birds were observed to commute between the fields and the intertidal, which one would suppose to be the best strategy of all). The relationship between flocking and food distribution may be to some extent obscured in some cases by the effect of cover (PINOWSKI, 1959). PINOWSKI, studying winter flocks of corvids, argued that even when the food distribution favours flocking, flocks will tend not to form in habitats with a great deal of cover, because the birds cannot easily see and follow others to rich patches of food.

The other question which has to be considered is the relationship between the variations in foraging behaviour (flocking versus territoriality) and colonial nesting. If colonial nesting is an adaptation for exploitation of food resources, one might expect it to show the same type of phenotypic adaptation as the behaviour of birds on the feeding grounds; the expectation being that birds would tend to be solitary nesters in areas where the food supply is scattered and more colonial where there is a clumped shifting food supply. Data for the Grey Heron (*Ardea cinerea*) in Britain and Holland suggest a trend in this direction (BURTON, 1956; BRAAKSMA & BRUNNS, 1950; LACK, 1954; GARDEN, 1958). In areas near large bodies of water, where flock feeding would be of benefit, colonies are larger. However, this evidence is certainly not totally convincing, since it could simply mean that there is more total food in large bodies of water, so more herons live there. This is the interpretation favoured by LACK (1954). For a really convincing piece of evidence, one would have to show that the total available food in the different areas was not different in quantity, but only in distribution. Nevertheless, the bit of evidence that is available goes in the predicted direction. In order to explain why herons do not always nest solitarily when they are solitary feeders, one would have to postulate that they have a basic tendency towards colonial nesting (which evolved in conditions where social feeding was advantageous) and that the phenotypic modification of this tendency is only partial, perhaps because there is no disadvantage in colonial nesting.

The question of whether or not interspecific variations in sociality of ardeids (for full account see MEYERREICHS 1960) are related to variations in feeding habits cannot be answered till more is known about the behaviour and distribution of food of solitary species. LACK (1968) argued that

solitary nesting species, because nesting in inland favour spacing cannot explain

In summary nesting and sociality an individual to conclude that colonial nesting

In this paper hypothesis that the efficiency of that individuals learn about ground feeding more social information collected in (*Ardea herodias* food intake of

The analysis birds used different supply is expected if tended to use if the overall group copy their near I did not collect successful ones

On the feeding in areas than by a single expect that flow A step-wise in fish caught per zo gets about success (i.e. st variation of effort and station I discuss we conclude that stirring up the flocks only by model to show

In conclusion are adaptation in the evolution

solitary nesting in ardeids is an antipredator adaptation in ground nesting species, because it reduces the conspicuousness of nests, while in species nesting in inaccessible places (trees over water, etc.) predation will not favour spacing out. LACK (1968) also pointed out that the "food" hypothesis cannot explain the formation of mixed colonies.

In summary, while I have presented fairly direct evidence that colonial nesting and social feeding act as adaptations that enhance the ability of an individual to exploit unpredictable food sources, it is not yet possible to conclude that this provides a sufficient explanation for the evolution of colonial nesting in herons.

SUMMARY

In this paper I present data collected to test certain predictions arising from the hypothesis that colonial nesting and social feeding in birds are adaptations that enhance the efficiency of exploitation of unpredictable food supplies. The hypothesis suggests that individuals benefit from nesting in colonies because they have the opportunity to learn about good feeding areas by following other birds from the nesting colony to the feeding grounds. If a bird is unsuccessful on one foraging trip, it will observe and follow more successful birds on subsequent trips; in this way the colony acts as an 'information centre'.

I collected two types of data to test this idea as applied to the Great Blue Heron (*Ardea herodias*). (i) I recorded flights of parent birds. (ii) I measured the rate of food intake of birds hunting for food in flocks of different sizes.

The analysis of foraging flights from the colony showed the following: (a) The birds used different feeding grounds on different days; this suggests that the food supply is ephemeral. (b) The birds tended to leave the colony in groups, which would be expected if they were following each other. (c) Birds from neighbouring nests tended to use the same feeding grounds and tended to leave the colony in groups (within the overall grouping of the colony as a whole). This would be expected if birds mainly copy their near neighbours. All these results support the idea of an information centre. I did not collect any data on whether successful birds were being followed by unsuccessful ones, but the data do seem to show that birds follow one another.

On the feeding grounds, I showed by use of models that herons are attracted to feed in areas where there are other birds, and that they are more attracted by a group than by a single bird. If flock feeding helps in locating good feeding places, we can expect that flock birds would do better in terms of food intake than solitary individuals. A step-wise multiple regression showed that rate of food intake of a bird (grams of fish caught per minute) is an asymptotic function of flock size. A bird in a flock of 20 gets about 5 times as much food per minute as a solitary bird. Further, the percent success (i.e. strikes resulting in a capture) is higher in flocks, and the coefficient of variation of feeding rate is lower. Thus flock birds get more food for relatively less effort and stand a smaller chance of doing very badly in terms of food intake.

I discuss various possible explanations of the advantage of the flock birds, and conclude that it is not a result of searching harder, less 'nervousness' of predators or stirring up the fish to make them easy to catch. It is a consequence of the fact that flocks only build up where feeding conditions are good. I present a simple graphical model to show how this happens.

In conclusion, my results support the idea that colonial nesting and social feeding are adaptations concerned with finding food, but there are also other factors involved in the evolution of sociality in ardeids and other birds.

REFERENCES

- ANDRZEJEWSKI, R. & WIERZBOWSKA, T. (1961). An attempt at assessing the duration of residence of small rodents in a defined forest area and the rate of interchange between individuals. — *Acta theriol.* 12, p. 153-71.
- BALDA, R. P. & BATEMAN, G. C. (1972). The breeding biology of the pinnon jay. — *Living Bird* 11, p. 5-42.
- BENT, A. C. (1926). Life histories of North American marsh birds. — U.S. Nat. Mus. Bull. 135, p. 1-491.
- BRAAKSMA, S. & BRUYNS, M. F. M. (1950). Overzicht van de broedkolonies van de Blaauwe Reiger *Ardea cinerea* L. in Nederland in 1949. — *Ardea* 38, p. 135-162.
- BROSSIER, A. (1968). La vie sociale des oiseaux dans une forêt équatoriale du Gabon. — *Biol. Gabon.* 5, p. 29-69.
- BROWN, J. L. (1964). The evolution of diversity in avian territorial systems. — *Wilson Bull.* 76, p. 160-169.
- BURTON, J. F. (1956). Report on the national census of heronries 1954. — *Bird Study* 3, p. 42-73.
- CHARNOV, E. L. (1973). Optimal foraging: Some theoretical explorations. — Ph. D. Thesis, U. of Washington.
- CODY, M. L. (1971). Finch flocks in the Mohave desert. — *Theor. Popul. Biol.* 2, p. 142-148.
- COURSON, J. C. (1971). Competition for breeding sites causing segregation and reduced young production in colonial animals. — *Proc. Adv. Study Inst. Dynamics*. Numbers Popul. (Oosterbeek 1971), p. 257-268.
- CROOK, J. H. (1964). The evolution of social organisation and visual communication in the weaver birds (Ploceinae). — *Behaviour Suppl.* 10; p. 1-178.
- (1965). The adaptive significance of avian social organisations. — *Symp. Zool. Soc. Lond.* 14; p. 181-218.
- (1970). Social behaviour in birds and mammals. — Academic Press.
- GROZE, H. J. (1970). Searching image in carrion crows. — *Z. Tierpsychol.*, Beiheft 5, p. 1-85.
- CURRY-LINDAHL, K. (1971). Systematic relationships in herons (Ardeidae) based on comparative studies of behaviour and ecology: a preliminary account. — *Ostrich Suppl.* 9; p. 53-70.
- DAVIS, J. W. F. (1973). Aspects of the breeding ecology and feeding of certain gulls. — D. Phil. Thesis, Oxford.
- DAWKINS, R. (1972). A cheap method of recording behavioural events, for direct computer access. — *Behaviour* 40; p. 162-173.
- EALLEN, J. M. (1973). Ecology: an evolutionary approach. — Addison Wesley.
- EMLEN, S. T. (1971). Adaptive aspects of coloniality in the bank swallow. — *Amer. Zool.* 11; p. 628.
- FRENCH, R. P. (1967). The dickcissel on its wintering grounds in Trinidad. — *Living Bird* 6, p. 123-140.
- FISHER, J. (1954). Evolution and bird sociality. — In: HUXLEY, J. S., HARRY, A. C. & FORD, E. B. eds. *Evolution as a process*. London Allen & Unwin.
- FRINGS, H., FRINGS, M., COX, B. & PEISSNER, L. (1955). Auditory and visual mechanisms in food finding behaviour in the herring gull. — *Vliss. Bull.* 67, p. 155-170.
- GARDEN, E. A. (1958). The national census of heronries in Scotland 1954 with a summary of the 1928/29 census. — *Bird Study* 5, p. 70-109.
- Goss-CUSTARD, J. D. (1970). Feeding dispersion in some overwintering wading birds. — In J. H. Crook (ed.). "Social behaviour of birds and mammals", p. 3-35. Academic Press.
- HEATHWOLE, H. (1965). Some aspects of the association of cattle egrets with cattle. — *Anim. Behav.* 13, p. 79-83.
- HOLLING, C. S. (196 in mimicry and (in press). *Social*
- HORN, H. S. (1968). *Bird Emphysem*
- JENNIT, D. A. (1969). season at Lake
- KARBS, J. R. (1973) of chickadees. —
- , MacROBERTS, Tit *Parus nizi* & Partridge.
- Nature 212, p. 3
- Karvur, H. (1964). *ridibundus*) —
- (1972). The sp
- Lack, D. (1954). *T*
- (1968). *Ecolog*
- MEYERRECKS, A. J. American Hero
- (1960b). *The s*
- (1962). *Diversi*
- MURSTEN, P. E. S. Heron. — *Arde*
- Mosse, D. H. (1970 — *Ecol. Monog*
- MURKIN, R. K. (19 behaviour of th
- (1971b). *Why* & ISAACSON, pigeon *Columb*
- , & WESTW clover supply ar
- , & — (stress in a pop
- p. 53-84. —, COONS, C. F. *Columba iria*
- p. 875-889. OROURT, H. G. (19 las). — *Calif.*
- OWEN, D. F. (196c availability of
- PAINE, J. M. (1971 Thesis U. B. C
- PALKER, R. S. (196 *ridibundus*. —
- PATTERSON, I. J. (*ridibundus*. —
- PIROWSKI, J. (1959) *fringillus*) in
- PULLIAM, H. R. (19 RAND, A. L. (1954) RECHER, H. F. & J
- p. 896-897.

- HOLING, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. — Mem. Ent. Soc. Canada 45, p. 5-60.
- (in press). Stability and resilience in ecological systems. — Ann. Rev. Ecol. Syst. 4.
- HORN, H. S. (1968). The adaptive significance of colonial nesting in the Brewer's Blackbird *Euphagus cyanocephalus*. — Ecology 49, p. 682-694.
- JENNI, D. A. (1969). A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida. — Ecol. Monographs 39, p. 245-270.
- KREBS, J. R. (1973). Social learning and the adaptive significance of mixed-species flocks of chickadees. — Can. J. Zool. 51, p. 1273-1288.
- , MACROBERTS, M. H. & CULLEN, J. M. (1972). Flocking and feeding in the Great Tit *Parus major* — an experimental study. — Ibis 114, p. 507-530.
- & PARRIDGE, B. (1973). The significance of head tilting in the great blue heron. — Nature 242, p. 533-534.
- KRUK, H. (1964). Predators and antipredator behaviour of the blackheaded gull. (*Larus ridibundus*) — Behaviour Suppl. 11, p. 1-127.
- (1972). The spotted Hyena. — Chicago University Press.
- LACK, D. (1954). The natural regulation of animal numbers. — O.U.P.
- (1968). Ecological adaptations for breeding in birds. — Methuen.
- MEXERRECKS, A. J. (1960a). Comparative breeding behaviour of four species of North American Herons. — Publ. Nuttall Ornithological Club 2, p. 1-158.
- (1960b). The success story of a pioneering bird. — Nat. Hist. 59, p. 46-57.
- (1962). Diversity typifies heron feeding. — Nat. Hist. 71, p. 48-59.
- MULSTEIN, P. LE S., PRESTR, I. & BELL, A. A. (1970). The breeding cycle of the Grey Heron. — Ardea 58, p. 171-257.
- MORSE, D. H. (1970). Ecological aspects of some mixed species foraging flocks of birds. — Ecol. Monogr. 40, p. 119-168.
- MURTON, R. K. (1971a). The significance of a specific search image in the feeding behaviour of the wood pigeon. — Behaviour 39, p. 10-42.
- (1971b). Why do some birds feed in flocks? — Ibis 113, p. 534-536.
- & ISAGSON, A. J. (1962). The functional basis of some behaviour in the wood pigeon. *Columba palumbus*. — Ibis 104, p. 503-521.
- , — & WESTWOOD, N. J. (1966). The relationships between wood pigeons and their clover supply and the mechanism of population control. — J. Appl. Ecol. 3, p. 55-96.
- , — & — (1971). The significance of gregarious feeding behaviour and adrenal stress in a population of wood pigeons *Columba palumbus*. — J. Zool. Lond. 165, p. 53-84.
- , COOMBS, C. F. B. & THERBLE, R. J. P. (1972). Ecological studies of the feral pigeon *Columba livia* var. II Flock behaviour and social organization. — J. Appl. Ecol. 9, p. 875-889.
- ORCUTT, H. G. (1950). The life history of the starry flounder *Platichthys stellatus* (Palas). — Calif. Div. Fish and Game Fish Bull. 52, p. 1-64.
- OWEN, D. F. (1960). The nesting success of the heron *Ardea cinerea* in relation to the availability of food. — Proc. Zool. Soc. Lond. 133, p. 597-617.
- PAINE, J. M. (1971). A study of colonial nesting in the Great Blue Heron. — B. Sc. Thesis, U. B. C.
- PALMER, R. S. (1962). Handbook of North American Birds. Vol. 1. — Yale Univ. Press.
- PATTERSON, I. J. (1965). Timing and spacing of broods in the blackheaded gull, *Larus ridibundus*. — Ibis 107, p. 433-459.
- PINOWSKI, J. (1959). Factors influencing the number of feeding rooks (*Corvus frugilegus* in various field environments. — Ekol. Polska Ser. A. 16, p. 1-48.
- PULLIAM, H. R. (1973). On the advantages of flocking. — J. Theor. Biol. 38, p. 419-422.
- RAND, A. L. (1954). Social feeding behaviour of birds. — Feldiana Zool. 36, p. 1-71.
- RECHER, H. F. & RECHER, J. A. (1972). Herons leaving water to defecate. — Auk 89, p. 896-897.

- SAUL, G. W. & WILLARD, D. E. 1971. The hunting behaviour and success of Forster's Tern. — *Ecology* 52, p. 989-998.
- SCALLER, G. (1972). The Serengeti Lion. — Chicago University Press.
- SIEGFRIED, W. R. (1971). Communal roosting of the cattle egret. — *Trans. Roy. Soc. S. Afric.* 39, p. 419-443.
- SMITH, J. N. M. & DAWKINS, C. R. (1971). The hunting behaviour of individual Great Tits in relation to spatial variations in their food density. — *Anim. Behav.* 19, p. 695-706.
- SOUTHERN, H. N. (1939). The flocking of immature herons. — *British Birds* 32, p. 346-349.
- SWYNNERTON, C. F. M. (1915). Mixed bird parties. — *Ibis* 3, p. 346-354.
- THOMPSON, W. A., VERTINSKY, J. & KREBS, J. R. (in press). The survival value of flocking in birds: a simulation model. — *J. anim. Ecol.* 43.
- TINBERGEN, N., IMBEROVEN, M. & FRANCK, D. (1967). An experiment on spacing out as a defence against predation. — *Behaviour* 28, p. 207-321.
- VERBEKE, N. A. M. (1973). The exploitation system of the yellow billed magpie. — *Univ. Calif. Misc. Publ. Zool.* 99, p. 1-58.
- WALTHER, R. (1972). Social grouping in Grant's Gazelle (*Gazella granti*) in the Serengeti National Park. — *Z. Tierpsychol.* 31, p. 348-403.
- WARD, P. (1965). Feeding ecology of the black-faced Diodia *Quercia quercia* in Nigeria. — *Ibis* 107, p. 173-214.
- (1972). The functional significance of mass drinking flights by sandprouse: *Provochidae*. — *Ibis* 114, p. 533-536.
- & ZAHAVI, A. (1973). The importance of certain assemblages of birds as "information centres" for food finding. — *Ibis* 115, p. 517-534.
- WEISS, E. F. (1969). The age and growth of the marine cottid *Leptocottus armatus*. — *Proc. Montana Acad. Sci.* 29, p. 63-71.
- WENNER, A. M. (1971). The Bee Language Controversy. — Educational Programs Improvement Corporation.
- WINTERBY, H. F., JOURDAIN, F. C. R., TRENKURST, N. F. & TRUCKER, B. W. (1939). The handbook of British Birds. Vol. 3. — London.
- ZAHAVI, A. (1971a). The social behaviour of the white wagtail *Motacilla alba alba* wintering in Israel. — *Ibis* 113, p. 203-211.
- (1971b). The function of pre-roost gatherings and communal roosts. — *Ibis* 113, p. 106-109.

ZUSAMMENFASSUNG

Die in diesem Artikel mitgeteilten Daten sammelte ich um bestimmte Annahmen zu prüfen, die von der Hypothese abgeleitet sind, dass Kolonienbildung und Nahrungssuche in Gruppen bei Vögeln Anpassungen an Umweltbedingungen sind, die sie nicht vorhersehender Nahrungsmengen effizienter ausbeuten lassen. Angenommen wurde dass individuelle Tiere von der Kolonienbildung dadurch profitieren, dass sie gute Futtergründe kennenlernen indem sie anderen Vögeln der Kolonie auf der Futtersuche folgen. Wenn ein Vogel auf einem Erkundungsflug keinen Erfolg hat, wird er demnach erfolgreichere Tiere beobachten, und ihnen auf weiteren Flügen folgen; auf diese Weise wird die Kolonie zum Informationszentrum.

Um diese Hypothese in Bezug auf den Blaureiher (*Ardea herodias*) zu überprüfen, habe ich zwei Arten von Daten gesammelt: (i) Ich beobachtete Flüge von Elternvögeln (ii) Ich bestimmte die Rate der Nahrungseinnahme von Vögeln, die in unterschiedlich grossen Scharen auf Futtersuche gingen.

Die Auswertung der von der Kolonie ausgehenden Erkundungsflüge ergab folgendes: (a) Die Tiere benutzen an verschiedenen Tagen verschiedene Futtergründe. Dies deutet darauf hin, dass das Nahrungsangebot von Tag zu Tag schwankt. (b) Die Vögel verliessen

die Kolonie in Gruppen aus benachbarten Kolonien in Gruppen zu erwarten, was stützen die Hypothese, dass die Rate der Futtersuche von der Rate der Erkundungsflüge abhängt. Dies deutet darauf hin, dass das Nahrungsangebot von Tag zu Tag schwankt.

Weiter diskutieren die Ergebnisse die "Barkeit" der Funktion der Vögel in Gruppen, die die Rate der Futtersuche von der Rate der Erkundungsflüge abhängt.

Zusammenfassend haben die Ergebnisse gezeigt, dass die Rate der Futtersuche von der Rate der Erkundungsflüge abhängt, was stützt die Hypothese, dass das Nahrungsangebot von Tag zu Tag schwankt.

die Kolonie in Gruppen. Das ist zu erwarten, wenn die Tiere einander folgen. (c) Vögel aus benachbarten Nestern neigten dazu, dieselben Futterplätze zu benutzen und die Kolonie in Gruppen, innerhalb der Gesamtgruppierung der Kolonie, zu verlassen. Dies ist zu erwarten, wenn die Tiere vor allem ihre Nachbarn nachahmen. Diese Ergebnisse stützen die Hypothese des Informationszentrums. Ob erfolgreiche Tiere von weniger erfolgreichen gefolgt werden habe ich nicht mit Daten belegen können; die Tatsache des Folgens ist jedoch ziemlich sicher.

Auf den Futterplätzen zeigte ich mit Hilfe von Modellen, dass Reihler dazu neigen, in Gebieten Futter zu suchen in denen sich bereits weitere Vögel aufhalten, und dass sie eher dazu neigen, sich einer Gruppe als einem einzelnen Tier anzuschließen. Wenn Nahrungssuche in Herden zum Auffinden guter Futterplätze verhilft, ist zu erwarten dass Vögel in Herden mehr Nahrung einnehmen als Einzeltiere. Eine stufenweise multiple Regression ergab, dass die Nahrungseinnahme eines Vogels eine asymptotische Funktion der Herdengröße ist. Ein Tier in einer Herde von 20 Tieren erhält etwa 5 mal so viel Nahrung pro Minute wie ein Einzeltier. Ausserdem ist die prozentuale Erfolgsrate (erfolgreiche Fangversuche) in Herden höher und der Variationskoeffizient der Nahrungseinnahme ist geringer. Folglich erhalten Herdentiere mehr Nahrung mit geringerem Aufwand und haben eine geringere Chance, gelegentlich sehr wenig Nahrung zu erhalten.

Weiter diskutierte ich verschiedenen Möglichkeiten, die Vorteile der Tiere in Herden zu erklären und schloss, das diese nicht auf angestrengteres Suchen, geringere „Erregbarkeit“ der Beutetiere, oder dem gemeinsamen Aufstöbern der Fische beruhen. Sie sind eine Folge des Umstandes, dass Herden sich nur bilden, wo die Nahrungsbedingungen günstig sind. In einem einfachen graphischen Modell demonstrierte ich, wie das vor sich geht.

Zusammenfassend stützen meine Ergebnisse die Annahme dass Kolonienbildung und gemeinsame Nahrungssuche Anpassungswert in Bezug auf die Nahrungsversorgung haben, jedoch sind wahrscheinlich noch weitere Faktoren an der Entstehung der Geselligkeit bei Reihern und anderen Vögeln beteiligt.

cess of Forster's

ans. Roy. Soc. S.

individual Great
chim. Behav. 19,

ish Birds 32, p.

survival value of

spacing out as a

magnie. — Univ.

in the Serengeti

in Nigeria. —

ndgrouse: *Petro-*

of birds as "in-

notus armatus. —

Programs Im-

B. W. (1939). The

alba alba win-

costs. — Ibis 113.

nte Annahmen zu
und Nahrungssuche
sie nicht vorherzu-
wurde dass indivi-
gute Futtergründe
uche folgen. Wenn
nach erfolgreichere
se Weise wird die

ce) zu überprüfen,
ge von Elterntieren.
e in unterschiedlich

ze ergab folgendes:
gründe. Dies deutet
Die Vögel verliessen

APPENDIX

A MODEL OF EQUILIBRIUM FLOCK SIZE IN HERONS

(written in collaboration with Dr J. M. CUREY)

The equilibrium flock model presented in Figure 13 can be developed as follows. Suppose that the catching of fish by a bird constitutes a Poisson process with a rate of catching p (Figure A 1 shows that this is in fact a reasonable assumption). The chance of a bird having caught 0, 1, 2, etc. fish after a time t is given by the Poisson series. The chance of having caught no fish is:

$$e^{-pt} \dots \dots \dots (1)$$

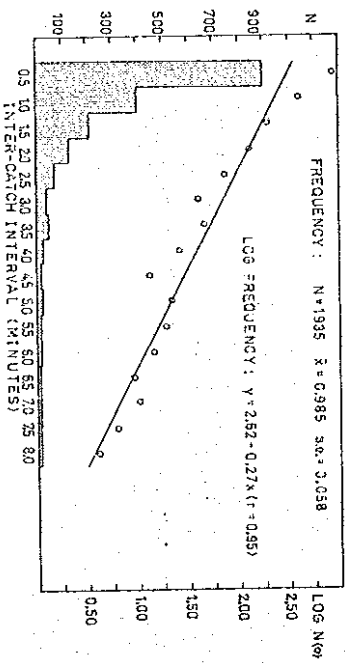


Fig. A1. The frequency distribution of inter-catch intervals. The intervals are combined into 0.5 minute groups. The open circles show the log₁₀ of the frequency distribution. These points fall close to a straight line, indicating that catching of fish by the herons approximates a Poisson process.

Consider a flock of size N in a steady state, i.e. the arrival rate is equal to the departure rate. The birds departing in the interval t to $t + dt$ will consist of two groups, birds who arrived and caught no fish by the time their giving up time (G.U.T.) expired (unsuccessful new birds) and birds who caught their last fish some time ago and whose G.U.T. has expired (unsuccessful old birds).

If we assume the giving up time to be a constant G , the number of new birds arriving in the interval $t - G$, to $t - G + dt$ is $F(N) \cdot dt$, where $F(N)$ is the rate of joining a flock of N , as shown in figure 14. Of these birds, a fraction e^{-ptG} will fail to catch a fish by the time their G.U.T. has elapsed. Therefore the number of new birds still unsuccessful at the end of G minutes is:

$$F(N) \cdot e^{-ptG} \cdot dt \dots \dots \dots (2)$$

The number of old birds that caught a fish in the interval $t - G$ to $t - G + dt$ will be $(N - F(N)) \cdot p \cdot dt$. A fraction e^{-ptG} of these will fail to catch another fish by the end of G minutes. Therefore the number of unsuccessful old birds is:

$$(N - F(N)) \cdot p \cdot e^{-ptG} \cdot dt \dots \dots \dots (3)$$

Therefore the total

(F

The number of bir

which can be read
In an equilibrium

or:

In order to see
we insert the mean
this is done, the le
side a value of 39.

Fig. A2. The fre

Thus the model
 $F(N)$. However t
(see Fig. A2). It
variance in G , as
responding to equ

The observed v
no solution of equ
variance) version
describing the sys
There are seven

HERONS

developed as follows. A process with a rate λ (life assumption). The given by the Poisson

Therefore the total number of birds departing in the interval dt is:

$$(F(N) \cdot e^{pG} + N - F(N) \cdot p \cdot e^{pG} dt) \dots \dots \dots (4)$$

The number of birds arriving in the interval dt is:

$$F(N) \cdot dt$$

which can be read off Figure 14.

In an equilibrium flock, where arrivals = departures:

$$F(N) \cdot dt = F(N) \cdot e^{pG} + N - F(N) \cdot p \cdot e^{pG} dt$$

or:

$$\frac{e^{pG}}{p} - 1 = \frac{N}{F(N)} - 1 \dots \dots \dots (5)$$

In order to see if this model really does describe the formation of equilibrium flocks, we insert the mean values of G , p , N , and $F(N)$ and see if the equation is true. When this is done, the left hand side of the equation gives a value of 37.73 and the right hand side a value of 39, a remarkably good agreement.

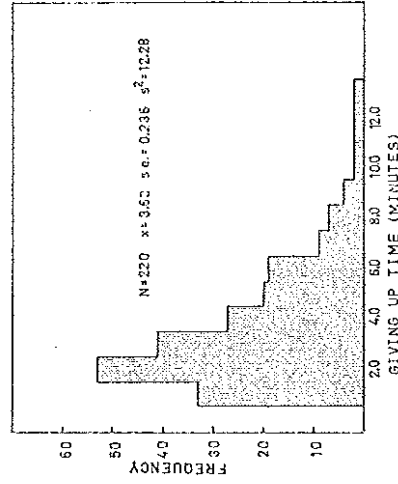


Fig. A2. The frequency distribution of giving up times. The variance (S^2) is too large to fit the model (see text).

Thus the model is successful in predicting the equilibrium flock size given p , G and $F(N)$. However this is assuming that G is fixed, whereas in fact G is quite variable (see Fig. A2). It is possible to develop a modified version of the model to allow for variance in G , assuming it is normally distributed. In this version, the equation corresponding to equation (5) is:

$$\frac{e^{pG - p^2 S^2 / 2}}{p} - 1 = \frac{N}{F(N)} - 1 \dots \dots \dots (6)$$

The observed variance (S^2) in G , shown in fig. A2, is much too high, and allows for no solution of equation (6). Thus the model, which was so successful in the simple ('no variance') version in predicting the mean stable flock size, does not seem to work in describing the system of flock formation in more detail.

There are several possible reasons we can suggest to explain why the model does not

work in the variance version. (i) The model assumes a normal distribution of the G.U.T., which is clearly not the real situation (Fig. A2). However, even allowing for this, the variance would clearly have to be extremely small to fit any variance model. (ii) The model assumes that the G.U.T. is independent of both flock size and feeding rate, because a regression analysis failed to show any such relationships. If these relationships, which seem intuitively reasonable, did exist, then the model would have to be more complicated. (iii) The G.U.T. may vary according to the type of fish last caught, for example a longer G.U.T. after a large capture. Again this seems intuitively reasonable, but without further evidence we do not know if it is true. In summary, the model works well in its simple form, but not in the more detailed version.

We thank Richard Sibley for checking the maths.

AROLLS

(Ethol.)

General ethologists & psychologists agree as to the "arousal" has effects partly physiology and

Some of the terms are large adopted into the for example, with the limb BEACH *et al.* specifically a

However, it is clear that it is a variable along states of high I shall be clear that a patible with the of the review

The varieties associated with in the under in some cases basis implied

¹ I am very on earlier data (TICK) for the