Distribution and foraging behaviour of Grey Herons *Ardea cinerea* in adjacent tidal and non-tidal areas

Dirk Draulans and Jan Hannon

Foraging activity and behaviour of Grey Herons were recorded in a tidal and an adjacent non-tidal brackish water area to investigate whether herons behaved differently in the two areas. This was not the case. Distribution of foraging herons and overall fishing success were similar, despite large differences in food availability. Foraging success did not vary much in the course of a day in the non-tidal area, but in the tidal area foraging was much more successful at high tide and almost impossible at low tide. This, however, did not seem to cause a shift of birds from the non-tidal to the tidal area. In neither area did numbers of foraging herons and fishing success vary much in the course of the winter. Weather variables, on the other hand, influenced heron distribution and foraging success, with herons shifting towards the tidal area during windy, rainy and cloudy weather, when foraging became relatively more efficient there. This could indicate that generally both areas are equally profitable to herons, despite large differences in the spatial and temporal availability of prey.

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Introduction

Different degrees of sociality in animals have been related to differences in predictability of resources in both space and time (Crook 1965, Ward and Zahavi 1973, Davies 1978). Where food distribution is highly predictable, animals are more likely to defend territories, as (1) territories are more defendable and (2) the location of food is known. Within some species the whole range of sociality can be found, dependent on habitat characteristics, to which differences in food predictability are usually linked.

Large herons (Ardeidae), such as the Grey Heron *Ardea cinerea* and the related Great Blue Heron *A. herodias*, breed either solitarily or in colonies of varying size (e.g., Cramp and Simmons 1977, Krebs 1978, Hancock and Kushlan 1984, van Vessem and Draulans 1986), and have been reported both to defend feeding territories and to forage in flocks (e.g., Lack 1968, Ward and Zahavi 1973, Krebs 1974, Cook 1978, van Vessem et al. 1984, Dowd and Flake 1985, van Vessem and Draulans 1987a). This variability has been related to differences in the predictability of food resources; rivers and fish ponds, for example, have been considered to provide spatially and temporally more predictable feeding conditions than tidal and drying-out swamp conditions (Ward and Zahavi 1973, Krebs 1978, van Vessem et al. 1984). Consequently, it has been assumed that herons living in or near tidal areas breed in large colonies and forage mainly in flocks (Lack 1968, Ward and Zahavi 1973, Krebs 1974). However, contrary to expectation, herons have been described to be territorial in tidal areas as well (Bayer 1978, Cook 1978, Richner 1986). This seems to suggest that food supplies here could still be predictable, but simply not readily available.
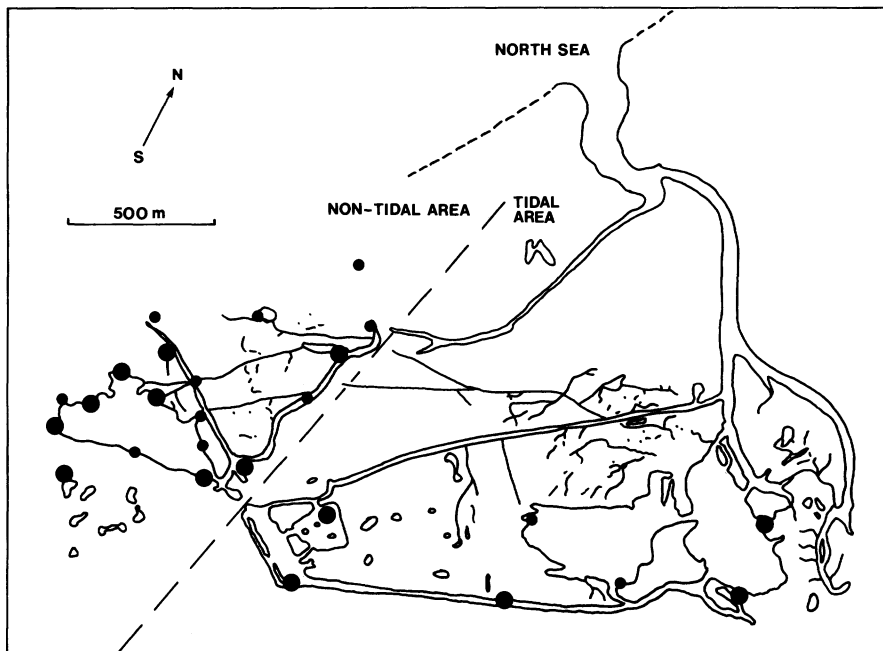
Fig. 1. Water areas in the Zwin reserve and positions of Grey Herons (large dots: more than ten records of a heron, small dots: between five and ten records of a heron; n = 88 counts).

In this contribution we compare the effects of several conditions on fishing success of Grey Herons in two areas of a brackish water habitat, one of which subjected to daily tidal fluctuations in water level and food abundance, the other not. Herons foraging in both areas roosted together in one large flock in the neighbourhood. We expected, from the above analysis, differences in distribution and success of herons in the two areas. From Richner's (1986) work we also predicted that herons should shift between the areas with changes in the relative availability of food: more herons should be foraging in the tidal area at high tide when pools are filled with water.

Methods

The study was performed in the Zwin reserve at Knokke-Heist in the extreme northwest of Belgium. The reserve is almost completely surrounded by dikes and dunes, and covers 125 ha adjacent to the North Sea. Contact with the sea is established through a small mouth in the north (cf. Fig. 1). During every high tide seawater fills most of the pools and creeks in the eastern part of the reserve (the "tidal" area). A similar area of ponds and creeks of about 30 ha in the west is unaffected by tide due to the presence of a few locks. This area, which we shall subsequently refer to as the "nontidal" area, is always filled with brackish water at a more or less constant level. The average number of herons present in the reserve decreases gradually from about 30 birds in September to 12 in January (Hannon and Draulans 1986). No data on prey abundance and availability were collected.

Between October 1984 and January 1985, we carried out 88 counts of herons in the area. All herons observed were plotted on a map and the general activity of each heron was recorded. We distinguished between foraging herons, birds present at a roost (which was situated in the non-tidal area), and birds present at a feeding site apparently without foraging (preening or looking around; for a detailed description of postures see Draulans and van Vessem 1986). These data were used to study the proportion of foraging herons in both areas in different conditions (month; time of the day: 04.00–10.00, 10.00–16.00 and 16.00–22.00 hours; height of the tide as recorded by the Hydrographical Service of the Administration of Bridges and Roads in Ostend, divided into three classes: <2 m above low water level, 2–4 m above l.w.l. and >4 m above l.w.l.; and four weather variables: temperature, amount of precipitation, wind speed and degree of cloudiness, as recorded by the Royal Meteorological Institute at Ukkel for a site very close to our study area). All statistical analyses were considered significant at the 95%-level.

In the same period we collected 475 5-min samples of heron foraging behaviour as a function of the same variables mentioned above. The herons were watched through a spotting telescope (20 × 60) and their behaviour recorded on tape. Behavioural variables included (1) the total number of strikes, (2) the number of successful and unsuccessful strikes, (3) the number of orientation movements, (4) the number of walks, and (5) the number of aggressive interactions. Strikes included all attempts to catch a fish, orientations all postures in which a heron focussed its attention on a potential prey (bill pointed towards the water), and walks all movements from one site to another. We also estimated the size of fish caught by comparison with the length of the

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Tab. 1. Proportion of Grey Herons foraging in the tidal and non-tidal area of the Zwin reserve during the course of the day and with changing tide.

	Tidal area		Non-tidal area	
	%	n	%	n
Time of day (hours)				
04–10	65	11	36	173
10–16	71	34	8	208
16–22	75	34	15	174
Height of tide (m)				
0–2	38	24	22	167
2–4	39	18	25	183
4–6	70	37	12	205

bill (ca 12 cm). The behavioural data were computer-analysed together with the environmental variables. At some stage in the analyses we performed a PCA-analysis on the entire data set to try and eliminate some of the two-sample comparisons (full procedures described in Draulans et al. 1986). However, this analysis did not reduce the underlying correlation matrix to a significantly smaller set of factors, so we will restrict the presentation to a series of two- and three-variable comparisons only.

Results

Differences between tidal and non-tidal area

The proportion of foraging herons in the tidal area was 53% (n = 79) and in the non-tidal area 49% (n = 191). The difference was not significant (test of equality of two percentages, Sokal and Rohlf 1969, P > 0.1).

The spatial distribution of foraging herons was similar for both areas: herons always foraged solitarily along the edges of creeks and pools, and there was no obvious indication from mapping positions of foraging birds that they were closer together or foraging in flocks in either area. Both areas had a number of sites where foraging was often recorded (and which could have been territories), but also sites where herons were seen more occasionally (Fig. 1). Grey Herons are rarely individually recognizable and we did not attempt to catch and mark the birds in the reserve, so we are not sure whether birds used the same site consistently. The frequency of aggressive encounters recorded during foraging behaviour sampling was the same for both areas (0.05 (5 min)$^{-1}$, S.D. = 0.12 and 0.13 for tidal and non-tidal area, respectively; n = 130 and 345). This again suggests that the distribution of foraging birds was similar for both areas.

We recorded exactly the same mean strike frequency in both areas (0.76 (5 min)$^{-1}$, S.D. = 0.84 and 0.98 for tidal and non-tidal area). However, only 38% (0.29 ± 0.74) of these strikes were successful in the non-

tidal area versus 50% (0.38 ± 0.93) in the tidal area, a difference which is statistically significant (test of equality of two percentages, P < 0.05). The average size of the prey caught was the same for both areas: 7 cm (n = 28 and 37 for tidal and non-tidal area, respectively, S.D. = 2.4 and 2.2). As the prey caught were small, they were readily swallowed, making it impossible for us to identify the prey to species.

Overall, the tidal area seemed to be a better foraging site than the non-tidal area due to the higher success rate of strikes. However, Grey Herons foraged more intensively in the tidal area where they performed significantly more orientations (5.06 ± 1.36 and 3.49 ± 1.13 for tidal and non-tidal area, respectively) and more walks per unit time (3.21 ± 2.05 and 2.77 ± 1.89, respectively) (U = 388 and 297 for orientations and walks, respectively; Mann-Whitney U-test, two-tailed, P < 0.05).

Within-day differences in foraging conditions

We looked at within-day differences in heron feeding behaviour to assess the effect of tide on foraging success, compared with an area with no such tide effect. The number of herons present did not vary significantly between the two areas in the course of the day ($\chi^2 = 3.2$, df = 2, P > 0.1), nor with height of the tide ($\chi^2 = 4.2$, df = 2, P > 0.1).

In the non-tidal area significantly more herons foraged in the morning twilight, fewer in the evening, and only few in daylight (Tab. 1) ($\chi^2 = 49.9$, df = 2, P < 0.005). No nocturnal observations were made. The trend for the tidal area was different, with significantly higher numbers of birds foraging in daylight and in the evening ($\chi^2 = 14.4$, df = 2, P < 0.005). Consequently, changes in the number of foraging herons in the course of the day were highly significantly different between the areas (G = 29.4, df = 2, P < 0.005; test of independance, Sokal and Rohlf 1969). Such a significant difference between the two areas was also recorded in relation to tidal changes (G = 17.9, df = 2, P < 0.005). The proportion of foraging herons increased significantly at high tide in the tidal area ($\chi^2 = 44.9$, df = 2, P < 0.005), as opposed to a significant decrease in the non-tidal area in the same conditions ($\chi^2 = 11.0$, df = 2, P <0.005). In the course of our study, the tide often rose in daylight and water levels were high in the afternoon or early evening on the sample dates. Hence, we assume that in the non-tidal area most herons foraged in the twilight periods (as also recorded in freshwater habitats; cf. Draulans and van Vessem 1985, van Vessem and Draulans 1987a and b, and references cited herein) and in the tidal area at high tide. The other trends could then be a consequence of the correlation between tide and time of the day.

In the non-tidal area the number of successful strikes did not vary much in the course of the day (ANOVA, F = 0.6, P > 0.5) or with changing tides (F = 0.9,
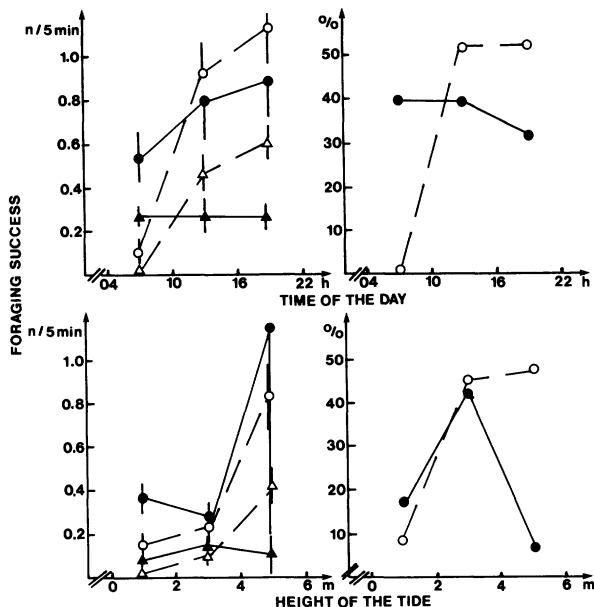
Fig. 2. Variation in foraging success of Grey Herons in the tidal (open symbols) and non-tidal (filled symbols) area of the Zwin reserve during the course of the day (upper graphs) and with changing tide (lower graphs); dots are frequency of strikes on the left graphs and proportion of successful strikes on the right graphs; triangles are number of successful strikes; vertical bars are standard errors.

$P > 0.5$), although the frequency of strikes increased significantly in the course of the day ($F = 3.4$, $P < 0.05$) (and probably as a consequence of the non-random distribution of high tides in the course of the day also with height of the tide; $F = 4.1$, $P < 0.001$) (Fig. 2). The proportion of successful strikes decreased in the course of the day. In the tidal area, on the other hand, foraging success did vary: both strike frequency ($F = 7.2$, $P < 0.001$) and strike success increased with the height of the tide, resulting in a significantly higher number of successful strikes at high tide ($F = 4.5$, $P < 0.01$) (and probably related to this tide effect also in the afternoon and the evening; $F = 6.5$ and 4.9 for strike frequency and strike success, respectively, $P < 0.01$). Variation in strike success was highly significantly different between both areas (2-way ANOVA, $F = 9.2$ and 7.1 for tide and time-of-the-day effect, respectively, $P < 0.001$). It seems that there was only little variation with time of the day, but that at high tide foraging was much more successful in the tidal area.

There was little variation in the frequency of walking at different water levels in the course of the day for both areas, apart from an increase in the evening (tidal area: $F = 2.4$, $P < 0.01$; non-tidal area: $F = 1.5$, $P > 0.1$), which seems unrelated to tidal conditions ($F = 0.4$ and 0.6 for tidal and non-tidal area, respectively, $P > 0.5$) (Fig. 3). The number of orientations was a little lower in the morning (and at low tide) in the non-tidal area, but

not significantly so ($F = 0.9$ and 1.3 for tide and time of the day, respectively, $P > 0.05$). It increased considerably, however, with height of the tide ($F = 2.2$, $P < 0.025$) and in the course of the day ($F = 3.8$, $P < 0.001$) in the tidal area: herons seemed to perform more orientations with increasing tide, which is in accordance with their increased frequency and success of strikes. Again, the changes between both areas varied significantly (2-way ANOVA, $F = 2.8$ and 2.6 for course of the day and height of the tide, respectively, $P < 0.05$). Heron foraging behaviour (orientation frequency and to a lesser extent also frequency of walks) seemed to vary during the day only in the tidal area, apparently as a consequence of tide effects.

Seasonal differences in foraging conditions

It has been reported that less fish move into a tidal area with high tide in the course of the winter. Consequently, we assumed that the tidal area should become relatively less good as a foraging place for Grey Herons, and we predicted that fewer herons should forage there in the course of the season and with a decreasing rate of success. We found indeed that the number of herons present in the tidal area decreased in the course of the winter, but in the non-tidal area it did not (Hannon and Draulans 1986). Consequently, heron distribution between the two areas changed significantly in the course of the winter ($\chi^2 = 17.1$, df = 3, $P < 0.005$).

However, there was no significant change in the proportion of herons foraging in the tidal area during the course of the season ($\chi^2 = 1.5$, df = 2, $P > 0.5$). In the non-tidal area, on the other hand, a significant decrease from 30% in October to 14% in December and 0% in January was recorded ($\chi^2 = 46.1$, df = 3, $P < 0.005$). This was a consequence of the increasing number of non-foraging herons in this area. The total number of foraging birds did not vary significantly between October and December ($\chi^2 = 1.5$, df = 2, $P > 0.1$), whereas no foraging was recorded in January, when most of the creeks and pools here were ice-covered. But also in the
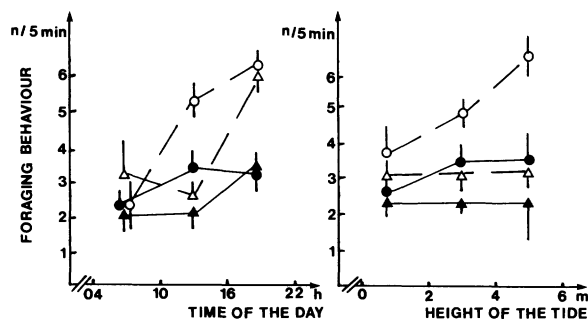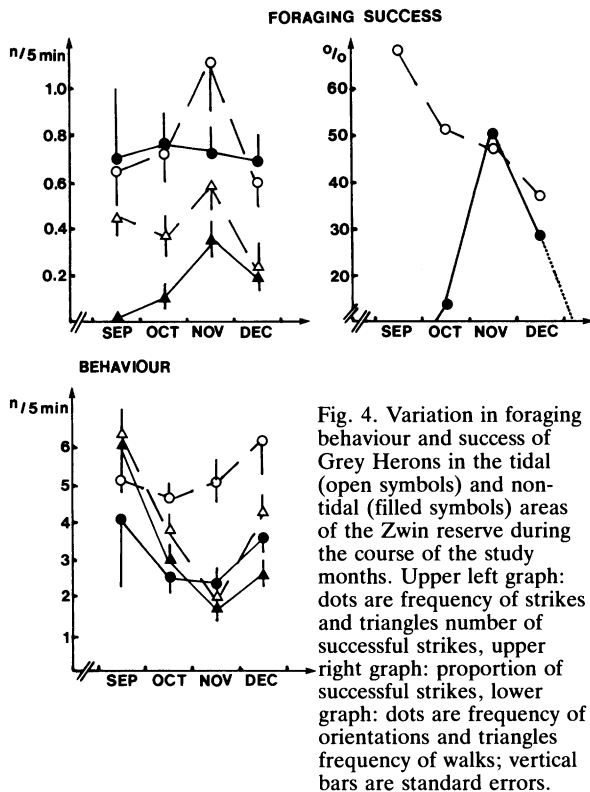

Fig. 3. Variation in foraging behaviour of Grey Herons in the tidal (open symbols) and non-tidal (filled symbols) area of the Zwin reserve during the course of the day (left graph) and with changing tide (right graph); dots are frequency of orientation movements and triangles frequency of walks; vertical bars are standard errors.

FORAGING SUCCESS

BEHAVIOUR

Fig. 4. Variation in foraging behaviour and success of Grey Herons in the tidal (open symbols) and non-tidal (filled symbols) areas of the Zwin reserve during the course of the study months. Upper left graph: dots are frequency of strikes and triangles number of successful strikes, upper right graph: proportion of successful strikes, lower graph: dots are frequency of orientations and triangles frequency of walks; vertical bars are standard errors.

tidal area, where the water was not frozen, foraging was almost non-existent in January. Many herons seemed to have foraged outside the reserve in the neighbouring polder streams and meadows in this period, where they hunted mainly for small mammals (unpubl. data).

Foraging success and behaviour varied in a more or less comparable way for both areas in the course of the winter (Fig. 4). Foraging success was highest in November (the September point for foraging success in the non-tidal area was based on a very small sample only). In December, birds were similarly successful in both areas, and, as mentioned earlier, in January none of the two areas seemed to house foraging herons. When we look at the changes in foraging success in the tidal area at high tide only, exactly the same pattern was found. None of the variation in foraging success was significant (tidal area: $F = 0.9$ for strike frequency and 1.0 for strike success, $P > 0.05$; non-tidal area: $F = 0.6$ and 0.7, respectively, $P > 0.5$), despite a clear decrease in success rate during the winter. The number of orientations did not show a consistent change in the course of the season ($F = 0.6$ and 0.9 for tidal and non-tidal area, respectively, $P > 0.1$). The number of walks, however, decreased in a significant way ($F = 3.6$ and 9.0 for tidal and non-tidal area, respectively, $P < 0.001$). The number of orientations was always higher in the tidal than in the non-tidal area, but variation in the number of walks in the course of the season was similar (2-way ANOVA, $F = 0.9$, $P > 0.1$). All these data seem to suggest that

there was only little consistent change in heron foraging in the course of the winter (although many birds seemed to go and forage elsewhere), and that the trends were comparable between the two areas.

Foraging in relation to weather

We assumed that if prey become more easily available in the tidal area during high tide, the success of foraging herons there should be less influenced by adverse weather conditions than those in the non-tidal area. We also assumed that cold, rainy, windy and cloudy conditions are worse for foraging herons than warm, dry, calm and sunny weather, which is supported by our as yet unpublished data. Hence, in these circumstances herons should shift towards foraging in the tidal area. There were indeed significant differences in heron distribution between the two areas, which confirmed these predictions (Tab. 2): significantly more herons were found in the tidal area during rainy, windy and cloudy weather conditions ($\chi^2 = 10.5$, 7.0 and 16.9, respectively, $P < 0.05$). There was no difference in the proportion of herons foraging in the two areas at different wind speeds ($\chi^2 = 0.1$ and 0.2 for tidal and non-tidal areas, respectively, $df = 2$, $P > 0.1$). Rainfall, on the other hand, increased the proportion of foraging herons in both areas, although the difference was significant for the non-tidal area only ($\chi^2 = 4.8$ and 9.0, $P > 0.1$ and < 0.025, respectively). Variation was similar for both areas ($G = 2.4$, $df = 2$, $P > 0.1$). Increasing cloudiness caused a significant increase in the proportion of herons foraging in both areas, but, again, the difference was significant for the non-tidal area only ($\chi^2 = 5.1$ and 18.3, $P > 0.05$ and < 0.005, respectively). Changes, again, were similar for both areas ($G = 0.2$, $df = 2$, $P > 0.5$). All this seems to indicate that bad weather caused a shift of birds from the non-tidal to the tidal area, but that the proportion of birds foraging was significantly affected in the non-tidal area only.

Tab. 2. The impact of weather on the proportion of Grey Herons foraging in the tidal and non-tidal area of the Zwin reserve.

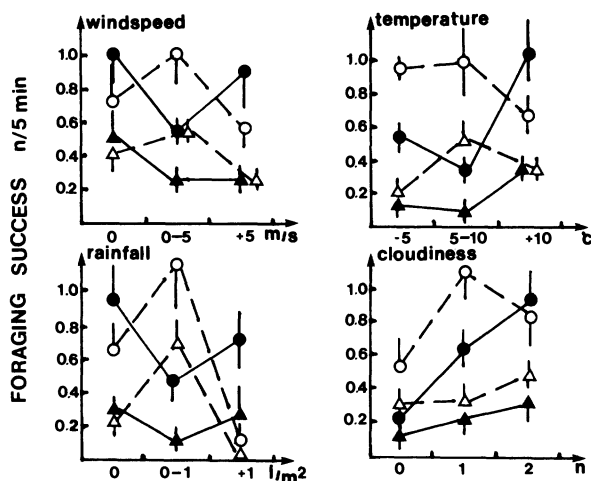|	Tidal area		Non-tidal area	
	%	ñ	%	n
Rain (l m^{-2})				
0	49	41	17	350
0.1–1	63	30	29	117
>1	38	8	14	88
Temperature (°C)				
<0	67	3	0	49
0–10	51	47	19	313
>10	55	29	23	193
Cloudiness				
no clouds	50	28	13	333
partly clouded	54	26	27	109
overcast	56	25	31	113

Fig. 5. Effect of weather on foraging success of Grey Herons in the tidal (open symbols) and non-tidal (filled symbols) area of the Zwin reserve; dots are frequency of strikes and triangles number of successful strikes; vertical bars are standard errors.

The effect of temperature was different, as temperature has more long-term effects than the three other weather variables studied. Temperature, however, did not significantly influence heron distribution between the two areas ($\chi^2 = 2.8$, df = 2, P > 0.1), suggesting that this variable was not entirely related to the seasonal changes described earlier. It is, however, unclear what exactly caused the difference between the areas. The proportion of foraging herons decreased significantly in cold weather in the non-tidal area ($\chi^2 = 22.9$, df = 2, P < 0.005), but not in the tidal area ($\chi^2 = 0.4$, df = 2, P > 0.5).

The question remains whether these changes relate to variation in foraging success. It seems that strike frequency and success show opposite trends for wind, rain and temperature in the two areas. The changes in success could support our predictions: success seems to decrease more slowly with worsening weather in the tidal area, although at extreme conditions values become similar again (Fig. 5). In conclusion, although obviously preliminary, these data seem to support the suggestion that on a short-term basis changing weather conditions may induce a shift in herons towards proportionally better foraging areas.

Discusssion

Our data suggest that Grey Herons forage more successfully in a tidal than in a non-tidal area, mainly due to a high strike success at high tide conditions when water fills pools and creeks. Shorebirds and gulls also tend to feed more rapidly during incoming tide (Puttick 1984, Curtis and Thompon 1985). Fish have been reported to move gradually into tidal areas with increasing

tide, so probably being most abundant at high tide (Tyler 1971, De Veen 1979). Herons, however, hunted in a more intensive way (more orientations and walks per unit time) in the tidal area, which is in contradiction to the finding of Black and Collopy (1982) that herons hunted less intensively in moving than in quiet water. However, the time available for hunting is clearly limiting in the tidal area, and a high temporary availability of prey could induce the birds to forage more intently (cf. Draulans 1987). It would be interesting to study individually-marked herons to try and calculate time budgets. It is possible that, on a daily basis, birds had a similar intake rate in both areas.

In our tidal area foraging was more efficient at high tide, which is in contrast to all other studies where herons foraged more efficiently in pools and at the water line during low tide (Krebs 1974, Quinney and Smith 1980, DesGranges 1981, Black and Collopy 1982, Draulans 1986, Richner 1986). The principle of changing foraging conditions, however, remains the same, as birds exploit the best options in each area (at our study site the birds could not forage at low tide, simply because of lack of water). There is no reason to suppose that food distribution differs during rising and falling water levels as we found no differences in foraging behaviour or success of Grey Herons at similar water levels during rising and falling tide.

It is remarkable that we did not find any significant changes in heron distribution in the course of the day or in different tide conditions. This seems in contradiction to the observations of Richner (1986). However, in Richner's study it was impossible for the Grey Herons to remain on their feeding grounds, as these became too deep during rising tide. DesGranges (1981) described Great Blue Herons perching in trees close to their foraging sites during high tides, and Draulans (1986) recorded Malagasy Herons Ardea humbloti resting on a beach until foraging in an adjacent tidal bay became possible again. Richner (1986) described Grey Herons switching between streams and tidal areas with changing foraging conditions in the tidal bay. Only three out of the 14 birds in his study area were involved, however. Such small changes are unlikely to be detected when analyses are made at the population level such as in our study. It would be interesting to know if Richner's herons also switched mainly during changing weather conditions, as in our study. Finally, Richner's data were collected in the winter period, so switchers might have been birds that were unable to fish properly in their stream territories. A similar behaviour was sometimes recorded in winter in a large fish pond area in Belgium, when ponds froze during cold weather. Grey Herons occupying permanent territories on ponds switched for short feeding bouts (without territorial defence) to a nearby fish farm where food remained highly available (Draulans 1984 and unpubl.).

Although foraging success and behaviour of Grey Herons in the non-tidal area were more or less similar

throughout the day, more birds foraged in the twilight periods, especially in the morning (when foraging intensity was lowest), which is consistent with what has been found elsewhere (e.g., Cramp and Simmons 1977, Draulans and van Vessem 1985, van Vessem and Draulans 1987a and b). A similar pattern was found for the tidal area when low and high tides were analysed separately, as also described by DesGranges (1981) and Black and Collopy (1982). Foraging seems to be more successful in twilight, especially at dawn. It was remarkable that herons did not seem to switch between the two areas in relation to the tidal cycle, whereas short-term shifts occurred in adverse weather conditions, when more herons moved to the tidal area, where foraging was less affected. It is puzzling why herons should respond to short-term changes in weather conditions and not to similar short-term changes in the height of the tide.

Changes in foraging behaviour and success in the course of the winter were similar for both areas, suggesting that fish availability decreased in a similar way. Fish are believed to become less active and to remain in deeper water during cold weather (Kushlan 1981), and less fish move in with the rising tide during winter (Cain and Dean 1976, Kuypers 1977). Grey Herons may switch from fishing to feeding on small mammals in the nearby polders when foraging in the Zwin reserve is becoming less profitable, but this remains to be investigated.

In conclusion, our data do confirm the suggestion of Richner (1986) that there are no clear differences in resource predictability between tidal and non-tidal areas. Consequently, it is hard to assume that herons in tidal and non-tidal areas should behave differently, as has been suggested earlier (Lack 1968, Krebs 1974, van Vessem et al. 1984). We believe that social feeding in Grey and Great Blue Herons (and regular switching between foraging areas) is common only in (rare?) situations where prey suddenly become accessible for a restricted period of time, such as in drying out marshes (Hafner et al. 1982) or at draining fish ponds (Draulans 1987). These conditions enable herons to flock, but also force them to switch readily between areas. Such behaviour does not seem to be obligate in tidal areas, suggesting that food availability is more predictable here.

References

Bayer, R. D. 1978. Aspects of an Oregon estuarine Great Blue Heron population. – In: Sprunt, A., Ogden, J. C. and Winckler S. (eds). Wading birds. National Audubon Society, New York, pp. 245–252.

Black, B. B. and Collopy, M. W. 1982. Nocturnal activity of Great Blue Herons in a North Florida salt marsh. – J. Field Ornith. 53: 403–406.

Cain, R. L. and Dean, J. M. 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. – Mar. Biol. 36: 369–379.

Cook, D. C. 1978. Grey Herons *Ardea cinerea* holding feeding territories on the Ythan Estuary. – Bird Study 25: 17–22.

Curtis, D. J. and Thompson, D. B. A. 1985. Spacing and foraging behaviour of black-headed Gulls *Larus ridibundus* in an estuary. – Ornis Scand. 16: 245–252.

Cramp, S. and Simmons, K. E. L. 1977. The birds of the western Palearctic. Vol. I. – Oxford Univ. Press, Oxford.

Crook, J. H. 1965. The adaptive significance of avian social organisations. – Symp. Zool. Soc. London 14: 181–218.

Davies, N. B. 1978. Ecological questions about territorial behaviour. – In: Krebs, J. R. and Davies, N. B. (eds). Behavioural ecology. An evolutionary approach. Blackwell Scientific Publications, Oxford, pp. 317–350.

De Veen, J. F. 1979. On the selective tidal transport in the migration of North Sea Plaice (*Pleuronectes platessa*) and other flatfish species. – Neth. J. Sea Res. 12: 115–147.

DesGranges, J. 1981. Observations sur l'alimentation du Grand Héron *Ardea herodias* en Quebec (Canada). – Alauda 49: 25–34.

Dowd, E. M. and Flake, L. D. 1985. Foraging habitats and movements of nesting Great Blue Herons in a prairie river ecosystem, South Dakota. – J. Field Ornith. 56: 379–387.

Draulans, D. 1984. Terreinkeuze, tijdsgebruik en gedrag van Blauwe Reigers (*Ardea cinerea* L.) in een uitgestrekt vijvergebied gedurende het winterhalfjaar. – Leuven, Ph.D. thesis.

– 1986. On the distribution and foraging behaviour of the Malagasy Heron *Ardea humbloti*. – Ostrich 57: 249–251.

– 1987. The effect of prey density on age-related differences in foraging behaviour and success of Grey Herons *Ardea cinerea*. – J. Anim. Ecol. 56: 479–493.

– and van Vessem, J. 1985. Age-related differences in the use of time and space by radio-tagged Grey Herons (*Ardea cinerea*) in winter. – J. Anim. Ecol. 54: 771–780.

– and van Vessem, J. 1986. Communal roosting in Grey Herons (*Ardea cinerea*) in Belgium. – Colon. Waterbirds 9: 18–24.

– , van Vessem, J. and Symons, F. 1986. Multivariate analysis of factors affecting foraging success of Grey Herons (*Ardea cinerea*) at a fish farm in winter. – Ann. Soc. r. Zool. Belg. 116: 211–226.

Hafner, H., Boy, V. and Gory, G. 1982. Feeding method, flock size and feeding success in the Little Egret *Egretta garzetta* and the Squacco Heron *Ardeola ralloides* in Camargue, South France. – Ardea 70: 45–54.

Hancock, J. and Kushlan, J. 1984. The herons handbook. – London, Croom Helm.

Hannon, J. and Draulans, D. 1986. Bestandsontwikkeling van overwinterende Blauwe Reigers (*Ardea cinerea*) in een slikken- en schorrengebied. – Wielewaal 52: 59–63.

Lack, D. 1968. Ecological adaptations for breeding in birds. – Methuen, London.

Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for the exploitation of food resources in Great Blue Herons *Ardea herodias*. – Behaviour 51: 99–134.

– 1978. Colonial nesting in birds, with special reference to the Ciconiiformes. – In: Sprunt, A., Ogden, J. C. and Winckler, S. (eds). Wading birds. National Audubon Society, New York, pp. 299–314.

Kuypers, B. R. 1977. On the ecology of juvenile Plaice on a tidal flat in the Wadden Sea. – Neth. J. Sea Res. 11: 56–91.

Kushlan, J. A. 1981. Resource use strategies of wading birds. – Wilson Bull. 93: 145–163.

Puttick, G. 1984. Foraging and activity patterns in wintering shorebirds. – In: Burger, J. and Olla, B. (eds). Behaviour of marine animals 6. Plenum Press, London, pp. 203–231.

Quinney, T. E. and Smith, P. C. 1980. Comparative foraging behaviour and success of adult and juvenile Great Blue Herons. – Can. J. Zool. 58: 1168–1173.

Richner, H. 1986. Winter feeding strategies of individually marked herons. – Anim. Behav. 34: 881–886.

Sokal, R. and Rohlf, R. 1969. Biometry. – San Francisco, Freeman.

Tyler, A. V. 1971. Surges of Winter Flounder *Pseudopleuronectes americanus* into the intertidal zone. – J. Fish Res. Bd. Can. 28: 1727–1732.

van Vessem, J. and Draulans, D. 1986. On the adaptive significance of colonial breeding in the Grey Heron *Ardea cinerea*: inter- and intracolonial variability in breeding success. – Ornis Scand. 17: 356–362.

– and Draulans, D. 1987a. Spatial distribution and time budget of radio-tagged Grey Herons (*Ardea cinerea*) during the breeding season. – J. Zool. Lond. 213: 507–534.

– and Draulans, D. 1987b. Patterns of arrival and departure of Grey Herons *Ardea cinerea* at two breeding colonies. – Ibis 129: 353–363.

– , Draulans, D. and De Bont, A. F. 1984. Movements of radiotagged Grey Herons (*Ardea cinerea*) in the breeding season in a large pond area. – Ibis 126: 576–587.

Ward, P. and Zahavi, A. 1973. The importance of certain assemblages of birds as "information centres" for food finding. – Ibis 115: 517–534.