

Winter feeding strategies of individually marked herons

H. RICHNER

Department of Zoology, Culterty Field Station, University of Aberdeen, Aberdeen, Scotland

Abstract. The winter feeding behaviour of individually marked herons was studied in an estuarine habitat with adjacent streams in north-east Scotland. Feeding rates in the estuary were highest around low tide, and no feeding took place 3 h before and after low tide. Feeding rates at streams were significantly lower than in the estuary, but were constant throughout the day.

Individual herons fed consistently with one of the following strategies: (1) feeding in a stream only; (2) feeding in the estuary only; or (3) switching between stream and estuary. The feeding rate was measured as a basis for a comparison of the benefits of alternative feeding strategies. A comparison between the three feeding strategies showed that herons that switched between estuary and streams achieved a significantly higher food intake than birds that used a stream feeding site only. The timing of arrival on the estuary and departure from the estuary to the streams was consistent with an energy maximization hypothesis. In mid-winter, switchers were significantly heavier than non-switchers.

In a recent survey of the literature, Krebs et al. (1984) point out the lack of quantitative tests of models of optimal foraging in field situations. In particular there have been, to date, very few field studies that discuss energy maximization (Davies & Houston 1981; Hodges 1981; Best & Bierzychudek 1982). In this study I examine the timing of switching between food patches in relation to an energy maximizing hypothesis. The rate of food intake is taken as a currency to compare the benefits of different strategies of individually wing-tagged herons (*Ardea cinerea*).

Hérons in estuarine habitats are faced with a complex feeding situation: they feed at the edge of the water-line which changes position throughout the tidal cycle; the timing and position of high and low tide changes each day; and prey density varies between high and low water-line. In contrast, tributary streams provide a more constant source of food over time. A heron feeding in an estuary with adjacent streams has, therefore, a choice of alternative feeding strategies: e.g. feeding in the estuary only; switching between the estuary and the streams; or feeding in the streams only. Furthermore, herons have a choice between remaining in one feeding site and establishing a feeding territory or moving between undefended feeding sites.

METHODS

Hérons wintering on the Ythan Estuary and adjacent streams were observed between 0800 hours and 1800 hours from 15 December 1981 to 20 March 1982 for a total of 67 h. When a bird under observation left the area, another heron was chosen and therefore, observation periods varied from 0.5 h to 4 h. Initially, 10 individuals were recognized by plumage characteristics. Nine of these individuals were subsequently caught at their communal night roost at the end of January by using a catapult elastic-powered net. All birds were individually wing-tagged. They returned to their respective feeding sites the following day and previous identification by plumage characteristics was confirmed. Juvenile herons (first and second year individuals recognized on the basis of plumage differences; Witherby et al. 1939) were considered separately from adult herons.

Locations of feeding sites throughout the whole estuary and on the two streams (Tarty Burn, Foveran Burn) are given in Fig. 1. Observations of individuals' feeding behaviour were restricted to the Insches area of the estuary (see Fig. 1) and to both of the streams. The number of herons, timing of arrival, prey captures, size and type of prey, search times (time from swallowing one prey item to catching the next one), timing of interactions and time of departure from feeding sites were recorded and mean values (± 1 SE) for each were calculated for each 0.5-h period. Since juvenile herons usually have lower feeding rates than adults

Present address: Département de Zoologie et d'Ecologie animale, Université de Lausanne, 1015 Lausanne, Switzerland.

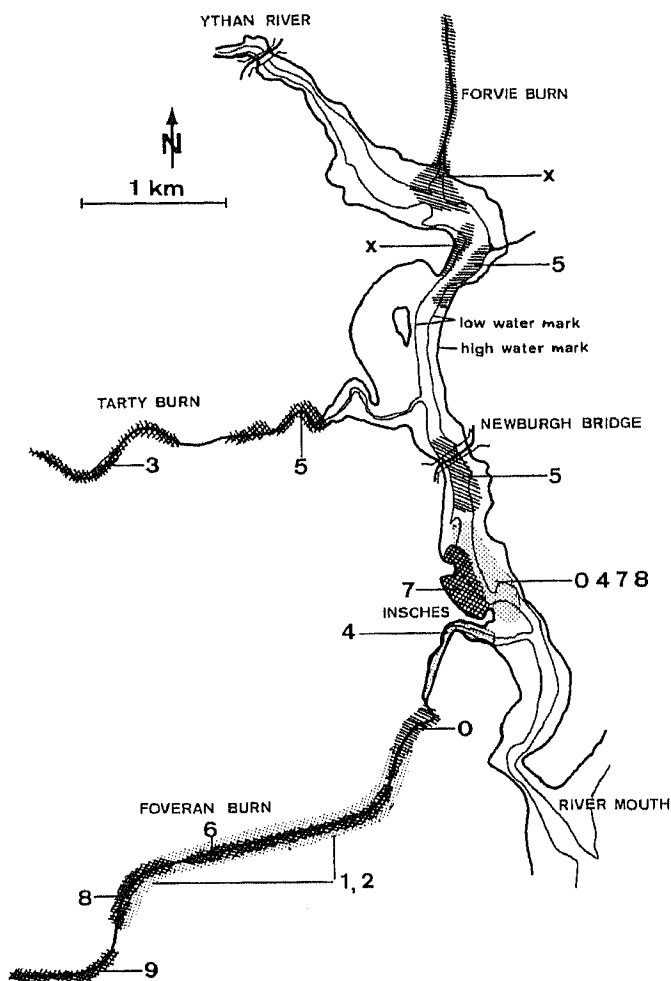


Figure 1. The Ythan estuary and adjacent streams with the positions of the feeding sites of individually marked herons, birds 0-9, and the unmarked adult X. Dotted: undefended area; hatched: undefended but exclusive area; cross-hatched: defended and exclusive area.

(Recher & Recher 1969; Quinney & Smith 1980) I restricted the collection of feeding data to adults only.

The prey items were categorized into four size classes in relation to the average bill length of the heron (120 mm): (1) fish smaller than 60 mm; (2) fish between 60 mm and 119 mm; (3) fish between 120 mm and 179 mm; (4) fish between 180 mm and 240 mm in length. Larger items required longer handling times and estimates of their length were relatively accurate. To estimate the weight of fish eaten, I used power equations for length (L , in cm) to weight (W , in g) conversions. The equations for the most common prey species were: $W=0.00125L^{3.16}$ for eel (*Anguilla anguilla*); $W=0.030L^{2.69}$ for flounder (*Platichthys flesus*); $W=0.015L^{2.91}$ for trout (*Salmo trutta*); $W=0.0014L^{3.50}$ for sprat (*Sprattus sprattus*); and

$W=0.0096L^{2.56}$ for butterfish (*Pholis gunellus*) (Harris & Hislop 1978; unpublished data). Since all prey items were fish and their calorific values varied within a small range (1.05 cal g^{-1} wet weight, to 1.18 cal g^{-1} wet weight) the feeding data here are presented in g, but can be transformed approximately into energy by multiplying by 1.1 cal g^{-1} . Small unidentified fish species were classified according to their shape, i.e. eel-shape, flounder-shape, trout-shape, and the appropriate equation used for length to weight conversions. Mean feeding rate (g wet weight min^{-1}) was calculated for each 0.5-h period. Means are given ± 1 SE.

The number and location of the feeding sites of individual herons were mapped for each day. Two types of feeding territories were distinguished: (1) undefended territory in the sense of an exclusive area (Pitelka 1959; Schoener 1968); (2) territory in the sense of a mutually exclusive area with rigidly defined boundaries and the presence of defence that keeps out rivals (Brown & Orians 1970).

RESULTS

Feeding Sites

Adults

Five adult herons (numbers 0, 5, 7, 8, X) used the estuary as a feeding area (Fig. 1, Table I). Two birds (5, X) occupied undefended territories; another bird (7) occupied a defended territory and also shared a larger feeding area with the non-territorial estuary users (0, 8). When the estuary was unsuitable for fishing (because of the state of the tide) the birds gathered at a roost or, with the exception of bird 7, fished at a stream. There they appeared to defend their territories. Heron 7 fished regularly at night under the light of a road lamp, where a small outlet of a pond reaches a mudflat on the edge of its territory.

Adults 3, 6 and 9 always fished at a stream and never switched to the estuary.

Juveniles

All three juvenile herons appeared to be non-territorial. Birds 1 and 2 fed exclusively in a stream using the feeding territories of adults 6, 8 and 9, but were chased off by these adults as soon as they were detected. One juvenile was actually killed by adult 9 during the course of a territorial interaction. Juvenile 4 had a feeding site at the outflow of the Foveran Burn into the estuary. There, it too was

Table I. Degree of territoriality of individuals* at their feeding sites

	Adults			Juveniles (non-territorial)
	Non-territorial	Undefended territory	Defended territory	
Stream			0, 3, 5, 6, 8, 9	1, 2
Estuary	0, 8	X, 5	7	4

* Birds 0-9 and the unmarked adult, X.

able to fish at night under the light of a road lamp. In addition to this, it shared a communal estuarine feeding area at the Insches with adults.

Feeding Rates

Four individuals, 0, 4, 7 and 8, were observed at their feeding sites in the estuary (Fig. 1) for a total of 36.5 h. Their feeding rate depended on the state of the tide (Fig. 2). If the time of low tide is taken as zero, their feeding rate was 0.0 g min⁻¹ for each 0.5-h period, 2.5 h or more before low tide. Feeding rates then gradually increased to a peak of 1.89 g min⁻¹ at -1 h. Over low tide they dropped to 1.1 g min⁻¹, then fell further between +0.5 h and +2 h to 0.27 g min⁻¹, finally dropping to zero at +2 h to +3 h. Birds were never seen fishing on the estuary more than 3 h before and 3 h after low tide. No correlation was found between time of day and feeding rate. Similarly, feeding rates were not related to changes in the low water mark, even though feeding sites became more exposed on spring than on neap tides. It was not possible to ascertain the effects of spring and neap tides on the duration of food availability since the tidal range is affected by many other factors including wind and air pressure.

The four adult herons, 3, 6, 8 and 9, feeding at the streams had an average feeding rate of 0.58 g min⁻¹ (Fig. 2; pooled data for 30.5 h observation). The rate of food intake did not differ significantly between the two streams or between individuals at streams and was not related to the time of day.

Search Times

Mean search times, like feeding rates, were related to the state of the tide (Fig. 3): they were longer than 30 min -2 h before low tide, dropped to 16 min at -1 h, and then fell to 7 min between

-1 h and low tide. After low tide, mean search times were 9 min in the first 0.5-h period and then increased rapidly to 22 min in the following 0.5-h period. After this they were, on average, longer than 30 min.

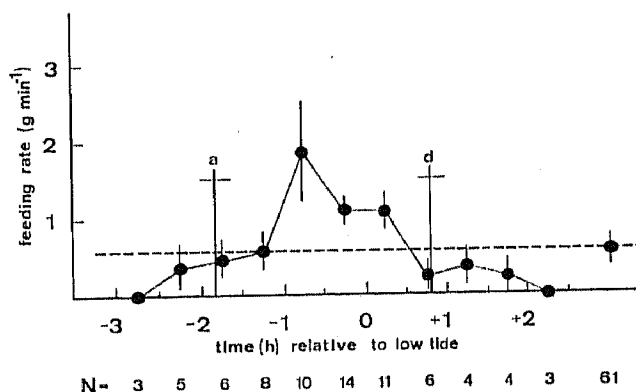


Figure 2. Pooled data of feeding rates in relation to low tide (low tide=0) of herons 0, 4, 7, 8 (solid line) feeding in the Insches area of the Ythan estuary and 0, 3, 6, 8, 9 (broken line) feeding at the streams. Mean (± 1 SE) feeding rates are given as g min⁻¹ in 0.5-h periods. Time of arrival (a) on the estuary and departure (d) from the estuary are indicated.

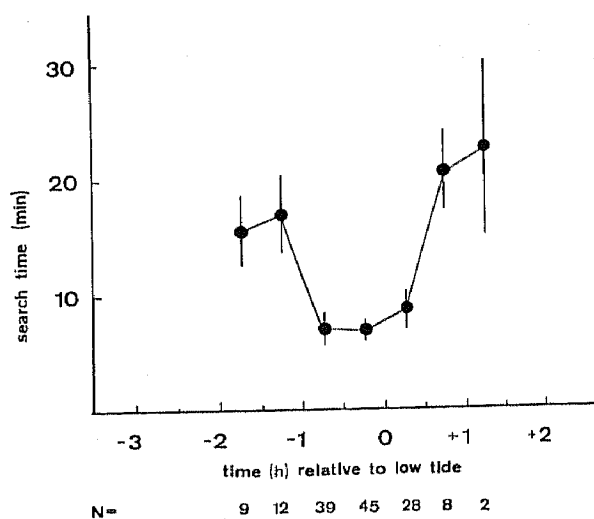


Figure 3. Mean (± 1 SE) search times per 0.5-h period at the Insches area of the estuary in relation to low tide.

Mean search times in the estuary ($\bar{X} = 11.7 \pm 0.8$ min) were significantly shorter than those in the streams ($\bar{X} = 36.0 \pm 0.4$ min; Mann-Whitney *U*-test, $z = 4.9$, $P < 0.0001$, $N = 183$).

Number of Birds

Changes in the number of herons present in the Insches area of the estuary in relation to low tide are given in Fig. 4. The first heron to arrive at its feeding site in the Insches area was always the territorial bird 7, the only bird that fed exclusively in the estuary. The number of herons started to increase at -2 h and reached a peak between -0.5 h and low tide. Then numbers dropped almost linearly and there were no herons left at $+2$ h.

Switching Behaviour between Stream and Estuary

Herons which feed in both stream and estuary are faced with the problem of optimal time allocation in the two patches. One patch, the stream, provides a constant low reward rate. The other, the estuary, provides a variable reward rate, determined by the tidal cycle. In this situation, the strategy with the highest food reward was to arrive in the estuary when the expected feeding rate in the estuary exceeded that in the stream, and to leave when the intake rate fell below that of the stream.

The switchers arrived, on average, 1.8 h (± 0.16) before low tide, i.e. 24 min before the mean feeding rate in both streams and estuary was equal. They moved from the estuary back to the streams at 0.8 h (± 0.16) after low tide. This was 15 min later than the 'optimal' switching time, when the mean feeding rate in both streams and estuary was equal. Individuals which moved between estuary and streams (switchers) improved their feeding performance over this time period from 0.58 g min^{-1} to 1.1 g min^{-1} , an increase of 53%! The mean feeding

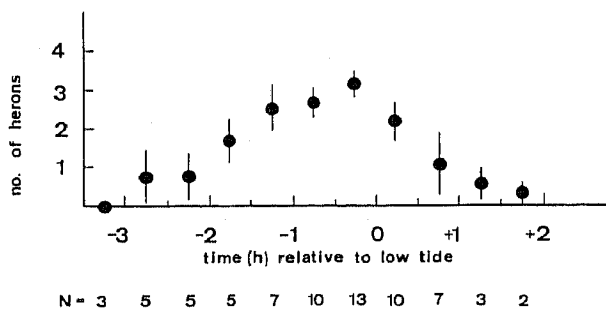


Figure 4. Mean (± 1 SE) number of herons per 0.5-h period at the Insches area of the estuary in relation to low tide.

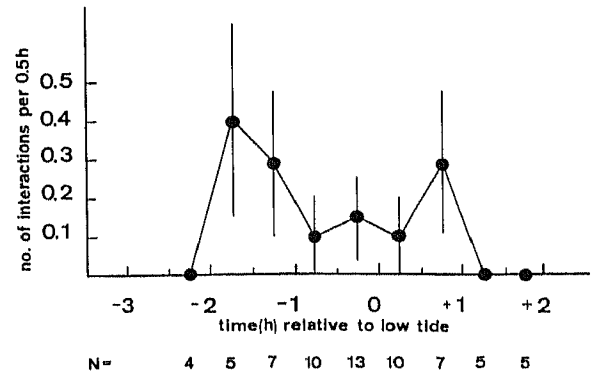


Figure 5. Mean (± 1 SE) number of interactions per 0.5-h period at the Insches area in relation to low tide.

rate of herons in the estuary was significantly higher (Mann-Whitney *U*-test, $z = 3.485$, $P < 0.001$) than the mean feeding rate of herons in the streams.

Differences in Body Weights between Switchers and Non-switchers

Herons which fed in both streams and estuary (switchers) were, in the middle of the study period, significantly heavier (*t*-test, $t = 6.51$, $P < 0.001$, $df = 7$) ($\bar{X} = 1993$ g ± 53) than those which fed exclusively in streams (non-switchers) ($\bar{X} = 1378$ g ± 72).

Intraspecific Interactions

Two types of intraspecific interaction were common. Territorial interactions occurred when one heron intruded into another's feeding territory and was chased off. Feeding interactions took place when an individual was chased after it had caught a large fish.

The mean rate of interaction was low, but followed a distinctive pattern in relation to the state of the tide (Fig. 5). Interaction rates were positively correlated with the mean search times ($r = 0.813$, $P < 0.05$, $df = 4$) and negatively correlated with the mean feeding rates ($r = 0.825$, $P < 0.05$, $df = 4$) for each 0.5-h period.

DISCUSSION

Patch Switching

To investigate the benefits of the alternative feeding strategies of herons, I will consider their

food intake in relation to their daily food requirements. Precise figures of a heron's daily food requirements are not available, but equations for existence metabolism of non-passerine birds are given in the literature (Kendeigh et al. 1977). This differs little from Kushlan's general equation (1978) which gives the daily food requirement as 268 g of fish per day for a heron weighing 1500 g.

A heron feeding exclusively in a stream with a feeding rate of 0.58 g min^{-1} has to fish for 7.7 h per day to obtain 268 g. A heron which switches to the estuary for 2.6 h per day catches an average of 172 g on the estuary and a further 177 g in the remaining 5.1 h at a stream, making a daily total of 349 g. This represents 30% more food per day for a switcher compared to a non-switcher. An exclusively estuarine bird such as number 7, fishing during the 4.5 h over low tide when food is available in the estuary, has a mean feeding rate of 0.8 g min^{-1} . This is lower than the 1.1 g min^{-1} achieved by switchers during their shorter stay of 2.6 h when more food is available. The total amount of food caught by the estuarine bird is 216 g per day, but it might make this up to the 268 g minimum daily requirement by fishing at night under the road lamp. A 1-h observation of bird 7 at night revealed a feeding rate of 2.4 g min^{-1} with very short search times. Prey items were small fishes that congregated under the light of the road lamp.

The significantly higher body weight of the switchers might arise from a benefit associated with switching behaviour, but it is impossible to separate cause and effect, e.g. switchers may have been heavier than non-switchers before taking up their winter feeding sites. For herons there is no significant difference in body weights between the sexes (Cramp 1977).

Obviously, switching between stream and estuary is the most rewarding strategy. Why then do not all birds switch between the two food sources? An analysis of the variances of daily food reward showed no significant difference between stream and estuary, which would be a necessary prerequisite for testing risk proneness in relation to foraging preferences. Preference for a variable food source (risk proneness) has been shown in other species to be associated with a negative expected daily energy budget (Caraco et al. 1980; Caraco 1981). The chosen time scale for comparing these variances might not be very relevant for large birds, such as herons. They might be able to sustain much longer periods of hunger than small birds.

In terms of Fretwell's (1972) theory of habitat distribution, the estuary might represent the better habitat and, in autumn, be filled up with herons first. Any additional arrivers might then be excluded by the estuarine herons and thereafter settle in the streams with lower feeding interaction rates between birds.

Territorial Behaviour

Three out of four birds at the Insches area of the estuary were non-territorial, whereas all adults at the streams defended their feeding sites vigorously. Long term benefits associated with these territories can be excluded since all territories were given up at the start of the breeding season and many birds dispersed after the winter and bred elsewhere.

It is more likely that patterns of food availability are the crucial factor leading to differences in social behaviour at the feeding site. Three aspects of food availability are considered.

First, the rate of food renewal is likely to be very different between stream and estuary. Renewal times are in the order of 12.5 h (one tide) in the estuary and probably days, or even weeks, at the streams. Renewal time to reach a certain profitability in the estuary is given by the tidal cycle, whereas renewal time at streams might be shortened if an individual prevents conspecifics from exploiting its territory.

Second, the time available for feeding in the estuary is very short (2–3 h per tide), whereas streams provide food throughout the whole day at a steady rate. This brief period of food availability in the estuary might explain the non-territorial behaviour of most of the herons there. Probably the benefits of spacing behaviour, e.g. higher feeding rates, do not offset the costs of territorial defence e.g. time or prey disturbance (Davies & Green 1976). The finding that interaction rates were low when feeding rates were high and search times short supports this hypothesis. Unlike other estuarine herons, the individual which defended a territory (7) fed in the estuary at night as well as during the day. Thus, for him, territorial defence might have paid over a longer time period.

Third, unpredictability of resources in time and space is associated with non-territorial behaviour in many other species (Crook 1965; Kruuk 1972; Davies 1976). In the heron's case however, there was no significant difference between the variances of daily food intake for estuary and streams and

therefore this cannot explain the difference in territorial behaviour between streams and estuary.

ACKNOWLEDGMENTS

I thank Professor G. M. Dunnet and Dr I. J. Patterson who provided facilities, encouragement and constructive criticism throughout the study. I am also very grateful to all other staff and students at Culterty Field Station (University of Aberdeen) for useful discussions during the project, and to G. M. Dunnet, I. J. Patterson, Mick Marquiss, Hilary Dow and Graham Pierce who commented on the manuscript. Two anonymous referees made very useful suggestions. I thank C. Thomson for his ingenious trapping devices. This study was financed by a grant from The Swiss National Science Foundation.

REFERENCES

- Best, L. S. & Bierzychudek, P. 1982. Pollinator foraging in foxglove *Digitalis purpurea*: a test of a new model. *Evolution*, **36**, 70–79.
- Brown, J. L. & Orians, G. H. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.*, **1**, 239–262.
- Caraco, T. 1981. Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behav. Ecol. Sociobiol.*, **8**, 213–217.
- Caraco, T., Martindale, S. & Whittam, T. S. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Anim. Behav.*, **28**, 820–830.
- Cramp, S. 1977. *The Birds of the Western Palearctic*. Oxford: Oxford University Press.
- Crook, J. H. 1965. The adaptive significance of avian social organisation. *Symp. Zool. Soc. Lond.*, **14**, 181–218.
- Davies, N. B. 1976. Food, flocking and territorial behaviour of the pied wagtail *Motacilla alba* in winter. *J. Anim. Ecol.*, **45**, 235–253.
- Davies, N. B. & Green, R. E. 1976. The development and ecological significance of feeding techniques in the reed warbler *Acrocephalus scirpaceus*. *Anim. Behav.*, **24**, 213–225.
- Davies, N. B. & Houston, A. I. 1981. Owners and satellites: the economics of territorial defence in the pied wagtail *Motacilla alba*. *J. Anim. Ecol.*, **50**, 157–180.
- Fretwell, S. D. 1972. *Populations in a Seasonal Environment*. Princeton: Princeton University Press.
- Harris, M. P. & Hislop, J. R. G. 1978. The food of young puffins (*Fratercula arctica*). *J. Zool., Lond.*, **185**, 213–236.
- Hodges, C. M. 1981. Optimal foraging in bumblebees *Bombus appositus*: hunting by expectation. *Anim. Behav.*, **29**, 1166–1171.
- Kendeigh, S. C., Dol'nik, V. R. & Gavrilov, V. M. 1977. Avian energetics. In: *Granivorous Birds in Ecosystems* (Ed. by J. Pinowski & S. C. Kendeigh), pp. 127–204. Cambridge: Cambridge University Press.
- Krebs, J. R., Stephens, D. W. & Sutherland, W. J. 1984. Perspectives in optimal foraging. In: *Perspectives In Ornithology* (Ed. by G. A. Clark), pp. 165–221. Cambridge: Cambridge University Press.
- Kruuk, H. 1972. *The Spotted Hyena*. Chicago & London: University of Chicago Press.
- Kushlan, J. A. 1978. Feeding ecology of wading birds. In: *Wading Birds* (Ed. by A. Sprunt, J. C. Ogden & S. Winckler), pp. 249–297. New York: National Audubon Society.
- Pitelka, F. A. 1959. Numbers, breeding schedule and territoriality in pectoral sandpipers in northern Alaska. *Condor*, **1**, 233–364.
- Quinney, T. E. & Smith, P. C. 1980. Comparative foraging behaviour and efficiency of adult and juvenile great blue herons. *Can. J. Zool.*, **58**, 1168–1173.
- Recher, H. F. & Recher, J. A. 1969. Comparative foraging efficiency of adult and immature little blue herons *Florida caerulea*. *Anim. Behav.*, **17**, 320–322.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. *Ecology*, **49**, 123–141.
- Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Rucker, B. W. 1939. *The Handbook of British Birds: Vol. 3*. London: H. F. & G. Witherby.

(Received 8 November 1984; revised 10 May 1985; MS. number: 2621)