JOURNAL OF AVIAN BIOLOGY 32: 345–350. Copenhagen 2001

Switching to a feeding method that obstructs vision increases head-up vigilance in dabbling ducks

Matthieu Guillemain, Patrick Duncan and Herve Fritz

Guillemain, M., Duncan, P. and Fritz, H. 2001. Switching to a feeding method that obstructs vision increases head-up vigilance in dabbling ducks. – J. Avian Biol. 32: 345–350.

A major assumption in most models of foraging is that feeding and vigilance are mutually exclusive. A recent experimental study challenged this hypothesis and demonstrated that birds are able to detect predators while pecking seeds on the ground (head-down vigilance). Experimental obstruction of head-down vigilance makes birds increase head-up vigilance (i.e. the classical overt vigilance posture). For many foragers in the wild, visibility varies between habitats and foraging methods. We compared the vigilance of Teal *Anas crecca* and Shoveler *Anas clypeata* when foraging with their eyes above the water surface (shallow feeding, only the bill submerged) and when foraging with their eyes underwater (deep feeding, head and neck underwater, or upending), at three wintering sites in western France. Birds of both species spent less time in head-up vigilance during shallow foraging than during deep foraging, with no significant difference between sites, which suggests that they are capable of some vigilance during shallow foraging. During deep foraging, the time spent vigilant increased because the frequency of scans was much higher, while scan length decreased. However, these differences could have resulted from variations in the availability of food at different depths. In an experiment where the food availability was constant, we observed the same pattern, with a higher frequency of scans during deep foraging. This study therefore provides strong support for the idea that vigilance and foraging are not always mutually exclusive and shows that switching between searching methods can cause vigilance time – and, as a consequence, loss of feeding time – to vary. This should be taken into account in future field and experimental studies of the trade-off animals make between vigilance and feeding.

M. Guillemain, P. Duncan and H. Fritz, Centre d'Etudes Biologiques de Chize, CNRS-UPR 1934, F-79360 Beauvoir-sur-Niort, France. Present address of M. Guillemain: Centre for Ecology and Hydrology, Winfrith Technology Centre, Winfrith Newburgh, Dorchester, U.K. DT2 8ZD. E-mail: magu@ceh.ac.uk

Most studies of compromises made by animals in allocating time to feeding or vigilance are based on the assumption that these activities are mutually exclusive, i.e. that animals cannot be vigilant while feeding (e.g. Bertram 1980, Hart and Lendrem 1984, Lima and Dill 1990, McNamara and Houston 1992). A recent study (Lima and Bednekoff 1999) challenged this assumption and showed that Dark-eyed Juncos *Junco hyemalis* pecking seeds on the ground were capable of detecting a predator when they were not in a position of head-up vigilance, suggesting that some vigilance is possible during feeding bouts. Lima and Bednekoff experimentally reduced the visibility around feeding birds (i.e. put them in a situation where head-down vigilance was impossible): this made the birds compensate by increasing time spent in head-up vigilance. A similar result had been obtained previously by Arentz and Leger (1997), who experimentally obstructed the visibility for foraging ground squirrels *Spermophilus tridecemlineatus*.

Reduced visibility during feeding also occurs naturally (Metcalfe 1984, Lima 1987, Lazarus and Symonds 1992, Bekoff 1995): in some species, switching between feeding methods causes variation in the extent to which vision is obstructed. This is the case in dabbling ducks feeding on water bodies: these birds can obtain their food at variable depths and use a wide range of feeding

© JOURNAL OF AVIAN BIOLOGY

methods from grubbing in mud or dabbling, when only the bill is submerged, to upending in deep water (Thomas 1982). These methods fall into two categories with respect to visibility: (1) shallow feeding where the eyes are above the substrate, which may allow some head-down vigilance (*sensu* Lima and Bednekoff 1999) and (2) deep feeding where the eyes are underwater, a situation in which vigilance and feeding are indeed mutually exclusive. Switching from one method to the other may therefore have consequences for the foraging individuals in terms of predator detection (Pöysä 1987). This adds to the list of confounding factors that may affect individual levels of vigilance (see Elgar 1989 for a review).

The objective of our study was to test whether ducks in the wild increase the time spent in head-up vigilance when they switch from shallow to deep foraging – a strong prediction from the experimental work of Lima and Bednekoff (1999). In addition, we investigated how the temporal structure of vigilance (length and frequency of scans) differs between the two feeding methods. Since any variations observed could be due to differences in food density (Elgar 1989), we also observed birds in an experimental set-up where food availability in different patches was identical, and tested if the birds still increased the time spent vigilant when using feeding methods in which their vision is obstructed.

Methods

Study sites and behavioural observations in the field

We studied the behaviour of Teal *Anas crecca* and Shoveler *A. clypeata* from September 1996 to March 1997 on water bodies ranging from 6.5 to 24 ha in three protected areas in the Marshes of Rochefort, western France: the municipal sewage works at Rochefort (Stepro), the nature reserve of Yves (Yves) and the hunting reserve of the Cabane de Moins at Breuil-Magné (Breuil). Observations took place at each site one day per week between 07:00 and 19:00, for a total of 57 study days. We used focal observations (10 min, Altmann 1974) on feeding individuals chosen by chance; each change in behaviour was recorded on a portable computer that automatically incorporated time to the nearest 0.5 s. Data were recorded by the same observers throughout the study. Analyses were restricted to the temporal organisation of behaviour during foraging, i.e. successions of feeding bouts and interruptions where birds were standing or swimming in an upright position (head-up vigilance bouts, hereafter scans). We considered foraging to be terminated by any activity other than feeding or scanning (Cézilly and Brun 1989) and, because scans were usually very short (i.e. 0.5 to 3 s), by exceptional scans >10 s. Foraging method was classified as shallow or deep (i.e. shallow when the bird had its eyes above the water surface, deep when the eyes were underwater). A total of 124 focal observations were made on Teal and 71 on Shoveler. Most birds used only one feeding method during a focal session and were therefore classified as shallow or deep feeding. We calculated the mean length of feeding bouts and scans (in seconds), the frequency of scans (no. $\min^{-1}$) and the percentage of time spent overtly vigilant during each foraging session. For each focal bird we then calculated the mean values of the parameters over all foraging sessions, which were weighted equally. Thirty out of 195 focal birds switched between the two types of feeding; we analysed the data from these individuals separately (see below).

As the ducks were not individually marked, we may have sampled the same bird twice. However, this is unlikely to have occurred frequently. Hence, we do not believe that this constitutes an important problem for the statistical analyses in view of the fact that (1) the turn-over of individuals can be rapid in wintering dabbling duck populations (Pradel et al. 1997), (2) the number of focal observations per species and site relative to the number of individuals present (mean numbers >100, except for Shoveler at Breuil: 93 individuals), (3) the small number of focal observations per species per day (1–7), and (4) the duration of the study (6 months).

Confounding factors

Group size, distance to nearest neighbour and the frequency of predator occurrences are likely to affect vigilance levels of individuals (e.g. Elgar 1989), thus confounding the effect of search method. Whenever possible, we noted the nearest neighbour distances (in duck-lengths) at the beginning and end of each session, and the feeding group size, i.e. the number of birds feeding together (<10 duck-lengths apart). We also monitored the frequency of fly-overs by large raptors (mostly Marsh Harriers *Circus aeruginosus*) for each three-hour period of the day during which a focal observation was carried out. This was used as an index of predation risk (Fritz et al. 2000).

Previous studies have shown that the foraging methods of dabbling ducks in western France may vary during the course of the day, with more shallow-foraging in early morning and late afternoon than during midday (Guillemain et al. 2000a), and across months during a winter (Guillemain 2000). Vigilance levels of dabbling ducks may also vary over the winter because of changing energy requirements (Gauthier-Clerc et al. 1998). These variables may therefore also confound the relationship between vigilance level and search method.

We used backwards stepwise General Linear Model procedures (GLM, SAS Institute 1990) to quantify the respective roles that Method (shallow or deep foraging), Species (Teal or Shoveler), Site (Stepro, Yves or Breuil), Time (i.e. before 11:00; 11:00–14:59; after 15:00) and Period (i.e. early [September–November] or late winter [December–15 March]) (as factors) and Group size, Neighbour distance and the Frequency of raptor fly-overs (as covariates), play in explaining vigilance patterns of foraging ducks (i.e. arcsine-transformed proportion of time spent in head-up vigilance, length and frequency of scans). The interaction between Species and the other factors and covariates was also included in the analyses to test for differential effects on Teal and Shoveler. Variations in feeding bout length were not analysed to prevent redundancy, since feeding bout length was closely related to the frequency of scans ($Y = 0.54X^{-1.13}$, $R^2 = 0.93$, df = 223). Only those individuals that used only one feeding method were considered in the analysis.

The 30 birds that used both shallow and deep foraging within a focal observation offered the opportunity to control for individual effects on the time spent in head-up vigilance. After ensuring that vigilance parameters during shallow and deep foraging by these individuals did not differ from those of ducks using either of these feeding methods (Student's t-tests, all $P > 0.05$), we used paired t-tests to compare shallow and deep foraging by these individuals for each species separately.

Laboratory experiments

Besides changes in vigilance behaviour, the main factor that may affect the temporal organisation of feeding bouts and scans by ducks using different foraging methods is the density of food at different depths. In order to test for this potentially confounding factor, we used behavioural data (i.e. feeding bout length and the frequency of head-up scans) from a laboratory experiment in another study, conducted to assess the food intake rate of Mallards *Anas platyrhynchos* feeding at several different depths (Guillemain et al. 2000b). Mallards were chosen because this species is easy to keep in captivity. Between tests, birds used in the experiments were kept outdoors in a 400 m^2 fenced area with a net-roof. Tests were performed in a 15 m^2 enclosure comprising a 2 m^2 tank where ducks were offered 100 g of wheat at a depth of either 5 cm (shallow feeding, eyes above the surface of water) or 35 cm (deep feeding, eyes under water) spread evenly over the bottom of the tank and covered by a thin layer of sand. The experimental enclosure was part of the 400 m^2 fenced area in which ducks were kept, to prevent them from being stressed by a new environment during the experiments. Ducks were safe from predation because of the fence and the net but, although this did not happen during the experiments, they were highly vigilant when Common Buzzards *Buteo buteo* or Black Kites *Milvus migrans* flew over the area. Groups of three birds were used for each test, randomly chosen from a set of nine. Five tests were conducted; the birds were observed for three hours between 09:00 and 12:00. On average, these experiments provided six measures of the duration of feeding bouts and three measures of scan frequency for each individual. A mean value was calculated for each bird and feeding depth (except for one bird that did not feed in shallow water in one test). Wilcoxon paired tests were used to compare these means within individuals since all Mallards could be individually identified.

Results

Feeding in the field

Only Species and Method had significant effects on the proportion of time spent in head-up vigilance by focal birds, with Method explaining the largest part of the variance (Table 1): deep-feeding ducks spent up to twice as much time in head-up vigilance as shallow-feeding ducks, the difference being greater in Shoveler (Fig. 1). Shoveler using the two types of feeding method within a focal session also increased the proportion of time spent in head-up vigilance when they switched from shallow to deep foraging (t = 3.59, P = 0.0058; Fig. 2). The same trend was found for Teal, however not significant (t = 1.58, P = 0.1296; Fig. 2).

Variations in scan frequency were best explained by Species and Method, again with a much larger effect of the latter factor (Table 1): the frequency of scans was low in shallow-foraging individuals (Teal: 8.4 scans

Table 1. Effects of foraging method (shallow or deep foraging) on percentage of foraging time spent in head-up vigilance*, scan length and scan frequency. N = 104 focal Teal and 61 focal Shoveler. Only the final models are presented. The significance of the effects was assessed by stepwise backwards GLMs.

	Model	F	df	P
% Time head-up		52.51	2	P < 0.0001
	Feeding method	90.34	1	P < 0.0001
	Species	8.53	1	P = 0.0040
Scan length	Feeding method	11.97	1	P = 0.0007
Scan frequency		224.05	2	P < 0.0001
	Feeding method	407.68	1	P < 0.0001
	Species	21.13	1	P < 0.0001

*Analyses were performed on arcsine-transformed proportions (Sokal and Rohlf 1995).

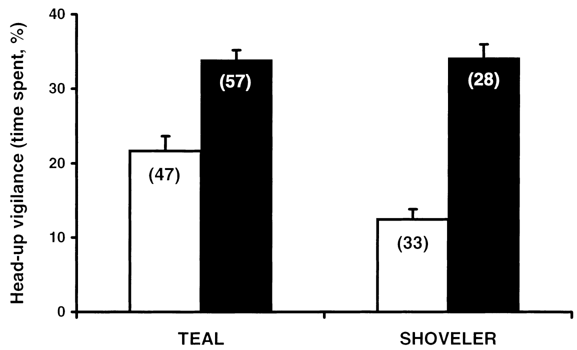

Fig. 1. Time spent in head-up vigilance by shallow- (white) and deep-foraging ducks (black). Columns are means + SE. Sample sizes (the number of focal individuals) are indicated in brackets. See text and Table 1 for statistics.

$min^{-1} \pm 0.6$ SE, N = 47; Shoveler: 6.0 scans $min^{-1} \pm 0.6$ SE, N = 33), and about three times higher in deep-foraging individuals (Teal: 22.2 scans $min^{-1} \pm 0.6$ SE, N = 57; Shoveler: 18.6 scans $min^{-1} \pm 0.6$ SE, N = 28).

Only Method explained a significant part of variations in mean scan length (Table 1): deep-foraging ducks made shorter scans than shallow-foraging ones (1.06 s $\pm$ 0.05 SE, N = 85 and 1.70 s $\pm$ 0.18 SE, N = 80, respectively).

Laboratory experiments

In the experiments, where food availability was the same at both depths, Mallards altered the temporal organisation of behaviour between shallow and deep foraging in a similar way to that of the wild ducks. Deep-feeding birds also had a higher frequency of scans (deep: 12.21 scans $min^{-1} \pm 1.24$ SE, N = 9; shallow: 2.56 scans $min^{-1} \pm 0.21$ SE, N = 8; Z = 2.52, N = 8, P = 0.012), and consequently shorter feeding bouts (deep: 2.3 s $\pm$ 0.1 SE, N = 9; shallow: 22.2 s $\pm$ 1.8 SE, N = 8; Wilcoxon paired test: Z = − 2.66, N = 8, P = 0.008). The short feeding bouts in deep water were not due to the need to breathe, since the nostrils were submerged in shallow-feeding as well as in deep-feeding (water depth 5 cm, bill tip to nostril 4.6 – 5.0 cm, the head being held diagonally). Shallow-feeding birds were able to scan the surrounding area while foraging since their eyes are 7.1–7.6 cm above the tip of the beak.

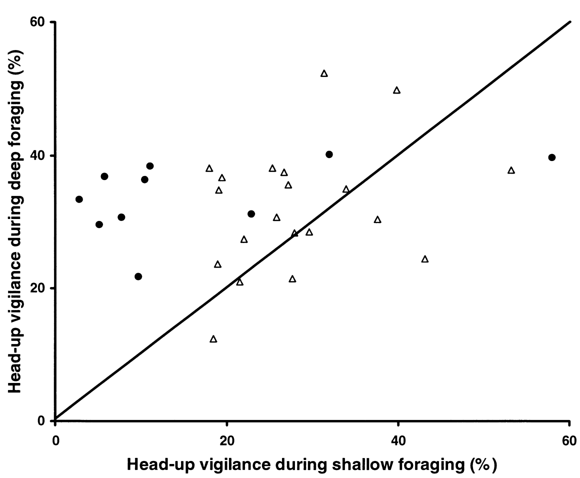

Fig. 2. Time (%) spent in head-up vigilance during shallow (X-axis) and deep foraging (Y-axis) by focal Teal (open triangles) and Shoveler (filled circles) that switched between the two methods. The line is Y = X, i.e. individuals spent the same time in head-up vigilance in the two methods. See text for statistics.

Discussion

Switching to a feeding method that obstructs vision increases head-up vigilance in Teal and Shoveler in the wild: both species spent more time overtly vigilant during feeding sessions when foraging deeply, with their eyes underwater, than when foraging with only the bill in the mud or water.

The fact that ducks increase head-up vigilance when deep-feeding is consistent with shallow-foraging birds performing part of their vigilance in the head-down posture (see also Pöysä 1987). Head-down vigilance should be less costly than head-up scans since it can be combined with foraging. This could help to explain that wintering dabbling ducks use shallow-foraging preferentially when food densities are similar at several depths (Guillemain et al. 2000a, b, see also Thomas 1982).

However, because shallow-feeding ducks interrupt their feeding to scan, both in the field and in laboratory experiments, head-down vigilance is probably less effective. Therefore, ducks may need to maintain a minimum level of head-up vigilance as well. Head-down vigilance may be adequate to observe the departure of congenerics caused by predator approaches, since dabbling ducks have large visual fields (Martin 1986). Head-up vigilance may provide more detailed information about the environment, e.g. allowing birds to detect a predator directly. Moreover, head-up scanning could provide information on congenerics' feeding strategies and their success, allowing birds to adjust their own feeding strategies ('public information', e.g. Valone 1989). It is most unlikely that deep-feeding birds maintain any surveillance while the head is below the water surface, and they are very vulnerable because their bodies are exposed to predators.

Shallow-feeding Teal spent more time in head-up vigilance than Shoveler, while group size, density of ducks and the frequency of fly-overs by harriers had no significant effect. This may be because the risk of predation is greater for Teal: they are smaller than Shoveler and, when foraging by shallow methods, are usually close to the shore, i.e. closer to the terrestrial vegetation regularly patrolled by harriers (Schipper et al. 1975, Fritz et al. 2000), whereas Shoveler generally feed in open water (Nudds and Bowlby 1984). Previous studies on dabbling ducks have shown that individuals closer to the shore had higher levels of vigilance (Lendrem 1983), though scan frequency has also been reported to be high for birds both close to and very far from shores, the frequency being lower for intermediate distances (Pöysä 1994, Gauthier-Clerc et al. 1998). An alternative explanation could be that Shoveler has a complete panoramic vision, while Teal may have a blind area to the rear of the head, as in some other duck species (G. Martin pers. comm.). Given that Teal grub the mud for seeds while holding their heads vertically (Thomas 1982), this behaviour may make it more difficult for them than for Shoveler to detect aerial predators while foraging.

Both Teal and Shoveler in the field, and Mallard in laboratory experiments, increased their vigilance during deep foraging through an increase in scan frequency. In Teal and Shoveler, scans were shorter during deep than during shallow foraging. The way the ducks distributed their vigilance time therefore differed from that of the juncos whose head-down visibility was obstructed in the study of Lima and Bednekoff (1999): juncos increased both the frequency and duration of scans. That the ducks increased vigilance through a higher frequency of head-up scans rather than through longer scans is consistent with a previous experimental study showing that the food intake rate of Mallard was more reduced by an increase in the length than by an increase in the frequency of scans (Fritz et al. in press). The short duration of scans suggests that ducks are able to estimate the level of risk rapidly, whatever their foraging method.

This study provides further evidence that switching to a feeding method which precludes predator detection leads to an increase in head-up vigilance in foraging ducks. These results strengthen the idea that vigilance can sometimes be combined with foraging activities (Lima and Bednekoff 1999). Studies of the trade-off animals make between feeding and anti-predator behaviour, both empirical and modelling, need to take this into account.

Acknowledgements – We thank Ola Olsson, Andy Green, Graham Martin, Vincent Bretagnolle, Francesco Bonadonna and an anonymous referee for useful comments on an earlier version of the manuscript, and also Noël Guillon, Stéphane Guérin, Sylvie Houte and Didier Portron for their help during the field work, and Sandra Blais for help in the laboratory experiments. We thank the Ligue pour la Protection des Oiseaux and the Fédération Départementale des Chasseurs de Charente-Maritime, especially Christophe Boucher, Alain Doumeret and Jacques Brun, for allowing us access to the field sites. This work is part of a research program on wetlands directed by Patrick Duncan and funded by the Centre National de la Recherche Scientifique and the Région Poitou-Charentes. Matthieu Guillemain was supported by a doctoral grant from the Région Poitou-Charentes.

References

Altmann, J. 1974. Observational study of behaviour: sampling methods. – Behaviour 49: 227–267.

Arentz, C. L. and Leger, D. W. 1997. Artificial visual obstruction, antipredator vigilance, and predator detection in the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). – Behaviour 134: 1101–1114.

Bekoff, M. 1995. Vigilance, flock size, and flock geometry: information gathering by Western Evening Grosbeaks (Aves, Fringillidae). – Ethology 99: 150–161.

Bertram, B. C. R. 1980. Vigilance and group size in Ostriches. – Anim. Behav. 28: 278–286.

Cézilly, F. and Brun, B. 1989. Surveillance et picorage chez la tourterrelle rieuse, *Streptopelia risoria*: effets de la présence d'un congénère et de la dispersion des graines. – Behaviour 110: 146–160.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. – Biol. Rev. 64: 13–33.

Fritz, H., Guillemain, M. and Guérin, S. 2000. Changes in the frequency of prospecting fly-overs by marsh harriers *Circus aeruginosus* in relation to short-term fluctuations in dabbling ducks abundance. – Ardea 88: 9–16.

Fritz, H., Guillemain, M. and Durant, D. The cost of vigilance for intake rate in mallard (*Anas platyrhynchos*): an experimental approach, – Ethol. Ecol. Evol. In press.

Gauthier-Clerc, M., Tamisier, A. and Cézilly, F. 1998. Sleep-vigilance trade-off in Green-winged Teals (*Anas crecca crecca*). – Can. J. Zool. 76: 2214–2218.

Guillemain, M. 2000. Le fonctionnement du peuplement de canards des marais de l'Ouest: compromis entre compétition et vigilance dans les stratégies d'alimentation individuelles. – Ph.D. dissertation, University of Paris VI, Paris.

Guillemain, M., Fritz, H. and Guillon, N. 2000a. Foraging behavior and habitat choice of wintering Northern Shoveler in a major wintering quarter in France. – Waterbirds 23: 355–364.

Guillemain, M., Fritz, H. and Blais, S. 2000b. Foraging methods can affect patch choice: an experimental study in Mallard (*Anas platyrhynchos*). – Behav. Proc. 50: 123–129.

Hart, A. and Lendrem, D. W. 1984. Vigilance and scanning patterns in birds. – Anim. Behav. 32: 1216–1224.

Lazarus, J. and Symonds, M. 1992. Contrasting effects of protective and obstructive cover on avian vigilance. – Anim. Behav. 43: 519–521.

Lendrem, D. W. 1983. Sleeping and vigilance in birds. I. Field observations of the Mallard (*Anas platyrhynchos*). – Anim. Behav. 31: 532–538.

Lima, S. L. 1987. Distance to cover, visual obstructions, and vigilance in house sparrows. – Behaviour 102: 231–238.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.

Lima, S. L. and Bednekoff, P. A. 1999. Back to the basics of antipredatory vigilance: can non-vigilant animals detect attack? – Anim. Behav. 58: 537–543.

Martin, G. R. 1986. Total panoramic vision in the mallard duck, *Anas platyrhynchos*. – Vision Res. 26: 1303–1305.

McNamara, J. M. and Houston, A. I. 1992. Evolutionary stable levels of vigilance as a function of group size. – Anim. Behav. 43: 641–658.

Metcalfe, N. B. 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? – Anim. Behav. 32: 981–985.

Nudds, T. D. and Bowlby, J. N. 1984. Predator-prey size relationships in North American dabbling ducks. – Can. J. Zool. 62: 2002–2008.

Pöysä, H. 1987. Feeding-vigilance trade-off in the Teal (*Anas crecca*): effects of feeding method and predation risk. – Behaviour 103: 108–122.

Pöysä, H. 1994. Group foraging, distance to cover and vigilance in the Teal *Anas crecca*. – Anim. Behav. 48: 921–928.

Pradel, R., Rioux, N., Tamisier, A. and Lebreton, J. D. 1997. Individual turnover among wintering Teal in Camargue: a mark-recapture study. – J. Wildl. Manage. 61: 816–821.
SAS Institute. 1990. SAS/STAT User's guide, version 6, 4th edn, Vol 2. – SAS Institute, Cary, USA.
Sokal, R. R. and Rohlf, F. J. 1995. Biometry, 3rd edn. – W.H. Freeman and Cie, New York.
Schipper, W. J. A., Buurma, L. S. and Bossenbroek, P. 1975. Comparative study of hunting behaviour of wintering Hen harrier *Circus cyaneus* and Marsh harrier *Circus aeruginosus*. – Ardea 63: 1–29.
Thomas, G. J. 1982. Autumn and winter feeding ecology of waterfowl at the Ouse Washes, England. – J. Zool. (Lond.) 197: 131–172.
Valone, T. J. 1989. Group foraging, public information, and patch estimation. – Oikos 56: 357–363.

(*Received 3 November 2000*, *revised 28 May 2001*, *accepted 30 May 2001*.)