Ornis Hungarica 2:37-44. 1992

The effects of the patchiness and the nest location on mean flight distance: a model

Z. Barta

Barta, Z. 1992. The effects of the patchiness and the nest location on mean flight distance: a model. - Ornis Hung. 2:37-44.

One of the advantages of colonial breeding may be the enhanced foraging efficiency through the location of colony. In a patchy environment a colonial breeder may experience a shorter distance between the nest and an average food patch than an average dispersed breeder. How are this distance influenced by nest location, and varying patchiness? To develop a model of a predator moving by random walk in a patchy foraging area I found that: (i) the nest location in a bounded area influenced sufficiently the mean flight distance and (ii) the growing patchiness increases this distance.

Z. Barta, Department of Zoology, Kossuth University, Debrecen, Egyetem tér 1., Hungary, H-4010

1. Introduction

Although colonial nesting may have disadvantages, many bird species breed in colonies throughout the world, (Lack 1968). A cost of this behaviour may be high infection rate by ectoparasites (Brown & Brown 1986) or increasing competition for food, for nest materials and for mates (Hoogland & Sherman 1976, Møller 1988).

Coloniality may have some advantages as well. One type of the gains is anti-predator behaviour such as mobbing or early detection of predator (Kenward 1978, Bertram 1980, Brown & Brown 1987). The other main advantage of coloniality may be the increased foraging efficiency (Brown 1988). One of the ways of the efficiency increasing may be the effect of colony location on the mean flight distance from the nest to a food patch as Horn (1968) has argued. He assumed that average individuals who breed in dispersed location over the foraging area could experienced an increased mean patch distance in a patchy environment than those breed in a single location, in a colony. On the basis of this model we should predict that the colony must be situated in the centre of the bounded foraging area. Wittenberger & Dollinger (1984) however, showed out that the acentric location of a colony do not influence the benefit of a colonial breeder over the disperse breeder upt o 60% of acentricity. All Horn (1968), Wittenberger & Dollinger (1984) assumed that the birds know about the location of food and they use all food patches in equal proportion, although the birds do not behave in this way. How do the search and the location of nest influence the mean flight distance? What is the effects of the different degree of patchiness on this distance?

In this paper I try to answer to these questions to develop a model of foraging area and of a search behaviour in this area.

Tab. 1. Parameters of the models

Parameters: Meaning
AF: amount of food in a patch
dtN,i: distance between N (nest) and *i*th squares
E(FP): number of food patch on the area
F: amount of food on the area
fkN,i: probability that random walker arrives first from *N* to *i*th square at *k* time unit
n: total number of squares
pi: probability that *i*th square becomes food patch
Pi: probability that the bird finds a food patch in *i*th time unit
P(food): probability that a square becomes food patch on a homogeneous area
Pi(to i): probability that the bird gets at least once from N to *i*th square
Rf: ratio of food patches
t: maximum searching time
tF: average distance of food patch in time units
tS: average searching time

2. The model

2.1. The model of the foraging area

The foraging area is considered as a two-dimensional surface divided into a grid of equal-sized squares. For each square i, p_i is the probability that square contains food (see the list of parameters in Tab. 1). There is at least one square which has $p_i > 0$ in the foraging area.

A main feature of the area is the number of food patches $\left[E(FP)\right]$ which is equal to the expected value of the number of food patches on the area.

$$E(FP)=\frac{\sum_{k=0}^{n} Pr(x=k)\,k}{\sum_{k=0}^{n} Pr(x=k)} \qquad (1)$$

where n is the total number of squares and $Pr\left(x=k\right)$ is the probability that there are k food patches on the area.

$$Pr(x=k)=\sum_{l=0}^{\binom{n}{k}}\left[\prod_{i=1}^{k} p_i \prod_{i=1}^{n-k}\left(1-p_i\right)\right] \qquad (2)$$

and the indices in the parentheses run so that all kth-class combination of n are arisen.

The area is homogeneous when

$$p_i=p_j=P\left(food\right) \qquad \text{for all } i \text{ and } j, \qquad (3)$$

namely there are no differences among the squares. In this case $E\left(FP\right)$ will equal to the mean of binomial distribution:

$$E'\left(FP\right) = n\ P\left(food\right) \qquad (4)$$

If we divide the number of food patches by the total number of squares we get the ratio of food patches (*Rf*).

$$Rf=\frac{E\left(FP\right)}{n} \qquad 1 \geq Rf > 0 \qquad (5)$$

If the ratio of food patches is great ($Rf \approx 1$), then the food is evenly distributed. On the other hand its small value ($Rf << 1$) shows us that the food is clumped.

A food patch contains the following amount of food (*AF*) in average:

$$AF=\frac{F}{Rf\ n} \qquad (6)$$

where F is the total amount of food on the area.

2.2. Random foraging of single predator

In this case the predator has no information about the location of food, so its foraging path is a random walk. No previous events influence the next step of the predator. Since the bird has no memory the process can be represented by a Markov chain. To define the process we have to give its matrix of transition probability which contains the probability of moving from one square to another. A normal element of this matrix is the following:

$$P_{ij} = \begin{cases} 0.25\left(1-p_i\right) & \text{if } i\text{th and } j\text{th squares are neighbouring} \\ p_i & \text{if } i=j \\ 0 & \text{otherwise} \end{cases} \qquad (7)$$

On the basis of this model the bird remains the ith square if it has found a food patch there, otherwise it moves to each of the neighbouring squares with an equal probability. The process was assumed to be reflection. From this matrix we can determine the probability of $f^k{}_{N,i}$ which gives us the chance a bird would be first in ith square at kth time unit if it was in N (nest) square when k equalled to 0 (for details see Karlin & Taylor 1975).

To sum $f^k{}_{N,i}$ up by k we can calculate the probability that the bird gets at least once from N to $i$ith square.

$$P_i\left(to\, i\right) = \sum_{k=0}^{t} f^k{}_{N,i} \qquad (8)$$

where t is the maximum time of search, for example one day.

The average distance of food patch (t_F) is an important feature of the movement of a what Orians & Pearson (1979) call 'central place' forager. We assume that it is equal to the means of distance of each square weighted by P_i(to i) and p_i. (The distances are in time unit.)

$$t_F = \frac{\sum_{i=1}^{n} P_i\left(to\, i\right) p_i d^t{}_{N,i}}{\sum_{i=1}^{n} P_i\left(to\, i\right) p_i} \qquad (9)$$

For homogeneous area:

$$t_F' = \frac{\sum_{i=1}^{n} P_i\left(to\, i\right) d^t{}_{N,i}}{\sum_{i=1}^{n} P_i\left(to\, i\right)} \qquad (10)$$

where $d^t{}_{N,i}$ is the distance of $i$ith square from N in time unit.

A significant parameter of predator's foraging is also the average time of food finding (or searching time t_S). Let this time equal to the mean of time of random steps at the end of which the bird finds a food patch. But it is not certain that a bird finds food in under t time units, so we must weight this mean by the inverse of probability that the bird find at least one food patch in t time unit.

$$t_S = \frac{\sum_{j=0}^{t} j\bar{P}_j \prod_{i=0}^{j-1}\left(1-\bar{P}_i\right)}{\sum_{j=0}^{t} \bar{P}_j \prod_{j=0}^{j-1}\left(1-\bar{P}_i\right)} \; \frac{1}{1-\prod_{i=0}^{t}\left(1-\bar{P}_i\right)} \qquad (11)$$

where $\bar{P}_i$ is the probability that the bird finds a food patch in i th time unit.

The expression of $\bar{P}_j \prod \left(1-\bar{P}_i\right)$ gives the probability that the bird first finds food in time unit j.

Let $\bar{P}_j$ equal the mean of probability of p_i weighted by probability of the first visit.

$$\bar{P}_j = \frac{\sum_{1=1}^{n} f^j{}_{N,i} p_i}{\sum_{i=1}^{n} f^j{}_{N,i}} \qquad j >= 1 \qquad (12)$$

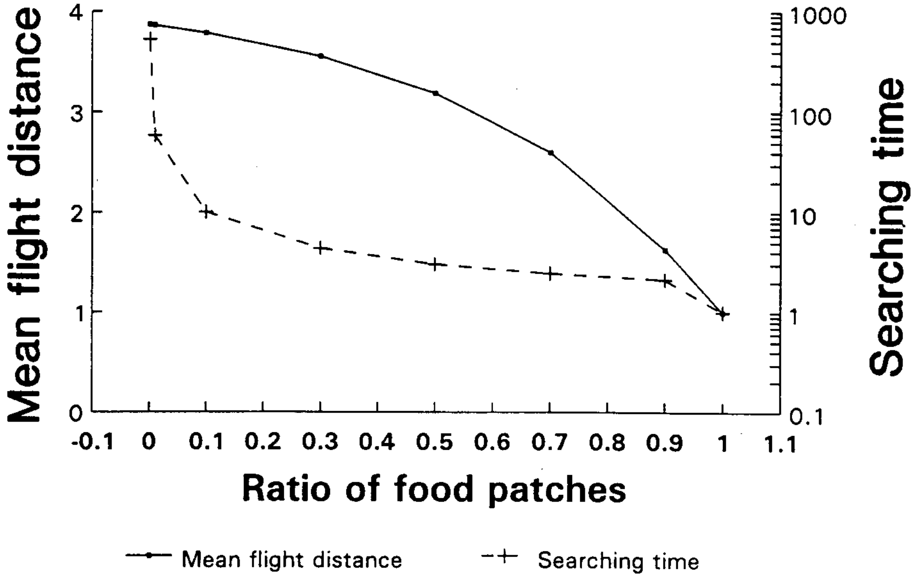

Fig. 1. The average distance of food patch from the nest and searching time, when ratio of food patches was manipulated from $1-10^{-6}$ (evenly distributed) to 0.001 (clumped). Area size was 9 x 9 squares and the nest was in the centre of the area. The maximum searching time was 30 units.

where $f^{j}{}_{N,i}$ is determined from a transition probability matrix of a same-sized area which has no square with $p_i > 0$.

For an homogeneous area equations (11) and (12) become the following:

$$\overline{P'}_j = P(food) \quad \text{for all } j \qquad (13)$$

and

$$t_S = \frac{\sum_{j=0}^{t} j\bar{P}_j \left(1-\bar{P}_j\right)^{j-1}}{\sum_{j=0}^{t} \bar{P}_j \left(1-\bar{P}_j\right)^{j-1}} \frac{1}{1-\left(1-\bar{P}_j\right)^{t}} \qquad (14)$$

3. Results

On the basis of the model, I determined the parameters of random walk on a homogeneous area sized 9 x 9 squares under different ratios of food patches (Fig. 1.). The maximum searching time was 30 units.

When the ratio of food patches is decreased the average distance of food patch from the nest (t_F) is increased (Fig. 1.). When the food is evenly distributed the simulated bird used the squares near the nest (Fig. 2a). On the other hand when food is clumped it exploits more frequently the farther parts of the area (Fig. 2b). The searching time (t_S) is also increased strongly (Fig. 1).

To study the effects of nesting place on the predator's movement, I changed the location of the nest – as showed by Fig. 3. – on a homogeneous area where the distribution of food was clumped ($Rf = 0.001$) and the maximum searching time was 30 units. The distance of an average food patch from the nest (t_F) was first decreased then increased when the nest was moved from the centre of the area to the edge (Tab. 2). The distance

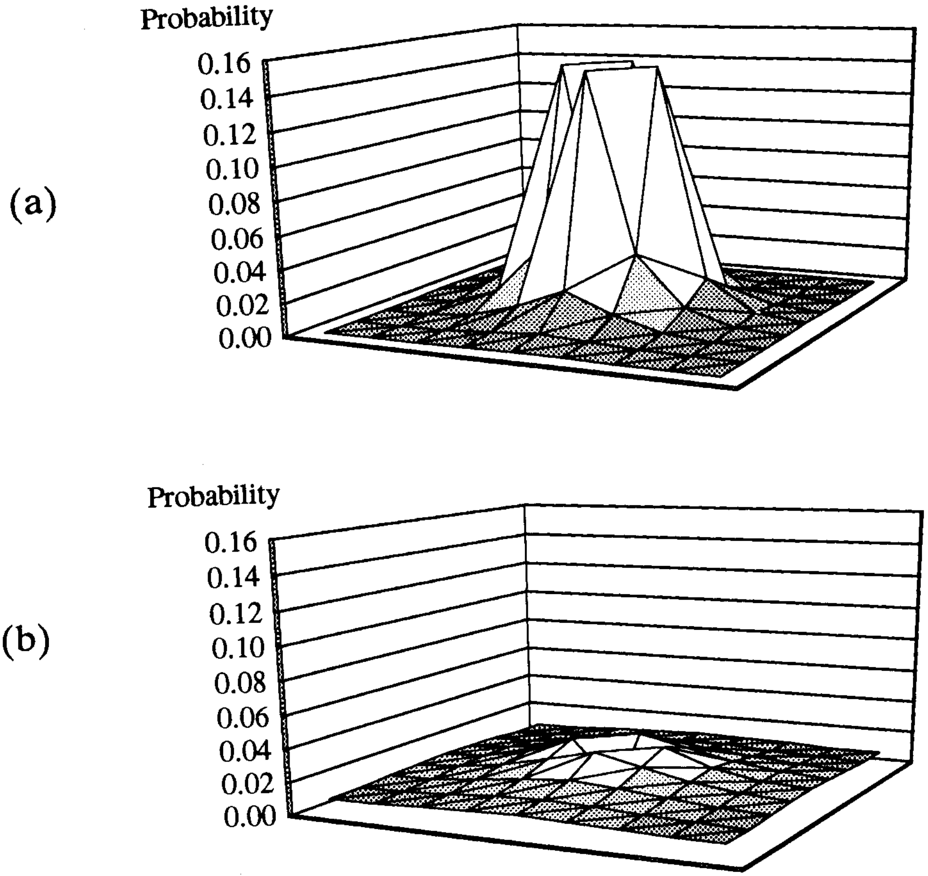

Fig. 2. Probabilities of at least once getting. The basis of figures is the area, and the surface represents the probabilities. The nest is in the centre of the area. (a) Food is evenly distributed, ratio of food patches equals to 0.9; (b) Food is very clumped, ratio of food patches is 0.001.

was the smallest when the nest was in the middle position, although the unweigthed mean of distance of squares $(d^{t}_{N,i}/n)$ was greater than in the case of the nest in the centre (Fig. 4a and 4b). It may be that the bird used the closer squares more frequently because of the nearness of edge of the area. When the nest was on the edge, the unweigthed mean of distance of squares (see above) was greatly increased and the bird could not use many near squares because of the location of nest, so the average distance of food patch (t_F) was increased too (Fig. 4c).

Furthermore I investigated the movement of a predator on an heterogeneous area. On this area all squares had a $p_i = 0.001$ except of one which had a $p_i = 0.8$, so there is a stationary food patch in the area. This stationary patch was further from the nest. The maximum

Tab. 2. The average distance of food patch and the unweighted mean distance of squares from the nest, when the nest was placed in the centre, in a middle position and on the edge. (See also Fig. 3.). Area size was 9 x 9 squares and the food was clumped (Rf=0.001). The maximum searching time was 30 units.

Place of the nest	Distance of food patch from the nest	Unweighted distance of squares from the nest
centre	3.865	360
middle	3.715	396
edge	3.992	504

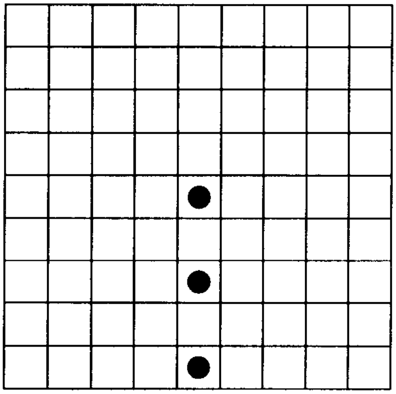

Fig. 3. The nest site in three investigated cases, the dots represent the nests. In baseline case, the nest is in the centre.

searching time was 30 and the nest was in the centre of the area. The searching time (t_S) decreased strongly compared to its value on a homogeneous area where all squares had a $p_i = 0.001$ (Tab. 3). On the other hand the average distance of food patches (t_F) was increased. The ratio of food patches (Rf) on this area was also greater than on the similar homogeneous area.

4. Discussion

To improve a model of foraging bird in a patchy environment in this paper I investigated the effects of patchiness and nest location on the mean flight distance in a bounded foraging area.

With decreasing patchiness the mean flight distance increased from which we may conclude that birds living in a patchy environment may collect and carry to their nest more food than those living in an even environment. On this basis we may expect that species foraging on clumped food has relatively larger bill or stomach compared to a relative species at evenly distributed food.

The location of nest influences strongly the mean patch-nest distance. Surprisingly a nest placed close but not on the edge of the area is the best for a breeder from the viewpoint of mean flight distance. This result may explain why the colonies are not located in the centre of the foraging area (Wittenberger & Hunt 1985). The insufficiency of my model is that it does not account the competition for food so it cannot

Tab. 3. The effects of a stable food patch of hetergeneous area on the predator's movement compared a homogeneous area. All squares have p_i=0.001 except of one which has p_i=0.8 in the heterogeneous area. On the other hand in the homogeneous area all squares have p_i=0.001. Both area size were 9 x 9 squares and the nest was in the centre of the both area. The maximum searching time was 30 units.

Area	Distance of food patch from nest	Searching time	Ratio of food patchess
heterogenous	4.832	68.749	0.0109
homogenous	3.865	521.662	0.0010

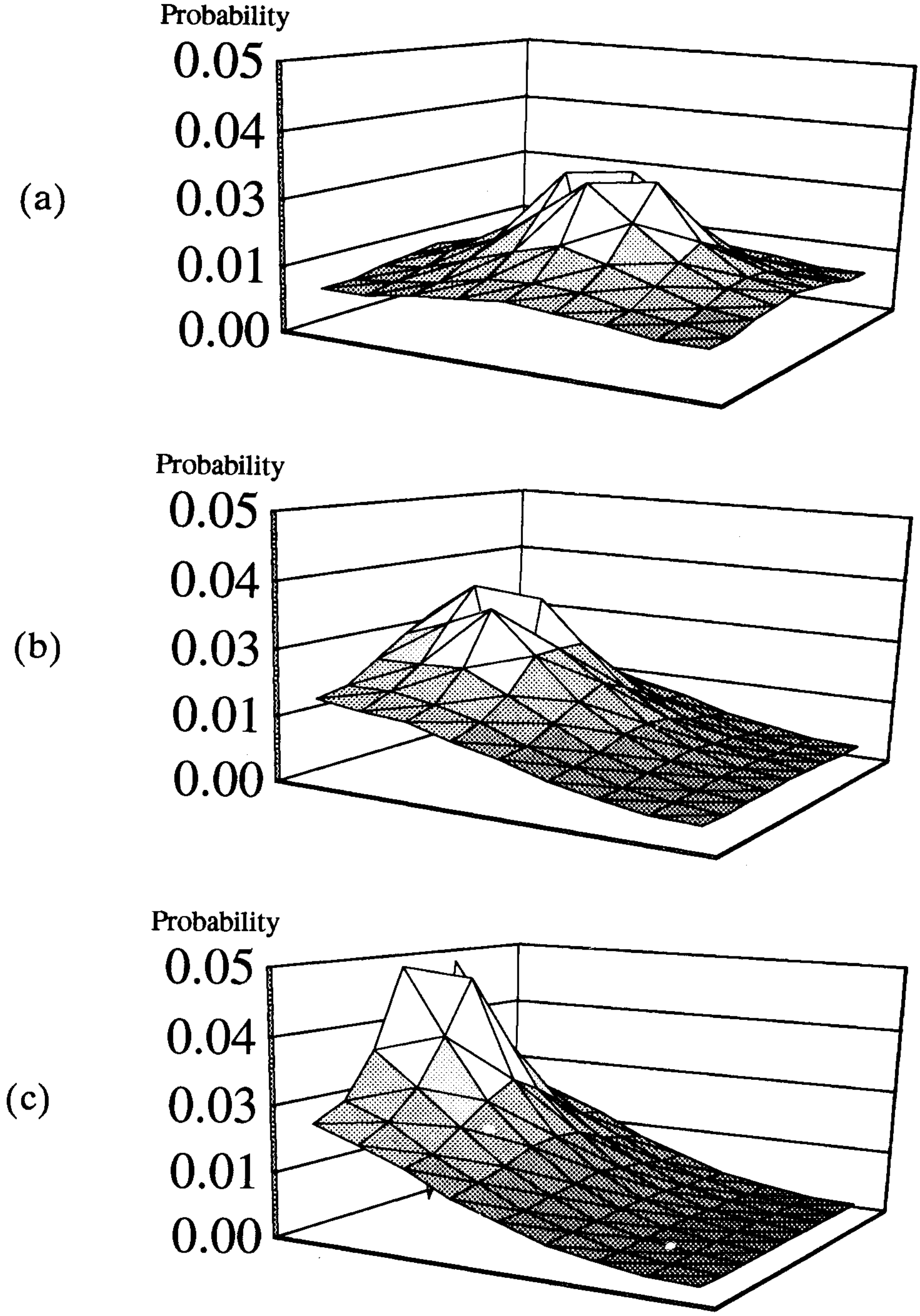

Fig. 4. Probabilities of at least once getting when the nest place was changed. The basis of figures is the area, and the surface represents the probabilities. The food was clumped, Rf=0.001. The nest was (a) in the centre, (b) middle and (c) on the edge of the area.

compare the solitary and colonial breeding.

The long search time in a patchy environment predicted by the model may show the importance of information transfer at a central place in such environment (Ward & Zahavi 1973).

In an heterogenous area the nest is expected to be placed near the most stationarious patch, otherwise the mean distance in this area increase considerably.

Acknowledgements. I am grateful to Alaisder Houston, Erzsébet Pásztor, Tamás Székely and Tibor Szép for helpful comments on this paper and I would like to thank Zoltán Varga for facilities.

Összefoglalás

A táplálék foltosságának és a fészek elhelyezkedésének hatása az átlagos repülési távolságra: egy model

A telepes fészkelének egyik oka lehet, hogy a madaraknak az időben és térben változó helyzetű táplálékfoltok miatt rövidebb távot kell megtenniük a fészek és egy átlagos táplálékfolt között, mintha a területen szétszórva fészkelnének. Mitől függ ezen távolság? Hogyan befolyásolja nagyságát a fészek területen belüli helyzete, a táplálék "csomósságának" (aggregáltságának) foka? A kérdésekre a választ egy modell kifejlesztésével próbálom megadni. A modell egy véletlen bolyongással kereső predátor mozgását írja le egy négyzethálón, ahol a táplálék eloszlása a csomóstól az egyenletesig változtatható.

A kapott eredmények: A fészek és a folt közötti távolság a táplálék csomósodásával egyre hosszabbá válik. Egy körülhatárolt területen a fészek helyzete jelentősen befolyásolja a táv hosszát. A modell alapján a kissé excentrikus fészekelhelyezés az optimális.

References

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

Brown, C. R. 1988. Enhanced foraging efficiency through information centers: a benefit of coloniality in cliff swallows. – Ecology, 69 : 602-613.

Brown, C. R. & M. B. Brown. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). – Ecology, 67: 1206-1218.

Brown, C. R. & M. B. Brown. 1987. Group-living in cliff swallows as an advantage in avoiding predators. – Behav. Ecol. and Sociobiol. 21: 97-107.

Hoogland, J. L. & P. W. Sherman. 1976. Advantages and Disadvantages of Bank Swallow (*Riparia riparia*) Coloniality. – Ecol. Mon. 46: 33-58.

Horn, H. S. 1968. The adaprive significance of colonial nesting in the Bewer's blackbird (*Euphagus cyanocephalus*). – Ecology 49: 682-694.

Karlin, S. & H. M. Taylor. 1975. A first course in stochastic process. – Academic Press, New York.

Kenward, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on wood-pigeons. – J. Anim. Ecol., 47: 449-490.

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

Møller, A. P. 1988. Infanticidal and anti-infanticidal strategies in the swallow *Hirundo rustica*. – Behav. Ecol. and Sociobiol. 22: 365-371.

Orians, G. H. & N. E. Pearson. 1979. On the theory of central place foraging. pp. 155-177. In: Horn, D.F. (ed.). Analysis of Ecological System. – Ohio State Univ. Press, Columbus.

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

Wittenberger, J. F. & M. B. Dollinger. 1984. The effect of acentric colony location on the energetics of avian coloniality. – Am. Nat. 124: 189-204.

Wittenberg, J. F. & G. L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. pp. 1-75. In: Farner, D. S. & J. R. King. (eds.) Avian Biology, Vol. 8. – Academic Press, New York.

Received 2 February 1992, revised 5 August 1992, accepted 20 September 1992