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FOOD AND FEEDING ECOLOGY OF GULL-BILLED TERNS (*GELOCHELIDON NILOTICA*) IN GREECE

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The Gull-billed Tern is a cosmopolitan species (Cramp, 1985), whose feeding habits have been studied in parts of its breeding range (Costa, 1984, see Cramp 1985 for earlier studies ; Cabo & Sanchez, 1986 ; Quinn & Wiggins, 1990 ; Sanchez *et al.*, in press and pers. comm.). The studies in the eastern part of the species' range were carried out in USSR (see Møller, 1982), but none were done in the eastern Mediterranean.

The main purpose of this paper is to describe the feeding habits of Gull-billed Terns in Greece and, by putting these results within the context of available information, to critically examine some problems related to the trophic diversity of Gull-billed Terns.

STUDY AREAS AND METHODS

This study of Gull-billed Terns in Greece took place in three areas :

1) The Evros Delta (40° 47′ N, 26° 05′ E). This delta is a Ramsar wetland and includes a great variety of habitats (Britton & Hafner, 1978 ; Goutner & Kazantzidis, 1989). In 1985 and 1986 the Gull-billed Tern colonies were situated in the lower delta (i.e. the seaward portion), in the Drana lagoon (see Goutner 1987 for description of the breeding area), but due to the drainage of this lagoon by local people in 1987 (Goutner & Jerrentrup, 1987), the colony shifted to a coastal islet's bare sand beach.

2) Alyki Kitrous (thereafter Alyki) (40° 21′ N, 22° 38′ E). This area is situated along the west coast and at the mouth of the Gulf of Thessaloniki (Fig. 1). It is made up of a lagoon with islets covered with halophytic vegetation in its southern part ; there are saltworks in its northern and south-western parts, and heaths and low sand dunes separate the lagoon from the sea (for a detailed description see Stubbs *et al.*, 1981). The area is of particular interest for herpetologists (Stubbs *et al.*, 1981, 1985) and ornithologists (Goutner, 1986 ; Papakostas, 1990) but it is still unprotected.

Small colonies of Gull-billed Terns occurred in the area from 1985 to 1989, but pellets were collected only in 1989, when two colonies were established about 500 m apart from each other (a colony was defined according to Erwin *et al.*, 1981). One was established on a small islet, and the other on a saline dike, both on bare sandy-muddy substrates.

3) The Messolonghi wetlands (38° 20′ N, 21° 20′ E). This is a large area extending over 28 000 ha included in the Greek Ramsar wetlands. They contain a

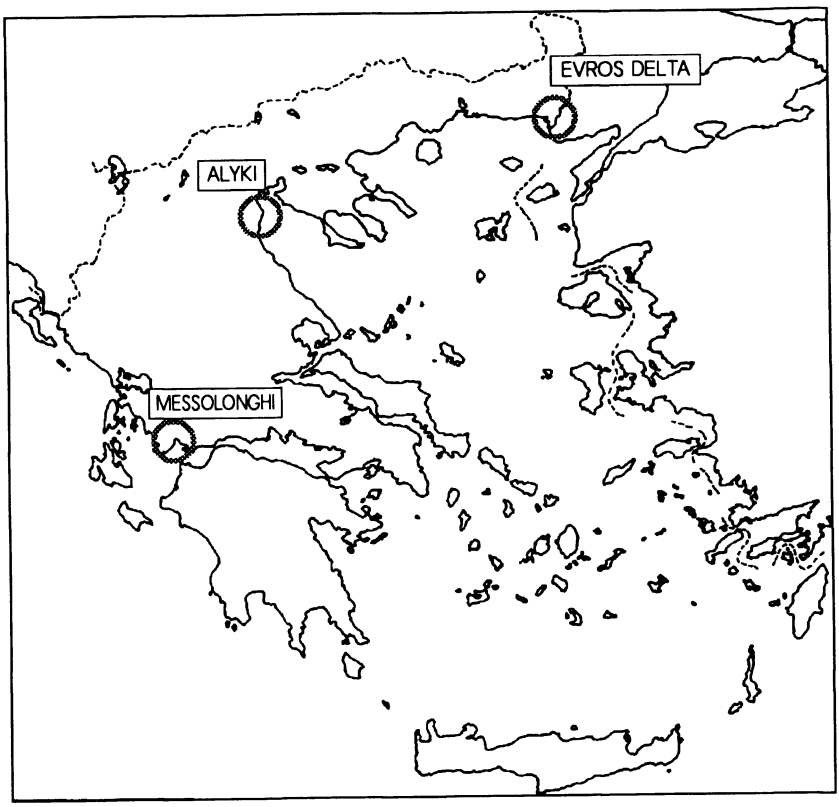

Figure 1. — Map of Greece where each study area is indicated by a circle.

great variety of habitats (Szijj, 1983) including extensive shallow lagoons. A colony of at least 83 pairs of Gull-billed terns was located in 1989 on a vegetation-free dike of the saltworks (Pergantis *et al.*, in press).

Regurgitated pellets were collected during the incubation and/or early chick stage : in the Evros Delta pellets were collected on the following dates ; 06.VI and 11.VI.1985, 08.VI.1986 and 13.VI.1987. At Alyki, collection dates were 21.VI and 22.VI.1989, and in Messolonghi 07-11.VI.1989. Some of the insect material was identified in the Entomological Department of the Museum of Natural History in Prague. Other material was identified by the author and other specialists in the Laboratory of Zoology, University of Thessaloniki, using reference books and reference collections.

Various authors have used indices of diversity to describe the frequency of various items in the diet of Gull-billed Terns. Møller (1977, 1982), Vargas *et al.* (1978), Costa (1984), Cabo & Sanchez (1986), and Sanchez & Blasco (1986) used either the Shannon-Wiener index H′ (Shannon & Weaver, 1963) or an equivalent index proposed by Lloyd & Ghelardi (1964), to estimate the « trophic diversity ». All of them (also Quinn & Wiggins, 1990), apart from Costa (1984) and Sanchez & Blasco (1986), used H′ to estimate the « Niche Breadth » B = exp H′ (MacArthur, 1969).

To help comparisons with the above mentioned studies I also used the same diversity indices. I considered the following systematic categories (classes) as groups : Insecta, Bivalvia, Crustacea, Arachnida, Osteichthyes, Amphibia, Reptilia, Aves, Mammalia.

To facilitate comparisons with my study area I also used the equitability index (evenness) proposed by Atalato (1981) :

$$F_{2,1} = (N_2 - 1)/(N_1 - 1)$$

where $N_2 = 1/\Sigma p_1^2$ and $N_1 = \exp H'$ (antilogarithmic Shannon's entropy). This index has been considered as more precise than other relative indices when species diversity (and in this case trophic diversity) is low (Atalato, 1981).

RESULTS

1. *PREY TYPE*

1.1. *Evros Delta*

Insects were the most important food of Gull-billed Terns in the Evros Delta during all our study years. Coleoptera were numerically most abundant and *Pentodon* spp. were the commonest prey-species at least in 1985 and 1986 (Table I). Other beetles were represented in the diet of Gull-billed Terns in moderate to low proportions (Curculionidae and Carabidae), whereas the other beetles were scarce. Orthoptera and Hymenoptera were of moderate abundance and, especially the former, increased numerically throughout the study years. Other insect groups were represented in low proportions in the diet. Non-insect taxa (Bivalves, Crustaceans, Fishes, Anurans, Reptiles, and Mammals) occurred in generally low proportions. In most prey groups, especially insects, various subcategories changed considerably in composition and/or abundance over the years.

TABLE I

Gull-billed Tern prey types in the Evros Delta from 1985 to 1987.

Figures are percentages of total items examined per year (A), and percentages of occurrence of each item in each pellet sample (B).

	1985		1986		1987	
Total items examined	N = 489		N = 57		N = 806	
Number of pellets collected	N = 90		N = 14		N = 132	
	A	B	A	B	A	B
INSECTA	96.7	98.9	86.0	62.3	84.6	81.8
Coleoptera	92.4	95.5	64.9	42.8	40.2	55.3
Scarabaeidae	86.5	95.5	45.6	28.6	13.8	24.2
Pentodon idiota	31.9	36.7	33.3	21.4	13.4	22.7

Total items examined Number of pellets collected	1985 N = 489 N = 90		1986 N = 57 N = 14		1987 N = 806 N = 132	
	A	B	A	B	A	B
Pentodon sp.	39.7	42.2			0.1	0.8
All *Pentoton* spp.	71.6	78.9	33.3	21.4	13.5	23.5
Anoxia sp.	14.3	20.0	12.3	7.1		
Anisoplia sp.	0.2	1.1				
Oryctes nasicornis	0.2	1.1				
Other Scarabaeidae	0.2	1.1			0.3	0.7
Curculionidae	5.3	3.3	12.3	21.4	18.1	28.0
Carabidae	0.4	2.2	7.0	7.1	7.1	18.9
Cicindela sp.					0.1	0.8
Calosoma sycophanta					0.1	0.8
Other Carabidae spp.					6.9	17.3
Tenebrionidae	0.2	1.1				
Buprestidae					0.4	0.8
Dytiscidae					0.5	0.8
Ilibius sp.					0.5	0.8
Unidentified Coleoptera					0.4	0.8
Orthoptera	4.3	13.3	10.5	35.7	28.3	54.5
Ensifera	4.1	12.2	8.8	21.4	12.1	26.5
Gryllotalpa gryllotalpa	3.1	11.1	7.0	14.3	10.5	24.2
Other Ensifera	1.0	1.1	1.7	7.1	1.6	2.3
Caelifera	0.2	1.1	1.7	7.1	16.0	30.3
Unidentified Orthoptera					0.1	0.8
Hymenoptera			10.5	1.1	13.0	3.0
Formicoidea			10.5	1.1		
Formicidae					5.3	2.3
Myrmicinae					7.7	0.7
Dermaptera					1.6	3.0
Diptera					1.5	3.0
Asilidae					1.5	3.0
CRUSTACEA	0.4	2.2			9.5	26.5
Carcinus aestuarii	0.2	1.1			8.7	22.0
Carcinus sp.	0.2	1.1			0.5	2.2
All *Cardinus* spp.	0.4	2.2			9.2	24.2
Unidentified Crustacea					0.3	2.3
AMPHIBIA	2.4	13.3	14.0	42.8	4.1	16.7
Anura	2.4	13.3	14.0	42.8	4.1	16.7
Ranidae			5.3	21.4	0.4	2.3
Rana sp.					0.4	2.3
Other Anura			8.7	21.4	3.7	14.4
REPTILIA					0.6	3.8
Sauria					0.6	3.8
BIVALVIA					0.5	3.0
OSTEICHTHYES					0.2	1.5
MAMMALIA	0.4	2.2			0.2	1.5
Soricidae	0.2	1.1				
Apodemus sp.	0.2	1.1				
Unidentified Vertebrata					0.1	0.8

1.2. *Alyki*

In the two Alyki colonies insects were also the most important prey making up to 97.4 % and 98.5 % of the total food items respectively found in all pellets collected (Table II). In both colonies Orthoptera were numerically the most abundant (Table II). However the relative abundance and composition of prey varied considerably between colonies. Orthoptera and Coleoptera differed significantly in numbers between colonies ($\chi^2 = 27.17$ and $\chi^2 = 30.04$, $P < 0.001$, respectively). Prey other than insects were minor components of the Gull-bill Terns' diet at Alyki.

TABLE II

Gull-billed Tern prey types at two colonies in Alyki, 1989.

Figures are percentages of total items examined per year (A), and percentages of occurrence of each item in each pellet sample (B).

	Colony 1		Colony 2	
Total items examined	N = 228		N = 124	
Number of pellets collected	N = 31		N = 23	
	A	B	A	B
INSECTA	97.4	100	98.5	100
Orthoptera	64.9	74.0	90.3	91.3
Ensifera	50.0	71.0	90.3	91.3
G. gryllotalpa	2.6	9.7	3.7	13.0
Other Ensifera	47.4	61.3	86.6	86.9
Caelifera	14.9	9.7		
Coleoptera	27.6	48.4	3.7	17.4
Scarabaeidae	15.8	32.2	2.2	13.0
Pentodon idiota	12.7	29.0	1.5	8.7
Melolonthinae	1.3	6.4	0.7	4.3
Anoxia sp.	1.7	3.2		
Carabidae	6.6	12.9		
Curculionidae	4.4	12.9		
Silphidae	0.4	3.2		
Unidentified Coleoptera	0.4	3.2	0.7	4.3
Odonata	3.1	3.2	4.5	8.7
Hemiptera				
Homoptera	0.4	3.2		
Hymenoptera	1.3	6.4		
Ichneumonoidea	0.4	3.2		
Formicoidea	0.9	6.4		
BIVALVIA	0.9	6.4	1.4	8.7
AMPHIBIA	0.4	3.2		
Anura	0.4	3.2		
AVES	0.4	3.2		
MAMMALIA	0.4	3.2		
Microtus sp.	0.4	3.2		

TABLE III

Gull-billed Tern prey types at Messolonghi, 1989.

Figures are percentages of total items examined (A) and percentages of occurrence of each item in each pellet sample (B).

	Total items examined N = 242 A	Number of pellets collected N = 122 B
INSECTA	39.2	55.7
Orthoptera	16.5	15.6
Ensifera	7.0	11.5
Gryllotalpa gryllotalpa	7.0	11.5
Caelifera	7.8	3.3
Other Orthoptera	1.6	3.3
Coleoptera	13.6	24.6
Carabidae	7.0	12.3
Scarabaeidae	1.6	3.3
Pentodon sp.	1.6	3.3
Curculionidae	1.2	1.6
Chrysomelidae	0.4	0.8
Other Coleoptera	3.3	6.5
Lepidoptera	7.4	14.7
Unidentified Insecta	1.6	3.3
ARACHNIDA	0.4	0.8
Araneae (Lycosidae)	0.4	0.8
CRUSTACEA	53.3	55.7
Carcinus aestuarii	6.2	4.9
Carcinus sp.	47.1	50.8
AMPHIBIA	5.8	4.9
Anura	5.8	4.9
Ranidae (*Rana* sp.)	0.4	0.8
Other Anura	5.4	4.1
OSTEICHTHYES	1.2	2.4
Syngnathus sp.	0.4	0.8
Belone belone	0.4	0.8
Other Osteichthyes	0.4	0.8

1.3. *Messolonghi*

Crabs (*Carcinus* sp.) constituted more than half of the prey items in the Messolonghi wetland colony, while insects were next in frequency, 39 % of the total (Table III, see also Pergantis *et al.* in press, for a preliminary analysis of the data). Orthoptera and Coleoptera were the most abundant insect groups in the diet. Other items (Arachnids, Fishes and Anurans) were much less numerous.

2. *TROPHIC DIVERSITY*

During the following analysis only the Shannon-Wiener index values were used, as being more useful in such situations.

In the Evros Delta, the trophic diversity values differed considerably among study years, increasing from 1985 to 1987. The evenness values also increased throughout the study (Table IV), although the high 1986 value might have been due to the small size of the sample. The trophic diversity values were similar in the two Alyki colonies, and results for the Messolonghi region provided the highest diversity values obtained in this study.

TABLE IV

Trophic Diversity of Gull-billed Tern food in Greece.

H′ is the Shannon-Wiener Index (Shannon and Weaver 1963) ; H is the Diversity Index of Lloyd and Ghelardi (1964) ; B is the Niche Breadth (B = expH′) ; and F is the Equitability Index (Evenness, Atalato, 1981).

Area	Year	H′	H	B	F
Evros Delta	1985	0.17	0.24	1.18	0.37
	1986	0.40	0.58	1.50	0.64
	1987	0.58	0.85	1.79	0.47
Alyki, col. 1	1989	0.14	0.23	1.15	0.36
col. 2		0.12	0.20	1.13	0.35
Messolonghi	1989	0.83	1.36	2.29	0.98

DISCUSSION

The data presented here relate to different areas of Greece and were, in part, assembled during different years ; therefore direct comparisons may not be always meaningful.

Although the majority of the food items in the Evros Delta were insects, there were considerable yearly variations in the proportions of particular insect groups. *Pentodon* spp. dominated among beetle prey at least in 1985, suggesting a specialization (perhaps due to a superabundance of *Pentodon*), but this became less obvious throughout the study period as suggested by the evenness values (Table IV). The material for diet analysis was collected each year during a limited period in June, and the variations observed do not forcibly imply seasonal differences in food abundance. These differences in food diversity may suggest year-to-year changes in prey availability. This may have been due to the dramatic habitat changes which took place in the Evros Delta during our study (Goutner & Jerrentrup, 1987 and pers. obs.), and such changes may have affected the feeding ecology of Gull-billed Terns. Furthermore, in the Evros Delta, part of the tern population moves for feeding in the Turkish territory, 5-6 km away from the colony sites (Goutner 1986 and this study), and it is impossible to locate all the foraging areas of the birds and their possible modifications with time. In a similar Mediterranean wetland the average foraging distance of Gull-billed Terns was 9.3 km (Fasola & Bogliani, 1990).

In the two Alyki colonies, just 0.5 km apart, the birds fed on different insect prey. This suggests a differential exploitation of the available feeding habitats by the members of each colony. In a similar situation in Spain, Costa (1986) suggested that these differences were due to differences in the nature of the environment exploited by each colony.

In contrast to the Evros Delta and Alyki, crabs (*Carcinus* sp.) dominated in the diet of Gull-billed Terns at Messolonghi. This can be due to the abundance of this kind of prey, which thrives in the large shallow lagoons that cover 16 400 ha, i.e. about 66 % of the total surface of this wetland area (Pergantis, 1988).

Previous studies suggest that Gull-billed Terns seem to be more generalists at northern latitudes and specialists further south (Møller, 1977, 1982). This hypothesis seems to hold true if we consider Møller's data only, the highest index value being that for Denmark and the lowest that for Spain (Møller, 1982). However, more recent studies show that although insects are the most important prey in southern latitudes, the Gull-billed Terns seem, at least on some occasions, not to specialize as suggested. Niche breadth values found in the southern areas (Table V) are much higher than expected by Møller's hypothesis. This is characteristic of e.g. the Camargue, where a recent niche breadth value (Table V) exceeded those given by Møller (1977) for the same Camargue and for Denmark.

It should be noted that in all food studies of Gull-billed Terns (Quinn & Wiggins, 1990, excepted) Niche Breadth values were calculated without distinguishing pellet samples collected at different times within the breeding season. Additionally, all studies seem to have been carried out within a single year ; there is no mention in the literature of year-to-year dietary differences. However, diet changes within a same breeding season and a same region (see Cramp, 1985 ; Cabo & Sanchez, 1986 ; Sanchez, pers. comm.), and also between years in a same region (this study and Table V for other regions) do occur. Therefore it is not surprising that niche breadth varies for different periods of the same season, and/or in different years, or for different colonies breeding simultaneously within the same region. Consequently, the methodology used up to now may not give a representative picture of the trophic diversity for some regions. If our study in the Evros Delta had been carried out only in 1985, the results would have « shown » that Gull-billed Terns were true specialists, but 1985 was an exception as the present study shows.

Furthermore, there is no significant correlation between latitude and species diversity, or niche breadth values, either for all the available values or for the highest within a single region only [For all values : $R_{s\ latitude\text{-}H'} = 0.30$, $P = 0.21$ NS, $R_{s\ latitude\text{-}B} = 0.28$, $P = 0.24$ NS. For maximum values : $R_{s\ latitude\text{-}H'max} = 0.08$, $P = 0.79$ NS, $R_{s\ latitude\text{-}Bmax} = 0.08$, NS (Table V). R_s is the Spearman Rank Correlation Coefficient ; Zar, 1984)].

Therefore it may be concluded that although a relationship between prey specialization and latitude in Gull-billed Terns may sometimes exist, the most recent evidence shows that it cannot be generalized. To begin with, trophic diversity must be studied throughout the whole breeding season because of possible shifts in the kinds of prey taken. One has also to establish whether or not different breeding pairs in a colony eat different prey at different periods of the same breeding season. Such studies have also to be carried out for a number of years and along a latitudinal gradient, and include both pellet analyses and direct

TABLE V

Trophic Diversity (H') and Niche Breadth (B) of Gull-billed Terns from studies throughout their breeding range.

Data are ordered by latitude. Values with an asterisk were estimated by the author, using the same parameters than those used in the literature mentioned. Values in parenthesis were calculated for comparison using (for insects) lower taxonomic categories (orders) than those used by the other authors.

Area	Co-ordinates	H'	B	Reference
Nordjylland, Denmark	57° 02′ N, 09° 54′ E	1.96*	7.09	Møller 1977
Denmark	" "	2.55	12.81*	Møller, in Sanchez and Blasco 1986
Changarskij, USSR	46° 17′ N, 32° 52′ E	1.5*	4.6*	Møller 1982
Chernomorskii, USSR	45° 31′N, 32° 36′ E	1.4*	3.9*	Møller 1982
Kuban, USSR	45° 05′ N, 38° 03′ E	0.8*	2.2	Møller 1982
Camargue, France	43° 20′ N, 04° 38′ E	1.08*	2.95	Møller 1977
Camargue, France	" "	2.11	8.24*	Walmsley et Johnson, in Sanchez and Blasco 1986
Evros Delta, Greece 1985	40° 47′ N, 26° 05′ E	0.17 (0.34)	1.18 (1.40)	This study
1986	" "	0.40 (1.03)	1.50 (2.80)	This study
1987	" "	0.58 (1.56)	1.79 (4.76)	This study
Alyki, Greece 1989, colony 1	40° 21′ N, 22° 38′ E	0.14 (0.92)	1.15 (2.50)	This study
colony 2	" "	0.12 (0.42)	1.13 (1.52)	This study
Messolonghi, Greece, 1989	38° 20′ N, 21° 20′ E	0.83 (1.33)	2.29 (3.78)	This study
Guadalquivir, Spain, colony 1	37° 20′ N, 06° 24′ W	1.80	6.05*	Costa 1984
colony 2	" "	1.25	3.49*	Costa 1984
colony 3	" "	1.37	3.93*	Costa 1984
Fuente Piedra, Spain	36° 43′ N, 04° 23′ W	0.35*	1.42	Vargas *et al.*, 1978
Fuente Piedra, Spain	" "	1.82	6.17*	Sanchez and Blasco 1986
Afso, Morocco	38° 73′ N, 0° 55′ W	0.98*	2.67	Cabo and Sanchez 1986

observations of prey brought to the nestlings (e.g. Quinn & Wiggins, 1990). One must not forget also that some prey do not leave identifiable remains in the pellets (Duffy & Jackson, 1986).

On the basis of the existing evidence, the trophic diversity of the Gull-billed Tern appears to be relatively independent of latitude. The flexibility of the feeding habits of the species suggests that it is able to adapt itself successfully to local changes in food availability.

SUMMARY

A study of the diet of Gull-billed Terns was carried out by analysis of regurgitated pellets during the breeding season in three Greek coastal wetlands: Evros Delta (1985-1987), Alyki Kitrous (1989) and Messolonghi (1989). In the Evros Delta, insects, especially Coleoptera, were the most important prey; non-insect taxa (Bivalvia, Crustacea, Osteichthyes, Reptilia and Mammalia) were much less important. At Alyki, insects, especially Orthoptera, were the predominant prey whereas other prey items (Bivalvia, Amphibia, Aves, Mammalia) were of little importance. At Messolonghi, crabs (*Carcinus* sp.) were the prey most often consumed; insects (mainly Orthoptera and Coleoptera) were less common in the diet and other prey types (Arachnida, Amphibia, Osteichthyes) were of minor importance. Trophic diversity indices differed between years in the Evros Delta. A brief review of the literature shows that, in contrast to what has been previously suggested, trophic diversity of Gull-billed Terns is independent of latitude. Methodological aspects are discussed in order to improve our knowledge of the feeding ecology of Gull-billed Terns.

RÉSUMÉ

Le régime de la Sterne hansel *Gelochelidon nilotica* a été étudié par analyse des pelotes de régurgitation dans trois zones humides de Grèce, le delta de l'Evros (1985-87), Alyki Kitrous (1989) et Messolonghi (1989).

Dans la première localité, les insectes, et en particulier les Coléoptères, constituent les proies principales, les autres taxons (Mollusques bivalves, Crustacés, Poissons téléostéens, Reptiles, Mammifères) n'ayant qu'une importance secondaire. A Alyki, ce sont les Orthoptères qui prédominent. A Messolonghi, les crabes arrivent en tête, suivis par les insectes (Orthoptères et Coléoptères principalement), puis les proies de moindre importance (Arachnides, Amphibiens, Poissons téléostéens).

Les indices de diversité trophique varient d'une année à l'autre dans le delta de l'Evros.

Contrairement à ce qui a été suggéré antérieurement, la diversité du régime de la Sterne hansel est indépendante de la latitude.

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