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Coordinated visual displays and vocal duetting in different ecological situations among Western Palearctic non-passerine birds

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The biological significance of mutual behaviours, like duet singing and visual displays, is not entirely clear. The main hypotheses (pair bonding and territorial defence) come from studies of tropical bird species. The aim of this work is to identify some behavioural-ecological parameters that characterize the birds of the temperate area showing duets and coordinated-visual displays (CVD).

To this end we performed a multivariate statistical analysis considering 122 non-passerine of the Western Palearctic, 46 of which make coordinated displays. Five main groups have been obtained, two of which are pure vocal duetters (owls/woodpeckers and swifts/shearwaters), and the other three consisting of birds where vocalisations are accompanied by CVD (some marine colonial species, Anatidae and divers). In agreement with previous studies of tropical birds, vocal duetting is typical of monogamous, monomorphic and territorial species. CVD is present in species living in open habitat with nidifugous offspring and migratory habits. It is suggested that in the latter birds, pair-synchronization and pair-strengthening needs are the main ecological pressures selecting for these mutual forms of communication.

KEY WORDS: duet singing, coordinated visual displays, non-passerine birds, Palearctic area, ecological correlates, multivariate analysis, comparative study.

INTRODUCTION

Duetting, a vocally synchronized behaviour of reproductive partners, that is «temporally and thematically coordinated in a sequential manner» (WICKLER 1980), has been described mainly in tropical birds (THORPE 1972, FARABAUGH 1982). The main characteristics of duetting birds are year-round territoriality, monogamous habits, and, an aspect which has been recently questioned by FARABAUGH, morphochromatic monomorphism.

Two functions have been suggested for duetting: territorial defence and pair bonding (FARABAUGH 1982). WICKLER investigated the complex nature of this phenomenon and pointed out that in different species one of these two functions prevails. In *Laniarius funebris* and *Trachyphonus usambiro* the territorial function seems more important (SEIBT & WICKLER 1977), while it has been suggested that the peculiar form of duetting observed in *Symplectes bicolor*, probably derived from a territorial display, may have evolved as a pair-bonding device (WICKLER & SEIBT 1980).

Other forms of synchronized behaviour (e.g., coordinated visual displays), have been compared to vocal duetting. Among birds, visual ceremonies, first described as «*Pas de Deux*» by ARMSTRONG (1942), have been observed in grebes, divers, penguins, albatrosses and cranes. Displays may be wholly visual or also have vocal components, as in Triumph Ceremonies of geese involving both calling in unison and coordinated visual displays. From a functional standpoint, all these behaviours may be considered as akin to duetting and may also function in pair bonding («mutual physiological adjustment», ARMSTRONG 1942). However different interpretations of the mutual water-displays of Gaviidae have been expressed. DUNKER (1974) stressed the pair-bond maintenance function, while SJOLANDER & AGREN (1972), felt that this mutual display had primarily a territorial significance.

In our opinion, insufficient attention has been devoted to duetting species in the temperate zone, such as those of the Western Palearctic area, where more than 40 non-passerine species exhibit duetting (data inferred from CRAMP 1977-1985). In about 50% of these species, vocal duetting is accompanied by mutual visual ceremonies, taking place mainly during the mating period. The aim of this comparative study is twofold: (1) to determine whether some of the eco-ethological characteristics of the tropical duetters are also found in the non-passerine duetter of the temperate area; (2) to identify, within the latter group, possible ecological and behavioural differences between vocal and vocal + visual displayers. To this end, we have performed a multivariate statistical analysis on a large sample of non-passerine Western Palearctic birds using the data obtained from the literature. Vocal duetting and coordinated visual display (CVD) were taken as the dependent variables and 11 relevant behavioural-ecological characteristics as the independent variables.

MATERIALS AND METHODS

The sample included 122 species of non-passerines of the Western Palearctic area, covering all the duetting species (46 in all, as inferred from the literature) and 76 non-duetting species sampled at random from all the systematic taxa of non-passerine Western Palearctic birds. Passerine birds were excluded from the analysis, because homogeneous sources of references (CRAMP 1988, in

progress; GLUTZ & BAUER 1988, in progress) are missing at present, and to keep the data set at a manageable size. The references are given in Table 1. For each species we took into account (see Table 2) 13 ecological and behavioural variables as reported in CRAMP & SIMMONS (1977-1985, vols I-IV). To 11 of them we assigned scores between 1 (characteristic absent) and 3 (fully expressed) while for the remaining two parameters («g» and «j») the score was between 1 and 4.

Table 1.
Duetting species and references.

Species	References
Accipiter badius	SMEENK & SMEENK-ENSERINK 1977
Accipiter nisus	CRAMP & SIMMONS 1979
Alle alle	EVANS 1981
Anser albifrons	CRAMP & SIMMONS 1977
Anser anser	RADESATER 1974
Apus apus	CRAMP 1985
Apus pallidus	MALACARNE & CUCCO 1990
Asio otus	CRAMP & SIMMONS 1977
Branta canadensis	RADESATER 1974
Branta ruficollis	CRAMP & SIMMONS 1977
Bubo bubo	CRAMP 1985
Ciconia ciconia	HAVERSCHMIDT 1949
Ciconia nigra	KAHL 1972
Cygnus cygnus	CRAMP & SIMMONS 1977
Cygnus columbianus	CRAMP & SIMMONS 1977
Cygnus olor	CRAMP & SIMMONS 1977
Dendrocopus major	CRAMP 1985
Dendrocopus minor	CRAMP 1985
Dendrocopus syriacus	RUGE 1970
Gavia adamsii	HUXLEY 1923
Gavia arctica	HUXLEY 1923
Gavia immer	HUXLEY 1923
Gavia stellata	HUXLEY 1923
Grus grus	CRAMP & SIMMONS 1979
Haematopus ostralegus	NEUMANN 1940
Jynx torquilla	CRAMP 1985
Larus argentatus	CRAMP & SIMMONS 1982
Larus canus	WEIDMANN 1955
Milvus migrans	CRAMP & SIMMONS 1979
Oceanodroma leucorrhoa	GRUBB 1973
Otus scops	CRAMP 1985
Phalacrocorax aristotelis	CRAMP & SIMMONS 1977
Podiceps auritus	CRAMP & SIMMONS 1977
Podiceps cristasus	CRAMP & SIMMONS 1977
Podiceps grisegena	CRAMP & SIMMONS 1977
Podiceps nigricollis	CRAMP & SIMMONS 1977
Puffinus griseus	CRAMP & SIMMONS 1977
Puffinus puffinus	CRAMP & SIMMONS 1977
Rallus aquaticus	CRAMP & SIMMONS 1979
Rissa tridactyla	CRAMP & SIMMONS 1982
Strix aluco	WENDLAND 1963
Sula bassana	CRAMP & SIMMONS 1977
Surnia ulula	CRAMP 1985
Tachybaptus ruficollis	CRAMP & SIMMONS 1977
Tito alba	BUNN 1974
Uria aalge	CRAMP 1985

Table 2.
Ecological and behavioural variables.

Dependent variables
a) *Duetting*
1) not duetting species
2) episodical or occasional
3) duetting species
b) *Coordinated visual display (CVD)*
1) not described
2) episodical or occasional
3) regularly exhibited
Independent variables
a) *Pair bond*
1) polygamy
2) seasonal monogamy
3) multiseasonal monogamy
b) *Movements*
1) migratory
2) partially migratory
3) sedentary
c) *Nesting habitat*
1) open
2) intermediate
3) sheltered
d) *Feeding habitat*
1) open
2) intermediate
3) sheltered
e) *Feeding habits*
1) vegetarian
2) mixed diet
3) flesh, insect of fish-eating
f) *Social pattern in reproduction*
1) coloniality
2) facultative or loose coloniality
3) isolated pairs
g) *Plumage-morphological and size sexual dimorphisms*
1) plumage-morphological and size sexual dimorphism
2) plumage-morphological sexual dimorphism
3) size sexual dimorphism
4) absence of sexual dimorphism
h) *Territoriality during reproduction*
1) territorial species
2) intermediate
3) non-territorial species

i) *Nest characteristics*
   1) hole nester
   2) intermediate
   3) open nester

j) *Parental care*
   1) both parents
   2) one mainly sex
   3) only one sex
   4) no care

k) *Young*
   1) nidicolous
   2) semi-nidifugous
   3) nidifugous

A cluster analysis (single linkage method with Euclidean distance) was performed to express similarities between duetting and CVD species. Discriminant Analysis has been choosen to provide new composite variables (factors) which maximize the differences among prespecified groups. Three categories both for duetting and CVD analyses were specified. Canonical loadings represent the relationships among the 11 ecological and behavioural variables and factors sorted by the analysis.

The choice of the taxonomic level used for the analysis may bias the outcome of any comparative study (HARVEY & MACE 1982). The species-level has been the usual unit of comparison in most studies, but this may bias the data in favour of a few species-rich genera. On the other hand, taxonomic comparison above the species-level may exclude significant variation at a lower taxonomic level. Therefore, we performed further discriminant analyses on a data set of 77 different genera of birds (obtained from the previous one by pooling the scores of the species, when more that one was present in the same genus), to show how these groupings affect the pattern of variation in duets and CVD.

Representation of duetting and CVD species with other non-passerine birds was obtained through Correspondence Analysis. For discriminant analysis, we used a Systat software package (WILKINSON 1986); for Correspondence Analysis, Lagoli software was used (LAGONEGRO & FEOLI 1985).

RESULTS

In the cluster (Fig. 1) the 46 species reported to duet or engaged in CVD are represented. The species showing only vocal duetting (diurnal raptors, owls, woodpeckers, swifts, petrels and shearwaters; 47.8%) are quite well separated from those in which duetting is coupled with CVD (grebes, divers, swans, geese, ducks and some gulls; 45.7%). In three species only (*Cygnus olor, Phalacrocorax aristotelis* and *Sula bassana*; 3.5%) CVD does not seem to be combined with duetting, but these species do show some kind of vocal interactions as well.

Upon a closer inspection, it is possible to identify five homogeneous groups in the cluster, two of which: (1) woodpeckers and owls, (2) swifts, petrels and shearwaters, display duetting only, and three: (3) gulls and auks, (4) grebes and divers, and (5) ducks, geese and swans, display both vocal duetting and coordinated visual displays.

Fig. 2 illustrates the position of the 122 species being considered as determined

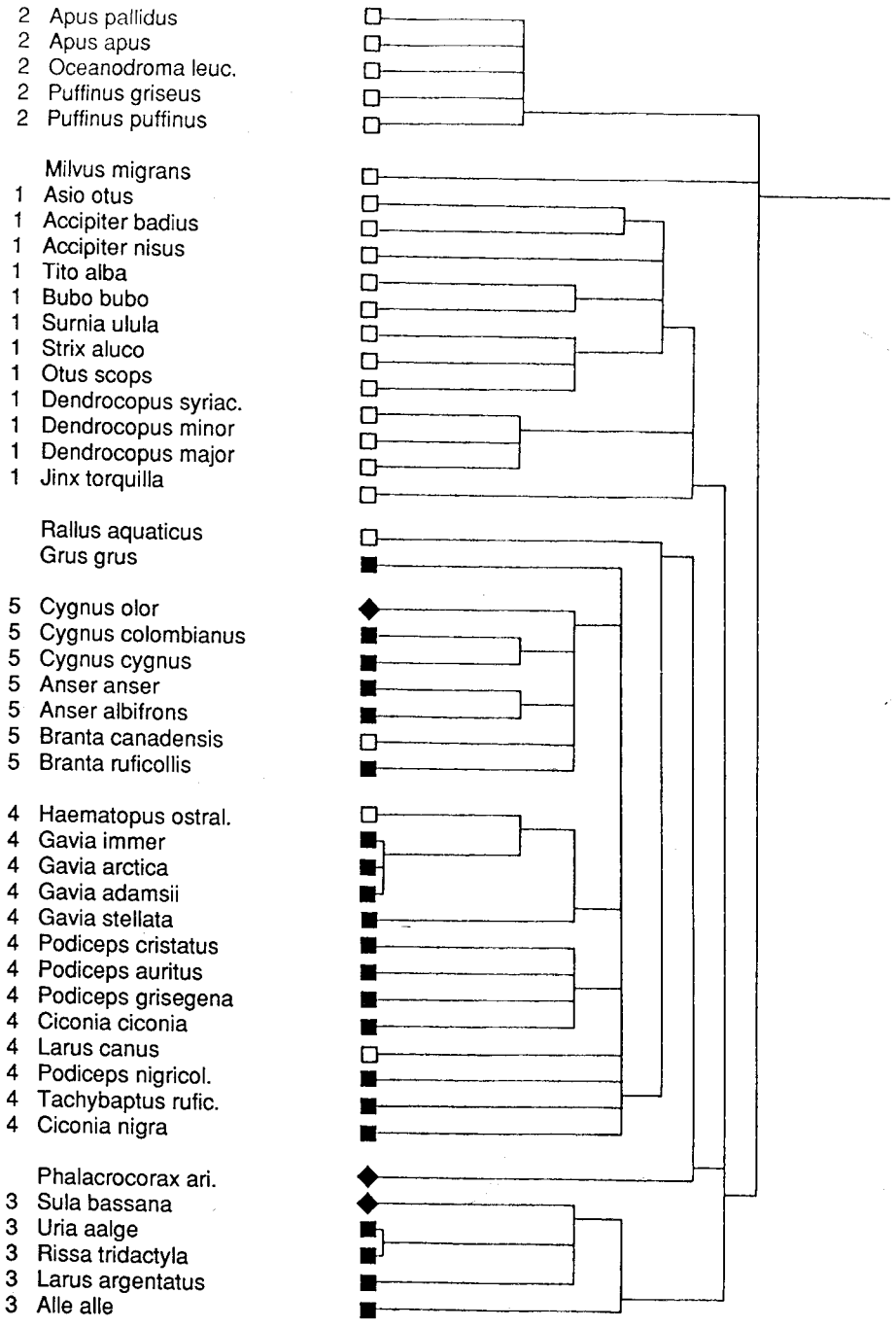

Fig. 1. — Relationships among the duetting or CVD species. (Distance metric is Euclidean distance, Single Linkage — Nearest Neighbor — method). Open square, duetting species; filled square, duetting + CVD species; filled rhomb, CVD species. Numbers indicate the five groups discussed in the text.

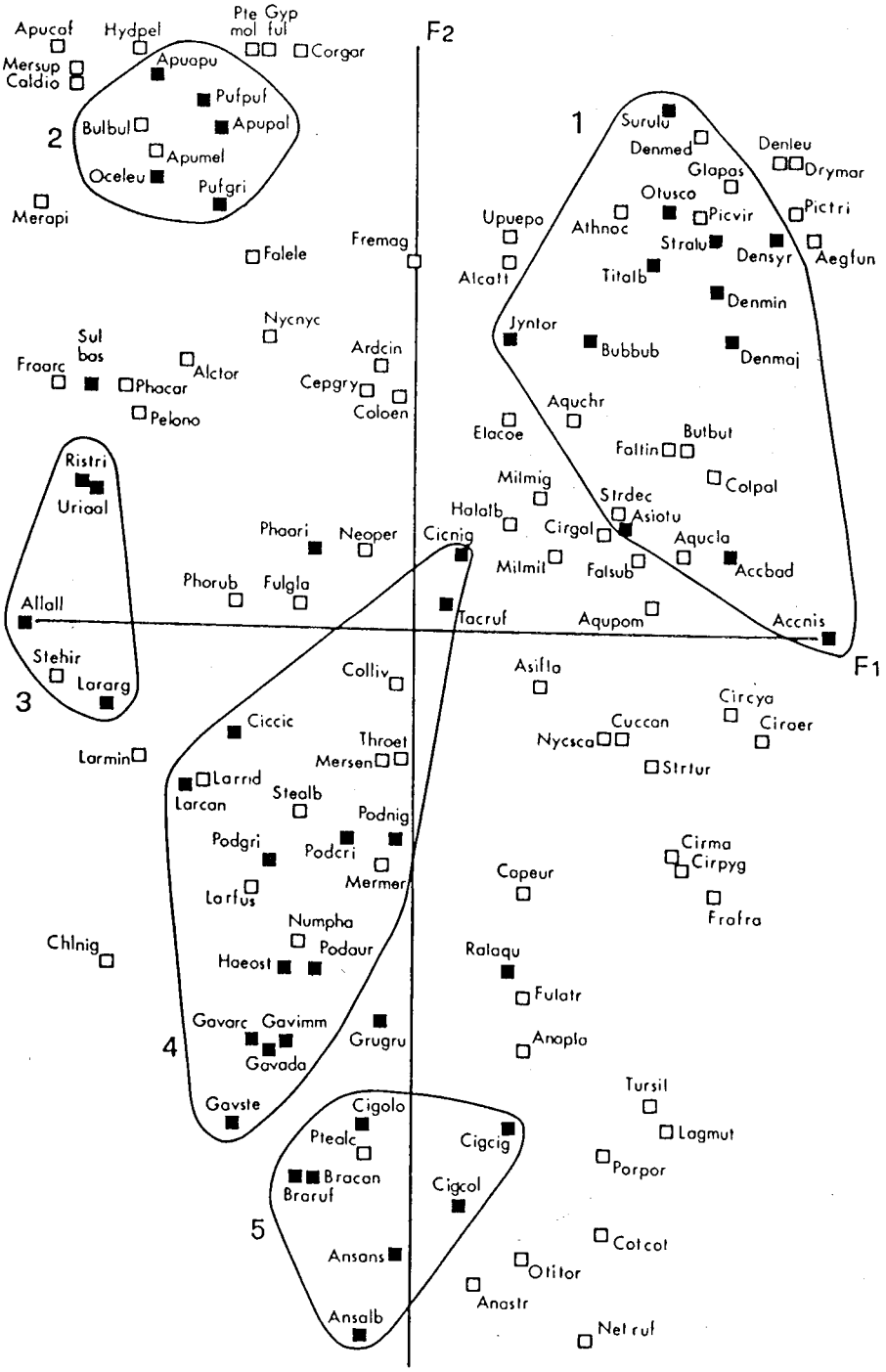

Fig. 2. — Plot of the first two factors (F1, F2, variance explained 27.9 and 21.9 respectively) of the Correspondence Analysis. The five groups outlined are discussed in the text. Filled square, duetting or CVD species; open square, non-duetting or CVD species.

Table 3.
Discriminant Analyses conducted at the species or at the genus level: canonical loadings (correlations between variables and the 1st canonical factor) and discrimination of the CVD species.

CVD variables	Canonical loadings (first factor)	
	Species n = 122	Genera n = 77
Young	0.822	0.814
Nest characteristics	0.620	0.690
Feeding habitat	−0.476	−0.301
Nest habitat	−0.446	−0.235
Feeding habits	−0.409	−0.512
Movements	−0.291	−0.253
Sexual dimorphism	0.237	0.015
Parental care	−0.182	−0.047
Social pattern in reproduction	−0.143	−0.210
Pair bond	0.123	−0.244
Territoriality in reproduction	−0.009	0.057
Canonical correlations: 1st factor =	0.631	0.657
2nd factor =	0.498	0.485

Table 4.
Predictability of the CVD on the basis of the two Discriminant Analyses.

		Predicted score 1	2	3	Total
Observed score	1	50	7	7	64
	2	6	23	5	34
	3	2	2	20	24
	Total	58	32	32	122 species

		Predicted score 1	2	3	Total
Observed score	1	34	6	2	42
	2	3	14	5	22
	3	1	3	9	13
	Total	38	23	16	77 genera

Species: $\chi^2 = 94.8$, df = 4, $P < 0.001$.
Genera: $\chi^2 = 17.8$, df = 1, $P < 0.001$.

through correspondence analysis. The five groupings obtained from the dendrogram are highlighted in the figure: they can be clearly distinguished along the axis of the first 2 canonical variables (cumulating 27.9% and 21.9% of the variance, respectively). Groups no. 1 (woodpeckers, owls, hawks) and no. 2 (swifts, petrels and shearwather), appear well separated in the upper part of the figure. Duetting + CVD species appear in the lower part: groups no. 4 (divers and grebes) and no. 5 (Anatidae) are close. Two vocal duetters, the Crane and the Water Rail, not included in the five groups, occupy intermediate positions.

Discriminant analyses (Tables 3, 5) show two sets of variables, associated with CVD and vocal duetting, respectively. Vocal duetting is seen to be correlated with monogamy, morphological and chromatic monomorphism, and with territoriality. CVD, on the other hand, is correlated with nidifugous chicks, open nests, open-nesting and open-feeding habitats, vegetarian feeding and migratory attitudes. The ecological and behavioural independent variables are statistically predictive for discriminating vocal and vocal + CVD displayers (Tables 4, 6).

Similar results were obtained considering the genus or the species as the taxonomic unit.

DISCUSSION

Vocal duets. Two of the variables characterizing tropical duetters apply to the species of the Western Palearctic area as well, and therefore are not exclusive of tropical birds. All the authors (PAYNE 1971, THORPE 1972, KUNKEL 1974, SEIBT & WICKLER 1977) agree on the first characteristic, monogamous pair bonds, that was confirmed by our analysis. As to the second characteristic, absence of plumage dimorphism, FARABAUGH, unlike other authors (PAYNE 1971, THORPE 1972), did not regard this as a variable associated with duetting. However, according to FARABAUGH (1982) too, some general differences between monomorphic and dimorphic species do exist since duets by the latter group are less elaborate. In Palearctic non-passerine birds, this variable is clearly associated with duetting species.

The third variable, territoriality during reproduction, seems to be characteristic of the Palearctic duetters, even if year-round territoriality (a typical feature of tropical duetters, FARABAUGH 1982) may replace it in the tropical zones.

On the other hand, a fourth characteristic observed in tropical birds, that is, a dense vegetation habitat, is not specific of Palearctic duetters. THORPE & NORTH (1965), trying to account for the predominantly tropical distribution of duetting species, suggested that duets replace visual pair bonding displays in species living in dense tropical vegetation where visual communication is hindered. Later on, WICKLER (1980) and TODT & FIEBELKORN (1980) questioned the complementarity of these forms of display in different habitats. Our results confirm the non-complementarity hypothesis: CVD is exhibited almost invariably in conjunction with vocal duets and, as in the tropics, vocal duets are not exclusive to sheltered woody habitats (WICKLER 1980).

Coordinated visual displays. The ecological characteristics correlated with CVD species, namely: open habitats (1) for nesting and (2) for feeding; (3) open-nests; (4) nidifugous offspring; (5) migratory attitudes, differ from those of vocal duetters.

Table 5.

Discriminant Analyses conducted at the species or at the genus level: canonical loadings (correlations between variables and the 1st canonical factor) and discrimination of the duetting species.

Duetting variables	Canonical loadings (first factor)	
	Species n = 122	Genera n = 77
Pair bond	0.675	0.588
Territoriality in reproduction	−0.501	−0.426
Sexual dimorphism	0.420	0.559
Social pattern in reproduction	0.319	0.341
Movements	−0.124	−0.050
Parental care	−0.103	−0.124
Nest characteristics	−0.090	−0.192
Feeding habits	0.087	0.151
Young	0.054	0.030
Nest habitat	0.048	−0.099
Feeding habitat	0.042	0.111
Canonical correlations: 1st factor =	0.527	0.586
2nd factor =	0.382	0.331

Table 6.

Predictability of the duetting on the basis of the two Discriminant Analyses.

		Predicted score 1	2	3	Total
Observed score	1	23	9	5	37
	2	9	22	11	42
	3	7	10	26	43
	Total	39	41	42	122 species

		Predicted score 1	2	3	Total
Observed score	1	14	9	7	30
	2	8	13	6	27
	3	1	6	13	20
	Total	23	28	26	77 genera

Species: $\chi^2 = 36.1$, df = 4, $P < 0.001$.
Genera: $\chi^2 = 17.9$, df = 4, $P < 0.001$.

Incidentally, vegetarian feeding habits are only present in anatids and therefore can hardly be debated on the basis of the available data.

According to LACK's hypothesis (1968), the first four variables could be unified into a single factor: the open habitat. It is well known that life history traits of hole nesters vs open nesting species, such as nestling period and clutch size, may differ to a considerable extent. In the case of hole nesters, the virtual absence of predators makes for a larger clutch size and a longer nestling time, whilst the opposite is true in open nesting species.

Many hypothesis can be advanced about the presence of CVD: here we propose a few, which are not mutually exclusive. In contrast to vocal duetting, there is little literature on CVD.

All earlier hypothesis on CVD have stressed the aspect of pair bonding synchronization, although it is very difficult, we believe, to keep this function separate from the territorial one. We can start by assuming that in open habitats the summation of acoustic and visual forms of display is the outcome of predatory pressure, affecting adults and chicks alike, and promoting quick and early reproductive synchronization. Similarly, CVD would be associated with the migratory tendencies of these species, since birds reaching the breeding territory in spring need fast and strong pair strengthening.

Nor can it be ruled out that CVD in duetting species takes place wherever this is possible, whenever visual contact is not prevented, i.e. in birds of nocturnal habits, those nesting in thick woods (e.g., woodpeckers), and hole nesters (petrels, shearwaters and swifts).

An examination of the five groups isolated in this study can shed light on the outlined differences between CVD and duetting species. The first group of duetting, non-CVD, species consists of woodspeckers and owls living in thick woods or having nocturnal habits. A common dense-vegetation habitat surely represents a factor of considerable importance for a large proportion of tropical duetting birds as well (THORPE 1972). In the second group of purely duetting species we have grouped together swifts, petrels and shearwaters. LACK & LACK (1951) pointed out a number of converging eco-ethological characteristics in these two groups, both of them consisting of hole nesters and species faced with unpredictability in the amount of food resources available to them (food availability being mainly affected by weather conditions). Procellaridae and Apodidae do not exhibit all the characteristics of duetting birds, as they are normally migratory (a typical aspect of CVD species) and colonial birds whose territoriality is limited to the nest area.

Within the species displaying duetting + CVD, we can single out the three remaining groups. The first one is heterogeneous and less clearly defined than the others, as it includes some gulls and auks, nesting on cliffs or open habitats, the latter being a fundamental requisite of the species that exhibit CVD. This is not an orthodox group since these birds, despite their being CVD's, have nidicoulos offspring, albeit with a certain interspecific variability. The best known, and best studied, CVD's are those of the fourth (grebes and divers) and fifth groups (swans, geese and ducks): all of them are migratory birds with nidifugous young. Gaviidae and Podicipedidae, however, feed of fish and hence the relationship between a vegetarian diet and CVD cannot be seriously discussed here as it would be based solely on the habits of

Anatidae and, within non-passerine birds, there are only a few other vegetarian species.

In conclusion, a definitive interpretation of duetting and CVD in non-tropical birds is not yet possible primarily on account of the insufficient number of studies dealing with this problem.

Future work should focus on: a) a more detailed study of this aspect of behaviour, especially in lesser known species, e.g. the Pallid Swift (*Apus pallidus*) was not defined as duetting in the past, but recent studies describe modulated antiphonal calls (MALACARNE & CUCCO 1990), hence, other species of the Palearctic area would probably be defined as duetters upon a more thorough investigation; b) studies devoted to this specific problem, for example aimed at exploring both the context in which duetting is displayed and the visibility of the singer; c) the use of playback technique or other experimental manipulations. These approaches would surely lead to a substantial improvement in our knowledge on this point.

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