Ökol. Vögel (Ecol. Birds) 2, 1980: 199-220

Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radolfzell

Morphological aspects of ecological specialization in bird genera[1)]

Morphologische Aspekte der ökologischen Spezialisierung von Vogelgattungen

By **Bernd Leisler**

Key words: Eco-morphology, adaptive radiation, basic properties, specializing adaptations, Old World warblers, Sylviinae, *Acrocephalus, Locustella, Sylvia, Hippolais,* coexistence, habitat segregation, multivariate analysis, morphological life form.

Summary

This study of adaptive radiation at the generic level investigates morphological adaptations and specializations of European warblers (Sylviinae) of the genera *Locustella, Acrocephalus, Sylvia,* and *Hippolais.* Forty-two ecologically relevant morphological characters of 4 functional complexes (foot, hind limb, feeding apparatus, and flight apparatus) were measured and principal components analyses (PCA) were performed on the pooled data. Within the genus *Acrocephalus* there is greater morphological differentiation than within *Sylvia,* which is related to different coexistence mechanisms in these two genera. *Locustella* and *Acrocephalus* are foot specialists whereas use of wing and therefore wing morphology is more important in *Sylvia* and *Hippolais.* PCA of the characters of single functional complexes show how far the various groups have remained similar or have specialized in the respective complexes. The intra- and intergeneric morphological specializations can be interpreted in terms of the habitat and behaviour of each species. Cluster analysis of the same characters analysed by PCA shows the division of these major generic groups according to major »morphological life forms«.

Zusammenfassung

Am Beispiel verschiedener Grasmücken- (Sylviinae) Gattungen *(Locustella, Acrocephalus, Sylvia, Hippolais)* wird die Formenaufspaltung (adaptive Radiation) von Vogelgruppen auf einem niedrigen taxonomischen Niveau untersucht. Gefragt wird nach dem Grad der morphologischen Differenzierung der einzelnen Gattungen, nach ihren Basisanpassungen und nach den spezialisierenden Anpassungen der einzelnen Arten.

Die mitteleuropäischen Sylviinen wurden für die Untersuchung gewählt, weil sie artenreiche Gattungen stellen, häufige Kleinvögel und Weitstreckenzieher sind und die Mechanismen ihrer Koexistenz gerade untersucht werden.

Die Form der ökologischen Sonderung von Rohrsängern wird untersucht und mit der von Grasmücken verglichen. Diskriminanzanalysen verschiedener Habitatvariabler zeigen, nach welchen Merkmalen sich die Arten einer Gattung am stärksten trennen. Die Rohrsängerarten sind durch eine ziemlich präzise unterschiedliche horizontale Habitatselektion voneinander räumlich getrennt (Abb. 1). Die Habitattrennung der Grasmücken ist weniger gut. Alle 5 Arten können in ähnlicher Vegetation vorkommen (Abb. 2, CODY 1978).

[1)] Expanded version of a paper presented in the symposium »The Systematics – Ecology Interface« at the 1979 Annual Meeting of the American Society of Zoologists, Tampa.
Erweiterte Fassung eines Vortrages beim Symposium »The Systematics-Ecology Interface« während des Annual Meeting of the American Society of Zoologists, 1979, Tampa.

Anschrift des Verfassers:
Dr. B. Leisler, Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radofzell, 7760 Radolfzell, 16 Am Obstberg.

Die Körperformen der 15 Arten werden anhand von 42 ökologisch bedeutsamen äußeren morphologischen Maßen, Skelett- und Fluggefiedermerkmalen untersucht. Die Merkmale gehören zu 4 Funktionskomplexen (»Fuß«, »hinterer Bewegungsapparat«, »Nahrungsapparat«, »Flugapparatur«, Tab. 6), deren Funktion weitgehend bekannt ist.

Mittels Hauptkomponentenanalysen der größenkorrigierten Merkmalsmaße wird gezeigt, in welchen der 4 Funktionskomplexe sich die Arten einer Gattung spezialisiert haben, bzw. sich nicht oder nur wenig geändert haben (Abb. 3-7, Tab. 2-5).

Soweit dies für 3 Arten geschlossen werden kann, haben sich die Schwirle in keinem der untersuchten Funktionskomplexe stark differenziert und stellen morphologisch einen recht einheitlichen Lebensformtyp dar. Die Rohrsänger haben sich in allen Funktionskomplexen stark differenziert, am wenigsten im Flügelbau, wo sie zwar verschieden gute Streckenfliegereigenschaften entwickelten, aber im Hinblick auf Manövrierfähigkeit sehr einheitlich blieben. Sehr unterschiedliche Flugfähigkeiten haben die Grasmücken entwickelt, die sich aber durch große Einheitlichkeit im Schnabelbau auszeichnen. Grasmücken- und Schwirlarten unterscheiden sich in der Körpergröße stärker als Rohrsänger, die sich bis auf den großen Sprung zum Drosselrohrsänger größenmäßig wenig differenziert haben (Abb. 9).

Die Spezialisierungen einzelner Arten werden im Zusammenhang mit den artspezifischen Habitaten und den verschiedenen Formen der Habitatnutzung diskutiert.

Hauptkomponentenanalysen des gesamten Merkmalsatzes zeigen folgendes (Abb. 8, 9, Tab. 6):

1) Die untersuchten Gattungen gruppieren sich in distinkten Lebensformtypen. Dem entspricht, daß sich über weite Teile der Paläarktis die einzelnen Sylviidengattungen getrennte Lebensraumausschnitte erschlossen haben, die nur wenig überlappen.

2) Die Rohrsänger haben sich in der Körperform stärker differenziert als die Grasmücken. Das könnte darin begründet sein, daß sich die Rohrsänger bei der Besiedlung verschiedener Ausschnitte der Verlandungszone sehr fein an geringe Unterschiede der Vegetationsstruktur anpassen mußten.

3) Eine inverse (gegenläufige) Ausbildung von Hinterextremität und Flugapparatur ist bei den Gattungen als eine Basisanpassung an ihre Adaptationszonen festzustellen. *Locustella* und *Acrocephalus* sind beinbetont, während mit Höher- und Komplexerwerden der besiedelten Vegetation *Sylvia* und besonders *Hippolais* stärker flügelbetont sind.

Eine Klassifikation der Arten nach den 42 Merkmalen bringt folgendes Ergebnis (Abb. 10): Ökomorphologisch steht der Mariskensänger den Schwirlen näher als den Rohrsängern. Die einfarbigen Rohrsänger sind von den gestreiften getrennt. Innerhalb der Grasmücken stehen sich Mönchs- und Klappergrasmücke und Dorn- und Sperbergrasmücke nahe. Der Gelbspötter zeigt die größte Ähnlichkeit zur Gartengrasmücke.

1. Introduction

The major emphasis of eco-morphological studies has been concerned with morphological variation within communities (Karr & James 1975, Ricklefs & Cox 1977, Baker 1979, Norberg 1979, Ricklefs & Travis, in press, Bairlein 1980, Sorjonen 1980, see also Findley 1976 and Gatz 1979 for bat and fish communities respectively). The examination of adaptive radiation of generic groups within families seems to be an especially interesting aspect of eco-morphology, since genera should be both systematic as well as ecological units (Inger 1958, Illies 1970).

In studies of Old World warblers (subfamily Silviinae) I have compared the adaptive radiation of 4 ecologically as well as systematically related bird genera of Central Europe represented by the 6 Reed and Marsh warblers of the genus *Acrocephalus*, the 3 Grasshopper warblers *Locustella* and the 5 *Sylvia* warblers and the Icterine warbler *Hippolais icterina*, an arboreal member of the genus *Hippolais*. As part of the analysis I have also typified the ecological role and the basic morphological properties of these generic groupings as well as the specializations of the individual species.

Three aspects of the biology of these warbler groups make them paritcularly interesting for an eco-morphological investigation of taxonomic differentation:

1) Sylviine warblers are represented by several species-rich genera in Europe.
2) Nearly all these temperate zone warbler species are long distance migrants which spend the winter in Africa.
3) They show varying degree of spatial segregation within their habitats: clear spatial segregation among species of *Locustella* and *Acrocephalus* and extensive spatial overlap among *Sylvia* species. Thus we should expect different ecological specializations to be reflected in corresponding morphological features of the genera (basic properties) and furthermore of the species comprising them (specializing adaptations, WRIGHT 1941, HUXLEY 1943).

Over much of the Palaearctic region the individual Old World warbler genera have occupied discrete habitat subdivisions which overlap only slightly. Two alternative mechanisms of resource allocation have been found within different warbler genera in which feeding ecologies are similar. On one hand, for example, in the New World warblers (Parulidae) in spruce forests a clear segregation is found among species of a genus by foraging behaviour (MACARTHUR 1958). On the other hand many Old World Sylviine warblers show a clear segregation by habitat selection, both among and within genera. Mechanisms of coexistence in Sylviine warblers are currently being examined by different investigators (e.g. CATCHPOLE 1973, CODY & WALTER 1976, CODY 1978, BLONDEL 1969, FERRY 1974, SPITZ 1972 and LEISLER, in prep.).

2. Materials and Methods

To describe quantitative characteristics of the breeding habitats in the 6 *Acrocephalus* warblers, I have measured the following habitat variables in 270 territories in 4 study areas (Hortobágy Puszta, Hungary; Lake Neusiedl, Austria; Lake Constance, southwest Germany; Camargue, southern France): water depth, vegetation height, number of emergent elements and vegetation foliage profile. Foliage profile was measured using the «half-covered board» method (MACARTHUR &MACATHUR 1961). The total profile area (F) and the areas of sections of 50 cm (F_1-F_8) were rated as variables, so that 12 habitat characters were used in the analysis. Further details will be published elsewhere.

For the 15 Sylviid species investigated I use the abbreviations listed in Tab. 1.

The 42 characters I used to analyse morphological life form of the 15 species are listed in Tab. 6. The characters belong to 4 functional complexes: 1-18 flight apparatus (single feathers or their elements were measured), 19-28 foot functional complex, 29-37 feeding apparatus, 38-42 pelvis girdle and hind limb (LEISLER 1977 b.) Characters were chosen the functions of which were already known (LEISLER, in press, b).

Sample sizes per species for the characters of the flight apparatus are: Lf 12, Ll 15, Ln 12, Aa 11, As 17, Ap 19, Am 24, Asch 10, Apa 4, Sa 18, Sb 13, Sco 12, Scu 10, Sn 11, Hi 6. External and skeletal characters (19-42) of at least 10 adult specimens were used except Apa 4, Hi 6. Specimens have been collected mainly in southwest Germany and Austria.

As species of different sizes are being compared all measurements were transformed by cube root of «body size», a compound measurement of the body core skeleton: (sternum length + pelvis length + coracoid length) x (sternum width + pelvis width) x height of crista sterni (HOERSCHELMANN 1966, STORK 1968, RÜGER 1972).

For analysis I use two multivariate techniques (principal components analysis and discriminant function analysis) which reduce a large number of correlated variables into a smaller number of identifiable factors that determine similarities and differences among the units investigated (SNEATH & SOKAL 1973).

Table 1. Abbrevations of the species investigated.

Tab. 1. Abkürzungen der untersuchten Arten.

River warbler *(Locustella fluviatilis)*	Lf
Savi's warbler *(L. luscinioides)*	Ll
Grasshopper warbler *(L. naevia)*	Ln
Great reed warbler *(Acrocephalus arundinaceus)*	Aa
Reed warbler *(A. scirpaceus)*	As
Marsh warbler *(A. palustris)*	Ap
Moustached warbler *(A. melanopogon)*	Am
Sedge warbler *(A. schoenobaenus)*	Asch
Aquatic warbler *(A. paludicola)*	Apa
Blackcap *(Sylvia atricapilla)*	Sa
Garden warbler *(S. borin)*	Sb
Whitethroat *(S. communis)*	Sco
Lesser whitethroat *(S. curruca)*	Scu
Barred warbler *(S. nisoria)*	Sn
Icterine warbler *(Hippolais icterina)*	Hi

3. Results

Habitat preferences and habitat separation

Acrocephalus:

Across the zone of shallow eutrophic water in suitable European lakes one can find up to 6 *Acrocephalus* species along a habitat gradient of decreasing moisture from open water to land (LEISLER 1977 b). One generally finds each species in a specific zone associated with a certain vegetation structure within the habitat gradient. The 3 plain-backed warblers (Marsh warbler, Reed warbler and Great reed warbler) are found more in vertical oriented elements whereas the 3 streaked species (Sedge warbler, Aquatic warbler and Moustached warbler) are found in mixed vegetation and undergrowth of sedges and grasses.

To see which habitat variable shows the most distinction among the *Acrocephalus* species, a discriminant function analysis of 12 habitat variables was performed (Fig. 1). Axis I is an expression of a gradient from open water to land. It is correlated with decreasing vegetation density in the upper layers, decreasing vegetation height, decreasing number of emergent elements, and decreasing water depth, and increasing ground cover. Axis II means decreasing vegetation profile. Centroids of the

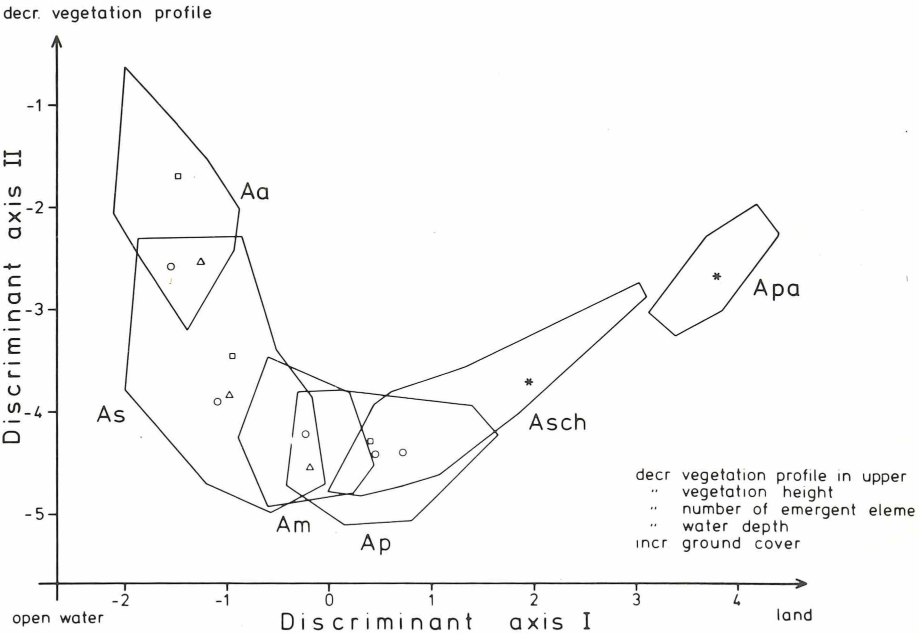

Fig. 1: Ordination of the habitats of 6 *Acrocephalus* species according to the first two discriminant axes. Axis I is a gradient from open water to land, axis II represents decreasing vegetation profile and decreasing vegetation profile in a layer at about 1 m. Centroids of the single study areas are: □ Lake Constance, ○ Lake Neusiedl, △ Camargue, ✳ Hortobágy. For species abbreviatons see Tab. 1.

Abb. 1: Ordinierung der Habitate von 6 *Acrocephalus*-Arten durch die ersten beiden Diskriminanzachsen. Achse I läßt sich als Gradient vom offenen Wasser zum Land interpretieren. Achse II bedeutet abnehmende Fläche des Vegetationsprofils und abnehmendes Pflanzenvolumen in ca. 1 m Höhe. Symbole sind Gruppenmittel aus den einzelnen Untersuchungsgebieten: □ Bodensee, ○ Neusiedlersee, △ Camargue, ✳ Hortobágy. Abkürzungen der Arten siehe Tab. 1.

individual species for different study sites are marked. This analysis shows a clear spatial segregation among species with little overlap. As a result the predictability of potential competitors is high at any given location in the gradient. Interspecific aggression seems to have evolved in *Acrocephalus* only in few species pairs which have locally overlapping ecological requirements (CATCHPOLE 1978).

Locustella:

The 3 *Locustella* warblers coexist in a heterogenous landscape because each species selects a different habitat in which to live, in a similar fashion to the situation in *Acrocephalus* (LEISLER 1977 a).

Savi's warbler has invaded the reed beds of the *Acrocephalus* zone whereas the River warbler occurs in boggy areas or in riverside meadows with long grasses with some bushes and trees. It is often in contact both with the Marsh warbler and the Grasshopper warbler, a weedy grassland species.

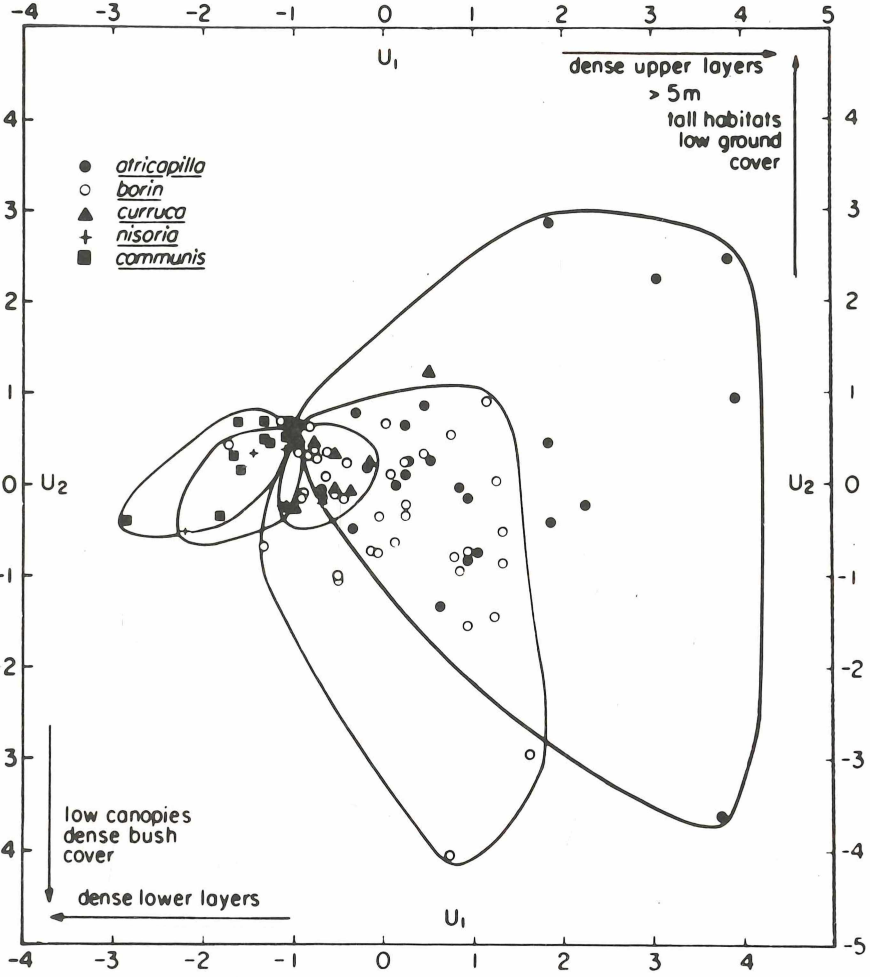

Fig. 2: Ordination of the habitats of 5 species of *Sylvia* in Sweden, based on the first two discriminant axes. Axis I is a gradient from dense lower layers to dense upper layers, axis II is a gradient from low canopies, dense bush cover to tall habitats and low ground cover (from CODY 1978).

Abb. 2: Ordinierung der Habitate von 5 *Sylvia*-Arten in Schweden durch die ersten beiden Diskriminanzachsen. Achse I führt von dichten unteren Schichten zu dichten oberen Schichten. Achse II führt von niedrigen Kronen und dichter Buschdeckung zu hohen Habitaten mit spärlichem Bodenbewuchs (Aus CODY 1978).

Sylvia:

Most species of *Sylvia* at middle latitudes in Europe are segregated by different habitat selection (LACK 1971), but many of them show extensive overlap (CODY 1978). Species of Sylvias are inhabitants of low woodland and tall scrub. The Lesser whitethroat inhabits scrubs of intermediate height. The Whitethroat can be found in the habitats with shortest vegetation, such as bramble patches and thorn hedges, whereas the Barred warbler inhabits dense bushes in an open clump like formation. Blackcaps and Garden warblers live in the tallest habitats. Blackcaps prefer dense canopy and dense middle layers and Garden warblers prefer dense but lower canopy.

In *Sylvia* species interspecific habitat segregation is less discrete than in *Acrocephalus* or *Locustella.* These warblers appear anomalous with respect to the mentioned alternative methods of resource allocation and show both ecological similarity and interspecific conflicts (CODY 1978, GARCIA 1979).

Figure 2 (taken from CODY 1978) shows habitat preferences of the 5 *Sylvia* species in Sweden, based on the first two discriminant axes describing changes in the height of dense vegetation and a gradient from low canopies with dense bush cover to tall habitats with low ground cover. Note that all five species can occupy common habitat at a point that represents 2-3 m open scrub. From this point each species appears to have radiated into different part of the habitat plane.

Hippolais:

The Icterine warbler is a canopy foraging member of the genus *Hippolais* in Central Europe (CODY 1978).

Table 2. Correlations of principal components I and II with 10 primary characters of the foot functional complex.

Tab. 2. Korrelationen der 10 Merkmale des Funktionskomplexes »Fuß« mit den ersten beiden Hauptkomponenten. Angegeben ist der Prozentsatz der durch die Komponenten erklärten Varianz.

Variables	Principal component I	II	
1 Foot span	**0,92**	0,35	
2 Foot span with hind and middle claw	**0,99**	0,09	
3 Hind toe	**0,92**	-0,34	
4 Inner toe	**0,66**	**0,74**	
5 Middle toe	**0,75**	**0,64**	
6 Outer toe	**0,87**	0,38	
7 Hind claw	**0,97**	-0,10	
8 Inner claw	**0,90**	-0,40	
9 Middle claw	**0,76**	**-0,63**	
10 Outer claw	**0,81**	**-0,56**	
			total
Percentage of total variance accounted for	74,32	22,21	96,53

Analysis of morphological life form

In examining the radiation of genera into adaptive zones, one must find out in which morphological complexes the animals differ distinctively and in which complexes they remain similar. Morphological similarity was examined by principal components analyses (PCA) in 42 ecologically relevant external characters and skeletal characters of 4 functional complexes (foot, hind limb, feeding apparatus and flight apparatus). I investigated 10 characters of the foot functional complex (Tab. 2), the functions of which are well known from morphological literature (RÜGGEBERG 1960). A clinging foot is characterized by long claws and a long hind toe, whereas a walking foot is characterized by short claws and inner and outer toe of equal lenght.

The loadings of the components to the original variables are listed in Tab. 2. Component I is positively correlated with all measurements of the foot, most strongly with characters of a clinging foot (hind toe, claw). Component II has positive loadings with inner and middle toe and negative ones with middle and outer claws, thus summarizes characters of a walking foot.

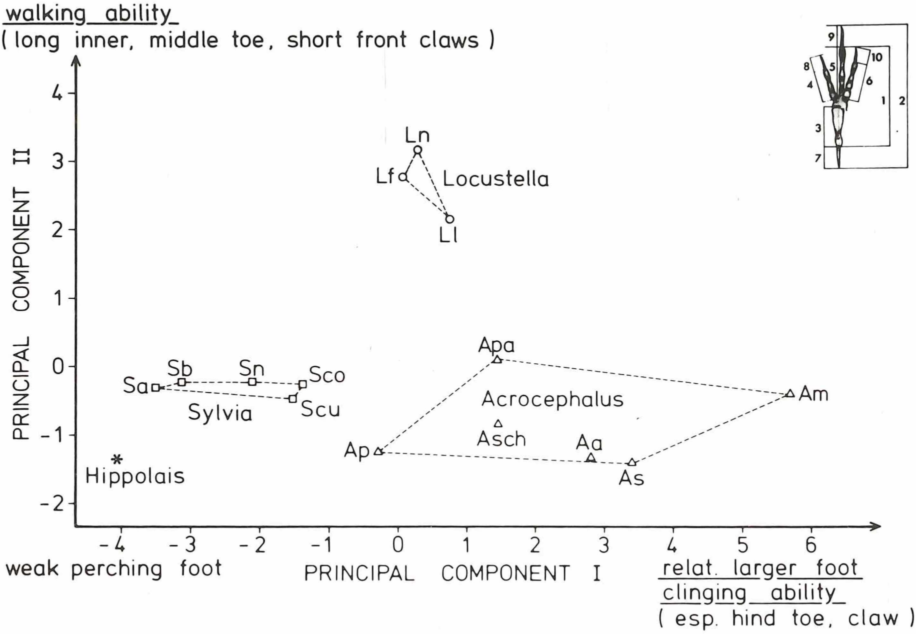

Fig. 3: Ordination of some Central European Sylviine warblers on the first two principal components constructed by analysis of 10 characters of the foot functional complex (inset). Symbols: ○ = *Locustella*, □ = *Sylvia*, △ = *Acrocephalus*, ✳ = *Hippolais*. For species abbreviations see Tab. 1.

Abb.3: Hauptkomponentenanalyse von 10 Merkmalen des Funktionskomplexes »Fuß« (Nebenbild) einiger mitteleuropäischer Sylviinen. Komponente I repräsentiert zunehmende Klammerfußeigenschaften, Komponente II zunehmende Stand/Lauffußeigenschaften. Symbole: □ = *Locustella*, □ = *Sylvia*, △ = *Acrocephalus*, ✳ = *Hippolais*. Abkürzungen der Arten siehe Tab. 1.

As figure 3 shows, component I leads from a weak perching foot to a relatively larger foot, suited for vertical clinging, whereas component II characterizes increasing features of a walking foot. *Hippolais* has a weak perching foot, as have the Blackcap and Garden warbler, which are the upper story warblers within the genus *Sylvia*. On the other hand the Whitethroat and Lesser whitethroat, which inhabit lower scrub, have stronger feet.

Acrocephalus warblers have evolved good clinging abilities associated with their locomotion on vertical stalks. As an adaptation to the herbaceous vegetation of its habitat the Marsh warbler has the weakest foot. At the right end of the picture the Moustached warbler shows a very specialized foot both for clinging and hopping in its very dense habitat. The Aquatic warbler which invaded meadows has developed a foot with good walking abilities somewhat similar to the Locustellas (LEISLER 1975).

As ground dwelling species, the 3 Grasshopper warblers have evolved good walking abilities. Savi's warbler which is more a hopping species in an *Acrocephalus* habitat has evolved the best clinging ability within the genus (LEISLER 1977 a).

I examined 5 characters of the pelvic girdle and the appendicular skeleton. From functional morphological investigations it has been shown that birds that climb on vertical surfaces and have no supporting tail need long, flexible legs (WINKLER & BOCK 1976). Component I has negative loadings with the three leg segments and pelvis length and can be interpreted as a decreasing capability for vertical climbing (see Tab. 3). Component II is decreasing pelvis length, the functions of which are not known. Fig. 4 shows the ordering of the species according to the 5 characters. The components demonstrating decreasing capability for vertical climbing and decreasing pelvis length separate the genera distinctively. All genera are widely spaced, that is the single species developed different methods of locomotion. Great reed and Reed warbler are the best vertical climbers which corresponds with their life in reed beds, whereas arboreal perchers, Blackcap, Garden warbler and *Hippolais* have short legs.

Table 3. Correlations of principal components I and II with 5 primary characters of the pelvis girdle and hind limb.

Tab. 3. Korrelationen der 5 Merkmale des Funktionskomplexes »Hinterer Bewegungsapparat« mit den ersten beiden Hauptkomponenten.

Variables	Principal I	component II	
1 Femur	**-0,84**	-0,41	
2 Tibiotarsus	**-0,94**	0,21	
3 Tarsometatarsus	**-0,82**	0,41	
4 Pelvis lenght	**-0,74**	**-0,62**	
5 Pelvis width	0,56	-0,48	
			total
Percentage of total variance accounted for	62,54	19,72	82,26

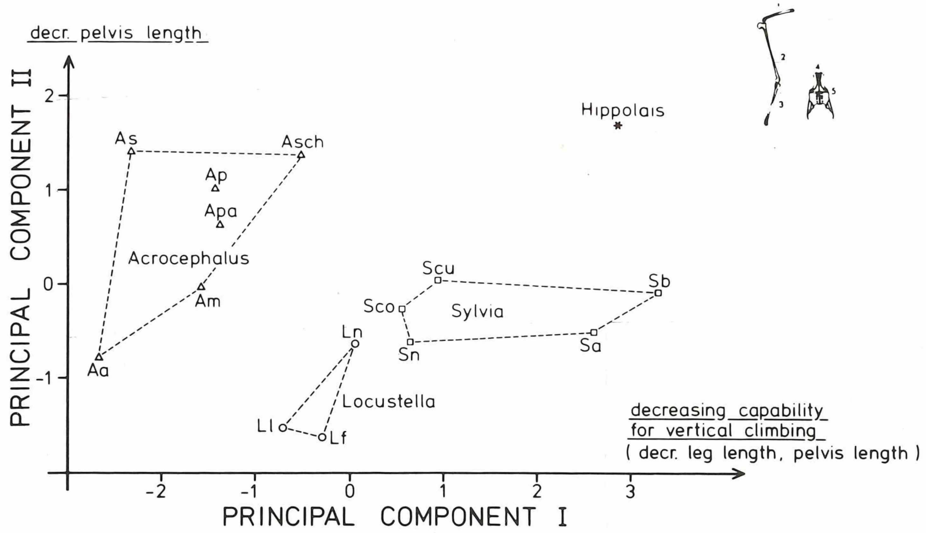

Fig. 4: Ordination of some Central European Sylviine warblers on the first two principal components constructed by analysis of 5 characters of the pelvic girdle and hind limb (inset). For symbols see Fig. 3, for species abbreviations see Tab. 1.

Abb.4: Hauptkomponentenanalyse von 5 Merkmalen des Funktionskomplexes »Hinterer Bewegungsapparat« (Nebenbild) einiger mitteleuropäischer Sylviinen. Komponente I bedeutet abnehmende Vertikalklettereigenschaften, Komponente II abnehmende Beckenlänge. Symbole wie in Abb. 3. Abkürzungen der Arten siehe Tab. 1.

Table 4. Correlations of principal components I and II with 9 primary characters of the feeding apparatus.

Tab. 4. Korrelationen der 9 Merkmale des Funktionskomplexes »Nahrungsapparat« mit den ersten beiden Hauptkomponenten.

Variables	Principal	component	
	I	II	
1 Bill length/feathering	0,27	**-0,91**	
2 Bill length/nostril	0,38	**-0,92**	
3 Bill length/skull	0,36	**-0,93**	
4 Bill length/flanges	0,39	**-0,88**	
5 Bill depth	**0,68**	0,36	
6 Bill width/nostril	**0,87**	-0,20	
7 Bill width/base	**0,93**	0,19	
8 Bill width/flanges	**0,91**	0,10	
9 Length of rictal bristles	**0,81**	-0,14	
			Total
Percentage of total variance accounted for	54,33	30,17	84,50

In the same way 9 elements of the feeding apparatus were examined the functions of which are well documented (BOCK 1964, 1966, Tab. 4). Surprisingly the functions of rictal bristles are not quite clear yet (LEDERER 1972, STETTENHEIM 1974). As accessory food capturing structures they might have an important function in mandibulating and directing food into the gape.

Component I has positive loadings to bill depth, width and length of rictal bristles, component II has negative loadings to bill length. In Fig. 5 the genera investigated are segregated by the first two principal components constructed by analysis of the 9 elements of the feeding apparatus. On the lower right bills suitable for capturing highly mobile prey which have high values in component I and low values in component II are found. The grassgleaning Locustellas and the foliage gleaning Sylvias

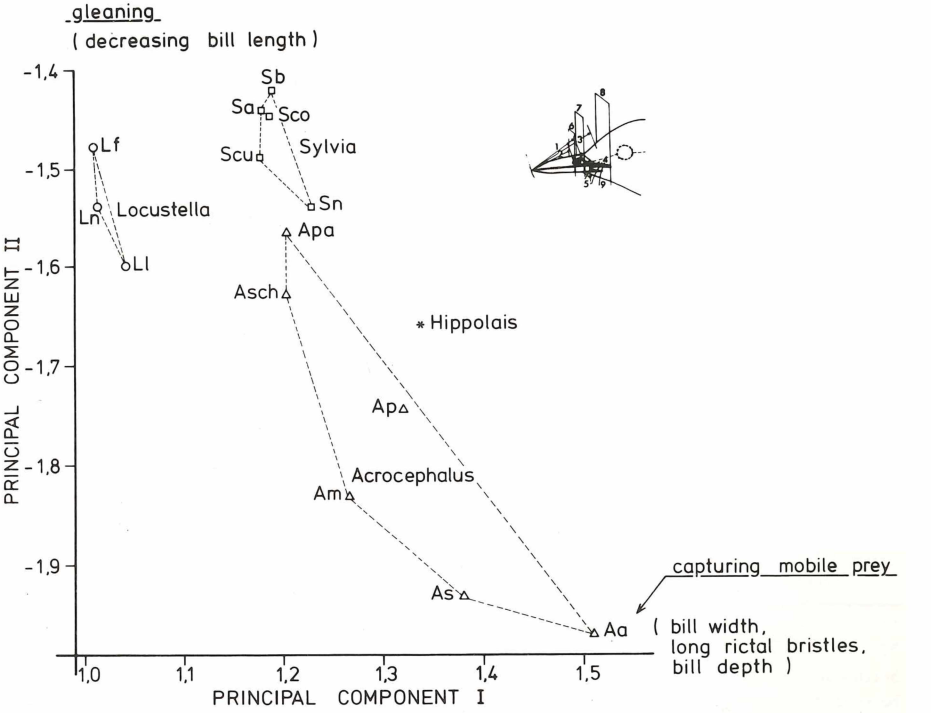

Fig. 5: Ordination of some Central European Sylviine warblers on the first two principal components constructed by analysis of 9 characters of the feeding apparatus (inset). For symbols see Fig. 3, for species abbreviations see Tab. 1.

Abb. 5: Hauptkomponentenanalyse von 9 Merkmalen des Funktionskomplexes »Nahrungsapparat« (Nebenbild) einiger mitteleuropäischer Sylviinen. Komponente 1 bedeutet zunehmende Schnabelbreite, -höhe, Länge der Vibrissen. Komponente II bedeutet abnehmende Schnabellänge. Symbole wie in Abb. 3. Abkürzungen der Arten siehe Tab. 1.

show small morhpological differences among species, that means these two genera have evolved little in the way of specific feeding adaptations. It would be interesting to investigate whether similarity in bill shape is linked to overlap in diet. The Reed warblers are widely spaced. At one end short-billed gleaning forms can be found (Aquatic warbler), whereas on the other Great reed warbler and Reed warbler are adept at capturing highly mobile prey.

The results of the analysis of 18 characters of the flight apparatus are shown in Tab. 5, where the loadings of the components to the original variables are listed. Component I is positively correlated with the distal primaries forming the wing tip and with the secondaries and with the length and pointedness of the wing. Component I is negatively correlated with the graduation of tail. As to functional morphology this component summarizes characters of high performance fliers: long pointed wings, and square ended tails (RÜPPELL 1975).

Component II is positively correlated with a round wing tip, with all notches, the first secondary and negatively correlated with pointedness. Avian wing tip slots reduce induced drag by limited span (HUMMEL, in press). Thus component II represents characters of extremely round wings with great manoeuvrability suited for numerous rapid take-offs.

Table 5. Correlations of the first three principal components with 18 primary characters of the flight apparatus.

Tab. 5. Korrelationen der 18 Merkmale des Funktionskomplexes »Flugapparatur« mit den ersten drei Hauptkomponenten.

Variables		Principal	component		
		I	II	III	
1 Alula		0,42	-0,07	**0,66**	
2 Primary	X	-0,12	**0,88**	0,11	
3 Primary	IX	**0,75**	**-0,62**	0,16	
4 Primary	VIII	**0,98**	-0,15	0,02	
5 Primary	VII	**0,98**	0,19	-0,07	
6 Primary	VI	**0,90**	0,42	0,00	
7 Notch of primary	X	-0,37	**0,70**	0,14	
8 Notch of primary	IX	0,40	**0,63**	-0,48	
9 Notch of primary	VIII	0,34	**0,80**	-0,23	
10 Notch of primary	VII	0,22	**0,87**	-0,13	
11 Secondary 1		**0,75**	**0,61**	0,11	
12 Secondary 9		**0,69**	-0,34	0,50	
13 Tail		0,37	0,44	**0,74**	
14 Graduation of tail		**-0,70**	-0,14	**0,63**	
15 Wing tip to prim.	X	**0,74**	**-0,60**	-0,05	
16 Wing tip to sec.	1	0,38	**-0,78**	-0,09	
17 Wing/tail		-0,29	0,41	**0,76**	
18 Wing		**0,97**	0,10	0,05	
					Total
Percentage of total variance accounted for		40,7	30,8	14,5	86,0

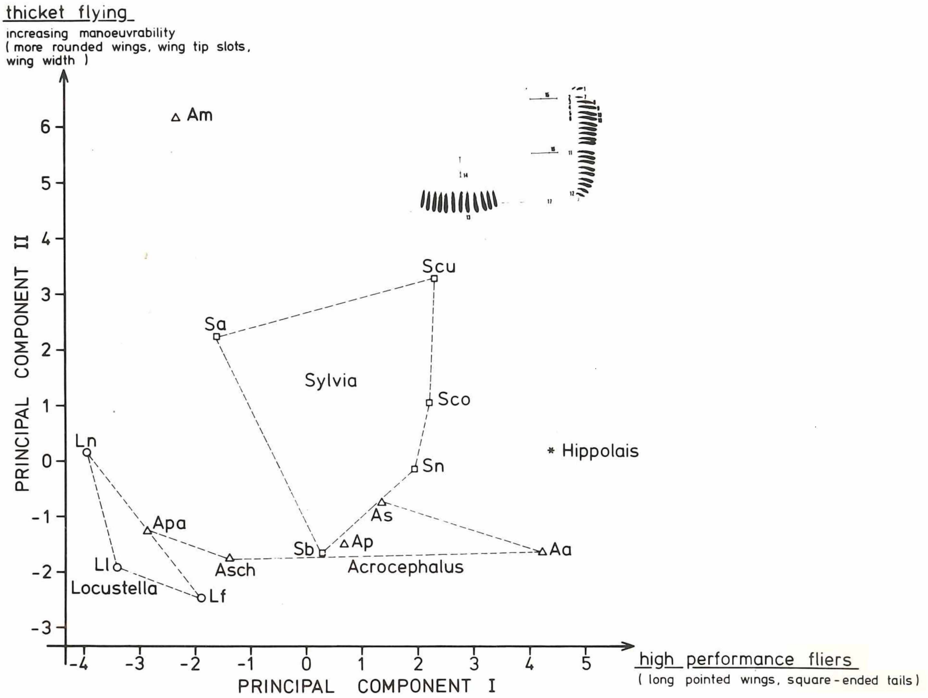

Fig. 6: Ordination of some Central European Sylviine warblers on the first two principal components constructed by analysis of 18 characters of the flight apparatus (inset). For symbols see Fig. 3, for species abbreviations see Tab. 1.

Abb. 6: Hauptkomponentenanalyse von 18 Merkmalen des Funktionskomplexes »Flugapparatur« (Nebenbild) einiger mitteleuropäischer Sylviinen. Komponente I repräsentiert zunehmende Eigenschaften von Streckenfliegern, Komopnente II zunehmende Eigenschaften von Eckenfliegern. Symbole wie in Abb. 3. Abkürzungen der Arten siehe Tab. 1.

In the morphological space represented by the first two principal components one sees poor fliers in the lower left. These are all the Grasshopper warblers, *Locustella*, and the Aquatic warbler. As ground-walking and skulking species of thick ground cover, they feed almost exclusively by pedestrian searching. They are reluctant to fly, and use the wings mainly for migratory flight (LEISLER 1977 a). The Reed warblers are widely spread over component I. As all of them except the Moustached warbler are trans-Sahara migrants (MOREAU 1972, LEISLER 1973, ZINK 1973), this means that from the Aquatic warbler to the Great reed warbler wing morphology plays an increasing role in habitat utilization, the higher the vegetation is.

Furthermore it is striking that the Reed warblers do not differ in manoeuvrability (component II), all are one line. The isolated position of the Moustached warbler apparently results from the fact, that it has not developed a special wing for migration. As a thicket dweller it could develop a wing especially suited for flying about the vegetation cover.

The *Sylvia* warblers have specialized very much in component II and developed different flight capacities which might be crucial in habitat exploitation. Lesser whitethroats have the most specialized wing.

In the functional complex for flight the results with the third component are instructive (Tab. 5). Component III shows positive correlations to alula and tail length, tail graduation and wing/tail ratio. As component III is composed heterogenously it might have different functions (for the functions of the alula, see NACHTIGALL & KEMPF 1971). The three dimensional picture (Fig. 7) shows the ordering of the species according to the three characters: (1) increasing length and pointedness of

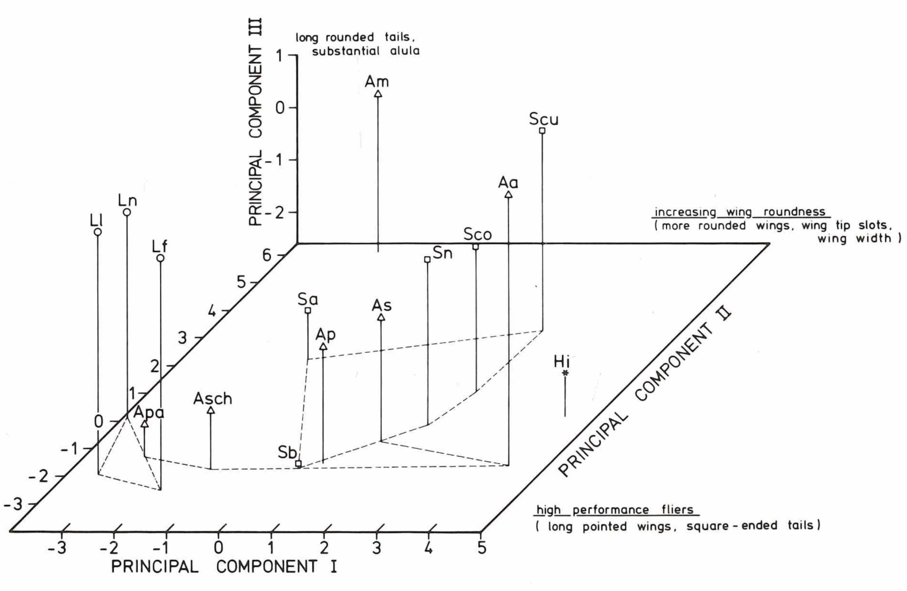

Fig. 7: Ordination of some Central European Sylviine warblers on the first three principal components constructed by analysis of 18 characters of the flight apparatus. For symbols see Fig. 3, for species abbreviations see Tab. 1.

Abb 7: Hauptkomponentenanalyse von 18 Merkmalen des Funktionskomplexes »Flugapparatur« einiger mitteleuropäischer Sylviinen. Komponente I repräsentiert zunehmende Streckenfliegereigenschaften, Komponente II zunehmende Eckenfliegereigenschaften, Komponente III bedeutet zunehmende Schwanzlänge und -stufung und zunehmende Alulalänge. Symbole wie in Abb. 3. Abkürzungen der Arten siehe Tab. 1.

wing, (2) increasing wing roundness, and (3) increasing length and graduation of tail together with length of alula. We have already discussed the configuration of species according to the first two components. With regard to the relation of component I and III we can recognize that in some species with increasing wing length and pointedness tail length and alula length increase. Single groups of species differ from this trend, which means that they have followed other evolutionary pathways. For example, the Grasshopper warblers, *Locustella,* as poor fliers, have extremely long, rounded tails. This suggest that their tail has another function than that in the other species examined. Probably it helps the birds to balance when creeping and threading through dense vegetation (GASTON 1974, LEISLER 1977 a).

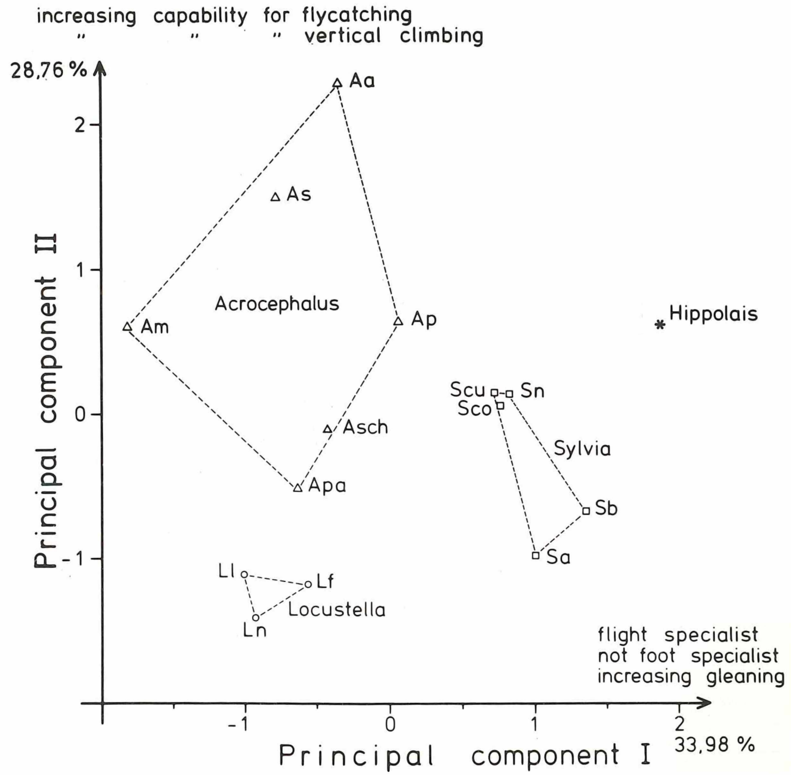

Fig. 8: Ordination of some Central European Sylviine warblers on the first two principal components, constructed by analysis of the pooled 42 character set. For symbols see Fig. 3, for species abbreviations see Tab. 1.

Abb. 8: Hauptkomponentenanalyse aller 42 morphologischen Merkmale einiger mitteleuropäischer Sylviinen. Komponente I bedeutet zunehmende Flügelbetonung, abnehmende Beinbetonung, zunehmendes Abklauben. Komponente II bedeutet zunehmende Flugjagd, zunehmende Vertikalklettereigenschaften. Symbole wie in Abb. 3. Abkürzungen der Arten siehe Tab. 1.

Table 6: Correlations of the principal components I and II with the pooled 42 character set with (A) and without size transformation (B). Only significant correlations are listed.

Tab. 6: Korrelationen der 42 Körpermaße (A größenkorrigiert, B ohne Größenkorrektur) mit den beiden ersten Hauptkomponenten. Nur die signifikanten Korrelationen sind aufgeführt.

		A		B	
	Variables	Principal	component	Principal	component
		I	II	I	II
1	Alula			-0,94	
2	Primary X				
3	Primary IX			-0,91	
4	Primary VIII	0,60	0,72	-0,92	
5	Primary VII	0,59	0,77	-0,90	
6	Primary VI	0,50	0,73	-0,89	
7	Notch of primary X	-0,56			
8	Notch of primary IX				0,74
9	Notch of primary VIII				0,73
10	Notch of primary VII				0,56
11	Secondary 1		0,69	-0,89	
12	Secondary 9		0,56	-0,94	
13	Tail, longest rectrix			-0,89	
14	Graduation of tail	-0,75			-0,94
15	Wing tip to prim. X		0,53	-0,90	
16	Wing tip to sec. 1			-0,80	
17	Wing/tail ratio				
18	Wing, longest primary	0,52	0,79	-0,93	
19	Foot span	-0,98		-0,82	-0,54
20	Foot span with claws	-0,95		-0,82	-0,51
21	Hind toe	-0,71	0,62	-0,91	
22	Inner toe	-0,87		-0,54	-0,74
23	Middle toe	-0,92		-0,68	-0,66
24	Outer toe	-0,91		-0,82	
25	Hind claw	-0,86		-0,70	-0,50
26	Inner claw	-0,66	0,70	-0,80	
27	Middle claw	-0,46	0,73	-0,72	
28	Outer claw	-0,53	0,74	-0,66	
29	Bill length/feathering	-0,55	0,69	-0,94	
30	Bill length/nostril		0,82	-0,90	
31	Bill length/skull		0,82	-0,92	
32	Bill length/flanges		0,80	-0,94	
33	Bill depth			-0,90	
34	Bill width/nostril		0,77	-0,83	
35	Bill width/base	0,74	0,62	-0,81	0,56
36	Bill width/flanges		0,61	-0,94	
37	Rictal bristles		0,76		0,68
38	Femur	-0,80		-0,91	
39	Tibiotarsus	-0,73	0,63	-0,96	
40	Tarsometatarsus	-0,57	0,69	-0,91	
41	Pelvis length	-0,69		-0,93	
42	Pelvis width			-0,74	
Percentage of total variance accounted for		33,98	28,76	60,75	16,36
total		62,74		77,11	

I investigated some basic morphological differences within and between genera by a PCA of the 42 pooled characters (see Tab. 6 A). Component I seemed most influenced by 2 sets of inversely related characters that is a contrast between elements of the flight apparatus and elements of hind limb and foot. Component I has also a positive loading with bill-width and a negative loading with bill-length, characters which can be interpreted as increasing capability for gleaning. From examination of component I in Fig. 8, it appears that *Acrocephalus* and *Locustella* are foot specialists, whereas *Sylvia* and especially *Hippolais* are flight specialists with increasing gleaning abilities.

Loadings with component II can be interpreted as an increasing capability for fly-catching (long wing tip, chord of wing, bill length and width and length of rictal bristles) and increasing capability for vertical clinging (long hind toe, front claws and distal leg segments). *Locustella* warblers have the lowest values on this axis whereas the plainbacked *Acrocephalus* warblers, which inhabit stiff stemmed plants, have the highest.

To reveal size differences as well as basic properties within and between genera the full 42 character set was analysed without transformation by body size (Tab. 6 B). Component I has high negative loadings to all characters except distal primary, notches, tail graduation and rictal bristles, and therefore serves to differentiate the units largely on the basis of decreasing size (Fig. 9). GIBSON et al. (1976) have stated that where a principal component can be interpreted as a general factor (high, equal-sign correlations with all characters) it does not describe mere size variation but variation both in size and shape. Thus we have to expect also some shape information in component I. Component II is effective in distinguishing the units chiefly on an inverse relationship between increasing use of wing and manoeuvrability (square ended tails, deep notches) and decreasing use of foot (decreasing walking and clinging abilities). Component II also loads positively to characters advantageous for capturing mobile prey in more open habitat (broader bills, long rictal bristles). According to component II the genera are nicely separated. This corresponds to the occupation of different adaptive zones by the single genera, from ground dwelling species in thick vegetation *(Locustella)* up to upper story warblers in more open situations *(Hippolais)*.

To assess eco-morphological affinities between species and to classify the position of single species, the 42 character set was used in a cluster analysis (correlation coefficients, weighted pair-group average clustering). The correlation phenogram (Fig. 10) shows the *Locustella* species clustered tightly. Note the isolated position of the Moustached warbler, which is in other aspects a typical *Acrocephalus* species (PARKER & HARRISON 1963, LEISLER 1971) and which has evolved some convergent similarities to the Locustellas. The other *Acrocephalus* species, plainbacked as well as streaked, are clustered tightly, whereas *Hippolais* is grouped in the *Sylvia* cluster, most closely to the Garden warbler. Within the Sylvias there are two groups in this

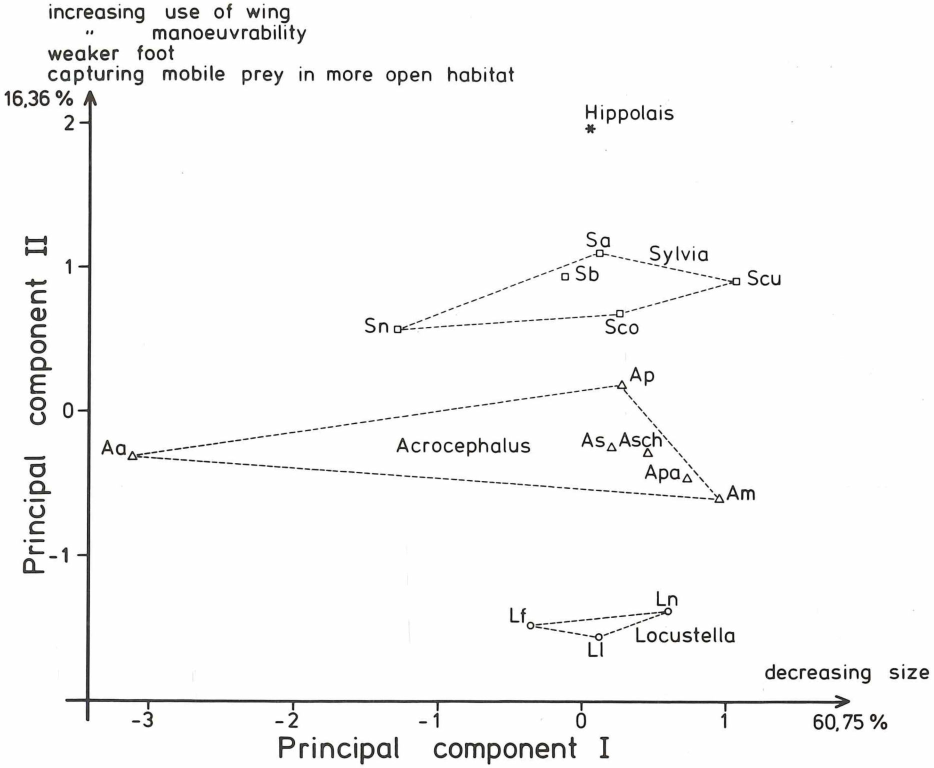

Fig. 9: Ordination of some Central European Sylviid warblers on the first two principal components constructed by analysis of the pooled 42 character set without size transformation. For symbols see Fig. 3, for species abbreviations see Tab. 1.

Abb. 9: Hauptkomponentenanalyse aller 42 nicht größenkorrigierten Körpermerkmale einiger mitteleuropäischer Sylviinen. Komponente I bedeutet hauptsächlich abnehmende Körpergröße. Komponente II bedeutet zunehmenden Flügelgebrauch, zunehmende Manövrierfähigkeit, zunehmend schwächere Fußausbildung und Zunahme von Schnabelbreite und Vibrissenlänge. Symbole wie in Abb. 3. Abkürzungen der Arten siehe Tab. 1.

regard: Firstly the Blackcap and the Lesser whitethroat and secondly the Whitethroat and the Barred warbler. A classification of the same units according to other systematically meaningful characters (e.g. variables like egg colour, tongue spots, downs of juveniles etc.) would have yielded yet another taxonomic grouping.

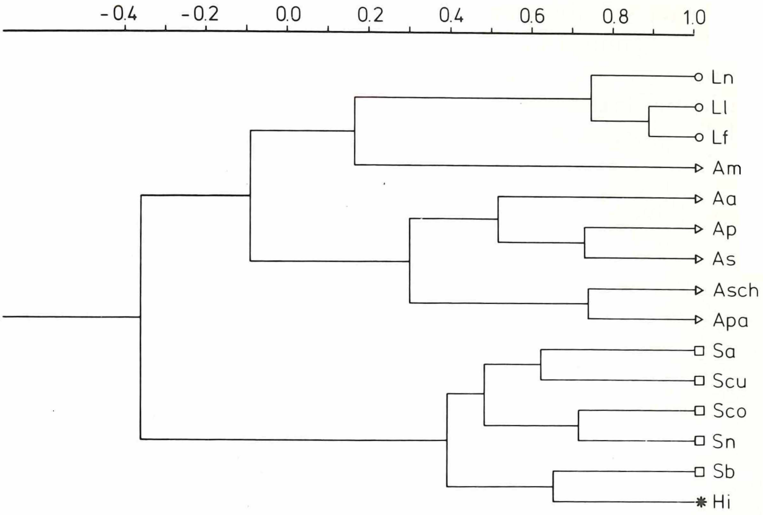

Fig. 10: A dendrogram of ecomorphological similarity in the species studied. For symbols see Fig. 3, for species abbreviations see Tab. 1.

Abb. 10: Dendrogramm der ökomorphologischen Ähnlichkeit der untersuchten Arten. Symbole wie in Abb. 3. Abkürzungen der Arten siehe Tab. 1.

3. Discussion

Sylvia and *Locustella* each show great intrageneric differences in body size. The *Acrocephalus* warblers were generally similar in size, except for the big difference of the Great reed warbler (Fig. 9, LEISLER, in press, a).

The species of *Locustella* showed little morphological differentation and thus represent a homogenous life from.

Most *Acrocephalus* species are isolated from each other by very precise species-specific horizontal habitat selection. Although the vegetation is successional *Acrocephalus* warblers encounter relatively high habitat reliability (high predictability both of resources and coinhabitants in a short structurally simple vegetation with high productivity). During their radation into different zones of the habitat gradient *Acrocephalus* warblers had to adapt precisely to slightly different vegetation structures. Thus they specialized very much in the structures of hind limb, foot, bill, and to some extent wing.

CODY (1978) has pointed out that particularly in the more northern and presumably younger *Sylvia* communities species exercise very broad habitat preferences with wide interspecific overlaps. Intermediate habitat, acceptable for all 5 species is 2-3 m shrub which often is successional or seral in nature. *Sylvia* warblers have remained similar in bill construction and have mainly differeniated in flight apparatus and not so much in leg construction.

As can be seen from Fig. 8 *Acrocephalus* warblers, although very similar in general appearance, have differentiated morphologically more than *Sylvia* warblers.

As we have seen the single genera are always separated from one another both in single functional complexes and in overall morphological similarity. The reasons for this may be that the different Sylviine genera have occupied discrete parts of the habitat, which overlap little.

During the occupation of new adaptive zones by the single genera, different use of foot and wing was important, accompanied by specializations of the bill. Fig. 8 and 9 clearly show the genera *Locustella* and *Acrocehpalus* to be foot specialists. With increasing vegetation height and structural complexity, use of wing becomes more important in *Sylvia* and *Hippolais*. An inverse relationship between elements of the hind limb and elements of the flight apparatus has been found by STORK (1968) in 6 European species of the genus *Turdus*. Also GIBSON et al. (1976) found a «contrast» between elements associated with the wing and with the leg in 11 North American and 2 European thrushes.

A comparison with ecological equivalents shows also that searching on foot might have been a key adaptation for exploiting thick ground cover in *Locustella* warblers. In *Acrocephalus* the evolution of vertical clinging seems to have been a basic property by invading the land succession zone (LEISLER 1977 b) while in *Sylvia* species of Central Europe differentiations of the flight apparatus and the foot might have been crucial.

Acknowledgements: I thank the following persons for assisting me during field work: R. BUCHWALD, CH. BUSSMANN, W. DORNBERGER, M. KASPAREK, A. SPITZNAGEL, K. WÜSTENBERG. PROF. FANCES JAMES commented on an ealier draft of the paper and made helpful suggestions. I am most grateful to DR.H. WINKLER who computed the multivariate analyses and to PROF. G.J.KENAGY who revised the English of the manuscript.

Literature

Bairlein, F. (1980): Ökosystemanalyse der Rastplätze von Zugvögeln: Beschreibung und Deutung der Verteilungsmuster von ziehenden Kleinvögeln in verschiedenen Biotopen der Stationen des »Mettnau-Reit-Illmitz-Programmes«. Diss. Univ. Konstanz. – Baker, M. CH. (1979): Morphological correlates of habitat selection in a community of shore birds (Charadriiformes). Oikos 33: 121-126. – Blondel, J. (1969): Synécologie des oiseaux résidents et migrateurs dans un échantillon de la région méditerranéenne francaise. C.R.D.P. Marseille. – Bock, W.J. (1964): Kinetics of the avian skull. J. Morphol. 114: 1-42. – Bock, W.J. (1966): An approach to the functional analysis of bill shape. Auk 83: 10-51. – Catchpole, C.K. (1973): Conditions of co-existence in sympatric breeding populations of *Acrocephalus* warblers. J. Anim. Ecol. 42: 623-635. – Catchpole, C.K. (1978): Interspecific territorialism and competition in *Acrocephalus* warblers as revealed by playback experiments in areas of sympatry and allopatry. Anim. Behav. 26: 1072-1080. – Cody, M.L. (1978): Habitat selection and interspecific territoriality among the Sylviid warblers of England and Sweden. Ecol. Monogr. 1978: 351-396. – Cody, M.L., & H. Walter (1976): Habitat selection and interspecific interactions among Mediterranean sylviid warblers. Oikos 27: 210-238. – Ferry, C. (1974): Fécondité et réussite de la reproduction chez le Grand Contrefaisant *Hippolais icterina* en allopatrie et en sympatrie avec le Petit *H. polyglotta*. Jean le Blanc 13: 1-10. – Findely, J.S. (1976): The structure of bat communities. Am. Nat. 110: 129-139. – Garcia,E.F.J. (1979): Interspecific territoriality in Blackcaps and Garden warblers. Abstracts Intern. Ethol. Congr. Vancouver. – Gatz, A.J.Jr. (1979): Community organization in fishes as indicated by morphological features. Ecology 60: 711-718. – Gaston, A.J. (1974): Adaptation in the genus *Phylloscopus*. Ibis 116: 432-450. – Gibson, A.R., M.A. Gates & R. Zach (1976): Phenetic affinities of the Woodthrush, *Hylocichla mustelina* (Aves, Turdinae). Can. J. Zool. 54: 1679-1687. – Hoerschelmann, H. (1966): Allometrische Untersuchungen an Rumpf und Flügel von Schnepfenvögeln (Charadriidae und Soclopacidae). Z. Zool. Syst. Evol. forsch. 4: 209-317. – Hummel, D. (in press): The aerodynamic characteristics of slotted wing-tips in soaring birds. Proc. XVII Intern. Orn. Congr. – Huxley, J. (1943): Evolution, the modern synthesis. New York, Harper. – Illies, J. (1970): Die Gattung als ökologische Grundeinheit. Faunist. ökol. Mitt. 3: 369-372. – Inger, R.F. (1958): Comments on the definition of genera. Evolution 12: 370-384. – Karr, J.R., & F.C. James (1975): Eco-morphological configurations and convergent evolution on species and communities. In: M.L. Cody & J.M. Diamond (eds): Ecology and Evolution of Communities: 258-291. – Lack, D. (1971): Ecological isolation in birds. Oxford and Edinburgh. – Lederer, R.J. (1972): The role of avian rictal bristles. Wilson Bull. 84: 193-197. – Leisler, B. (1971): Vergleichende Untersuchungen zur ökologischen und systematischen Stellung des Mariskensängers *(Acrocephalus, Lusciniola melanopogon, Sylviidae)*, ausgeführt am Neusiedler See. Diss. Univ. Wien. – Leisler, B. (1973): Die Jahresverbreitung des Mariskensängers *(Acrocephalus melanopogon)* nach Beobachtungen und Ringfunden. Vogelwarte 27: 24-39. – Leisler, B. (1975): Die Bedeutung der Fußmorphologie für die ökologische Sonderung mitteleuropäischer Rohrsänger *(Acrocephalus)* und Schwirle *(Locustella)*. J. Orn. 116: 117-153. – Leisler, B. (1977) a: Die ökologische Bedeutung der Lokomotion mitteleuropäischer Schwirle *(Locustella)*. Egretta 20: 1-25. – Leisler, B. (1977) b: Ökomorphologische Aspekte von Speziation und adaptiver Radiation bei Vögeln. Vogelwarte 29, Sonderheft: 136-153. – Leisler, B. (1980) a: Morphologie und Habitatnutzung europäischer *Acrocephalus*-Arten. Proc. XVII Intern. Orn. Congr. In press. –

LEISLER, B. (1980) b: Ökomorphologische Freiland- und Laboratoriumsuntersuchungen. Proc. XVII Intern. Orn. Congr. In press. – MACARTHUR, R.H. (1958): Population ecology of some warblers of Northeastern coniferous forests. Ecology 39: 599-619. – MACARTHUR, R.H., & J.W. MACARTHUR (1961): On bird species diversity. Ecology 42: 594-598. – MOREAU, R.E. (1972): The Palaearctic-African bird migration systems. Academic Press. London, New York. – NACHTIGALL, W., & B. KEMPF (1971): Vergleichende Untersuchungen zur flugbiologischen Funktion des Daumenfittichs (Alula spuria) bei Vögeln. Z. vergl. Physiol. 71: 326-341. – NORBERG, U.M. (1979): Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest, and the treecreeper in relation to locomotor pattern and feeding station selection. Phil. Transact. Royal Soc. London 287 (B 1019): 131-165. – PARKER, S.A., & C.J.O. HARRISON (1963): The validity of the genus *Lusciniola* Gray. Bull. Brit. Orn. Cl. 83: 65-69. – RICKLEFS, R.E., & G.W. COX (1977): Morphological similarity and ecological overlap among passerine birds on St. Kitts, British West Indies. Oikos 29: 60-66. – RICKLEFS, R.E., & J. TRAVIS: A morphological analysis of bird communities in scrub habitats. In press. – RÜGER, A. (1972): Funktionell-anatomische Untersuchungen an Spechten. Z. wiss. Zool. 184: 63-163. – RÜGGEBERG, T. (1960): Zur funktionellen Anatomie der hinteren Extremität einiger mitteleuropäischer Singvogelarten. Z. wiss. Zool. 164: 1-118. – RÜPPELL, G. (1975): Vogelflug. Kindler, München. – SNEATH, P.H.A., & R.R. SOKAL (1973): Numerical taxonomy. Freeman, San Francisco. – SORJONEN, J. (1980): Selection of breeding habitat by the Thrush Nightingal *Luscinia luscinia* and its position in bird communities. Ornis. Scand. 11: 125-134. – SPITZ, F.M. (1972): Etude du déterminisme de la répartition de quatre espèces du genre *Phylloscopus* (Oiseaux, Passériformes) par l'analyse factorielle des correspondances. Comptes rendus Acad. Sc. Paris 275, Ser. D.: 857-860. – STETTENHEIM, P. (1974): The bristles of birds. Living Bird 12 (1973): 201-234. – STORK, H.J. (1968): Morphologische Untersuchungen an Drosseln. Eine Analyse von Anpassungsstrukturen im Körperbau von sechs europäischen Arten der Gattung *Turdus* L.Z. wiss. Zool. 178: 72-185. – WINKLER, H., & W. BOCK (1976): Analyse der Kräfteverhältnisse bei Klettervöglen. J. Orn. 117: 397-418. – WRIGHT, S. (1941): The «age and area» concept extended. Ecology 22: 345-347. – ZINK, G. (1973): Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel. 1. Lieferung.

Zeitschrift/Journal: Ökologie der Vögel. Verhalten Konstitution Umwelt

Jahr/Year: 1980

Band/Volume: 2

Autor(en)/Author(s): Leisler Bernd

Artikel/Article: Morphological aspects of ecological specialization in bird genera. Morphologische Aspekte der ökologischen Spezialisierung von Vogelgattungen 199-220