Niche partitioning of two Palearctic passerine migrants with Afrotropical residents in their West African winter quarters

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In bird migration systems, the question of coexistence and competition of migrants with residents in the nonbreeding season and their role in shaping the evolution of present avian communities is much debated. However, conclusions are often drawn in a speculative way. In the Palearctic-African bird migration system, many studies have addressed the question of coexistence of Palearctic breeding birds with Afrotropical species in the former's wintering grounds. These studies have led to some generalizations concerning habitat selection and foraging ecology about the traits that might enable migrants to coexist with residents. Migrants were therefore assumed to forage in more open habitats, in more peripheral parts of the vegetation and with a higher foraging speed than residents. Furthermore, they were also assumed to be more flexible in foraging behavior by using a wider range of foraging tactics, but some studies revealed contradicting results. We studied the ecology of Palearctic migrants in Comoé National Park, Ivory Coast, West Africa, during three successive winters to explore the factors of niche partitioning between migrants and residents and to test the hypothesis of whether there are common behavioral traits in migrants. Therefore, we compared the ecology of two Palearctic breeding species: pied flycatcher, *Ficedula hypoleuca,* and willow warbler, *Phylloscopus trochilus*, with resident members of the respective guilds. With respect to use of microhabitat, foraging speed, and intake rates, we could not confirm the above-mentioned generalizations, showing that care has to be taken into account when drawing conclusions from few studies for a whole migration system on a huge continent. However, both migrating species were more flexible in foraging behavior than were their Afrotropical counterparts. As there are hints that this is also the case when migrants are compared with residents on their breeding grounds, we suggest that this flexibility enables migrants to partition resources with residents and, therefore, coexist with Afrotropical species. We discuss, however, whether this flexibility is an adaptation to migratory behavior or a prerequisite for the evolution of migration. The role that competition plays in present communities cannot be solved with a few observational studies because of the following problems. First, it is difficult to detect competition in the field. Second, there are constraints of performing field experiments that have not previously been performed in Africa, and third, there are several possible hypothetical scenarios about the role of competition in shaping present communities, including factors that might have been important in the past and are therefore impossible to detect at present. *Key words:* bird migration, Africa, *Ficedula hypoleuca*, niche partitioning, *Phylloscopus trochilus*. *[Behav Ecol 14:493–502 (2003)]*

The role of interspecific competition in shaping animal and plant communities is poorly understood and much debated, especially in tropical ecosystems (Huston, 1994; Lehman and Tilman, 2000; Wright, 2002). The main problem is the difficulty in measuring competition directly in the field and, therefore, the lack of empirical data (Huston, 1994; but see Abramsky et al., 2001). In addition, its calculation needs the consideration of a multiple set of factors (Abrams, 1980), and the structure of animal communities might have been shaped by factors, including but not limited to competition, which may have acted long time ago and which is impossible to detect at present (ghost of competition past; Connell, 1980). Furthermore, possible competitive situations between organisms might vary with habitat and season in the same area (Korb and Linsenmair, 2001). Recent stochastic nonequilibrium models conclude that in the tropics, interspecific competition does not play as great a role in communities as has been suggested before by deterministic equilibrium models (De Angelis and Waterhouse, 1987; Huston, 1994) and may play

a minor role compared with intraspecific competition (Rees et al., 1996), or species can coexist when relying on the same resource (Richards et al., 2000). One approach to detect the competitive influence of one species on another is the estimation of the competition coefficient (α), for example, through experimental removal of certain species in the field or under laboratory conditions, and the monitoring of any possible broadening of niches through competitive release (Fox and Luo, 1996; Greiner La Peyre, 2001; Munday et al., 2001; Shanker, 2001) or to provide additional resources like food (Abramsky et al., 2001; Jones et al., 2001). However, even this method can have problems with eliminating alternative hypotheses or may reveal misleading results (Huston, 1994; Underwood, 1986), and it is often not feasible in the field. Therefore, it is often only possible to monitor mechanisms that enable species to coexist through niche partitioning, and to discuss the possible role of competition on a rather speculative level (see Wauters et al., 2001).

In the Palearctic-African bird migration system, an estimated 5000 million birds migrate annually from Palearctic to Afrotropical regions, where they might compete temporarily for resources with other migrants and especially residents, even in times with lowest resource abundance within the annual cycle (Moreau, 1972), a situation paralleled in the Neotropics (Greenberg, 1995). Previously, it was thought that

tropical bird communities niches were so tightly packed that there was no vacant space for intruders at all (Diamond, 1975; McArthur, 1972; Rabøl, 1993), ignoring the fact of long-distance migration totally. Later Herrera (1978) claimed that migrants do not fit into a resident community but can do so when enough food resources are available, and in the Neotropic-Nearctic migration system, migrants "may in general not be fully integrated into tropical communities" (Holmes et al., 1989). Similarly, Lack (1983) assumed that migrants can only occur where food is superabundant. More recent publications, however, see migrants as integral parts of tropical avian communities, which are absent temporarily, and sometimes discuss their co-evolution with residents (Berthold, 2000; Cox, 1985; Jarry, 1985; Jones, 1998; Leisler, 1992; Salewski, 1999).

The role of interspecific competition in shaping migrant/resident communities has been reviewed by Greenberg (1986) and Leisler (1992). They concluded that evidence suggesting that competition is important in shaping winter distributions is tentative at best, and evidence for niche shifts induced by migrants is weak. Rabøl (1987) found habitat displacement of resident species by willow warblers, *Phylloscopus trochilus*, in Kenya. Later, however, Rabøl (1993) rejected his own conclusions, stating that interspecific competition plays a lesser role than previously thought and pointing to the role of coevolution for the shape of the existing species.

Food is probably the most important ecological factor affecting migrants in their winter quarters (Sherry and Holmes, 1996), and Palearctic migrants do not, aside from a few exceptions (Fry, 1992), breed in Afrotropical regions. Therefore, there should be no intraspecific or interspecific competition for mates or breeding sites, and potential niche partitioning should mainly affect foraging ecology, microhabitat selection, and habitat selection. With regard to foraging ecology, studies on niche partitioning and the mechanisms to allow coexistence between Palearctic migrants and resident species in sub-Saharan Africa (Baumann, 2001; Bruderer, 1994; Lack, 1985, 1986; Leisler et al., 1983; Rabøl, 1987, 1993; Salewski, 2000b) have led to some general assumptions. Palearctic migrants were assumed to forage higher and in more peripheral parts of the vegetation and, in general, in more open vegetation with a higher foraging speed than do their Afrotropical counterparts in their respective guilds (Lack, 1990; Leisler, 1992). This relation concerning microhabitat was recently found in orioles (Baumann, 2001). Palearctic migrants were also assumed to be more flexible and opportunistic in the utilization of resources and to use a wider range of foraging tactics (Leisler, 1992, 1993). However, there is no publication that compares heterogeneity of foraging behavior of residents and migrants in Africa. The three studies cited by Leisler (1993) in a review to promote this theory were performed in the Neotropics (Tramer and Kemp, 1980) or in the European Mediterranean (Herrera, 1978), or conclude that they do not support the assumption that migrants have a wider range of foraging tactics than residents with a coarse classification of foraging tactics (Lack, 1986). Further studies about comparative foraging ecology of residents and migrants (Baumann, 2001; Leisler et al., 1983; Rabøl, 1987, 1993) do not mention heterogeneity of foraging tactics at all.

The willow warbler is a Palearctic migrant that winters throughout sub-Saharan Africa, whereas the wintering grounds of the pied flycatcher *Ficedula hypoleuca* are mainly restricted to West Africa (Urban et al., 1997). Comparative ecological studies of willow warblers and residents have been performed in Kenya (Rabøl, 1987, 1993) and Zimbabwe (Salewski et al., 2002b), but there are no studies on the foraging ecology of pied flycatcher in its winter quarters

except a preliminary investigation with a limited number of observations and a comparison with willow warbler in the Ivory Coast (Salewski, 2000b; Salewski et al., 2002a).

We studied the ecology of willow warblers and pied flycatchers in Comoé National Park, Ivory Coast, during three European winters. The aim of our study was to assess how willow warblers and pied flycatchers partition resources with resident species. The question of habitat selection will be addressed elsewhere (Salewski et al., in press). Here we test the predictions whether the Palearctic species (1) differ from residents in selection of microhabitat, (2) differ in foraging ecology from residents with regard to intake rates and search area, and (3) are more flexible in foraging behavior.

METHODS

Study area

The Comoé National Park $(11,491 \text{ km}^2)$ is located in the northeastern Ivory Coast at $8°30'-9°35'$ N, $3°00'-4°30'$ W. Average altitude is 250–300 m, with the highest peak at 635 m. The climate is characterized by a rainy season from March–October and a dry season from November–February. Average annual rainfall varies from 1100–1300 mm. The average annual temperature is 27°C. The northeast section of the park belongs to the Sudan savanna zone and the southwest section to the northern Guinea savanna zone (Thiollay, 1985). The habitats comprise mainly savanna, with gallery forests along the main rivers (Comoé, Iringou). There are scattered isolated forests of varying size without any connections to rivers, mainly in the south of the park (Poilecot, 1991). For details of the study area, see Salewski (1999). Our study was conducted in the southwest of the park (about $8°45'$ N, $3°49'$ W).

Target species

Thirty species of Palearctic passerine species have been recorded in the park (Salewski, 2000a), but only the pied flycatcher, *Ficedula hypoleuca*, and willow warbler, *Phylloscopus trochilus*, were observed in sufficient numbers to be analyzed. The pied flycatcher with a sit-and-wait foraging tactic was assigned to the flycatcher guild. Afrotropical species with enough observations in this guild were Gambaga flycatcher, *Muscicapa gambagae*; Senegal batis, *Batis senegalensis*; red-bellied paradise flycatcher, *Terpsiphone rufiventer* (paradise flycatcher); and brown-throated wattle-eye, *Platysteira cyanea* (wattle-eye). The Gambaga flycatcher is an exception, as it is assumed to be an intra-African migrant that migrates to the area at about the same time as the pied flycatcher (Salewski et al., 2003). The African blue flycatcher, *Elminia longicauda*, was also assigned to this guild, although it moves along branches in search of food rather than using a sit-and-wait tactic and it catches its prey in a typical flycatcher manner by chasing it in the air. The willow warbler was assigned to the gleaner guild and was compared with the resident green-backed Eremomela, *Eremomela pusilla* (Eremomela), with which it often foraged in mixed species flocks (Salewski et al., 2002a), and the grey-backed Camaroptera, *Camaroptera brachyura* (Camaroptera).

Data collection

We stayed in the area during the European winter in 1994–1995 and the two following winters, in general from mid-September to the end of April. The study was performed in different habitats that comprised bush/tree savanna, an isolated forest, and gallery forest (for details, see Salewski,

1999; Salewski et al., in press). We observed individuals of the target species whenever possible and often in short intervals between other tasks. It is therefore not possible to give a number of field hours during which we performed our observations.

When performing field observations, we walked around randomly and searched for individuals of the target species. We then followed the individual for as long as possible, although flycatchers were followed for a maximum of 10 min, after which a search for another bird was started. When the bird was foraging, we recorded the microhabitat in which it fed and its foraging behavior. Microhabitat parameters were estimated height of the tree in which the bird was foraging, estimated height of the bird, cover above and below the bird (percentage of an area with 2-m diameter around the bird, for birds on the ground cover below was defined zero), and, in warblers, whether the bird foraged at the edge of the crown or in its center. For further analysis, the tree height index was later calculated by dividing the height of the bird by the height of the tree (Nyström, 1991). An index of one means that the bird is foraging on the top of the crown, and an index of zero means that it is foraging on the ground.

Parameters of foraging behavior were numbers of movements during an observation, estimated distance traveled during foraging, number of feeding attempts, substrate from which the bird was attempted to take prey (which were leaf, twig, trunk, air, and ground), and techniques with which the bird attempted to take prey (which were slightly modified after Remsen and Robinson [1990]: gleaning, picking prey while standing with both legs on the substrate and with both wings closed; sallying, flying toward a prey item and attempting to take it in flight; hovering, hovering in front of an attempted prey; jumpsally, jumping toward a prey item with open wings to keep the balance or accelerate the movement but not as the main force to drive the bird forwards; leaping, jumping toward prey without the use of the wings; and pouncing, flying from a perch to the ground). In most cases, we were unable to assess whether a foraging attempt was successful. We refrained from using the "snap" sound of some flycatchers when they close their bill as an indication of successful foraging because it indicates only that the bill was closed in a feeding attempt rather than that the attempt was successful. The time of each foraging bout was measured with a stopwatch.

Data analysis

For further analysis, we used only those observations for flycatchers that lasted longer than 30 s, after which the variance of foraging behavior of the pied flycatcher dropped only insignificantly (Stünzner-Karbe, 1996). In the warbler guild, only observations longer than 20 s were used for further analysis. Microhabitat parameters of the fast moving warblers were estimated after each observation, but in the flycatchers, for each feeding attempt. For the latter, the mean for each bird was calculated after the whole observation. When a bird was observed repeatedly, this was treated as one observation, and the same was applied to color-ringed individuals that were observed several times. Therefore, we tried to minimize any potential bias owing to nonindependent observations, but we cannot rule out that some birds were observed repeatedly. However, we assume that the bias is low, because of the high number of observations in the area during several years. For foraging techniques and foraging substrates, we calculated the percentage of each character a bird used, and used the mean of the total observations for further analysis. The use of absolute numbers would have biased our results owing to

nonindependence of the data because of different numbers of observed actions per individual.

We used the Shannon-Wiener diversity index (Magurran, 1988) to calculate diversity and Horn's index to calculate niche overlap (Krebs, 1999). The Shannon-Wiener diversity index is moderately sensitive to sample size (Magurran, 1988). Therefore, we used a random subsample of 60 of all pied flycatcher observations to calculate diversities of foraging substrates ($n = 263$) and foraging techniques ($n = 267$). In the warbler guild, we refrained from doing so, although the number of observations for Camaropteras (substrate $n = 34/$ technique $n = 38$) was much lower than in the other species (willow warbler, 86/97; Eremomela, 66/81). The Camaroptera differs from the other warblers by microhabitat, and we preferred to compare a higher number of observations of the species that often forage together in flocks. All other differences in numbers of observations between species were thought to be negligible. Despite the criticism of Hurlbert (1971) or Lande (1996), we used the index as a measure of heterogeneity of behavior because it allowed us to use percentages for the analysis, and values can be compared with a t test (Magurran, 1988). Other studies have used the index to calculate foraging diversity of birds or behavioral diversity in mammals (Brandl et al., 1994; Di Bitetti, 2000, and references therein).

We tested the robustness of discriminant analyses by dividing each original data set into two data sets of the same size and analyzing them separately. As in all analyses, the result was very similar compared with the analyses of the whole data sets; therefore, we refrain from giving details of those tests.

For statistical analysis, the program SPSS for Windows 6.0.1 was used (Norusis, 1993). For significance tests, $p \leq .05$ was accepted, but when multiple comparisons were made within a data set, a sequential Bonferroni correction was applied by using the Dunn-Šidak method (Sokal and Rohlf, 1995). Probability levels are given when these remained significant after such correction. All percentages were arcsine-transformed before analyses, with the exception of the foraging data used for the calculation of Shannon-Wiener diversity.

RESULTS

Flycatchers

Microhabitat
The medians of the microhabitat parameters showed that pied flycatchers had intermediate values in all characters (Table 1). There were Afrotropical species foraging under higher, as well as lower, vegetation cover or absolutely, as well as relatively, higher or lower in the vegetation. The Gambaga flycatcher had similar values to those of the pied flycatcher in all parameters.

A stepwise discriminant analysis included only the parameters cover above the bird (Wilks's λ: 0.66, $p < .0001$) and height index (Wilks's λ: 0.62, $p < .0001$). For the other parameters, the F level was insufficient for further analysis.

The first canonical function of the analysis was highly positively correlated with cover (Table 2). The second function was highly correlated with height index. The pied flycatcher has relatively low values along function 1 (Figure 1), indicating that it is foraging under relatively low vegetation cover, but the Gambaga flycatcher and Senegal batis show even lower values. The pied flycatcher has an intermediate position on the second function, but because of the low explained variance of factor 2, this is not of great significance, and the low eigenvalues of both functions (Table 2) show that the model can explain the variances between the species only

Table 1

Medians of the microhabitat parameters in the flycatcher guild

Species	Cover above		Cover below		Tree height		Height of bird	Height index
Pied flycatcher	10	(187)	1	(185)	10	(203)	6 (219)	0.59 (199)
Gambaga flycatcher	10	(41)	1	(37)	9	(45)	6 (45)	0.64 (42)
Senegal batis	4.1	(36)	0	(36)	10.7	(37)	6 (37)	0.63 (36)
Blue flycatcher	80	(41)	40	(41)	14	(42)	5 (42)	0.42 (41)
Wattle-eye	40	(31)	11.6	(30)	15	(39)	9 (36)	0.58 (36)
Paradise flycatcher	60	(68)	15	(67)	12	(75)	4 (76)	0.37 (73)

Numbers are the covers in percentage and heights in meters. Numbers in parentheses are numbers of observations.

to a limited extend. This was also shown by the fact that only 24.4% of all cases were correctly classified. For the pied flycatcher, this was even only 4.8%, indicating that it uses a wide range of microhabitats. Other species were correctly classified between 19.4% (African blue flycatcher) and 70.6% (Senegal batis).

Foraging rates

The analysis of the distances traveled and number of movements made while foraging showed that pied flycatchers have intermediate medians, indicating that there are Afrotropical species traveling either greater or lesser distances for foraging (Table 3). However, pied flycatchers show the lowest foraging rates of all species concerned.

A stepwise discriminant analysis of the parameters included only the character movements per minute (without foraging actions; Wilks's λ: 0.48, $p < .0001$). Distance and feeding rate were excluded from further analysis owing to an insufficient F level. Consequently, movements per minute was identical (correlation coefficient, 1) with the one canonical discriminant function extracted (eigenvalue, 1.09), whereas distance traveled (correlation coefficient, 0.26) and foraging rate (correlation coefficient, 0.11) showed a weak correlation with the function. The group centroids of the discriminant function shows that the pied flycatcher is well separated from other species by fewer movements per minute, with the exception of the Gambaga flycatcher (Figure 2). Of all cases, 38.7% were correctly classified. For the pied flycatcher, the proportion of correctly classified cases was 28.2%. The corresponding proportions for other species varied between 0% (wattle-eye) and 70.0% (Gambaga flycatcher), indicating that characteristics related to foraging speed and distance traveled while foraging are not discriminating well between species.
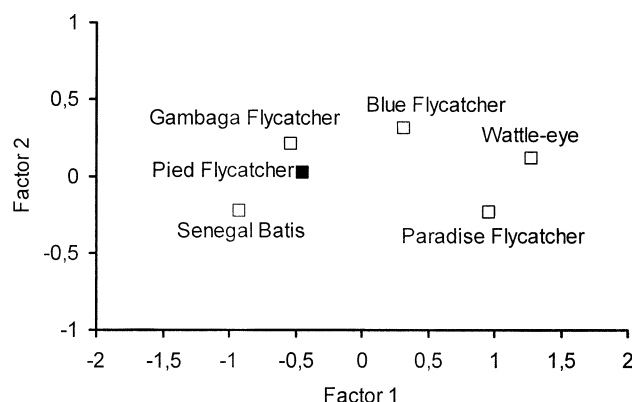
Foraging techniques and substrates

Only pied flycatcher and Gambaga flycatcher used all six foraging techniques recorded (Figure 3). Pied flycatchers used direct sallies toward a prey item less frequently than did other flycatchers. Pouncing toward prey on the ground played an important role but was hardly used by other flycatchers. Other techniques important for pied flycatchers were hovering and jumpsallies. Diversity of feeding techniques was highest in pied flycatchers (Table 4). A high diversity was also shown by paradise flycatcher and wattle-eye. The difference between pied flycatcher and paradise flycatcher was significant (t test, $t = 4.10$, df $= 226$, $p < .001$). Niche overlap of pied flycatcher was also greatest with paradise flycatcher and with wattle-eye (Table 5).

Pied flycatchers directed most foraging attempts to prey on leaves (Figure 4) and on the ground. The latter substrate was hardly used by other species. Other important substrates for pied flycatcher were twigs, trunks, and foraging attempts directed to prey in the air. Important substrates for other species were leaves (wattle-eye, paradise flycatcher) or foraging on prey in the air (African blue flycatcher, Gambaga flycatcher). For African blue flycatcher, this could be misleading, because it seemed to chase insects within the vegetation that were chased off leaves before. Diversity of foraging substrates (Table 4) was highest in pied flycatcher and Gambaga flycatcher. The least diverse species was the wattle-eye. The difference between pied flycatcher and Gambaga flycatcher was not significant (t test: $t = 1.60$, df $= 249$, $p =$ ns), but the difference of pied flycatcher to the African blue flycatcher with the next highest index was (t test, $t = 5.96$, df $= 342$, $p < .002$). The Gambaga flycatcher was also the species that showed the highest overlap of foraging substrates with the pied flycatcher (Table 5).

Warblers

Microhabitat

Willow warbler and Eremomela did not differ much in the medians of the microhabitat parameters (Table 6), whereas the Camaroptera foraged under much higher cover, in lower

Figure 1
Discriminant analysis of the microhabitat parameters in the flycatcher guild.

Table 2

Correlation coefficients of the microhabitat parameters with the canonical functions of a stepwise discriminant analysis of the flycatchers

Parameter	Function 1	Function 2
Cover above the bird	0.91	0.47
Height index	−0.27	0.98
Eigenvalue	0.56	0.03
Explained variance (%)	95.2	4.8
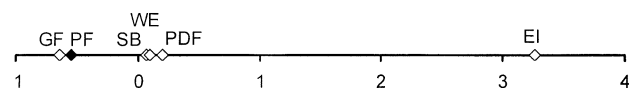
Figure 2
Group centroids of the one canonical function of a discriminant analysis of the foraging parameters in the flycatcher guild. GF indicates Gambaga flycatcher; PF, pied flycatcher; SB, Senegal batis; WE, wattle-eye; PDF: paradise flycatcher; and El, blue flycatcher.

Table 3
Medians of the foraging parameters of the flycatchers

Species	Distance	Movements	Intake rate
Pied flycatcher	8.6 (116)	1.3 (124)	0.5 (124)
Gambaga flycatcher	9.7 (27)	1.0 (30)	1.0 (30)
Senegal batis	13.4 (36)	3.6 (37)	0.6 (37)
Blue flycatcher	6.3 (10)	3.7 (10)	0.7 (10)
Wattle-eye	8.8 (21)	14.4 (25)	1.2 (25)
Paradise flycatcher	12.6 (46)	3.8 (48)	0.8 (48)

Numbers are the distance in m/min, movements/min, and intake rate/min. Numbers in parentheses are the numbers of observations.

trees at lower height, which led correspondingly to a lower height index.

A stepwise discriminant analysis between all species included the parameters height of the bird (Wilks's $\lambda = 0.63$, $p < .0001$), cover above (Wilks's $\lambda = 0.66$, $p < .0001$), and cover below (Wilks's $\lambda = 0.76$, $p < .0001$) the bird. Height index and tree height were excluded because their F level was insufficient for further analysis. Cover above the bird showed a high negative correlation with the first canonical function of the analysis (Table 7). The second canonical function was highly positive correlated with cover below the bird. Willow warblers and Eremomelas show group means along the first function (Figure 5), which are close to each other, indicating that they forage under similar cover and at a similar height. The Camaroptera foraged under distinctly higher cover and lower in the vegetation. Along the second function, the Eremomela is separated from the willow warbler by foraging with more cover under the bird, indicating that willow warblers might forage more in the lower parts of crowns. However, the low eigenvalues of both functions (Table 7), together with the low rate of correctly classified cases (all cases, 60.3%; willow warbler, 67.1%; Eremomela, 49.5%; Camaroptera, 81.5%), show that the model can explain the variances between the species only to a limited extend.

The Camaroptera foraged on the ground to a large extend (70.3%). This was never observed in willow warbler and Eremomela. The latter species showed a high niche overlap (0.91) in microhabitat use, whereas the overlap with the Camaroptera was low for both willow warbler (0.12) and Eremomela (0.40).

Eremomelas were found foraging at the edge of the vegetation in 39% ($n = 35$) of all cases and in 61% ($n = 54$) in the vegetation. For willow warblers, the respective numbers

are 15% ($n = 10$) and 85% ($n = 55$). The difference was significant ($\chi^2 = 10.4$, df = 1, $p = .001$), indicating that willow warblers foraged more within the vegetation than did Eremomelas. No differences were detected in either species whether they foraged in monospecific flocks or mixed species flocks, and therefore, there are no indications of habitat displacement.

Foraging rates
The medians of the foraging rates were highest in willow warblers, but they showed the lowest numbers of movements when foraging (Table 8). However, a stepwise discriminant analysis included only movements as sufficient to separate the species (Wilks's $\lambda = 0.93$, $p < .0001$). Therefore, movements per minute (correlation coefficient, 1) is identical with the one canonical discriminant function (eigenvalue, 0.07) extracted. However, the low eigenvalue and high Wilks's λ, together with the low proportion of correctly classified cases (all cases, 40.7%; willow warbler, 66.3%; Eremomela, 11.7%; Camaroptera, 48.1%), indicate that there is a high within-species variance.

Foraging techniques and substrates
All warbles preferred gleaning as the main technique to catch prey (Figure 6). However, it was least used by willow warblers that also hovered a lot and tried to catch prey by jumpsallies. The letter technique was used by the Camaroptera, even to a higher degree when foraging on the ground. Gleaning played
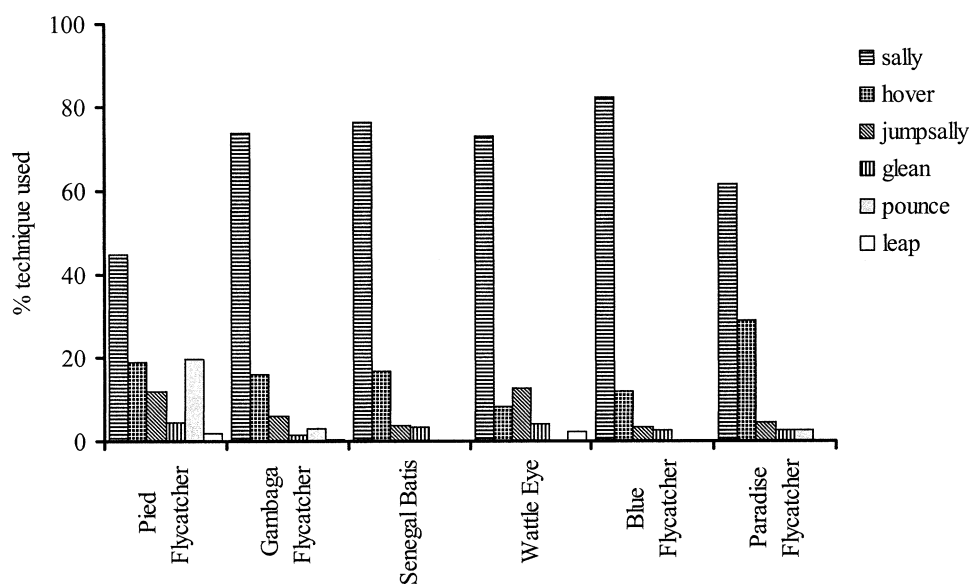
Figure 3
Percentages of foraging techniques used by the flycatcher species.

Table 4

Diversity (Shannon-Wiener diversity index) of foraging techniques and foraging substrates of the target species

Species	Diversity of foraging techniques	Diversity of foraging substrates
Pied flycatcher	**1.45**	**1.55**
Gambaga flycatcher	0.85	1.39
Senegal batis	0.74	0.95
Wattle-eye	0.91	0.65
Blue flycatcher	0.62	1.00
Paradise flycatcher	0.99	0.97
Willow warbler	**0.96**	**0.74**
Eremomela	0.35	0.51
Camaroptera	0.53	1.14

Bold indicates Palearctic species.

also the most important role but was still exceeded by the Eremomela. In total, willow warblers used the wings for their foraging attempts in 33.6% of cases, whereas this was only the case in 12.7% and in 8.7% for Camaroptera and Eremomela, respectively.

Diversity of foraging techniques (Table 4) was highest in willow warblers, followed by Camaroptera and Eremomela. The difference between willow warblers and Eremomela was significant (*t* test: $t = 5.5$, df = 229, $p < .001$). Both species showed a high degree of niche overlap (0.92), which was higher than between willow warbler and Camaroptera (0.87) but lower than between Eremomela and Camaroptera (0.96).

Leaves as foraging substrate (Figure 7) were most frequently used by willow warblers and Eremomelas. Camaropteras attempted to take more food from the ground than from leaves in the vegetation. All species foraged also on twigs to a considerable amount. Substrate diversity (Table 4) was highest in Camaroptera and lowest in Eremomela. The difference between willow warbler and Eremomela was significant (*t* test: $t = 2.4$, df = 264, $p < .02$). Niche overlap was highest between willow warbler and Eremomela (0.98).

Table 5

Niche overlap of the pied flycatcher with Afrotropical species

Species	Overlap in foraging techniques	Overlap in foraging substrates
Gambaga flycatcher	0.81	0.90
Senegal batis	0.85	0.73
Wattle-eye	0.87	0.76
Blue flycatcher	0.83	0.72
Paradise flycatcher	0.91	0.84

DISCUSSION

In both guilds, we could detect a certain amount of niche partitioning between Palearctic migrants and Afrotropical species, as indicated by different foraging ecology. Niche partitioning was mainly expressed by differences in foraging techniques and substrates rather than by microhabitat or foraging rates, but in the warblers, willow warblers foraged more within the vegetation than did Eremomelas and changed positions less while foraging. Therefore, previous statements that Palearctic migrants, when foraging together with Afrotropical residents, forage in more open microhabitats and in higher, more peripheral strata of the vegetation, and have a lower intake rate (Leisler, 1992; Lövei, 1989) could not be confirmed for both guilds. For willow warblers, this contradicts former findings in Kenya (Lack, 1985). In Zimbabwe, willow warblers foraged lower in trees than did burnt-necked Eremomela, *Eremomela usticollis*, with which it occurred in mixed-species flocks frequently. In other microhabitat parameters (cover), there were no differences between the species (Salewski et al., 2002b). In mixed-species flocks of tits in Europe, as well as in Korea, heavier species were foraging more in the central parts of the vegetation than did lighter ones (Jablonski and Lee, 1998). It seems therefore doubtful that migration status is the only factor influencing microhabitat selection. In addition, Rabøl (1987) found different foraging relationships on the edge of the vegetation between willow warbler and black-breasted Apalis, *Apalis*
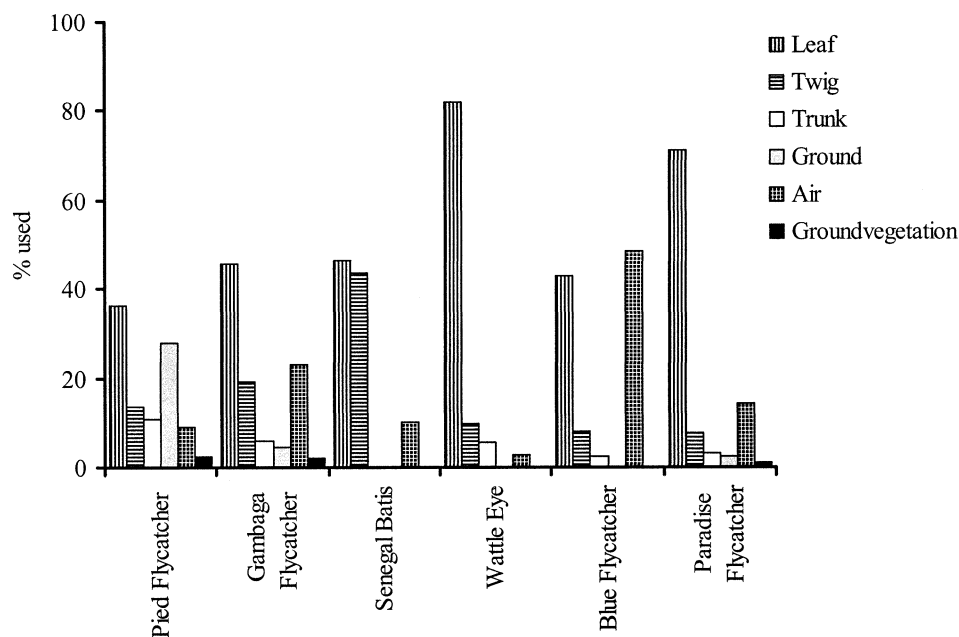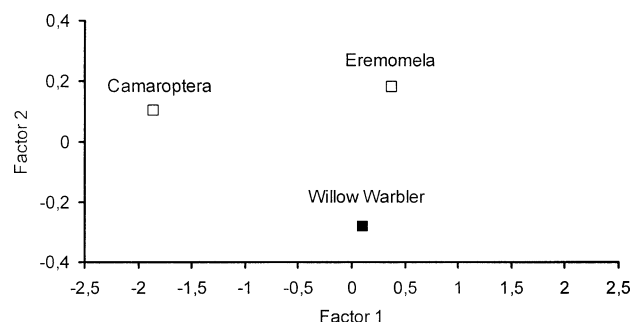

Figure 4
Foraging substrates of flycatchers.

Figure 5
Result of a discriminant analysis of the microhabitat parameters of the warblers.

Table 7

Correlation coefficients of the microhabitat parameters with the canonical functions of a stepwise discriminant analysis of the warblers

Parameter	Function 1	Function 2
Cover above the bird	−0.75	0.21
Cover below the bird	0.35	0.85
Height of bird	0.66	0.13
Eigenvalue	0.51	0.05
Explained variance (%)	91.5	8.5

flavida, in different habitats in Kenya. With regard to foraging techniques, willow warblers used their wings more often than did other species in their guild, which coincides with results of other studies (Baumann, 2001; Leisler, 1993; Rabøl, 1993). However, the assumption that migrants use their wings to a greater extent for foraging than do residents in general (Lack, 1986; Leisler, 1990) could not be confirmed in the flycatcher guild. When pouncing, pied flycatchers catch their prey by pecking on the ground while standing and, therefore, use their wings to a lesser extent for the actual foraging action than do all other flycatchers.

A comparative study of the wintering strategies of pied flycatchers and willow warblers in Comoé National Park showed that strategies differed widely between the two species in several traits (Salewski et al., 2002a). Therefore, it is difficult to characterize the wintering ecology of migrants with simple generalizations that do not take species-specific differences or different environments and local seasonal changes in a vast continent into account.

However, Palearctic migrants showed the highest diversity in foraging techniques and, in the flycatchers, also in foraging substrates. This confirms assumptions that migrants in general are less specialized in their foraging habits than are residents (Herrera, 1978; Leisler, 1993; Lövei, 1989; Salewski, 2000b; but see Lack, 1986), which is also the case in the neotropics (Greenberg, 1986). We cannot assess the nature of the prey the species were foraging on, but Lovette and Holmes (1995) showed that different feeding techniques reflect different kind of prey taken. Therefore, we assume that migrants have a wider range of prey that they utilize opportunistically. This enables them to forage successfully among resident species of the same guilds. That flexibility might be a factor that enables bird species to establish themselves in another community in different habitats. It was shown by Lefebvre et al. (1998) that behavioral flexibility is associated with learning ability in captivity, and behavioral flexibility allows animals to respond more rapidly to changes

in the environment. This can therefore be of advantage when invading novel habitats. Consequently, a positive correlation was shown between behavioral flexibility and success of establishment of introduced bird species to New Zealand (Sol and Lefebvre, 2000). There are indications that pied flycatchers adjust their behavior to food availability. With the progress of the dry season, when less leaves are on the trees, they forage more on the ground and increase the percentage of food taken out of the air after the first rains, when more insects are swarming (Stünzner-Karbe, 1996). Resident flycatchers do not show such a change in behavior (Salewski et al., 2002a). Additionally, it was found that pied flycatchers on their breeding grounds at their geographical distribution limit in the north react to spells of cold weather, when insects of the air and on the vegetation are inactive by taking more food from the ground. This behavior was not shown by the resident Siberian tit, *Parus cinctus* (Veistola et al., 1997). Therefore, flexibility might be an important feature for migrants to cope with unfavorable situations to which they are otherwise not adapted or to coexist with residents in the wintering area, as well as in the breeding grounds. However, when flexibility is a general feature of all migrants, which enables them to coexist with resident communities temporarily in the wintering areas, and in the breeding ground, there remains the question what adaptive value it had for the evolution of bird migration. Is flexibility an adaptation to migration to areas with a resident community, or is it a prerequisite for the evolution of migration out of a resident community?

In the flycatcher guild, the Gambaga flycatcher, which is an intra-African migrant (Salewski et al., 2003), showed less diversity in foraging techniques than did some resident species, but had the highest diversity in foraging substrates apart from the pied flycatcher. The Gambaga flycatcher was the species that showed the highest niche overlap with the pied flycatcher in both foraging substrates and techniques as well as microhabitat. Therefore, the Gambaga flycatcher might be the highest potential competitor to the pied flycatcher (Salewski, 1999), but it has to be kept in mind that niche overlap measures are no measures for actual intensity of competition (Abrams, 1980). However, for habitat choice, the Gambaga flycatcher was the species that overlapped least with

Table 6

Medians of the microhabitat parameters of warblers

Species	Cover above	Cover below	Tree height	Height of bird	Height index
Willow warbler	10 (79)	5 (78)	10 (90)	7 (83)	0.67 (86)
Eremomela	10 (111)	10 (108)	12 (126)	8 (112)	0.70 (111)
Camaroptera	85 (30)	0 (48)	6,5 (30)	0.4 (62)	0 (49)

Numbers of the covers are in %; heights, in m. Numbers in parentheses are numbers of observations.

Table 8

Medians of the foraging parameters of the warblers

Species	Distance	Movements	Intake rate
Willow warbler	4.36 (94)	19.15 (101)	2.64 (102)
Eremomela	4.12 (89)	22.76 (103)	2.45 (103)
Camaroptera	4.58 (52)	24.05 (54)	1.45 (53)

Numbers are the distance in m/min, the movements/min, and the intake rate/min. Numbers in parentheses are numbers of observations.
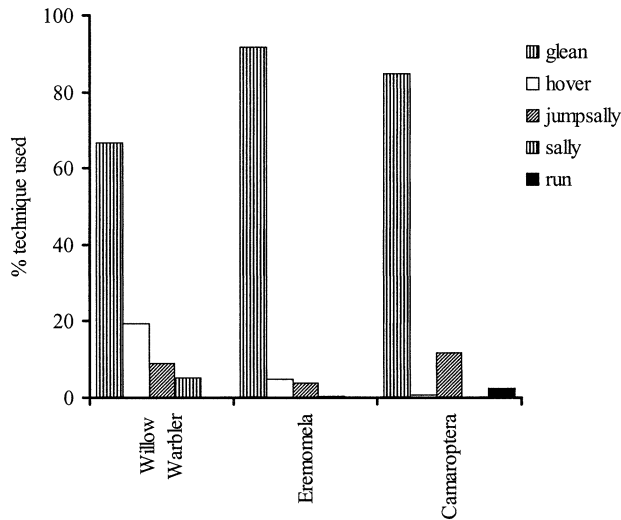
Figure 6
Foraging techniques of warblers.

Figure 7
Foraging substrates of the warblers.

the pied flycatcher compared with all other species of the guild (Salewski, 1999), and therefore, both species might be able to coexist because of the use of similar niches in different habitats. This difference in the two related species (family Muscicapidae) also shows that other similarities between the two migrant species might not be a mere reflection of phylogeny and, therefore, the misuse of species as independent data points (Sol and Lefebvre, 2000).

In the warbler guild, the Camaroptera was distinctly separated by microhabitat from the other species. It usually foraged under dense cover and low in the vegetation or on the ground, which explains the higher feeding substrate diversity compared with that of the other species. Willow warbler and Eremomela used the same microhabitat and were observed foraging in mixed species flocks regularly. In foraging techniques and substrates, the Eremomela was the species that showed the highest niche overlap with the willow warbler, although the overlap of techniques between the Eremomela with the Camaroptera was higher. As willow warblers take more food on the wing, we assume tentatively that they differ from Eremomelas in prey composition and that there are more possible food items available for the migrant.

There are few studies in Africa that might hint to interspecific competition between migrants and residents, although Moreau (1972) stated that 28% of migrant species are potential competitors to residents. In Kenya, Leisler et al. (1983) found competition between wintering and resident chats (*Oenanthe* sp.) expressed by interspecific aggression over territories in which the migrant species were inferior to the resident ones. In shrikes, *Lanius* sp., Bruderer (1994) could not confirm a general superiority of residents over migrants. Microhabitat displacement of resident warblers by willow warblers was described from Kenya by Rabøl (1987). This conclusion was later withdrawn by the author (Rabøl, 1993). However, in Zimbabwe, burnt-necked Eremomelas, *Eremomela usticollis*, foraged more in the center of the vegetation in monospecific flocks than when willow warblers were present (Salewski et al., 2002b), indicating possible microhabitat displacement.

In this study, there were no hints of active displacements in any characters, and therefore, previous suggestions of microhabitat displacement of Eremomelas by willow warblers (Salewski, 1999) could not be confirmed. There was also hardly any observation of interspecific aggression, which
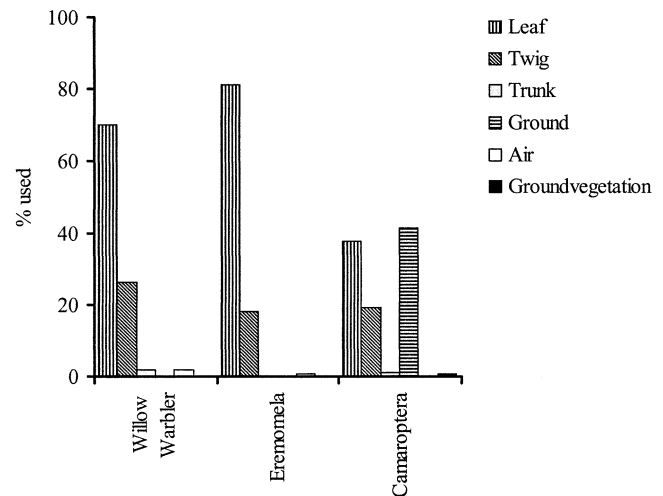
might provide a hint of potential competitive situations, and intraspecific territorial pied flycatchers did not defend their territories interspecifically (Salewski et al., 2002a). We assume therefore that present competition between Palearctic migrants and residents plays a minor role in shaping the bird community in the study area. Nevertheless, the flexibility of Palearctic migrants in feeding ecology might allow them to utilize resources that are not available for residents, and they might therefore be able to coexist in the same habitats.

It has been stated that the high numbers of migrants must have an influence on tropical communities (Jones, 1998; Rabøl, 1987). Microhabitat shifts of warblers (Rabøl, 1987) or geographical shifts of warblers, shrikes (*Lanius* sp.), and chats (*Oenanthe* sp.) in East Africa (Lack, 1985), as well as chats (Jones, 1985) or raptors (Thiollay, 1992) in West Africa (reviewed by Jones, 1998), were discussed as an indication of this relation (Leisler, 1992). However, this may not necessarily be the case. Several scenarios for the evolution of present avian communities are possible: (1) the present communities evolved by chance, and species never competed; (2) competition in the past played a role in the evolution of the communities, which led to niche differentiation through coevolution, and therefore, species do not compete at present; (3) competition plays a role at present, and competing species influence each other mutually; and (4) the present communities evolved/evolve under a set of stochastic environmental variables with competition playing a minor role. We do not intend to claim which scenario is most likely, but we want to point out that a multifactorial approach is probably necessary for the understanding of the Palearctic-African migration system, and the question of the role of competition for the evolution of the system might never be solved. Were scenario 1 or 2 to be true, it will be impossible to detect them and to distinguish between them at present. The validity of scenario 3 could theoretically be tested in field experiments. To our knowledge, no such experiments concerning migrants have been performed in Africa so far, and they might be hindered by the technical setup necessary to solve the question addressed here. Stochastic models have become more widely used in recent decades in the field of tropical ecology. However, even when more questions can be solved with these models, they fail to explain all occurring phenomena (Linsenmair, 1990), and at least in intermediate time scale, the arrival of migrants is a more deterministic event in tropical avian

communities, at least in our study area (Salewski et al., 2002a). In addition, we lack the basic data in most cases to test such models in the Palearctic-African bird migration system. The task for the future will be to collect such detailed species-specific data on the whole continent.

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