Different wintering strategies of two Palearctic migrants in West Africa – a consequence of foraging strategies?

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The wintering strategies of Pied Flycatchers *Ficedula hypoleuca* and Willow Warblers *Phylloscopus trochilus* in their West African winter quarters were compared. Pied Flycatchers arrived early in the season (September) and stayed in the study area throughout the winter. They were territorial and showed a high return rate. Intraspecific relationships were mostly expressed by territorial behaviour. Interspecific relations seemed to be unimportant. Willow Warblers arrived relatively late (November) and were absent from the area for some weeks in January and February, a behaviour which was interpreted as itinerancy. Willow Warblers were non-territorial and never returned to a site. Willow Warblers usually moved through the area in monospecific or mixed-species flocks. Habitat and microhabitat choice of these species were similar but in feeding ecology they differed by the higher diversity of feeding substrates and feeding techniques of Pied Flycatchers. The differences in the winter strategies are explained by the ability of Pied Flycatchers to defend a territory because of their diversity in foraging behaviour, whereas Willow Warblers are more specialized and are therefore forced to be more mobile to find their patchily distributed food.

Moreau (1972) estimated that at least 5 billion individual birds migrate each year from the Palearctic region to tropical Africa south of the Sahara to spend the winter there. When arriving at the wintering grounds they face the problem that they meet a resident bird community with which they might have to compete for space and food. Still rather little is known about the strategies used by Palearctic passerines to facilitate their coexistence. Most studies of the ecology of migrants in sub-Saharan Africa have been conducted in the eastern and southern parts of the continent (Pearson & Backhurst 1976, Leisler *et al.* 1983, Lack 1986, Herremans 1993) but seldom in West Africa (Morel & Morel 1992) where most migrants from central and western Europe overwinter (Bairlein 1985, Zink 1973–1985). These studies concluded that Palearctic migrants prefer to use more open and more seasonal habitats than resident species, and that migrants are more flexible in their choice of food and feeding techniques (Leisler 1992, Herremans 1997). Few studies of interspecific competition between migrants have been conducted in Africa (Leisler *et al.* 1983, Herremans 1997), although this question has received some attention in Nearctic migrants in South America (Greenberg 1986, Greenberg *et al.* 1994).

Previous studies have generally treated Palearctic migrants as a homogeneous group. This may be reasonable in some contexts because all long-distance migrants have to adapt morphologically and physiologically to, for example, the trans-Saharan flight, and ecologically to competition with resident species or to habitat changes. However, if there is interspecific competition for space and food it can result from the presence of either resident or other migrant species, although it is most likely to occur within guilds (Huston 1994).

In this paper we compare the phenology, habitat choice, microhabitat choice, territoriality, feeding ecology and intra- and interspecific relationships of the Pied Flycatcher *Ficedula hypoleuca* and the Willow Warbler *Phylloscopus trochilus* to investigate

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how their strategies differ and to explain the adaptive value of each strategy. The species were chosen because they were the two most abundant in the study area and they do not belong to the same guild (flycatcher with 'sit and wait' strategy vs. skulking leaf-gleaner). Any differences are therefore probably not due to strong recent interspecific competition. This makes it easier to test the hypothesis that wintering strategies of migrants are similar.

METHODS

Study area

The Comoé National Park (11 491 km²) is located in north-east Ivory Coast (8°30′–9°35′N, 3°00′–4°30′W; Fig. 1). Altitude is 250–300 m with the highest peak at 635 m. The climate is characterized by a distinct change between the rainy season from March to October and the dry season from November to February. Average annual rainfall varies between 1100 and 1300 mm. The average annual temperature is 27 °C. Maximum daily temperatures are highest in March (37 °C) and minimum daily temperatures are lowest in January (15 °C). The north-east of the park belongs to the Sudan savanna zone and the south-west to the northern Guinea savanna zone (Poilecot 1991). The habitats comprise mainly savanna (70%) with open woodland and riparian forest along the main rivers (Comoé, Iringou). In the south of the park there are scattered isolated forests of varying size without any connections to the riparian forest (Poilecot 1991). The change from the rainy season to the dry season is characterized by the drying out of the herbaceous layer in the savanna. The savanna is burned annually by humans mainly in December,
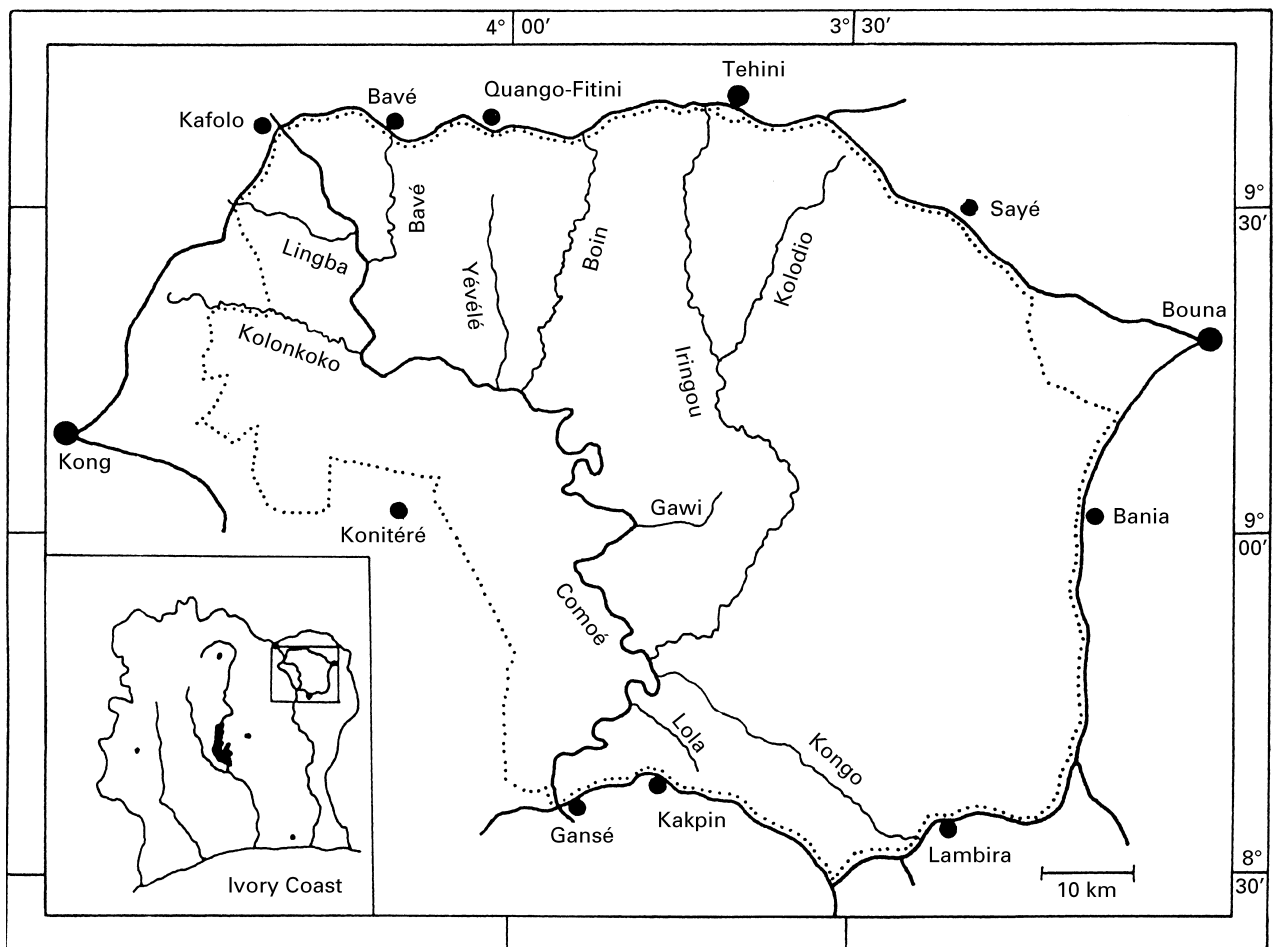

Figure 1. Comoé National Park. Dotted Line: Park boundary. Solid line outside park boundaries: Road.

when the majority of trees lose their leaves. In the savanna leaf-loss is induced by the fires and new leaves start to grow shortly afterwards, whereas in the forest leaf-loss is due to the dry season and new leaves do not start to grow before the first rains.

The study was mainly conducted near the mouth of the river Lola (Fig. 1) in the south-west of the park (about 8°45′N). Permanent study plots of 4.25 ha each were established in three different habitat types (savanna, isolated forest, riparian forest). Tree cover (percentage cover over the ground, Salewski 1999) in the savanna (*Daniella olivieri*, *Lophyra lanceolata*, *Burkea africana*, *Crossopteryx febrifuga*, *Terminalia avicenoides*) in 17 plots (50 × 50 m) varied between 5% and 10% in the rainy season and between 3% and 5% at the peak of the dry season. In the isolated forest (*Anisogeisus leiocarpus*, *Tapura fisheri*, *Diospyros abissinicus*, *Malacantha alnifolia*, *Ceiba pentandra*) the corresponding values for tree cover were 5–70% and 3–20%, and in the gallery forest (*Cynometra megalofolia*, *Creibia atlantica*, *Tapura fisheri*) 80–95% and 50–90%. Tree density was greatest in the gallery forest and least in the savanna (Salewski 1999). A herbaceous layer was well developed in the savanna but burned completely during the fires. It was found only on the fringes of the isolated forest, never in the gallery forest. An additional study area of about 1 ha, where regular mist-netting was carried out about every 10 days, was an alluvial plain supporting *Dichrostachys cinerea* bushes 5 km north of the main study area.

Phenology

The presence of Pied Flycatcher and Willow Warbler in the study area (study plots and the area between the plots) was recorded every day by opportunistic observation. A species was recorded when at least one individual was heard or seen or was mist-netted. The occurrence of a species was recorded as a percentage of days it was observed from the total number of days on which observations were made in a pentad. The numbering system for pentads followed Berthold (1973). Abundance is given following the system of Morel and Tye (1995).

Habitat choice

In the winters 1995/96 and 1996/97 standardized transect counts were performed about every 10 days in the study plots in all three habitats (Salewski 1999). Each count covered an entire plot and allowed estimations of the densities of migrants there. For comparison of the two target species every record during the two seasons of a Pied Flycatcher or a Willow Warbler in each habitat was treated as an independent event. The same individual (colour ringed) Pied Flycatchers were counted on several occasions but the effect of any possible bias due to non-independent data was thought to be negligible because of the high total number of records for this species. For Willow Warblers, it was not possible to identify individuals because of the small number of ringed birds in the study plot. However, the low resighting frequency of marked birds made it unlikely that individuals were counted twice.

Territoriality

Birds were mist-netted in the study area and marked with aluminium rings and an individual combination of two or three colour rings. Direct observations revealed territorial behaviour where territoriality of a bird was defined as ranging in a limited area and defending it temporarily against conspecific individuals for more than one day.

Feeding ecology

Direct observations of foraging birds were performed to investigate their feeding ecology, focusing on microhabitat choice, feeding techniques and feeding substrate. When an individual of the target species was detected it was observed for as long as possible but up to a maximum of 5 min. The total time for each observation was measured. We recorded the substrate from which a bird fed, and the technique used. Feeding substrates were classified as air, leaves, twigs, trunk, ground and ground vegetation (herbaceous layer). Feeding techniques were pecking (taking food from a substrate without using the wings or legs to approach), flying (flying directly towards prey), hovering (hovering in front of a food item), jumping (jumping towards a food item without using the wings), jump-flight (jumping towards a food item, using the wings for balance but not as the main force to drive the bird forward), running (running towards an item on a branch without using the wings) and pouncing (pouncing from a perch in a tree to the ground).

For the Pied Flycatcher, data on microhabitat choice were collected for every site where a feeding action started. These were: height of the vegetation,

height of the feeding bird and vegetation cover above and below the foraging bird (as per cent coverage in a space 2 m above and below the bird with a radius of 2 m). From the heights of the birds (H_B) and the heights of the trees (H_T) the foraging height index F_h was calculated (Nyström 1991): $F_h = H_B/H_T$.

The feeding rates of the Willow Warbler were too high to record microhabitat choice for every feeding action but this was given for the total time of an observation.

For further data analysis the mean values of the microhabitat parameters and the percentages of certain feeding techniques and feeding substrates of all feeding actions of a single bird during one observation period were calculated to avoid pseudo-replication. Additionally, the data from 10 colour-ringed Pied Flycatchers which were observed between two and 13 times were treated in the same way. In the Willow Warbler marked birds were never observed feeding. Therefore, Willow Warblers and unringed Pied Flycatchers could have been observed more than once, but due to the high number of observations (97 and 263, respectively) over the period of three winters and the fact that individual Willow Warblers did not stay in the area, a possible bias due to repeated observations was assumed to be negligible.

When a feeding bird was observed all other birds in the vicinity and their reaction towards it were recorded. Similar data were recorded for longer territorial interactions among Pied Flycatchers.

Statistical analyses

The data were analysed using SPSS 6.0.1 for Windows®. The accepted significance level for all tests was 95%. The Shannon-Wiener index was used to calculate diversities. It was criticized by Hulbert (1971). The index is moderately sensitive to sample size (Magguran 1988) and increases with numbers of categories (Krebs 1999). However, we are confident that possible bias is low as our sample sizes, although different, should be large enough to be representative and we have not missed any category because the percentages are based on a much higher number of observed foraging actions (foraging techniques: Pied Flycatcher = 608, Willow Warbler = 382; foraging substrates: Pied Flycatcher = 574, Willow Warbler = 331). Despite possible shortcomings the index gives an estimate of the differences in the techniques and substrates used, allows the use of proportions and samples can be compared with a *t*-test.

RESULTS

Phenology of Palearctic migrants

Pied Flycatcher

Pied Flycatchers arrived in the study area in mid-September with the earliest record on 17 September in 1996. By the end of September each year Pied Flycatchers were abundant in any suitable habitat (Fig. 2a), remaining in high numbers until they started to leave in April. During the last days of systematic observations in the 1996/97 season they were still present on 23 April. Colour-ringed Pied Flycatchers showed that a high percentage spent the whole
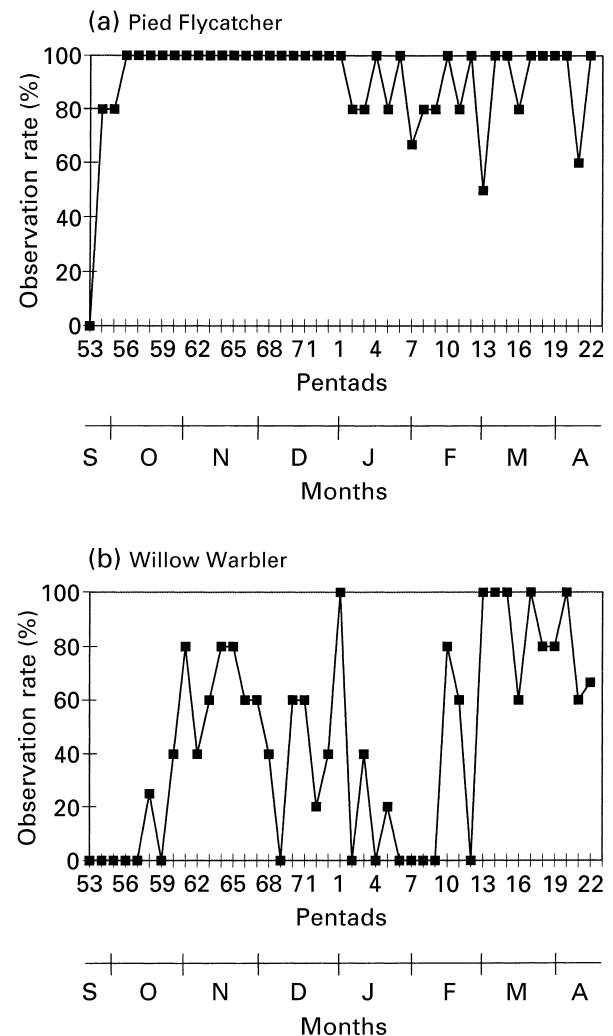

Figure 2. Observation rates of Pied Flycatcher (a) and Willow Warbler (b) in the winter 1995/96 as percentages of days of all days of the pentad when observations were performed, when at least one individual of the species was recorded.

Table 1. Numbers of Pied Flycatchers and Willow Warblers recorded in three habitats during transect counts between September and April in the seasons 1995/96 and 1996/97.

	Isolated forest	Savanna	Gallery forest
Pied Flycatcher	191	48	50
Willow Warbler	29	5	3

European winter in the area with a maximum recorded period of residence of 188 days.

Willow Warbler
Single Willow Warblers were observed as early as mid-October but mass arrival did not occur before November (Fig. 2b). Willow Warblers were then observed in the region frequently until the end of January or beginning of February. They were then absent for a period of 3–4 weeks in each winter to reappear again by the end of February. Throughout the next two months they were observed frequently before they left the area at the end of April.

Habitat choice

Both Pied Flycatchers (66%) and Willow Warblers (78%) were recorded most frequently in the isolated forest (Table 1). The savanna (17%/14%) and the gallery forest (17%/8%) were also used to a lesser extent. The two species showed no significant differences in habitat choice ($\chi^2 = 2.63$, n.s.).

Territoriality

Pied Flycatcher
Pied Flycatchers occupied territories and defended them intraspecifically throughout the winter. Ninety-five Pied Flycatchers were caught at sites which were checked regularly. Fifty (53%) were observed or mist-netted again in the same winter indicating that they were at least temporarily territorial but the rate of territoriality varied in different habitats and was highest in the isolated forest, expressed by the long time some individuals remained (Stanzer-Karbe 1996, Salewski 1999).

Willow Warbler
Territorial behaviour was never observed in Willow Warblers although they sang frequently in November and to a lesser extent in spring. Of 110 ringed birds only one was retrapped (1 day after it was ringed). Two birds were re-observed with a maximum residence period of 17 days.

Feeding ecology

Microhabitat choice
In a stepwise discriminant analysis of the micro-habitat parameters (Table 2), none of the following characters was found to be useful to separate the two species (Wilk's λ for all parameters: > 0.99): height of the vegetation ($F = 0.15$), height of the bird ($F = 0.0$) and cover above ($F = 0.48$) and below ($F = 0.88$). The foraging height index for Pied Flycatchers was 0.57 ± 0.25 ($n = 199$), and for Willow Warblers 0.63 ± 0.25 ($n = 86$). Willow Warblers fed significantly higher in the vegetation than Pied Flycatchers (Mann–Whitney *U*-test: $Z = -2.08$, $P = 0.04$).

Feeding techniques
The two species differed in the percentage of feeding techniques used (Table 3). Pied Flycatchers took most (66.7%) of their prey on the wing (flight and hovering). Pouncing (20.9%) was also important whereas other techniques played a minor role. Willow Warblers used the wings (flights, hovering, jumpflights) only in 33.4% of all feeding attempts, in the rest the food items were almost exclusively taken

Table 2. Microhabitat choice of Pied Flycatcher and Willow Warbler. Shown are the mean values and standard deviations of cover above and below the bird (%) and height of the vegetation and height of the foraging bird (m) and *F* and Wilks' *R* values of a stepwise discriminant analysis of these parameters. In parentheses are the number of observations.

	Pied Flycatcher (164)	Willow Warbler (72)	*F*	Wilks' *R*
Cover above the bird	23.6 ± 27.7	22.0 ± 23.0	0.48	> 0.99
Cover below the bird	12.4 ± 18.8	10.2 ± 11.1	0.88	> 0.99
Height of vegetation	11.9 ± 6.1	12.2 ± 5.6	0.15	> 0.99
Height of the bird	7.3 ± 5.3	7.4 ± 2.9	0.0	> 0.99

Table 3. Feeding techniques of Pied Flycatcher and Willow Warbler (%). In parentheses are the number of observations.

	Pied Flycatcher (267)	Willow Warbler (97)
Flight	50.9	5.0
Hovering	15.8	19.5
Jumpflight	8.9	8.9
Jumping	0.4	0.2
Pouncing	20.9	–
Pecking	2.4	66.5
Running	0.7	–

Table 4. Feeding substrates of Pied Flycatcher and Willow Warbler (%). In parentheses are the number of observations

	Pied Flycatcher (263)	Willow Warbler (86)
Air	7.9	1.8
Leaf	42.4	70.2
Twig	14.7	26.1
Trunk	11.1	1.9
Ground	21.3	–
Ground vegetation	2.3	–

by pecking (66.5%). The diversity index *H′* for Pied Flycatchers (1.32) was higher than for Willow Warblers (0.97) ($t_{177.8}$ = 2.19, $P < 0.05$).

Feeding substrates

Pied Flycatchers and Willow Warblers used various foraging substrates to a different extent (Table 4). Both species took most of their food from leaves but Willow Warblers did so to a greater extent (70.2%) than Pied Flycatchers (42.4%). The only other important substrate for Willow Warblers was twigs (26.1%) whereas Pied Flycatchers took a considerable amount of food from the trunks of trees (11.1%) and especially from the ground (21.3%). The diversity index *H′* for Pied Flycatchers (1.51) was significantly higher (t_{188} = 8.76, $P < 0.001$) than for Willow Warblers (0.75).

Intra- and interspecific relationships

Pied Flycatcher

Of 237 observations of feeding Pied Flycatchers during three winters seven (3%) ended by intraspecific aggression (only foraging bouts which were observed for more than 30 s were included). Only once was another Pied Flycatcher seen near (< 5 m) the observed bird without a reaction from the latter. Intraspecific aggression was especially observed in autumn shortly after the birds arrived and again in spring in the savanna and could last for several hours with several birds involved (Stünzner-Karbe 1996, Salewski 1999). Feeding in mixed-species flocks was never observed and interspecific aggression was rare (Salewski 1999).

Willow Warbler

Of 76 recorded observations in three winters only 29 (38.1%) single individuals were encountered; on 23 occasions (30.2%) it was a conspecific flock and on 24 occasions (31.6%) Willow Warblers were in

a mixed-species flock mainly with Green-backed Eremomela *Eremomela pusilla*. Intraspecific aggression was observed only three times during the whole period. Interactions always occurred between individuals foraging together in a flock and were short single supplants after which the birds continued feeding immediately. Willow Warblers were frequently heard singing, especially in November and March, but there was no indication that this was connected with the establishment of any territory, and occasionally several birds were singing within a feeding flock. Interspecific aggression was observed only twice. Both times Willow Warblers were attacked, once by a Spotted Flycatcher *Muscicapa striata* and once by a Yellow-fronted Canary *Serinus mozambicus*.

DISCUSSION

The wintering strategies of the two Palearctic species differed markedly in territoriality, intraspecific behaviour and recurrence (Salewski *et al.* 2000). Differences were also found in phenology and in feeding behaviour, but not in habitat and microhabitat choice. These features cannot be seen independently from each other and differences in phenology, territoriality and recurrence might be only consequences of the different feeding strategies which separate Pied Flycatcher and Willow Warbler.

After breeding, Pied Flycatchers leave Europe in a south-westerly direction (Winkel & Frantzen 1991, Lundberg & Alatalo 1992). In Spain and Portugal, where migration peaks in September (Veiga 1986), they occupy temporary feeding territories for up to 9 days (Bibby & Green 1980) which might be re-used in subsequent winters (Veiga 1986). During this time they prepare their onward migration (Bibby & Green 1980). After arriving south of the desert they probably rush to the final wintering grounds, as indicated by the early arrival in northern Ivory Coast, to occupy and defend a territory where they stay during the whole European winter. Birds which perform the migration again tend to re-occupy the territories used in previous winters (Salewski 1999, Salewski *et al.* 2000). Similar observations of recurrence have been made in territories at stopover sites in Portugal (Bibby & Green 1980), and on the breeding grounds birds show recurrence when breeding was successful in previous years (Lundberg & Alatalo 1992). It should not be surprising therefore that the same applies to successful wintering. Recurrence has been found among many Palearctic species in their wintering grounds or stopover sites in Africa (Moreau 1969,

Curry-Lindahl 1981, Kelsey 1989, Sauvage *et al.* 1998, Salewski *et al.* 2000).

Willow Warblers leave the European breeding grounds between the end of July and the beginning of September, depending on latitude (Tiainen 1991). Passage at Gibraltar occurs between the end of August and the second half of October (Tiainen 1991); through Morocco from mid-September to mid-October (Urban *et al.* 1997) with the median at the coast on 24 September (1997, *n* = 504, unpublished data of the European-African Songbird Migration Network, Bairlein & Gießing 1997). It is likely that the crossing of the Sahara, for which 2–3 days are needed, starts shortly afterwards (Moreau 1972, see also Bairlein 1992, Biebach 1995). Considering that the first birds start to cross the desert by mid-September there is a gap of 6–8 weeks until they arrive in southern Comoé National Park in the first half of November. It can be assumed that Willow Warblers remain south of the Sahara (Sahel) until this region becomes too dry and inhospitable due to the southward shift of the Inter-Tropical Convergence Zone (ITCZ) (Jones 1998).

That the Comoé National Park is not the final wintering area is shown by the fact that Willow Warblers disappear again for 4–6 weeks in January/February. It is unlikely that Willow Warblers were overlooked for this time because at least one, and usually two or three observers watched birds throughout the day in the area. Willow Warblers undergo a complete moult during the winter, a process during which birds behave more secretively (Jenni & Winkler 1994). However, this also could not explain the absence of records because some individuals started primary moult as early as December and birds still moulting remiges were found until the beginning of April (Salewski 1999). The most likely explanation is that this area becomes unsuitable for the species at the peak of the dry season, and that they reappear as the situation improves when the first rains are expected. The lack of ringing controls in this study suggests that Willow Warblers continue to move southwards, following the ITCZ until they reach a 'turning point' from which they return. In the course of these movements they are not attached to particular localities, as shown by the lack of recurrence. This contrasts with the situation on the breeding grounds in Europe, where recurrence rates of between 33% and 48% (Tiainen 1991) or 24% and 44% (Lawn 1994) and 23% for territorial males (Hogstad 1999) have been reported. The strategy of moving with the ITCZ was called 'itinerancy' by Moreau (1972) and

it appears to be common for Palearctic migrants in West Africa (Jones 1998).

It appears that Willow Warblers show more plasticity in their winter quarters than Pied Flycatchers. That this plasticity in site selection must be adaptive follows from the general assumption that all birds have highly sophisticated spatial orientation systems (Terrill 1991) which enable them to reach any place if this is within their physiological limits, and a motivation to do so exists (Berthold 1996). As Willow Warblers are long-distance migrants and show breeding-site fidelity it follows that there is no selective advantage in showing recurrence on the wintering grounds. Furthermore, Willow Warblers often feed in monospecific or mixed-species flocks and show no sign of territoriality. A similar situation was observed for Wood Warblers *Phylloscopus sibilatrix* in Gabon (Brosset 1971).

Brown (1964) introduced the 'economic defendability model' to explain the relation between territoriality, territory size and food resources in birds. If this model is applied to the Pied Flycatcher it shows that territorial birds can find enough food in a restricted area throughout the winter despite the seasonal changes in vegetation and insect supply (Salewski 1999). That this strategy is successful is shown by the fact that birds that once held a territory are likely to reappear in the following winters at the same site. That there is a food shortage for Willow Warblers in Comoé National Park during the peak of the dry season is suggested because they are mainly leaf-gleaners and dependent on a substrate which becomes less abundant with the proceeding of the dry season along with a decrease of insect numbers on leaves and branches of trees (Salewski 1999). Correspondingly, Martin and Karr (1986) found a positive correlation of foliage density with the numbers of insectivorous leaf-gleaning migrants but not in other guilds in the USA. During the peak of the dry season the situation becomes so unfavourable that Willow Warblers move further south where the situation is better, which leads to the gap of records in January/February. A similar situation was found for leaf-gleaning Palearctic migrants in Tsavo National Park, Kenya (Lack 1983).

Pied Flycatchers are more diverse in the use of feeding substrates and feeding techniques than Willow Warblers. The use of a variety of feeding substrates (foraging patches) close to each other enables Pied Flycatchers to stay in a limited area and to defend it economically. In contrast Willow Warblers appear to lack the ability to use a wide variety of

feeding substrates, one consequence of which might be that suitable feeding patches are distributed over a wider area. Therefore, Willow Warblers are forced to show greater mobility because they might deplete available food resources in a restricted area faster than Pied Flycatchers, which thus prevents them from establishing territories. It is indicative in this context that some resident members of the fly-catcher guild (Red-breasted Paradise Flycatcher *Terpsiphone rufiventer*, Brown-throated Wattle-eye *Platysteira cyanea*, African Blue Flycatcher *Elminia longicauda*) form mixed-species flocks in the dry season too and that they also show a lower diversity in feeding substrates than Pied Flycatcher and take most of their food from leaves (Salewski 1999).

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