

LETTER

Switching behavior, coexistence and diversification: comparing empirical community-wide evidence with theoretical predictions

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Abstract

Theory shows that the presence of behavioural switching between alternative resources can contribute to coexistence when competitors differ in trophic-related traits. In addition, switching can generate disruptive selection on such traits in a low-diversity community, increasing the number of species. Both of these processes should produce communities in which species differ in their values of the trophic trait, and display corresponding differences in the time-course of their switching from one resource to another. Here we present evidence for widespread switching behaviour for a diverse Mediterranean scrubland bird community. We show that species differ in a beak character related to their relative use of insect and fruit resource channels, and that the timing of switching is correlated with the relative use of resources. These patterns are consistent with theoretical predictions, suggesting a possible role of switching behaviour in promoting avian coexistence and diversification.

Keywords

Adaptation, birds, coexistence, diversification, foraging theory, fruits, insects, resource seasonality, species richness, switching behaviour.

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INTRODUCTION

The impact of adaptive behaviour on species diversity in natural communities has periodically received attention from both ecologists and evolutionary biologists. A positive role of adaptive behaviours in allowing coexistence and/or promoting morphological diversification of competing species has been demonstrated in several models over the years (Roughgarden & Feldman 1975; Wilson & Yoshimura 1994; Kondoh 2003; Abrams 2006a,b; Beckerman *et al.* 2006; Rooney *et al.* 2006; Eveleigh *et al.* 2007; Rueffler *et al.* 2007). Switching behaviour is the ability of consumers to adaptively increase the consumption of one resource at the expense of decreased consumption of an alternative resource. Behavioural switching has been shown to enhance coexistence of consumer species (Wilson & Yoshimura 1994; Abrams 2006a,b; Rueffler *et al.* 2007). A second potential diversity-enhancing impact of switching behaviour is its role in generating new species and promoting

morphological diversification. While such a role has been suggested several times (Wcislo 1989; Price *et al.* 2003; West Eberhard 2003), rigorous theoretical support has only recently appeared (Abrams 2006a, 2006b, Rueffler *et al.* 2007). These articles examine evolution in the context of a system that initially has a single lineage of consumers exploiting two resource types, with a trade-off in their abilities to use both based on the evolution of a morphological foraging trait. Rueffler *et al.* (2007) showed that adaptive diet choice based on energy content and handling time could allow evolution of two coexisting morphological types when only one type would exist in the absence of this behaviour. Abrams (2006b) demonstrated that behavioural switching between two food types in a variable environment promotes evolutionary diversification of a morphological trait that is related to the relative use of the food types. Different morphological traits cause the competing consumers to exhibit different temporal patterns of resource switching, and the resulting temporal resource segregation

allows coexistence. Switching expanded the conditions for evolution of multiple morphological types compared to an analogous model that lacked switching behaviour (Abrams 2006c), acting as a behavioural driver of morphological diversification in foraging traits.

The use of two alternative resources by consumer species is one of the prerequisites for evolutionary diversification by foraging adaptive behaviour (Abrams 2006b; Rueffler *et al.* 2007) and empirical evidence suggests that it is a common feature in natural communities. For instance, Rooney *et al.* (2006) have recently summarized empirical evidence for the use of two alternative 'resource channels' by top consumers in a number of terrestrial and marine food webs. However, empirical evaluations of switching behaviour have usually focussed on one or few species (Murdoch 1969), and community-wide evaluations of the relative importance of switching have usually been precluded due to the lack of precise data (Eveleigh *et al.* 2007). Similarly, none of the works reviewed by Rooney *et al.* (2006) has described the temporally staggered switching responses associated with morphological feeding traits that are predicted by the models of Abrams (2006b).

Here we evaluated the existence, ecological basis and morphological correlates of switching behaviour in a scrubland bird community located in Southern Spain during 2 years (Jordano 1987, 1988). The community was composed of 20 passerine bird species that were found to use invertebrates and/or fleshy fruits as food resources throughout the year. Species might act as generalists and adaptively adjust their relative use of two resources (invertebrates and fruits) in response to the marked seasonality of these resources. Alternatively, bird species might be specialists on one resource channel. The two resource types were found to vary asynchronously with contrasting seasonal peaks (Fig. S1), a characteristic feature of Mediterranean scrubland habitats. For each bird species, temporal changes in the proportions of invertebrates and fruits in the diet were evaluated during 2 years using faecal samples from periodical censuses (Jordano 1987, 1988). The existence of strong temporal switching events in the proportions of both resources in response to resource fluctuation was evaluated.

The observed patterns in switching behaviour were compared with theoretical predictions derived from a model of consumer–resource interactions by Abrams (2006b). This model incorporates switching behaviour and morphological evolution in a foraging trait (e.g. bill shape) by means of two variables. Figure 7 in Abrams (2006b) and supplementary Fig. S2 provide an example of the patterns of diversification in the morphological trait and the corresponding between-species differences in switching behaviour predicted by Abrams' model. The more specialized morphologies exhibit less extreme switching; they also switch back to their

preferred resource before less specialized morphological types when that resource increases in relative abundance, and switch away from it later when the preferred resource decreases. This pattern of switching generates temporal resource partitioning and thus contributes to coexistence when there is competition for resources.

To determine whether observed seasonal changes in diet composition were consistent with the theoretical results of Abrams (2006b), we contrasted five specific predictions derived from his model with empirical data. Specifically, we used the most numerous genus *Sylvia* (seven species out of 20 passerine species recorded in the area) to test predictions about the expected relationships between morphology and switching for species in a single evolutionary lineage (Blondel *et al.* 1996). The five predictions studied were as follows. First, switching was expected in all the species that behaved as generalists, i.e. that consumed the two resources (prediction 1). This pattern was expected because generalists seasonally switched between alternate resources as their abundance fluctuated in all theoretical simulations (Abrams 2006b; and see supplementary Fig. S2). Secondly, previous theoretical work (Abrams 2006b) showed that species differed qualitatively in their response to an increase in the proportion of a resource in the environment. We examined whether, as one resource (e.g. fruits) first becomes more abundant, the generalist switching species that are most similar to a fruit specialist, in terms of average diet, switch first, and if the species most similar to the opposite specialist (more insectivorous species, with a lower proportion of fruits in the diet) switch later (prediction 2). Thirdly, in theoretical simulations species were found to differ in the proportion of both resources in the diet by the effect of specific behavioural and morphological adaptations that modify consumer capture rates (Abrams 2006a,b,c). Thus, we asked whether species differed in the averaged proportion of both resources in the diet in natural communities [$MR^*_{ij} = \text{mean } R^*_{ij}$; where MR^*_{ij} is the averaged proportion of resource j used by species i , and R^*_{ij} is the proportion of resource j used by species i in each sample (see Materials and Methods)] (prediction 3). Fourth, for switching to favour evolutionary divergence in morphology, there must be a correlation between one or more morphological traits and relative abilities to use different resources (Abrams 2006b). To empirically evaluate the effect of morphology on consumer capture rates, we determined whether the difference in the averaged proportion of resource j used by species i (MR^*_{ij}) was correlated with specific values of a morphological foraging trait related to the relative ability to utilize the two resource types (prediction 4). Fifthly, in Abrams' model, resource consumption by generalist species tracks temporal fluctuations in resource abundance. We evaluated whether this

occurred in the natural communities, by analysing if the proportion of resource use (R_{ij}^*) was correlated with the temporal variation in resource abundance (R_1 , R_2) (prediction 5).

MATERIALS AND METHODS

Data

Temporal changes in the proportion of fruits and invertebrates in the diet were derived from periodical faecal samples of birds captured in mist-nets (Jordano 1987, 1988). A total of 6–10 mist-nets were operated weekly, 2 days per week. The nets were opened from dawn to dusk and checked at hourly intervals. Resource data were logarithmically transformed. The relative ratio between R_1 and R_2 was calculated normalizing fruit and invertebrate abundance (i.e. setting maximum abundance = 1). The percent volume in the faecal samples of species i consisting of invertebrates and fruits ($R_{i1}^* \approx 1 - R_{i2}^*$) was estimated (Jordano 1987, 1988). An averaged value was obtained every 15 days for each species. Variation in fruit production was estimated by transect counts of the total number of ripe fruits per unit area that were checked every 15 days (Jordano 1987, 1988). Relative variation in invertebrate abundance was calculated using adhesive traps that were set hanging from vegetation and on the ground (Jordano 1987, 1988). These traps were monitored weekly. Bird abundances were estimated by performing weekly counts following the procedure of Emlen (1971). Morphological measures were obtained from birds captured in the mist-nets using standard procedures (Jordano 1987, 1988).

Abrams' model

Abrams' model (2006b) simulates the population dynamics of two resources (R_1 , R_2), several consumer lineages (N_i) and the dynamic evolution of a foraging morphological trait (x_i) and a switching behavioural trait (α_i) for each consumer lineage. A detailed mathematical description of the model is provided in Abrams (2006b). We carried out a number of simulations using different parameter values and considering cases with evolution of the morphological trait (x_i) and with several species having x_i values fixed at their evolutionary equilibrium determined by the full model. A robust result is that evolution produces specialists and one or more generalist type, and that the different patterns of switching produced by the different species lead to temporal resource partitioning. Figure 7 in Abrams (2006b) and supplementary Fig. S2 provide examples of the dynamics of the behavioural traits as a function of resource densities in a set of four species whose morphological traits have attained an evolutionary equilibrium.

Statistical methods

Differences in switching rates between species were quantified by plotting the percentage of fruits in the diet (R_{i1}) against the resource ratio in the environment ($R_1/(R_1 + R_2)$) for each species. Sigmoid curves (four-parameter logistic equations) were fitted using nonlinear regression methods. We estimated switching delay for each species by calculating the relative environmental resource ratio at which 25% of fruits in species' diet was achieved [$R_1/(R_1 + R_2)_{25}$]. PRISM software (version 5.0) was used to interpolate values from the sigmoid curves fitted. A graphical illustration of this procedure is provided in supplementary Fig. S3. To model resource consumption as a function of temporal resource availability (prediction 5), ordinary least-squares regression models were applied assessing normality assumptions and logarithmically transforming resource variables. Temporal switching curves were fitted using the cubic spline method (JMP package, version 5). This method uses a set of third-degree polynomials spliced together such that the resulting curve is continuous and smooth at the splices (knot points). The estimation is done by minimizing an objective function composed by a combination of the sum of squares error and a penalty for curvature integrated over the curve extent. Lambda (λ) = 100 values were used for all the curves shown (unless otherwise indicated). Curves obtained for other λ values ($\lambda = 0.1$ –1000; not showed) were qualitatively similar.

RESULTS

We found that switching is a common behavioural strategy. The bulk of the species (14 out of 20) were generalists that switched between invertebrates and fruits following the resource peaks (prediction 1), suggesting that switching behaviour might be a pervasive and widespread phenomenon, at least in Mediterranean bird communities (Fig. 1). Switching behaviour was observed in all the groups in the studied community (residents, autumn- and spring-passage migrants, breeding and wintering species), suggesting that switching is a common strategy in most bird functional migratory groups. Among the species that did not switch, five ate mostly invertebrates, whereas only one ate both seeds and fruits [see Fig. S4 for detailed trends]. All *Sylvia* warblers exhibited switching behaviour.

Species differed in the speed of switching responses observed. Two main types of switching patterns were discernable. Some species rapidly increased the proportion of fruits in the diet following a relatively small increase in the relative ratio of fruits/insects in the environment. Other species switched more slowly and to a lesser extent, and appeared to need much larger fruit/insect resource abundance ratios in the environment to start switching

(Fig. 2a,b). Switching delay was negatively associated with the percentage of fruits in the diet ($R^2 = 0.54$, $P < 0.01$; Fig. 3), indicating that switching delay increased progressively with reduced proportion of fruits in the diet (prediction 2).

Interestingly, we also found empirical support consistent with the other three predictions outlined above. First, species were found to differ consistently in MR^*_{i1} , the averaged proportion of resource 1 used (prediction 3; Tukey–Kramer test, $P < 0.0001$; Fig. 4). Second, we analysed several morphological traits in a single evolutionary lineage, the species-rich genus *Sylvia* (Jordano 1987, 1988; Blondel *et al.* 1996). As expected, we were able to find a foraging trait (x_1 = gape width) that was associated with specific differences in the proportion of the two resources used (prediction 4; Fig. 2c). Moreover, when considering all the species in the study zone, insectivore specialists were characterized by significantly smaller gape widths (Fig. 5). Finally, the temporal variation in the proportion of resources used (R^*_{ij}) was found to be a function of the variation in resource abundance (R_1 , R_2) (prediction 5; Tables S1 and S2, Fig. 2a).

DISCUSSION

Our results provide the first empirical community-wide evaluation of switching behaviour in bird natural communities. We showed that switching behaviour is a pervasive and widespread phenomenon in Mediterranean bird communities characterized by strong resource fluctuations. Given that switching has been theoretically associated with diversification processes (Abrams 2006b), our empirical findings should encourage community-wide evaluations of switching responses in other systems characterized by sustained resource fluctuations (Eveleigh *et al.* 2007). Interestingly, tropical habitats with sustained resource fluctuations (i.e. forest canopies, ecotones and altitudinal gradients; Loiselle & Blake 1991; Levey 1988) have been also identified as important centres of morphological and behavioural diversification in birds (Levey & Stiles 1992; Smith *et al.* 1997; Hawkins *et al.* 2006; Weir 2006; Boyle & Conway 2007). Further, existing evidence states that a number of Palearctic and Nearctic bird species are derived from tropical ancestors specifically adapted to resources that fluctuate seasonally (Berthold 1976; Levey & Stiles 1992; Smith *et al.* 1997; Boyle & Conway 2007). Observational data from vertebrate communities cannot establish whether a particular ecological mechanism is involved in speciation, or whether that mechanism is essential for coexistence. While it is likely that many mechanisms play a role in bird coexistence (Martin & Martin 2001; Lovette & Hochachka 2006), theory demonstrates that the patterns of switching observed in

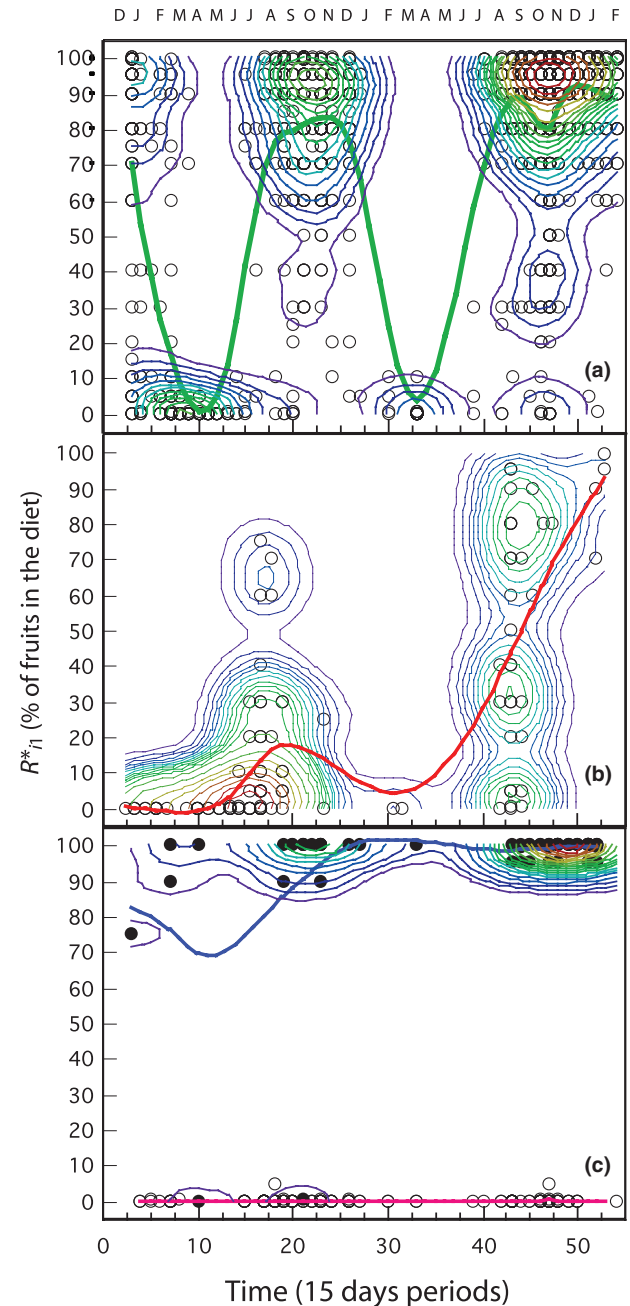


Figure 1 Observed foraging behaviours. Spline fits describing switching trends are shown. Each dot represents a faecal sample. Species are grouped by switching behaviour types: (a) Species that respond rapidly to a relative small increase in the availability of fruits (fast switchers, green line, switching delay values ranging from 0.1 to 0.3). (b) Species that showed delayed switching (delayed switchers, red line, switching delay values from 0.4 to 0.9). (c) Specialist species in fruits (black dots, blue line) and invertebrates (white dots, pink line, switching delay > 0.9). A smooth surface showing the density of data points is provided (except for invertebrate specialists for which all points lie on a line). Red contour lines indicate maximum point density.

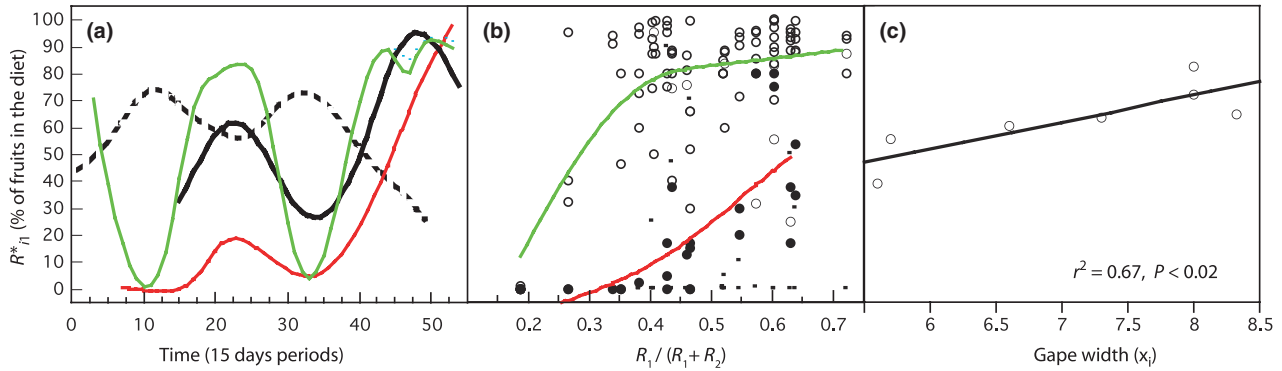


Figure 2 Switching behaviour in fast and delayed switchers. (a) Observed switching behaviour in fast switchers (green line) and slow switchers (red line). The black line indicates temporal variation in fruit production (R_1); the black-dashed line describes variation in invertebrate production (R_2). (b) Observed switching compared to the relative increase in the ratio of fruits/(invertebrates + fruits) in the environment. Rapidly switching species (green line, white dots) and delayed switching species (red line, black dots) are compared. (c) Observed relationship between a foraging morphological trait (ξ : gape width) and the averaged proportion of fruits used (MR^*_{i1}) in the genus *Sylvia*.

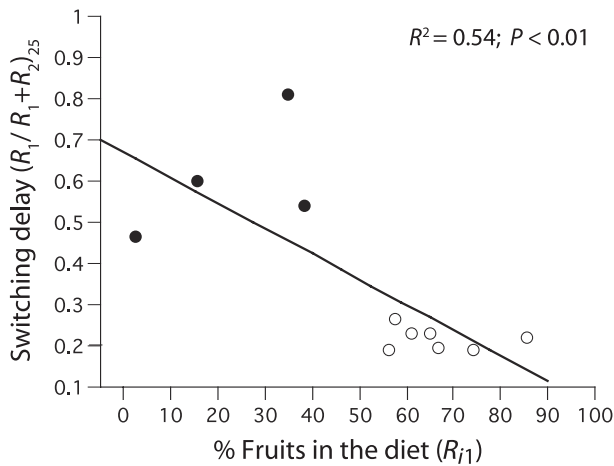


Figure 3 Regression between switching delay and mean percentage of fruits in the diet (MR_{i1}). Rapidly switching species (white dots) and delayed switching species (black dots) are compared.

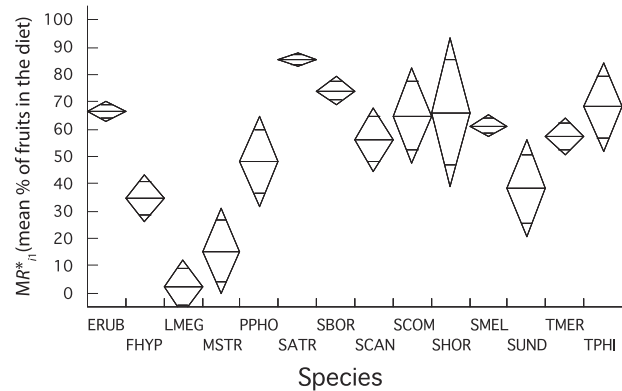


Figure 4 Specific differences in the averaged proportion of fruits in the diet (MR^*_{i1}) between switching species. A description of species codes is provided in Table S1. Significant interspecific differences in the values of MR^*_{i1} were statistically supported (Tukey–Kramer test; $P < 0.0001$).

the community we studied should at least contribute to coexistence if there is competition for food (Wilson & Yoshimura 1994; Abrams 2006b, 2006c). Locally, switching behaviour might combine with other factors to enable the persistence of populations at the local scale (Abrams 2006b; Rooney *et al.* 2006). For instance, coexistence has been shown to be favoured by the asynchronous variation in the abundance of resources using theoretical simulations (Egas *et al.* 2004; Rooney *et al.* 2006). Finally, our results suggest that the presence of switching behaviour might itself be under strong natural selection. In accord with these expectations, Berthold (1976) demonstrated the continued existence of switching behaviour in captured blackcaps, *Sylvia atricapilla* that were provided with constant availability of fruits and invertebrates and maintained in

controlled conditions during several years. This suggests that the ability to switch between resources represents a phenotypic plastic response that could be genetically assimilated to some extent in a number of species (sensu Price *et al.* (2003)).

Our study also provides evidence for the association between the temporal patterns of switching behaviour and morphological foraging traits. In line with these findings, both diversification in beak shape and feeding generalization have recently been associated with avian diversification processes (Ricklefs 2004; Grant & Grant 2006; Phillimore *et al.* 2006). Similarly, the genetic and developmental paths for diversification in beak shape have also been identified and related to avian diversification processes (Wu *et al.* 2004; Fitzpatrick *et al.* 2005). Overall, our

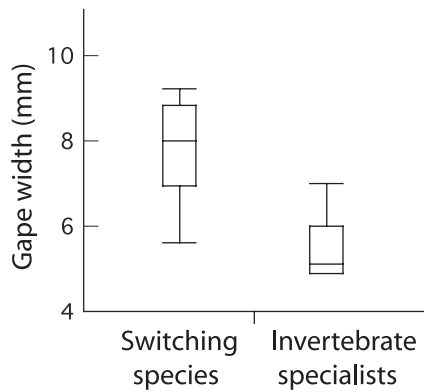


Figure 5 Differences in gape width between switching species and insectivore specialists. Significant differences were statistically supported (Tukey–Kramer test; $P < 0.0001$).

work highlights the need to consider the switching responses of consumers in understanding the organization of bird communities with non-constant resource availabilities. Such community-wide evaluations of switching responses in other tropical and temperate systems may also shed light on the patterns of morphological diversification observed in those communities. Overall, we conclude that experimental testing of the role of switching behaviour in promoting morphological diversification might be a promising research line in evolutionary ecology.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 Temporal variation of the production of resources in the study zone.

Figure S2 Behavioural dynamics predicted by Abrams' model.

Figure S3 An illustrative example of the estimation of switching delay (*Sylvia melanocephala*, *Sylvia undata*).

Figure S4 Switching trends for each bird species.

Table S1 List of the species, specifying diet and switching behaviour.

Table S2 Least square regression models of the proportion of resources in the diet as a function of resource productivity and morphological traits.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01195.x>

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Table S1. Community species. S = species that showed switching between R_1 and R_2 (fruits and invertebrates) characterized with low switching delay values < 0.4 (figure 4) and fast response curves (see figure S4); S°= Species characterized by fast switching responses (figure S4) and small sample size (no switching delay estimate allowed); S* = species that showed delayed switching behavior (switching delay >0.4 ; figure 4); F = species mostly using fruits and seeds; I = species that consumed mostly invertebrates; N= Number of fecal samples examined for each species.

GROUP	CODE	Species	CODE	N
Fast Switchers	S	<i>Sylvia cantillans</i>	SCAN	27
	S	<i>Sylvia borin</i>	SBOR	183
	S	<i>Erithacus rubecula</i>	ERUB	291
	S	<i>Sylvia atricapilla</i>	SATR	643
	S	<i>Sylvia communis</i>	SCOM	12
	S	<i>Sylvia melanocephala</i>	SMEL	238
	S	<i>Turdus merula</i>	TMER	77
	S°	<i>Sylvia hortensis</i>	SHOR	5
	S°	<i>Turdus philomelos</i>	TPHI	14
	S°	<i>Phoenicurus phoenicurus</i>	PPHO	14
Delayed Switchers	S*	<i>Luscinia megarhynchos</i>	LMEG	48
	S*	<i>Sylvia undata</i>	SUND	12
	S*	<i>Muscicapa striata</i>	MSTR	15
	S*	<i>Ficedula hypoleuca</i>	FHYP	50
Specialists	F	<i>Carduelis chloris</i>	CCHL	74
	I	<i>Hippolais polyglotta</i>	HPOL	34
	I	<i>Phylloscopus collybita</i>	PCOL	84
	I	<i>Phylloscopus trochilus</i>	PTRO	25
	I	<i>Phylloscopus bonelli</i>	PBON	8
	I	<i>Regulus ignicapillus</i>	RIGN	8

Table S2. Variables associated with the proportion of resources in the diet. Test effects of a least squares regression model of the variation in the proportion of resource 1 used (R_{i1}^* : fruits) as a function of fruit productivity (R_1), invertebrate productivity (R_2), species (Sp), species gape width (x_i) and year (y).

Dependent variable	Independent variables	Fit	Sum of squares	F	P
<i>All the species</i>					
R_{i1}^*	R_1	$R^2 = 0.47$	645245.0	137.79	0.0001
	R_2	$p < 0.0001$	42326.0	90.39	0.0001
	Sp	$DF=17, 1061$	274405.2	45.08	0.0001
	x_i		5362.1	11.45	0.0007
	y		64309.2	137.79	0.0001
<i>Sylvia genus</i>					
R_{i1}^*	R_1	$R^2 = 0.36$	74970.6	213.5	0.0001
	R_2	$P < 0.0001$	19893	56.7	0.0001
	Sp	$DF=10, 756$	21741.1	10.3	0.0001
	x_i		5631.2	16.0	0.0001
	y		38705	110.2	0.0001

Fig. S1. Temporal variation in the availability of fruits (R1) and invertebrates (R2) in the study area. Production of fruits is measured in kJ/ha and invertebrate production is measured in relative abundance units (number of invertebrates/ sample surface unit). Lines are spline fits for the data points showed.

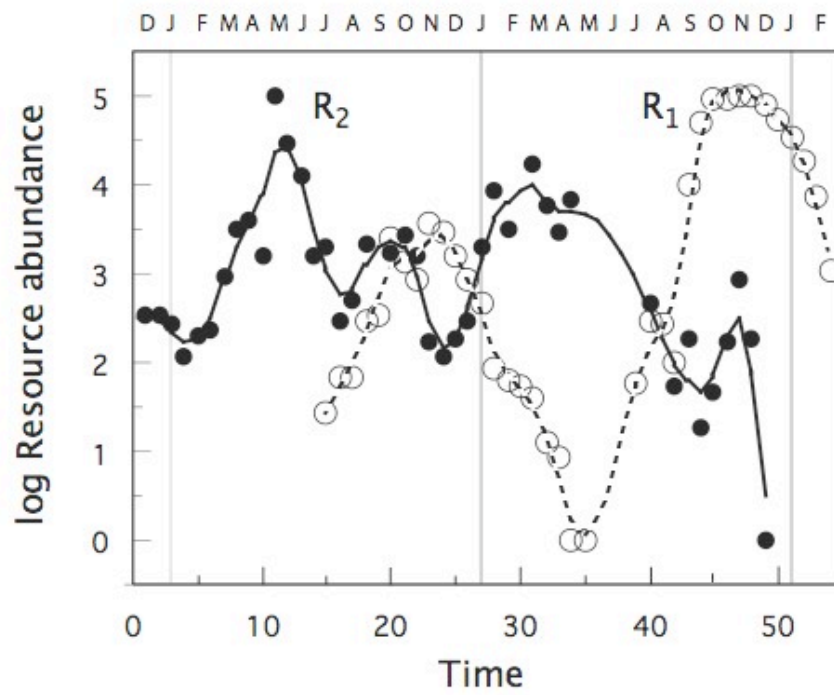


Fig. S2. Theoretical expected behavioral dynamics of the evolutionary stable coalition for four generalist species derived from Abrams' model. The parameters used are $I_1=0.25$, $I_2=0.25$, $E_1=0.15$, $E_2=0.15$, $C_{1\max}=5$, $C_{2\max}=5$, $h=1$, $b=0.1$, $d=0.03$, $v_x=0.005$, $v_z=20$, $\int_x=0.001$, $\int_z=0.000001$, $q_1=100$, $q_2=100$, $L=50$, $v_1=0.8$, $v_2=0.8$, $n=0.75$, $m=1$. **(A)** Resource abundance variation (R_1, R_2) when resource input rates are described by sinusoidal functions. Resource 1 is denoted by the solid line and resource 2 by the dashed line. There are very low amplitude fluctuations in the four consumer populations (not shown) as a result of the resource cycles. **(B)** Switching behavior (z_i) observed in four generalist species that coexist. The evolutionarily stable phenotypes in this model are: $x_i = 0.152$ (red line), 0.328 (solid black line), 0.573 (green line) and 0.845 (dashed black line). This represents a spectrum of increasing specialization on resource 1, with $x_i = 0.845$ being the most specialized on resource 1. The evolutionary rate is low enough that these values are effectively constant.

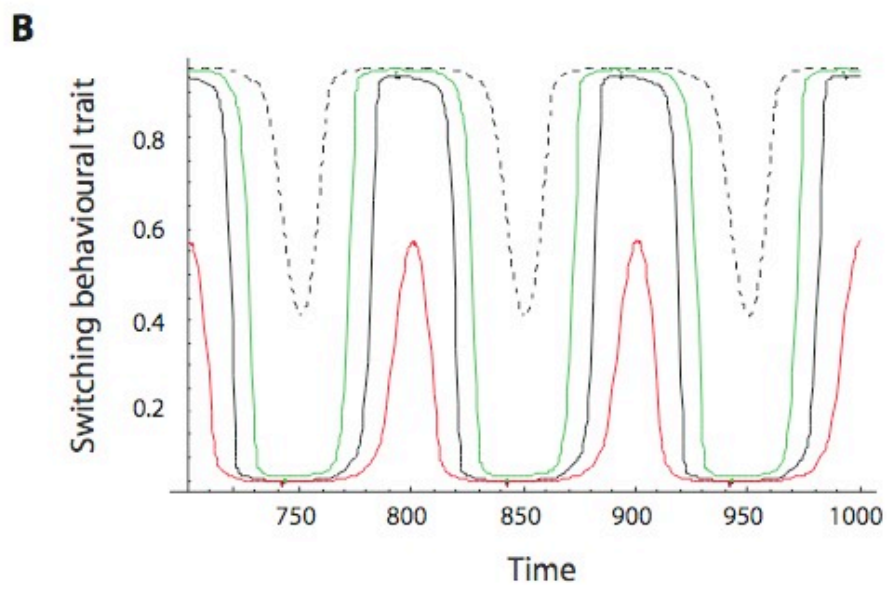
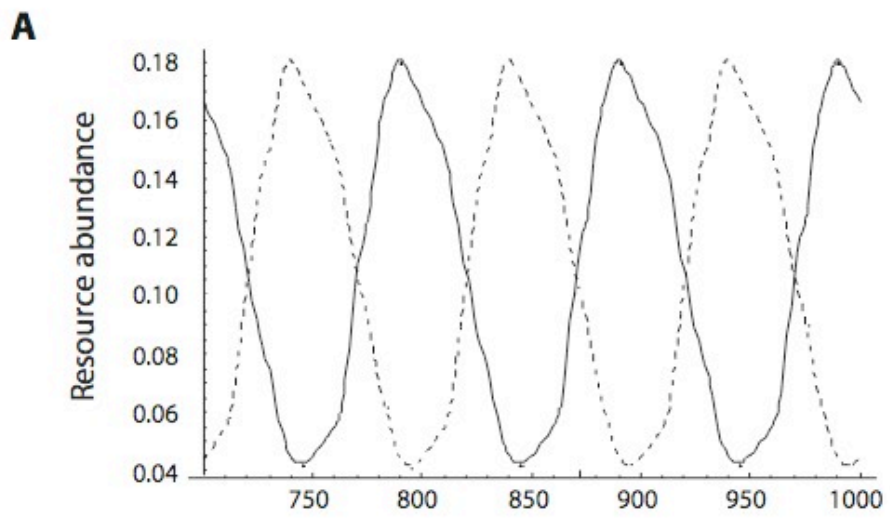


Figure S3:

An illustrative example of the calculation of switching delay using a sigmoid fit (four-parameter logistic equation). Switching delay was estimated as the ratio $R_1 / (R_1 + R_2)$ in the environment required to achieve a %25 of fruits in the species' diet. R^*_{i1} corresponds to the averaged percentage of fruits of several faecal samples (diet estimates of individual birds) collected during a period of 15 days.

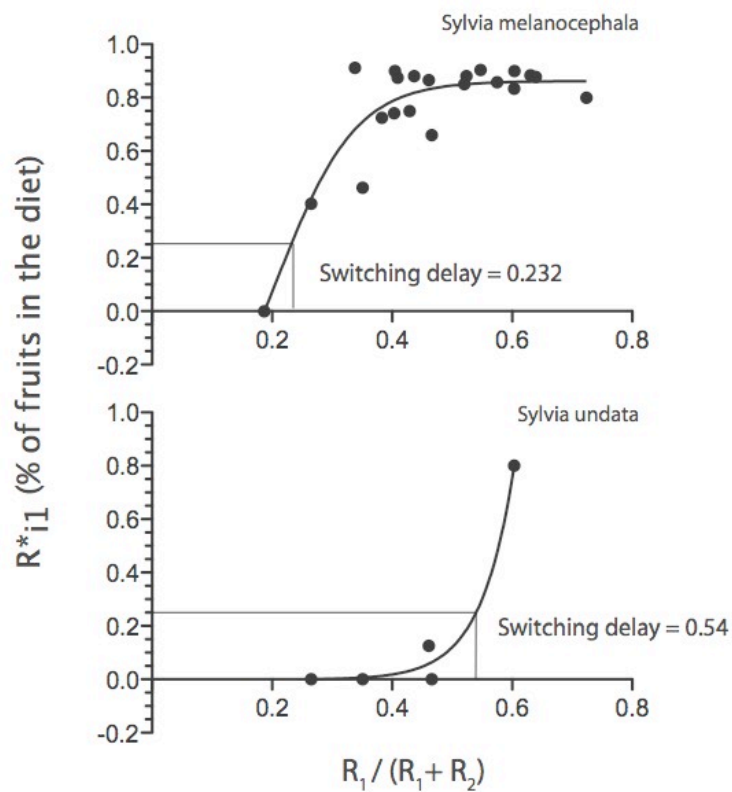


Figure S4: Switching trends for the studied species. **(A)** Species that switch rapidly due to a small increase in the proportion of fruits (Fast switchers): *Erithacus rubecula* (orange), *Phoenicurus phoenicurus* (light blue), *Sylvia atricapilla* (dark blue), *S. borin* (violet), *S. communis* (orange), *S. melanocephala* (red), *S. cantillans* (green), *Turdus merula* (grey), *T.philomelos* (pink). **(B)** Species that behaved as delayed switchers (Slow switchers): *Ficedula hypoleuca* (black), *Luscinia megarhynchos* (grey), *Sylvia undata* (pink) and *Muscicapa striata* (orange). **(C)** Species that behaved as specialists. Seeds and Fruits: *Carduelis chloris* (green); Invertebrates: *Phylloscopus collybita* (red), *P. bonelli* (pink), *P. trochilus* (blue), *Regulus ignicapillus* (yellow), *Hippolais polyglotta* (orange).

