



Singing the Popular Songs? Nightingales Share More Song Types with Their Breeding Population in Their Second Season than in Their First

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Abstract

Signals used in communication often change throughout an individual's life course. For example, in many song bird species, males modify their song especially between their first and second breeding season. To address one possible reason of such modification, we investigated whether common nightingales *Luscinia megarhynchos* adjust their song type repertoires to sing the song types commonly occurring in their breeding population. We analysed nocturnal singing of six nightingales in their first and second breeding season and compared their repertoire composition and usage to the 'typical' repertoire and usage on the breeding ground (represented by seven reference birds). Songs that were maintained between the first and second season by the six focal birds occurred in most of the repertoires of the seven reference birds and were sung often. In contrast, song types that were dropped from the repertoires occurred less often in the reference birds' repertoires and were sung less often. Furthermore, in the first year, each focal nightingale's repertoire was less similar to the reference birds' repertoires than in the second year. Thus, nightingales adjusted their singing towards the songs popular in the breeding grounds by keeping song types that were common and frequently sung by other individuals in their breeding area and by disposing of infrequently performed ones. This resulted in increased similarity with the population's repertoire from the first to the second year. We discuss possible ontogenetic processes that may lead to such an adjustment and suggest an improved ability to match song types as possible adaptive value.

Introduction

Learned communication signals of song birds often exhibit age-dependent changes. In 'closed-ended learners' like zebra finches *Taeniopygia guttata* (Immelmann 1969) and Bengalese finches *Lonchura striata* (Soma et al. 2009), learning is restricted to an early sensitive phase and no major changes in song characteristics take place afterwards. In contrast, 'open-ended learners' are able to acquire new song patterns after this period: European starlings

Sturnus vulgaris (Eens et al. 1992; Mountjoy & Lemon 1995) or canaries *Serinus canaria* (Nottebohm et al. 1986) exhibit a lifelong ability to change their vocal repertoires. In other oscines, pronounced changes occur between the first and second breeding season: the song of willow warblers *Phylloscopus trochilus* (Gil et al. 2001), brown-headed cowbirds *Molothrus ater artemisia* (O'Loughlen & Rothstein 1993), and common nightingales *Luscinia megarhynchos* (Kipper et al. 2004; Kiefer et al. 2006, 2009) are examples. Different mechanisms might lead to such

vocal plasticity: either new song material might be acquired later in life (e.g. Nottebohm et al. 1986) or an overproduction of previously learned song material might be preceded by a selective attrition process (e.g. Marler & Peters 1982; Nelson & Marler 1994). Both processes may result in increased similarity with the song of the breeding population or neighbours (Liu & Nottebohm 2007; Nelson & Poesel 2009). Sharing at least a part of the vocal repertoire with conspecifics can indicate the affiliation of an individual to a population which has been referred to as 'dialect'. Song dialects have been reported for e.g. puget sound white-crowned sparrows *Zonotrichia leucophrys pugetensis* (Baptista 1977; Nelson et al. 2004), European starlings (Hausberger et al. 2008), savannah sparrows *Passerculus sandwichensis* (Burnell 1998) and other song bird species (Krebs & Kroodsma 1980; Handley & Nelson 2005; Podos & Warren 2007). Song sharing in general can be beneficial for males in terms of e.g. reduced aggression (Briefer et al. 2008) or territory tenure (Beecher et al. 2000a). Song type sharing might be of particular importance in vocal interactions between neighbouring males in nightingales (Todt 1981; Geberzahn et al. 2002; reviewed in Todt & Naguib 2000), and the outcome of such interactions or 'song contests' may have implications for pairing success (Kunc et al. 2006, 2007; Schmidt et al. 2006).

In this study, we investigated whether and, if so, how nightingale's repertoire composition and use changes in successive years, and whether this is leading to an increased sharing level with the population repertoire. Male nightingales have large song type repertoires (mean 190 song types per male, Kipper et al. 2004) and imitate learned song types

very precisely (see Fig. 1 for examples). This allows comparisons of song types within and between individuals in different breeding seasons and populations (e.g. Hultsch & Todt 1981; Kipper et al. 2004; Kiefer et al. 2009). Learning experiments confirmed that nightingales are capable of incorporating new song types into their repertoires later in life: song types heard shortly before song crystallization (i.e. the onset of stereotyped full song) were incorporated within a few days, whereas song types heard shortly after this crystallization were integrated only in the following breeding season (Todt & Geberzahn 2003). It has been shown that nightingales stored more song types in memory than they actually sang in spontaneous singing. When confronted with tutored, but not performed song types in (simulated) interactions they performed those 'silent song types' (Geberzahn et al. 2002; Geberzahn & Hultsch 2003). Both processes (learning and incorporating new song types and activating silent song types) might potentially lead to a repertoire adjustment – e.g. to the breeding population.

Analysing the singing of nightingales in the wild did show that males of a population usually share song types, varying from about 23% (Hultsch & Todt 1981) to about 50–60% shared song types (Kipper et al. 2004). Shared song types are used in male-male encounters for song type matching, but we lack experimental evidence on the exact amount and function of song type matching in nocturnal counter singing (reviewed in Todt & Naguib 2000). Nightingales change their repertoires particularly between the first and second breeding season (Kiefer et al. 2009), but not thereafter (Kipper et al. 2004). From first to second breeding season, a pronounced reper-

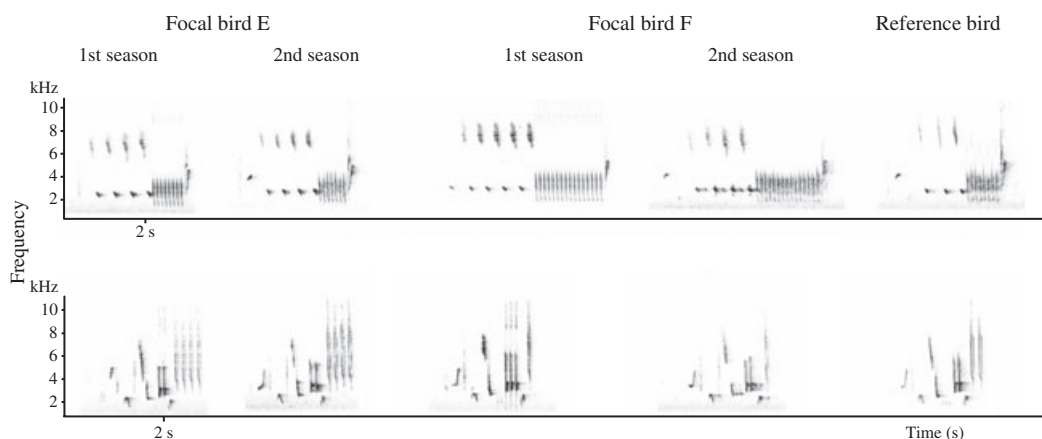


Fig. 1: Example of song stereotypy within and between individuals. Two representative song types were sung by focal bird E and F (in their first and second season) and by one reference bird.

toire turn-over, that is dropping some and adding other song types with a total increase of repertoire size, takes place. Given that repertoire changes appear to happen between seasons rather than within a season, another pre-requisite for increasing similarity with the breeding population would be a strong site fidelity. This is indeed the case in nightingales, where migrating birds tend to return to their breeding grounds. (e.g. Kipper et al. 2004; Kiefer et al. 2009). To conclude, nightingales possess all pre-requisites to re-arrange their repertoires between the first and the second breeding seasons to adjust their singing to the song types sung in their breeding population. If the considerable repertoire turn-over between years one and two indeed served to adjust repertoires in order to sing the most common songs in the population, we would expect 2-yr-old birds to share more song types with the population. Specifically, we expected birds to drop song types that were not (or only rarely) heard in their breeding grounds and to maintain and add the 'common' song types.

Methods

Subjects and Study Site

We recorded nocturnal song of free ranging nightingales in a municipal park in the city of Berlin. The park provides many nightingale breeding habitats, including grassy meadows, bushes, shrubs, woods, a river, small creeks and a pond. Males were individually distinguishable by colour-rings. A few days after their arrival in the park, unringed birds were captured with mist nets using brief song playbacks. Ringing was done by C. Sommer and R. Mundry and with the permission of the Senatsverwaltung für Stadtentwicklung und Umweltschutz and on behalf of the Vogelwarte Radolfzell (Beringungszentrale am Max-Planck-Institut für Ornithologie). No bird deserted its territory after having been captured. Individuals were identified by the location of their territories. To confirm this, we identified the colour-rings repeatedly during daytime, always including the day after nocturnal recording.

Age (1 yr or older) was determined by feather features by C. Sommer and R. Mundry (Svensson 1992; Mundry & Sommer 2007). The focal subjects were 6 birds that were first captured as yearlings in 2005 or 2006 (each: $n = 3$) and that returned to the study site in their second breeding season. About half of the 1-yr-old individuals returned to the breeding ground for a second season (seven of fifteen). Data of three of these birds were used in a previous study

to determine repertoire increase and repertoire turn-over (Kiefer et al. 2009).

We recorded nocturnal song using Sennheiser ME 80/K3U or ME66/K6 directional microphones (Sennheiser, Wedemark, Germany) with windbreak, and a Sony TCD 5 tape recorder, Sony WMD 6 walkman (Sony, Tokyo, Japan) or a Marantz PMD 660 solid state recorder (Marantz Corporation, Kanagawa, Japan). Recordings used in the study had a duration of at least 60 min, which corresponds to song sequences of at least 533 consecutive songs, a sufficient number to capture the majority of a birds' repertoire (e.g. Kipper et al. 2004).

Assessment of Song Type Repertoires and Similarities

The program Avisoft-SASLab Pro 4.40 (R. Specht, Berlin, Germany) was used for all acoustic analyses. Analogue recordings were digitized at 44,100 Hz, 16-bit resolution. Spectrograms of song recordings (settings: sample rate 22,050 Hz, FFT = 256 points, Hamming-Window, Overlap: 50%) were printed and visually compared. The high stereotypy of song type performance within and between individuals allowed a reliable determination of the song type repertoire for each bird and a comparison of repertoires across birds (operational criteria described in Hultsch & Todt 1981; examples in Fig. 1).

Recordings of males were obtained shortly after arrival from their wintering sites and within the first days of nocturnal singing of each male (Apr. 26–May 24). Such nocturnal singing indicates an unpaired status or a status very early in the breeding cycle (Amrhein et al. 2002, 2007). For each of both years, we analysed a sequence of 533 complete songs for each bird, yielding repertoire curves reaching saturation. We used this song sample to determine the number of song types a bird sang only in its first season, only in its second season, and in both seasons (referred to as maintained song types).

To investigate whether second year repertoires were more similar to the population repertoire than first year repertoires, we further inquired into the population repertoire that the focal birds had heard during their first breeding season. High population density (2005: 33, 2006: 29 territorial males) made it impossible to analyze repertoires of all males of the population in order to determine the population repertoire. Instead, we selected seven birds in 2005 and seven birds in 2006 (i.e. approximately a quarter of the respective populations; in the following referred to as reference birds). Reference birds were selected by criteria reflecting the age composition and life

stage of the whole population. Accordingly, for each year we included five recaptured birds, being at least in their second breeding year, one-first breeding season bird and one bird new in the population (a bird of unknown age but being at least in its second breeding year when firstly captured and ringed in the year of interest). We selected different reference birds for the 2 yr. Furthermore, we only included males that sung for at least three nights during our study period. For these selected reference birds, we again determined the repertoire composition based on sequences of 533 successive songs from one nocturnal recording.

Determining repertoires for many birds and years, it appears that song types and frequency of their occurrence are overall rather stable (S. Kiefer & S. Kipper, unpublished data). To test this assumption in the present study, we compared the reference birds' repertoires of the year 2005 with those of the year 2006. For all song types we summed up how many reference birds sang these types and how often each type was sung. The repertoire composition of the 2005 reference birds was very similar to that of the 2006 reference birds: The occurrence of the song types sung by the 2005 reference birds and by the 2006 reference birds was positively correlated (Spearman rank correlation test: r_s : 0.72, $n = 428$, $p < 0.001$). Additionally, the same song types were sung with similar frequencies by both groups of reference birds (Spearman rank correlation test r_s : 0.69, $n = 428$, $p < 0.001$ (see below)).

In order to investigate whether the focal birds changed their singing in relation to the songs in the breeding ground, we compared whether and how often song types that were dropped, added or maintained by the focal birds from first to second season were sung by the reference birds. Our aim was to test for an adjustment to the population's song between seasons. Therefore, we compared the three individuals which were 1-yr-old in 2005 with the reference birds of the year 2005 and the three 2006 yearlings with the reference birds of 2006. We refer to the same reference birds when focal birds were in their second season. We calculated two measures: The first one describes repertoire similarities between each focal bird and the reference birds. To do so, we considered every song type of each focal bird and determined how many of the reference birds were singing it (numbers of birds in %, averaged across song types). This resulted in a percentage of occurrences of song types in these repertoires (e.g. 100% equalling a song type that was performed by all seven reference birds). The frequency of song types

is assumed to be a second measure of the 'popularity' of song types. Therefore, we also determined the total occurrence of each song type, irrespective of which reference bird(s) had sung it (absolute frequencies of occurrence, averaged across song types). Whereas the first measure is a proxy for how many birds were singing a song (irrespective of how often it was sung), the second one reflects the frequency of performance of a song (independent of who was singing it).

As a measure of adjustment to the population's repertoire we calculated repertoire similarity of focal birds with reference birds for both seasons: (1) repertoire similarity of focal birds' repertoires in the first season with the repertoires of the reference birds in the first season and (2) similarity of focal birds' repertoires in the second season with the reference birds' repertoires in the first season. Repertoire similarities were determined by calculating mean DICE-coefficients C_D [with $C_D = 2 \times \text{mean number of shared song types} / (\text{repertoire size focal bird} + \text{mean repertoire size reference birds})$: C_D can reach values between 0 and 1, with 0 = no sharing and 1 = identical song repertoire compositions].

Data Analysis

All calculations (except for *post hoc* tests, see below) were done with the statistic software SPSS 15.0 using non-parametric, two-tailed tests. Because of small sample sizes, we calculated exact tests throughout (Mundry & Fischer 1998). DICE-coefficients of focal birds with reference birds (see above) between the two seasons were compared using Wilcoxon matched-pairs signed-ranks test (all $n = 6$). For comparisons of occurrence and use of song types that were added, maintained or dropped by the focal birds in reference birds' repertoires, we used Friedman tests and a *post hoc* multiple pairwise comparison procedure to accompany a Friedman test using the function 'FR.multi.comp' of the *asbio* package by Aho (2010) in R (R Development Core Team 2009, Kutner et al. 2005).

Results

Firstly, we analysed whether song types that birds had added, maintained, or dropped between first and second season were sung by different proportions of the reference birds. There were differences in the occurrence of the song types of the different categories in the reference birds' repertoires (Friedman Test: $F = 10.3$, $n = 6$, $p = 0.002$; Fig. 2). All six

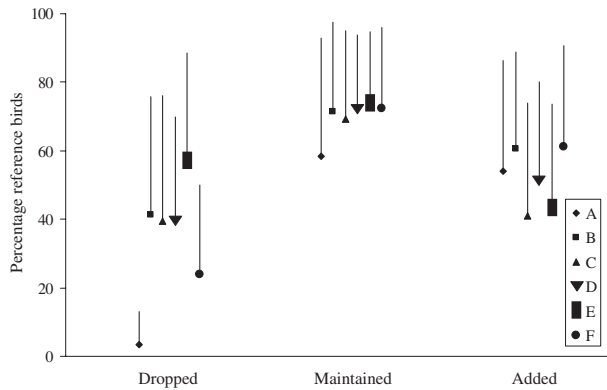


Fig. 2: Occurrence of added, maintained and dropped song types of focal birds (A–F) in the repertoires of the seven reference birds (%; $\bar{x} \pm SD$).

focal birds followed the same pattern: maintained song types occurred in more reference birds' repertoires than dropped ones (*post hoc* comparison: $n = 6$, difference = -1.83 , 95% confidence interval: -3.22 – -0.45 , $p = 0.004$), but there was no difference between the occurrence of maintained and added song types ($n = 6$, difference = 1.17 , 95% confidence interval: -0.22 – 2.55 , $p = 0.13$). There was no difference in the occurrence of added and dropped song types in reference birds, although in five of six focal birds added song types were sung by more reference birds than dropped song types ($n = 6$, difference = -0.67 , 95% confidence interval: 2.05 – 0.72 , $p = 0.74$). Song types of the categories 'added, maintained, or dropped' were also sung with different occurrence frequencies by reference birds ($F = 10.3$, $n = 6$, $p = 0.002$). Maintained song types were sung more often than dropped song types (*post hoc* comparison: $n = 6$, difference = -1.83 , 95% confidence

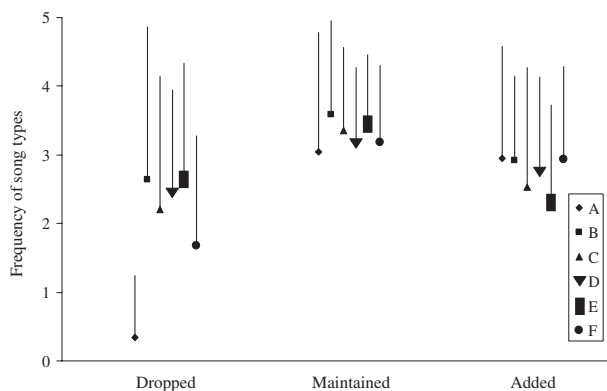


Fig. 3: Frequency of occurrence with which added, maintained and dropped song types of the focal birds A–F were sung by the reference birds ($\bar{x} \pm SD$).

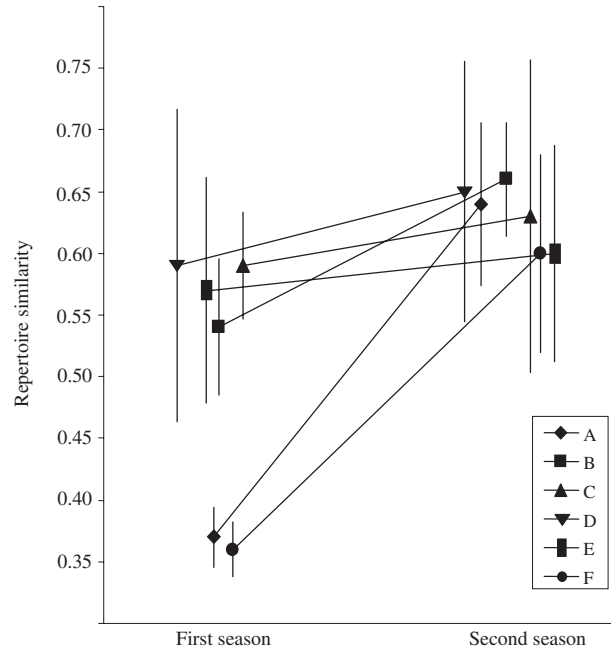


Fig. 4: Comparison of repertoire similarity between focal birds (A–F, subjects depicted by the same symbol in both seasons, connected with dotted lines) and each of the seven reference birds, expressed as mean DICE-coefficients ($\bar{x} \pm SD$, sample sizes for number of shared song types: A_{1st season}: 63 ± 10 , A_{2nd season}: 119 ± 22 , B_{1st season}: 69 ± 5 , B_{2nd season}: 99 ± 11 , C_{1st season}: 88 ± 13 , C_{2nd season}: 112 ± 20 , D_{1st season}: 95 ± 240 , D_{2nd season}: 116 ± 24 , E_{1st season}: 63 ± 17 , E_{2nd season}: 109 ± 20 , F_{1st season}: 49 ± 6 , F_{2nd season}: 98 ± 18). Higher coefficients reflect stronger repertoire similarity.

interval: -3.22 – -0.45 , $p = 0.004$; Fig. 3), but there was no difference in the occurrence frequency between maintained and added song types ($n = 6$, difference = 1.17 , 95% confidence interval: -0.22 – 2.55 , $p = 0.13$). There was no difference in the occurrence frequencies of dropped and added song types in reference birds, although for all except one focal bird added song types were sung more often by reference birds than dropped song types ($n = 6$, difference = -0.67 , 95% confidence interval: -2.05 – 0.72 , $p = 0.74$).

Finally, we calculated DICE-coefficients for each focal bird in each season with all of its seven reference birds, separately. DICE-coefficients (mean overall comparisons) for all focal birds were larger for their second year ($T^+ = 21$, $n = 6$, $p = 0.03$; Fig. 4). On average (mean of means) similarity increased from 0.50 ± 0.12 – 0.63 ± 0.02 .

Discussion

By comparing nightingales' repertoires in their first and second breeding season we could show that

maintained song types were those that were sung by more birds in the breeding population. In contrast, uncommon songs in the population were eliminated from the actual repertoires of second year birds. This led to an increased similarity of second year repertoires with the repertoires of a representative sample of the entire population. These results are consistent with the hypothesis that birds adjust their singing according to the common song types in their population. This is further corroborated by a comparison of song type usage in the population. Maintained song types were sung frequently by the reference birds whereas dropped as well as added song types were sung less often. With regard to maintained and dropped songs, these results are in line with our expectations – adjusting repertoires resulted in a larger proportion of shared song types between focal and reference birds. The numbers for added song types ranged intermediate between those of dropped and maintained song types in song type occurrence as well as usage in reference birds. The results for the added song types only partly fit our expectations – we did expect that newly incorporated song types were the ones sung by many birds and at high frequencies in the population, but added and dropped song types also did not differ in occurrence and usage in reference birds. We hypothesise that the category of added song types might be mixed, containing both, song types that occur frequently and are frequently sung as well as song types that occur rarely and are sung seldom by the reference birds. Three explanations might possibly account for this. Firstly, added song types might be types that were not performed by first year birds because of motor or neurological constraints and only older birds are competent to produce these ‘challenging’ song structures (reviewed in Podos et al. 2009; Ballentine 2009). A second explanation might be that birds also add song types which are rare in the population because these provide the opportunity to use them in terms of de-escalation in vocal interactions as suggested by Beecher & Campbell (2005). Thirdly, these new song types might have been added to emphasize individuality – which might be achieved by singing song types that occur rarely in the population. Studies conducted in the laboratory support these findings: Young song sparrows copied and retained song types of presumable neighbours in the next season on the one hand and on the other hand they tended to modify song types individually (Nordby et al. 2007). Even though nightingales do mostly not modify within a given song type, the explanation might nevertheless hold true for nightingales, too, as

nightingales do indeed possess a certain proportion of ‘individual’ song types that are shared only with a minority of neighbours (Sprau 2006). However, it remains open why the males then not simply kept the dropped song types that are uncommon in the population.

Our results indicate that nightingales adjust their singing towards the population repertoire of the breeding population: common song types are maintained, rare song types are no longer sung and second year repertoires are more similar to the population repertoire than first year repertoires. This pattern might be achieved by one or both of two mechanisms: (1) birds might incorporate new song types after their early sensitive phase, e.g. by learning song types they hear in their first breeding season and (2) birds might have acquired all these songs in early ontogeny already, but not performed them in the first season (selective attrition) (Marler & Peters 1982; Nelson & Marler 1994). In nightingales findings from learning experiments in the laboratory support both notions. Males can acquire new song types that are presented after song crystallization in the first season. These new song types are not immediately imitated, but only performed in their next season’s repertoires (Todt & Geberzahn 2003). Hand-reared nightingales memorize more song types during the early sensitive phase than they actually sing as adults. These ‘silent song types’ can be elicited by simulated vocal interactions (Geberzahn et al. 2002; Geberzahn & Hultsch 2003).

As a result of these processes, we might consider that in spontaneous singing, nightingales do not perform all songs stored in memory. They rather sing only a sub-set of these which might have been selected by preceding experience with the songs common in their breeding population. The finding that nightingales in their second season sing song types that are more common and are sung more often by reference birds than first year birds do, is consistent with the idea that the actual use of song types is biologically more relevant than what is stored in memory. Regarding nightingales as part of a communication network, singing shared song types might be beneficial. Besides using song types to communicate aggressive intent (Beecher et al. 2000b) or addressing individuals (Todt & Naguib 2000), an additional explanation for the adaptive value of song type sharing has recently been proposed by Logue & Forstmeier (2008): singing the same song or motif might allow participants of an interaction as well as bystanders such as listening males or females to directly compare the signal quality of two contes-

tants. Nightingales are a good model species to test predictions derived from this explanation. Despite their large repertoires and the high stereotypy of song type performance within and between individuals, nightingales are capable of immediate song type matches (Todt 1981), but the motivation to engage in this interaction pattern appears to be very different. In future studies we will address whether the decision to match a song with the same song is indeed depending on the performance quality of the matching bird, or which other variables might best explain song type matching.

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