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Heterospecific rival recognition in the Black Redstart (*Phoenicurus ochruros*)

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It has long been hypothesized that birds learn to recognize heterospecific competitors and for that reason males behave more aggressively against intruders in areas of local sympatry. Recently, it has been confirmed that individuals of one species are able to learn species-specific visual and acoustic characteristics of heterospecific rivals and that they are able to remember these associations. Here, we test hypotheses about the importance of learning in interspecific interactions, long-term memory of species-specific traits and early timing of this learning to the post-fledging period in the Black Redstart *(Phoenicurus ochruros)*. We show that Black Redstart males respond to playbacks of Redstart *(P. phoenicurus)* only in the areas where the two species come into close contact. This result demonstrates that Black Redstart males learn individually to recognize the rival species in areas of local coexistence. Black Redstart males responded in heterospecific experiments before the arrival of Redstarts from wintering grounds. This means that birds are able to retain the memory of specific traits of heterospecific competitors to the next breeding season. Moreover, yearling and older males, which differ in plumage colouration, responded in heterospecific experiments with the same frequency and intensity. This result indicates that young males learn to recognize Redstarts in the post-fledging period before a first contact with heterospecific rivals in a territorial context.

1. Introduction

Birds often defend resources against individuals of another species with similar ecology living in local sympatry (Cody 1969). The original view of interspecific aggression (Simmons 1951, Orians & Wilson 1964, Cody 1969) supposes that it is an adaptive behaviour, which reduces interspecific competition between sympatric species. On the other hand, Murray (1971, 1976, 1981) suggests that some interactions may result from misdirected intraspecific aggression, which is a consequence of a failure to discriminate a different species with similar appearance and/or song.

Catchpole (1978) predicted that if a general failure to recognize different species is responsible for interspecific aggression (Murray 1981), individuals should show the same response to hearing a playback of another species in a population where this other species also occurs (sympatric population) as in a population where this other species does not occur (allopatric population). Many experimental playback studies addressed this question about the origin and ecological relevance of interspecific aggression. Lower levels of aggression in sympatry were found for *Dendroica* warblers (Murray & Gill 1976), *Vermivora* warblers (Crook 1984), *Acrocephalus* warblers (Leisler 1988) and *Fringilla* finches (Slater & Catchpole 1990, Lynch & Baker 1991). Although the occurrence of stronger heterospecific response in allopatric populations implies misidentification (Murray 1981), this result could be interpreted alternatively as an adaptive ability to distinguish species which poses no ecological threat (Slater & Catchpole 1990).

Stronger interspecific aggression in sympatry was seen in *Passerina* buntings (Emlen *et al.* 1975), *Empidonax* flycatchers (Prescott 1987), *Luscinia* warblers (Lille 1988, Sorjonen 1986) and *Certhia* treecreepers (Gil 1997). This aggressive behaviour has been interpreted as being adaptive in these cases as it results in interspecific territoriality, which prevents exploitation competition. Martin and Martin (2001a, b) confirmed that behavioural responses of *Vermivora* warblers to heterospecifics reflect ecological interactions of the species.

Catchpole (1978) and Catchpole and Leisler (1986), who studied the interspecific aggression of *Acrocephalus* warblers, confirmed stronger heterospecific response in the area of coexistence with the opposite warbler species. As in previous cases, they suggest that this behaviour serves as the territorial exclusion of competing species. Moreover, they first pointed out that birds individually learn to recognize and respond to the songs of congeneric competitors only in areas of the species' close contact.

A number of recent studies have shown the importance of learning as a source of heterospecific recognition ability in other contexts such as brood parasitism (Payne *et al.* 2000, Slagsvold & Hansen 2001), sexual rival and mate recognition (Hansen & Slagsvold 2003, Slagsvold *et al.* 2002), the establishment of mating preferences during speciation and premating reproductive isolation of sympatric species (Grant & Grant 1996, 1998, Price 1998, Irwin *et al.* 2001).

Although it has long been hypothesized that birds are able to learn species-specific signal traits (song, plumage, behaviour etc.) (Gill & Murray 1972, Irwin & Price 1999), there was no direct evaluation of whether individuals of one species are able to learn species-specific characteristics of heterospecific intruders and if they are able to remember these associations.

Matyjasiak (2005) tested in his dual-choice experiments the heterospecific recognition ability and long-term memory of Blackcaps *(Sylvia atricapilla)* that behave aggressively towards Garden Warblers *(S. borin)*. He showed that male Blackcaps can associate species-specific songs with species-specific plumage type. As he carried out the playback experiments on Blackcap males before the arrival of Garden Warblers, he showed that birds retain the memory of these associations from year to year. He also asked when Blackcap males learn to recognize heterospecific intruders and assumed that this ability develops before the first breeding attempt in young Blackcaps. However, he was unable to estimate the age of tested males and he documents his result only indirectly using a proportion of particular age categories of males living in the study area.

The Black Redstart *(Phoenicurus ochruros)* and Redstart *(P. phoenicurus)* provide a unique opportunity to test hypotheses about the origin of interspecific aggression, learning of heterospecific recognition and long-term memory of this learned identification ability.

New molecular data support the view that the Black Redstart and the Redstart are not very closely related (Ertan 2002). There are major differences in the song structure (for spectrograms see e.g. Cramp 1988) and male colouration between them. Both species have a slate-grey head and upperparts, orange-chestnut tail and rump. However, the Redstart male has black sides of the face and throat, white forehead and orange-chestnut flanks, whereas the Black Redstart has black flanks and white wing-patches.

The two species inhabit different types of habitats under natural conditions. Black Redstarts primarily breed in open rocky terrain while Redstarts favour open woods (Cramp 1988). Both redstart species can associate with human beings and they may come into close contact in a mosaic urban environment. In such a situation, they occupy exclusive territories of different habitat compositions.

Each of the two species occupies habitat similar to that preferred under natural conditions (Sedláček *et al.* 2004). Nevertheless, spontaneous interspecific conflicts were frequently observed in areas where territories adjoin and the interspecific aggression was reliably confirmed in playback experiments. The Black Redstart is dominant in both natural and simulated encounters (Sedláček *et al.* 2004). Both redstart species are migratory. Redstarts migrate to sub-Saharan Africa, whereas Black Redstarts winter in the Mediterranean area (Cramp 1988). Black Redstarts arrive at breeding areas about 3 weeks before Redstarts and leave about 1 month later. Thus the two species cannot interact with each other during migration and in their winter quarters.

In Black Redstarts, males exhibit delayed plumage maturation during their first breeding season. The young males entering their second year of life are female-like dull grey, whereas older males are black with a white wing-patch (Cramp 1988).

In this study, we investigated the response of the Black Redstart to playback of Redstart songs in a larger city where Black Redstarts occur separately (České Budějovice) and in a small town (Březnice) where the two species come into close contact. The objective was to address three questions: (1) Is the interspecific aggression of Black Redstarts stronger in the area where territories of the two species are mixed and heterospecific individuals are immediate neighbours? (2) Do Black Redstart males respond in heterospecific experiments before the arrival of Redstart males from their wintering grounds? (3) Do yearling males respond to heterospecific playback before the arrival of Redstarts?

Stronger responses in sympatry would imply that Black Redstarts learn heterospecific recognition and aggressive response to Redstarts. Positive answers to the other questions would demonstrate that Black Redstarts remember once-learned heterospecific intruders from year to year and that young Black Redstart males learn to recognize a heterospecific competitor in the year of their birth, before they use this ability in a territorial context.

2. Material and methods

2.1. Study sites

Experiments were conducted in two towns (50 km apart) located in the south of the Czech Republic – Březnice (3500 inhabitants; 13°56'E, 49°34'N) and České Budějovice (100,000 inhabitants; 14°29'E, 49°00'N).

The study area in Březnice is very heterogeneous, consisting of a mosaic of diverse urban habitats – industrial sites, several types of built-up areas (urban villas, terraced houses and apartment houses), sports fields, gardens, tree alleys, three small and one larger park. Populations of both species are mixed and heterospecific individuals may frequently be immediate neighbours, thanks to the mosaic nature of diverse urban habitats. We label this site as 'sympatric'.

In the larger town, České Budějovice, the two redstart species are present, but they are spatially well separated due to the much coarser mosaic of urban habitats. Black Redstart males were tested within two large housing estates where only this species is present. These housing estates consist of large blocks of flats alternating with open, grassy areas with interspersed trees and shrubs. We label this site as 'allopatric'.

2.2. Mapping of redstart territories

In 1999, we investigated the number of territories of both redstart species in Březnice and České Budějovice. We carried out three surveys during the breeding season – at the end of April, middle of May and middle of June. If a male was seen in the same general area in at least two of three censuses a territory was recorded at the location. The mapping covered the whole area of Březnice (about 200 ha) and the northern part of České Budějovice (about 770 ha), representing all urban habitats including the largest park.

2.3. Experiments

We carried out the playback experiments between the 1st and 20th of April in the years 2002 and 2003, before the arrival of Redstarts from spring migration. The experiments consisted of song playback with a fixed artificial stuffed dummy. We used two differently coloured dummies for conspecific playback because of the occurrence of delayed-plumage-maturation in the Black Redstart (Landmann & Kollinsky 1995) and the possible weaker response of 1-year-old males (in their second calendar year of life) to older males (Cucco & Malacarne 1999). Males were presented with dummies of an age class identical to their own age class (gray dummy presented to 1-year-old males, black dummy to older males). For auditory playback we used a CD-player (Sony D-EJ611) with two loudspeakers (Panasonic RP-SP70). We used the same equipment at both localities, the amplitude was standardized and it was similar to that of natural singing. Loudspeakers were placed 1.5–15.0m above the ground. We did not perform control tests, because we did not record any aggressive responses to control playback (Robin *Erithacus rubecula*) in our previous study (Sedláček et al. 2004) and pilot experiments.

Playback tapes were prepared from recordings of Pelz (1993). These recordings consist of a typical song of one male of each species. The Black Redstart recording was 73 s long with 6 songs; the Redstart recording was 58 s long with 8 songs. These recordings were repeated continually during experiments. Although the use of a single song sample for each playback treatment could be considered as pseudoreplication (Kroodsma *et al.* 2001), there are reasons to justify it. We suppose that the problem of intraspecific song variation is not that severe in our case. Firstly, songs from two different species with very distinct songs are used. It is likely that the specific traits outweigh local or individual differences in the song structure that might affect the response. Secondly, we did not find any differences in intraspecific responses between the two localities suggesting that males at both localities recognized species-specific playback. Thirdly, we cannot definitely exclude an influence of dialectal differences of Redstart songs between the two studied localities in heterospecific experiments. However, the recording of Redstart comes from Prušánky village (16°59'E, 48°50'N), South Moravia, Czech Republic. This locality is ca 220 km from Č. Budějovice and 260 km from Březnice. It is highly improbable that the song recording of Redstart used in our experiments belonged to the same Redstart song dialect at only one of the studied localities, which are only 50 km apart, and that this might strongly influence the responses of Black Redstart males in heterospecific experiments.

The sample was 25 males (15 in 2002 and 10 in 2003; 11 1-year-old and 14 older males) in the sympatric and 33 (20 in 2002 and 13 in 2003; 12 1-year-old and 21 older males) in the allopatric area.

We located territory boundaries before experiments and we placed the sound-producing dummy at distances of 2–40 m from a singing or foraging male inside the territory at a site where each male could definitely see the dummy. The experiment duration was 10 min. This time was measured from the first response (approach, threat display or pass attack) of the male. If we did not record any response (no approach to the dummy, no threat displays, or the male flew away), the experiment was finished after 10 min from the start of song playback. Behaviour and position of a focal male was continuously tape-recorded during the whole trial period.

Each male was tested first with conspecific and second with heterospecific playback. We used this sequence to be sure of accurate location of the experimental apparatus inside a territory and that Black Redstart males were prepared to respond to playback, at least to the conspecific song. As all birds tested gave some initial response in conspecific experiments, all of them are included in the analysis. The two trials in a given territory were separated by at least 2 hours and the speaker was placed in an identical location.

The observed response of the bird was recorded continuously during the experiment and dictated into a dictaphone. We recorded locality, playback presented to a male, date and time of the trial and age of the experimental bird. The following variables were measured: 1. latency of response, 2. nearest distance to the loudspeaker, 3. time spent within a 15 m circular plot around the loudspeaker, 4. time spent singing during the experiment, 5. number of pass flights over the dummy (flying back and forth over the dummy within 10 m), 6. time spent in threat display (ruffled feathers, frequent tail-shivering and squatting, shaking) (Landmann & Kollinsky, 1995) and 7. number of physical attacks ("kicking" the dummy, pecking).

2.4. Statistical analyses

We compared the proportions of males that responded by approach, threat displays, pass flying and physical contacts using Fisher Exact Tests; P-values were adjusted for multiple testing (Bonferroni adjustment). Significant levels refer to α = 0.0125 in these tests.

Principal Component Analysis (PCA) was performed for visualizing the differences and the variability in response of Black Redstart males in conspecific and heterospecific trials at the two localities. PCA was computed using CANOCO 4.5 and visualized in CANODRAW 4.0 (ter Braak & Šmilauer 2002). PCA is a noncanonical multivariate statistical technique that enables one to reduce the dimensionality of the original set data by extracting a few complex orthogonal variables, and it describes variation with a minimal loss of information (ter Braak & Šmilauer 2002).

3. Results

3.1. Population size of the two Redstart species in Březnice and České Budějovice

In Březnice, we located 74 territories of Black Redstarts (density 43.9/km^2) and 26 territories of Redstarts (density 15.4/km^2). Within the study area of České Budějovice, we mapped 323 Black Redstart territories (density 41.8/km^2) and 30 Redstart territories (density 3.9/km^2). The Black Redstart is commoner in both towns, but the proportion is much higher in Č. Budějovice. Moreover, the two species are more spatially separated in this locality. In 2002, 57 Black Redstarts and only one Redstart occurred in the area of housing estates where the playback experiments were conducted.

3.2. Playback experiments

The Black Redstart males responded strongly to their own species' dummy (Fig. 1). There was no significant difference between 'sympatry' and 'allopatry' (Fisher's Exact Test; α = 0.0125 after Bonferroni adjustment; $n_1 = 33$, $n_2 = 25$; p > 0.76 for all four measures of aggression).

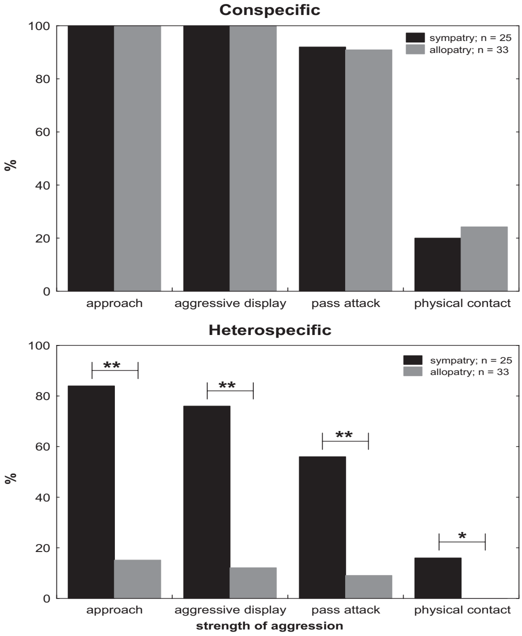

Fig. 1. Responses of Black Redstart to conspecific and heterospecific playback and dummies in populations allopatric and sympatric with Redstart. Histograms show proportions of males responding by approach within 15 m, aggressive display, pass-flight attack or physical attack. Fisher's Exact Tests; α = 0.0125 after Bonferroni adjustment for multiple testing: * p = 0.0298, NS; ** p < 0.001.

Black Redstarts responded more strongly to a heterospecific dummy in 'sympatry' (Fig. 1). The proportion of responding birds was significantly higher for three measures of aggressive behaviour (Fisher's Exact Tests; α = 0.0125 after Bonferroni adjustment; $n_1 = 33$, $n_2 = 25$; p < 0.001.). The proportion of males responding by physical attack was slightly higher in 'sympatry', but the difference was not significant (α = 0.0125 after Bonferroni adjustment; p = 0.0298).

In 'allopatry', the proportion of males responding to the heterospecific playback was significantly lower than to the conspecific one (Fisher's Exact Test; α = 0.0125 after Bonferroni adjustment; n = 33; p < 0.01 for all four measures of aggression). In 'sympatry', heterospecific reaction was less frequent than conspecific for only one measure of aggression – pass-flights (Fisher's Exact Test; α = 0.0125 after Bonferroni adjustment; n = 25; p = 0.008).

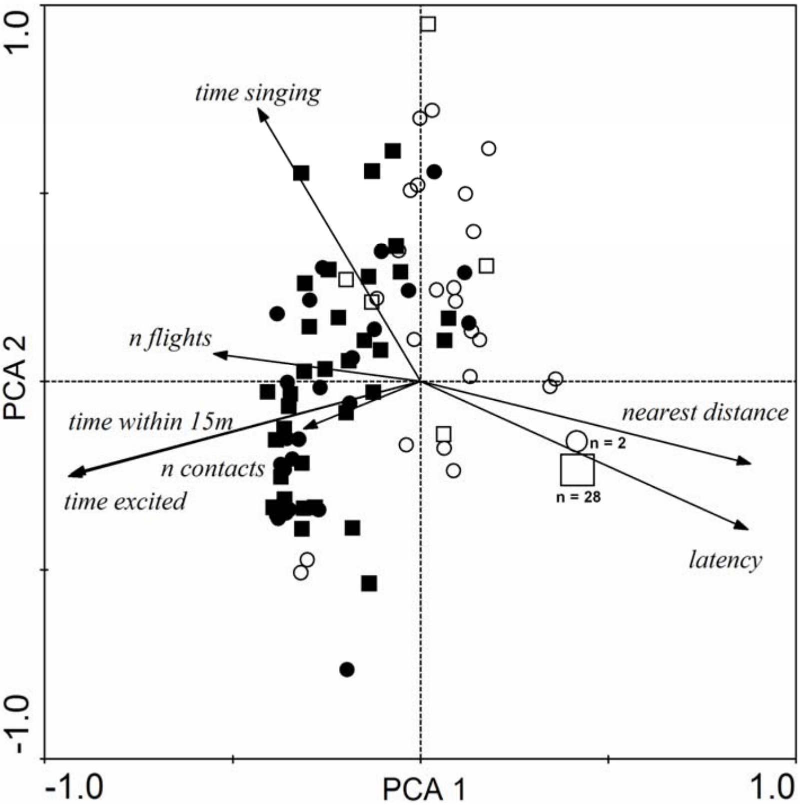

Fig. 2. Responses of Black Redstart males to conspecific and heterospecific playback in allopatric and sympatric populations with Redstart visualized using the two first principal components (PCA ordination) drawn from 7 response variables. The two PCA axes together explain 90.1% of variability. Black symbols – response in conspecific experiments; blank symbols – response in heterospecific experiments. ○ – sympatry, □ – allopatry. Larger symbols in the lower right corner indicate overlap of more samples in the biplot. These symbols represent males that did not respond in heterospecific experiments.

The variability of conspecific and heterospecific responses of the Black Redstart males at both localities is visualized by PCA ordination (Fig. 2, both axes together explain 90.1% of the variance). The first component accounts for 75.8% of the variance. This axis separates conspecific and heterospecific responses and the heterospecific responses in 'sympatry' and 'allopatry'.

All variables, except time spent singing, are correlated with the first axis and explain most of the response variability. The aggression of a male is characterized mostly by the time spent within a 15 m circular plot around the loudspeaker, time spent in threat display, number of pass-flights and number of physical attacks on the dummy. On the other hand, longer latency of response and longer distance of an approach to the loudspeaker are characteristic of less intensive aggression. The second axis (14.3% of variance) separates males according to time they spent singing during the experiments. This variable did not correlate with aggression either in conspecific or heterospecific responses.

In the 'sympatric' situation, we found no differences in the proportion of responding 1-year and older males in either conspecific (Fisher's Exact Test; $\alpha = 0.0125$ after Bonferroni adjustment; $n_1 = 11$, $n_2 = 14$; $p \sim 1$ for all four measures of aggression) or heterospecific playback experiments (Fisher's Exact Test; AAA = 0.0125 after Bonferroni adjustment; $p > 0.35$ for all four measures of aggression).

4. Discussion

Our results show that the aggression of Black Redstart males to Redstarts is a local feature of the 'sympatric' population in Březnice, and we suggest that this results from the coexistence of the two species at this locality. The Redstart inhabits some parts of České Budějovice as well, but it does not occur in the vicinity of the experimental sites.

This points to the fact that the origin of the aggression is related to immediate contact between the two species.

We found that the densities of the Black Redstart and intraspecific aggression rates are similar at the two localities. This demonstrates that the increased rate of aggression towards heterospecifics is not a simple consequence of local differences in intraspecific aggression rates.

For several reasons, results presented here cannot be explained by Murrays' (1971, 1976, 1981) hypothesis. He suggests that responses to coexisting closely related heterospecifics originate from misdirected intraspecific aggression. Firstly, Catchpole and Leisler (1986), who studied the interspecific aggression in *Acrocephalus* warblers, suggested that if a general failure to distinguish closely related species is responsible for interspecific aggression, then sympatric and allopatric populations would show similar responses to the other species. Secondly, the "mistaken identity" hypothesis is proposed for closely related species with similar appearance and song (Murray 1971, 1976). The principal differences in appearance and song morphology between the two redstart species suggest that failure to discriminate is unlikely. Thirdly, we did not record any mixed songs (i.e. song convergence) of the two species such as might evoke misidentification (see Sorjonen 1986 or Thielcke 1986 for such cases).

On the contrary, Catchpole (1978) and Catchpole & Leisler (1986) pointed out that birds learn to recognize and respond to the songs of congeners "who are regularly heard and encountered in a competitive situation". These experienced birds respond aggressively in subsequent heterospecific encounters. Catchpole & Leisler (1986) demonstrated a clear differential response of Reed Warbler *(Acrocephalus scirpaceus)* to Great Reed Warbler *(A. arundinaceus)* song playback at two localities separated by only 5 km. Thus, they suggested that local occurrence of interspecific aggression can be explained only by individual experience with interspecific competitors. Our results are consistent with these assumptions. The hypothesis of learning can well explain increased rates of interspecific aggression of the Black Redstart in Březnice, where the two species come into close contact.

Catchpole (1978) and Catchpole & Leisler (1986) consider the ultimate cause of learning of heterospecifics as the prevention of interspecific competition by means of interspecific territoriality. We suggest that the Black Redstart can readily encounter the Redstart as a competitor. Despite their different colouration, the two species have very similar morphology and they use the same foraging techniques (mainly a sit-and-wait strategy) and foraging substrates (mainly on the ground) (Sedláček *et al.* 2004). Moreover, both species breed in cavities. But the spatial distribution of redstarts differs from the other examples of interspecific territorial birds. Contrary to the other pairs of congeners for whom increased interspecific aggression has been confirmed in sympatry (Catchpole 1978, Catchpole & Leisler 1986, Emlen *et al.* 1975, Gil 1997, Prescott 1987, Sorjonen 1986), the two redstarts are strictly habitat separated at the sympatric locality. Therefore, it is not clear if they could be considered as interspecifically territorial and to what extent the clear habitat separation could be the result of interspecific aggression (Sedláček *et al.* 2004).

The questions worth stressing are when do Black Redstart males learn to recognize heterospecifics and if they remember associations from year to year. Matyjasiak (2005) first confirmed the long-term memory of these associations in birds. In his experiments, Blackcap males responded to Garden Warbler song playback before the arrival of the latter species to the study area. As the winter quarters of the two species are geographically separated, according to Matyjasiak (2005) Blackcap males must recall the species association after 8 months without contact with Garden Warblers. We were able to test the same hypothesis. Although Black Redstarts behave territorially in winter areas (Cuadrado 1995) they cannot interact with Redstarts during the winter. The Black Redstart winters around the Mediterranean, whereas the Redstart migrates to sub-Saharan Africa (Cramp 1988). As Black Redstart males respond aggressively in heterospecific experiments before the arrival of Redstarts, it means that the once-learned aggression persists at least to the next breeding season. According to Matyjasiak (2005), this long-lasting memory could be an evolutionary adaptation in cognitive abilities in migrants, because it may allow birds to remember relevant opponents and avoid wasting time and energy evicting heterospecific intruders which pose no threat. We suggest that this “associations memory” could result in site-specific levels of interspecific aggression in species which are faithful to their breeding sites. In the Black Redstart, an extremely high rate of between-year site fidelity was confirmed (Weggler 2000).

Matyjasiak (2005) also assumed that the ability to identify heterospecific competitors must develop before the first breeding attempt, because yearling Blackcap males responded before the arrival of the other species used in the playback experiments. We were able to test this hypothesis more directly thanks to the age differences in plumage colouration in the Black Redstart. Our results are consistent with the suggestions of Matyjasiak (2005). We did not find any significant differences between the heterospecific response of yearling and older males, suggesting that young males are able to learn to recognize heterospecifics during the post-fledging period.

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Mustaleppälinnut tunnistavat kilpailijansa, vaikka ne eivät olisi samaa lajia

Lintujen on pitkään oletettu oppivan tunnistamaan kilpailijansa myös muista lintulajeista. Tästä johtuen reviirinhaltijat reagoivat aggressiivisesti myös toisen lajin edustajia kohtaan silloin, kun lajien elinalueet menevät päällekäin. Hiljattain on osoitettu, että yksilöt voivan oppia tunnistamaan kilpailijansa niiden ulkonäön ja ääntelyn perusteella. Testasimme mustaleppälinnuilla oppimisen merkitystä lajien välisessä kanssakäymisessä, lintujen pitkäaikaista muistia sekä oppimisen ajoittumista. Mustaleppälintukoiraat reagoivat leppälinnun lauluun vain alueilla, joilla nämä kaksi lajia esiintyvät yhdessä. Tämä osoittaa, että mustaleppälinnut oppivat tunnistamaan kipailijoidensa laulun vain, jos kyseisten lajien yksilöt ovat tekemisissä keskenään. Alueilla, joilla tavattiin molempia lajeja, mustaleppälinnut reagoivat leppälinnun lauluun jo ennen kuin leppälinnut olivat saapuneet talvehtimisalueiltaan. Mustaleppälinnut siis oppivat edellisenä vuonna kohtaamiensa leppälintujen perusteella yhdistämään niiden laulun kilpailuun resursseista.

Tämän lisäksi vuoden ikäisten ja vanhempien koiraiden reaktioiden voimakkuudessa ei ollut eroa. Tulos tarkoittaa sitä, että nuoret mustaleppälinnut oppivat yhdistämään leppälinnun laulun kilpailuun jo ensimmäisenä syksynään ennen ensimmäistä omakohtaista reviirikiistaansa leppälintujen kanssa.

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