ORIGINAL ARTICLE

Host nest defense against a color-dimorphic brood parasite: great reed warblers (*Acrocephalus arundinaceus*) versus common cuckoos (*Cuculus canorus*)

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Abstract We tested great reed warbler (*Acrocephalus arundinaceus*) discrimination against two common cuckoo (*Cuculus canorus*) female color morphs (gray and rufous) in two areas with different parasitism rates and proportions of the two morphs. Hosts recognized the two cuckoo morphs from a control, the feral pigeon (*Columba livia*), at Apaj, Hungary (where brood parasitism was heavy), whereas no significant differences among the models were recorded at Lužice, Czech Republic (where the parasitism rate was moderate). At Apaj, the hosts discriminated the rufous morph (which is slightly predominant there) better than the gray morph from the control. Between-site comparison (after controlling for background aggression) revealed that great reed warblers were more aggressive towards the rufous morph at Apaj than at Lužice, whereas their responses to the gray morph did not differ, corresponding with much higher between-site difference in the relative abundance of the rufous morph. Our re-sults suggest that both local parasitism pressure and relative abundance of two female color morphs of a brood parasite may significantly influence host nest defenses.

Keywords Apostatic selection · Brood parasitism · Color polymorphism · Cuckoo · Nest defense

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Introduction

In the common cuckoo, a plumage color dimorphism limited to females occurs, manifested in two distinct morphs: gray, which looks similar to a Eurasian sparrowhawk (*Accipiter nisus*), and rufous (also called hepatic), resembling a Eurasian kestrel (*Falco tinnunculus*) (Harting 1895). Data on the distribution of the morphs are scarce and inconsistent. Although there might be a geographical gradient with an increasing proportion of the rufous morph to the south (Naumann 1826; Löhrl 1979), the real situation is probably much more complicated, as proportions of the two morphs vary locally (Voipio 1953). No studies have evaluated host responses towards the rufous morph of the common cuckoo.

The great reed warbler (*Acrocephalus arundinaceus*) is one of the favorite hosts of the common cuckoo (Moksnes and Røskaft 1995), but rates of parasitism vary across its breeding range: e.g., 0% in central Greece (Moskát et al. 2002), 5–39% in the southeast of the Czech Republic (Moksnes et al. 1993; Kleven et al. 2004) and 66% in Hungary (Moskát and Honza 2000, 2002).

Since occurrence of parasitism is not uniform over the breeding range of a host species, different host

populations may show different levels of defense against parasitic eggs. Indeed, this has been documented in studies which have shown that populations not currently used as hosts may retain good egg discrimination ability for a longer time, probably because of the low costs associated with rejection in the absence of parasitism (Briskie et al. 1992; Moksnes and Røskaft 1992; Sealy and Bazin 1995; Moskát and Fuisz 1999; Soler et al. 1999; Procházka and Honza 2003, 2004), and may thus simply reflect historical events of interspecific brood parasitism in the population (Davies 1999). Alternatively, such population differences reflect different stages in the co-evolutionary arms race between the cuckoo and its hosts (Davies and Brooke 1989b; Soler and Møller 1990; Briskie et al. 1992). Another explanation of the differences in the rejection behavior is the phenotypic plasticity hypothesis (Brooke et al. 1998; Lindholm 2000; Lindholm and Thomas 2000). These results are, however, based mostly on experimental studies on egg discrimination. As recently stressed by Røskaft et al. (2002b), egg recognition experiments can be supplemented by tests of aggressive behavior of cuckoo hosts.

In this paper, we report on a field experiment where we compared nest defense of two populations of the great reed warbler in Hungary and the Czech Republic against two color morphs of the common cuckoo. Great reed warblers in Hungary suffer from heavy cuckoo parasitism (ca. 66%; Moskát and Honza 2000), with slight predominance of the rufous morph, whereas the Czech population is parasitized with lower intensity (15 and 17% for the two years of this study, respectively; M. Honza et al., unpublished data; Table 1), and with rare exceptions, only the gray cuckoo morph occurs in this area.

This is a novel study as there is no experimental study testing specific recognition of a color polymorphic brood parasite. Also, there are only a few data documenting intensity of nest defense against the brood parasite in areas with different parasitism pressure. Røskaft et al. (2002b) found that populations breeding in sympatry with the cuckoo were more aggressive than allopatric populations. Thus, we expect Hungarian great reed warblers to show better discrimination (i.e., be more aggressive in more behav-

ioral measures) of the gray and rufous cuckoo morph from the pigeon, than Czech birds (prediction 1), thus revealing the influence of the parasitism pressure on the recognition of the parasite.

In accordance with the apostatic selection hypothesis which states that the phenotype, which is under selection pressure dependent on its recognition, is favored according to its rarity in a population (Paulson 1973), hosts will discriminate the commoner morph better (i.e., we will find differences in more measures) than the rarer morph from the control, and/or in each locality the nest defense will be higher against the commoner morph—hosts will be more aggressive against the commoner morph in at least one of the measures (prediction 2). In theory, considering that the less recognized (and thus attacked) morph would increase in relative abundance, then the finding that the rarer morph is less recognized supports the apostatic selection hypothesis.

Since the between-sites difference in parasitism rate by the rufous morph is much higher than by the gray morph (Table 1), the between-sites difference in specific aggression (see Methods) will be higher (i.e., we will find differences in more measures) against the rufous morph than against the gray morph (prediction 3), supporting that the relative abundance of the morphs together with the parasitism rate affects the cuckoo color morph discrimination by the hosts.

Alternatively, if great reed warblers developed discrimination against specific traits of the parasite (shape, posture), and plumage coloration is not important, we would predict no difference in response between the two morphs in the study areas. This phenomenon should then be considered as a result of a long-term adaptation of the host against brood parasitism (Swynnerton 1918; Davies and Brooke 1989a, b; Stokke et al. 1999).

Methods

Study areas

The study site in the Czech Republic was a fishpond area, located about 50 km SE of Brno in the vicinity of

Table 1 Parasitism rates of great reed warblers (*Acrocephalus arundinaceus*), proportions of the two common cuckoo (*Cuculus canorus*) female color morphs and calculated parasitism rates of the two morphs at Apaj and Lužice

Site	Parasitism rate total (% nests)	Proportion of rufous females (%)	Proportion of gray females (%)	Parasitism rate rufous (% nests)	Parasitism rate gray (% nests)
Apaj	66	60	40	40	26
Lužice	16	10	90	2	14

the village Lužice (48°50′N, 17°04′E). Nests of great reed warbler were found in narrow (3–6 m wide) reedbeds surrounding the ponds. The fieldwork was conducted between 15 May and 15 July in 2002 and 2003. The Hungarian study site was about 300 km from the Czech site, ca. 40 km S of Budapest, in the area surrounding Apaj (47°09′N, 19°05′E). Here the study was carried out between 15 May and 15 July in 2000. We searched for great reed warbler nests in habitats similar to those at the Czech site, i.e., narrow reedbeds, but in this case grown along both sides of irrigation channels, crossing arable fields and grasslands.

The ratios of the two morphs of the common cuckoo have been established by counts of calling cuckoo females during the breeding period in the years of study. When the female bubbling call was heard, the color morph and position of the individual was recorded on a map. Since the cuckoo females are known to be strictly territorial at their laying sites (Honza et al. 2002), we believe that the overlap between individual females did not lead to over-estimation of numbers. The numbers of females of the two color morphs at Lužice was 9 and 1, at Apaj 12 and 18 (gray and rufous, respectively). The proportion of the two color morphs differed significantly between the two study areas (Yates corrected χ^2 = 5.65, P = 0.02; Table 1).

The experimental bird models

Knight and Temple (1986) found that the posture of a predator influenced aggressive response by birds. Sealy et al. (1998) also recommended that the posture of the models should be consistent for comparable studies. Moreover, shape is an important cue in recognition of enemies as has been documented by Klump and Curio (1983) and Evans et al. (1993). However, not only the cues mentioned above, but also small dimensional parts of the parasite body, such as the bill, can play an important role for recognition (Gill et al. 1997). As we were unable to find stuffed cuckoo dummies differing only in color in museum collections, we made model cuckoos from polystyrene and balsa, identical in shape, size and posture, and painted them to mimic the gray and rufous morphs. The eyes were made of glass. As a control, we used a mount of a stuffed gray feral pigeon (*Columba livia* f. *domestica*). This species is similar in size to the common cuckoo and prefers different habitats.

This method could be criticized from the following aspect: avian vision differs substantially from that of humans (Cuthill et al. 2000; Cherry and Bennett 2001) and birds are spectrally sensitive near the ultraviolet (UV) part of the spectrum (Chen et al. 1984; Cuthill

et al. 2000). Therefore, there is a possibility that tested birds may react differently towards color-painted models and stuffed cuckoos. Nevertheless, our pilot study in 1999 revealed no difference in responses of great reed warblers towards a stuffed gray dummy and the gray polystyrene model in any respect of the measured behavior. As we were mainly interested in comparison of differences between the two color morphs, we believe that this approach did not affect our results.

Generally, we followed recommendations of the field protocol compiled by Sealy et al. (1998). Following the protocol, we presented models in random order at each nest (each pair was tested once) for 5 min and separated successive tests by a 15-min period. This period was adequate to allow nest owners to resume their normal behavior. Models were fixed on a pole, level with and 0.5 m from the great reed warbler nest, and facing the nest. At each site, experimental nests were watched from the furthest possible distance. All observations were made by two persons (M.H.—who made the majority of them—or V.Š.) who continuously recorded behavior onto a datasheet or a tape recorder from the time when the experimental model was exposed. As soon as any host entered a 5 m diameter circle round the nest (hereafter ''nest vicinity''), we regarded the trial as successful. In this case, we noted latency to response, contact attack, and recorded distance from the nest and presence of alarm calls for each bird at each 10-s interval. Sometimes, sample sizes for different elements of behavior may vary due to difficult observational conditions (e.g., when birds could not be seen while alarm calls could still be heard).

Statistical analysis

From the recordings, we derived the following variables: percentage time alarm calling and percentage time <1 m (both in percentage of the total presence of the bird in the nest vicinity), minimum distance and mean distance of birds from the mount. We used these variables and the latency of response as continuous characteristics of hosts' aggressive behavior.

As they were strongly correlated (Table 2), we carried out a PCA (Manly 1986; Olendorf and Robinson 2000) and used the first of the factors (Table 3), which explained 60% of total variability of all continuous variables (PC 1 Eigenvalue 2.985, PC 2 Eigenvalue 0.996).

In this way, we obtained a new characteristic of behavior called ''aggression'', increasing in value with increasing aggressivity in the behavioral characteristics from which it was derived (see correlations in Table 3).

Table 2 Correlations of measured continuous characteristics of the response to the different models

Measured response	Model	% time <1 m	% time alarm calling	Minimum distance to the dummy	Mean distance to the dummy
Latency to response	Gray	–0.63*	–0.52*	0.21	0.53*
	Rufous	–0.67*	–0.41*	0.08	0.68*
	Pigeon	–0.46	–0.68*	–0.22	0.52
% time <1 m	Gray		0.43*	–0.53*	–0.77*
	Rufous		0.71*	–0.68*	–0.81*
	Pigeon		0.57*	–0.58*	–0.62*
% time alarm calling	Gray			–0.38*	–0.43*
	Rufous			–0.51*	–0.66*
	Pigeon			–0.39*	–0.54*
Minimum distance to the dummy	Gray				0.62*
	Rufous				0.60*
	Pigeon				0.68*

Values of Spearman correlation coefficient (R) are shown. *$P < 0.05$

Table 3 Results of PCA of the continuous characteristics of the response to the dummies (component correlations, eigenvalues, and variance explained by the first component)

Measured response	PC 1
Latency to response	–0.462
% time <1 m	0.897
% time alarm calling	0.766
Minimum distance to the dummy	–0.764
Mean distance to the dummy	–0.892
Eigenvalue	2.985
% of total variance	59.707

According to the continuous character of data from which it was derived, we further regard this variable as the most precise, and hence main, measure of hosts' aggressive behavior. This variable was tested using Friedmann ANOVA, Wilcoxon matched pairs test ("post hoc") and Mann–Whitney U-test, as appropriate.

In addition, we used three supplementary nominal variables: presence of alarm calls, close approach (within 1 m), and contact attack. These were tested by Cochran's Q test and χ^2-test, according to data arrangement.

In comparisons between the two sites, we controlled for the "background aggression" in analyzed variables by subtracting values of the pigeon from the values of the cuckoo, thus gaining "specific aggression" (Grim 2005). Consequently, in nominal variables, a third type of the value (–1) appeared (in rare cases where the response to the control was stronger than to the cuckoo), such cases being pooled with cases with zero values.

As we compared hosts' behavior by four characteristics which may not be independent, we employed a Bonferroni adjustment (see Lindholm and Thomas 2000) to maintain the overall probability of a type I

error at 0.05. Consequently, we rejected the null hypothesis if $P < (0.05/4)=0.0125$. In Results, we give only significant values of tests after the Bonferroni correction, and of the insignificant only those which were significant before the Bonferroni adjustment.

All statistical tests were carried out by Statistica version 6.0 (StatSoft 2001).

Results

Enemy recognition within sites

Firstly, we analyzed responses towards different models at each site using "aggression" and three nominal characteristics (Table 4).

Apaj

As measured by "aggression", great reed warblers responded more strongly to the rufous morph than to the control, whereas such a difference was not found for the gray morph (Table 5, Fig. 1). However, there were no significant differences between the two color morphs in this measure.

Significantly fewer cases of close approaches (vs gray: Cochran $Q = 7.1$, $P < 0.01$, $n = 26$; vs rufous: $Q = 15.0$, $P < 0.001$, $n = 26$) and contact attacks (vs gray: $Q = 10.3$, $P = 0.001$, $n = 27$; vs rufous: $Q = 18.0$, $P < 0.001$, $n = 28$) were recorded towards pigeons, corresponding with our assumption that the great reed warblers recognize this species as a non-threatening intruder. There were no significant differences in all these responses of the great reed warblers towards the two cuckoo color morphs (before Bonferroni adjustment only contact attack was significant: $Q = 4.6$, $P = 0.033$, $n = 30$).

Table 4 Nominal characteristics of great reed warblers responses to different models. Numbers before slash represent number of nests in which the behavior was observed, numbers after slash total number of nests

Model	Gray		Rufous		Pigeon	
Site	Apaj	Lužice	Apaj	Lužice	Apaj	Lužice
Trials with alarm calls	28/30	15/23	32/33	19/24	25/28	13/23
Trials with close approach	18/30	18/22	25/33	15/22	7/28	10/22
Trials with contact attack	15/30	4/23	24/33	5/24	3/28	2/23

Table 5 Comparison of aggression (PC 1) between the models at each site (Wilcoxon matched pairs test; significance level was adjusted by Bonferroni correction to 0.0125; see Methods)

| Site	Model	Rufous	Pigeon
Apaj	Gray	$Z = 1.823$, $P = 0.06$ (NS), $n = 33$	$Z = 2.450$, $P = 0.014$ (NS), $n = 33$
	Rufous		$Z = 4.189$, $P < 0.001, n = 33$
Lužice	Gray	$Z = 1.331$, $P = 0.183$ (NS), $n = 27$	$Z = 1.186$, $P = 0.236$ (NS), $n = 27$
	Rufous		$Z = 1.886$, $P = 0.059$ (NS), $n = 27$

Lužice

No significant differences in "aggression" were found among any of the tested models (Table 5, Fig. 1). Interestingly, contrary to the situation at Apaj, there were no significant differences among models in any variable (before Bonferroni adjustment only differences in the number of cases with alarm calls towards the rufous morph were significant: vs gray: Cochran $Q = 5.00$, $P = 0.025$, $n = 21$; vs control: $Q = 6.00$, $P = 0.014$, $n = 21$; see Table 4)

Enemy recognition between sites

Secondly, we compared responses towards both cuckoo morphs between the two sites. "Aggression" (after controlling for background aggression) towards the rufous morph was higher at Apaj than at Lužice ($Z = 2.6$, $P < 0.01$), whereas there were no differences towards the gray morph between the two sites in this main measure of aggressive behavior. Moreover, great reed warblers attacked the rufous morph significantly more often at Apaj ($\chi^2 = 12.3$, $P < 0.001$) than at Lu-

žice (the gray morph was attacked in more cases at Apaj than at Lužice only before Bonferroni adjustment: $\chi^2 = 6.1$, $P = 0.014$).
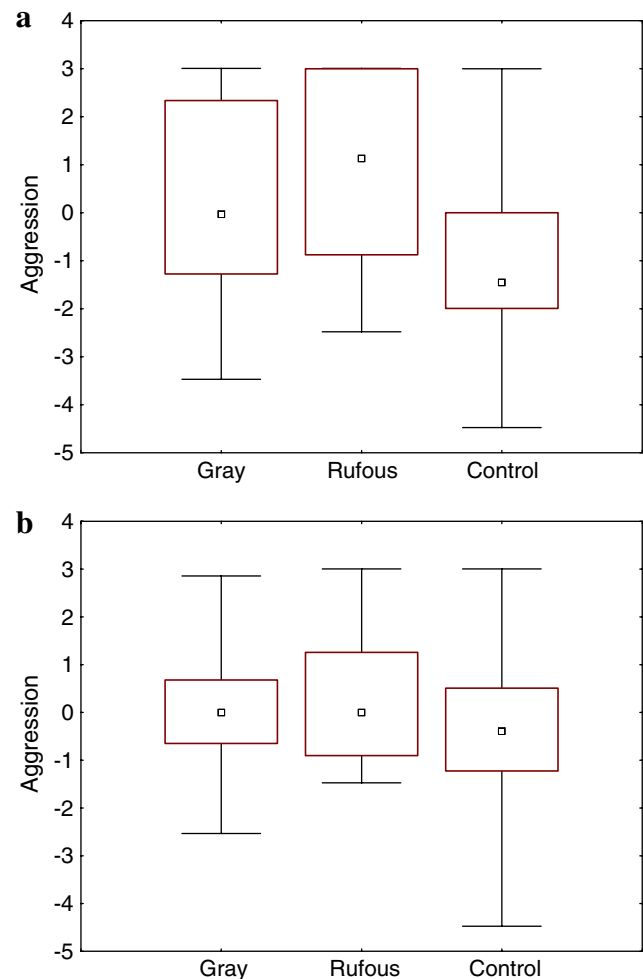
Fig. 1 Aggression of the great reed warblers towards the three experimental models computed by PCA from five measured variables (see the text) at Apaj (**a**) and Lužice (**b**). Medians, quartiles, min, max are shown

Discussion

Evolved recognition or generalized response?

There was a higher aggression towards both gray and rufous morph, compared with the control, at Apaj. In contrast, we found no differences in nest defense among models at Lužice (prediction 1).

Bird species which have been involved in a co-evolutionary arms race with the cuckoo should also be able to recognize it as a brood parasite (Moksnes et al. 1991). Why, in an area with low parasitism pressure, did great reed warblers respond towards control species in the same way as to cuckoos? It is possible that hosts do not need to recognize parasites in order to accrue the benefits of nest defense—they could simply respond defensively to any intruder of similar shape and size (Sealy et al. 1998; Honza et al. 2004; Grim 2005). This relationship applies not only to nest defense tactics, but also to egg discrimination. Egg rejecters do not recognize cowbird eggs per se, but eject any egg that differs substantially from their own eggs (Rothstein 1978, 1982; Sealy and Bazin 1995; see also Moskát et al. 2003 for nest cleaning behavior). A similar mechanism may operate in nest defense whereby hosts react defensively towards a range of intruders. Nevertheless, a generalized response to any intruder near the nest may be costly to nest owners in terms of time and energy, especially responses to species that do not present a threat. However, for evolution of fine-tuned recognition, a certain level of intensity of interaction between the parasite and host is necessary. For example, Smith et al. (1984) found that recognition of the brown-headed cowbird (*Molothrus ater*) as an enemy is based mainly on experience gained through encounters near hosts' nests. Similarly, Robertson and Norman (1977) suggested that aggressive individuals should be favored by selective pressures proportional to the frequency of parasitism and thus occurrence of the parasite. This has also been documented by Røskaft et al. (2002b), who concluded that populations breeding in sympatry with the cuckoo were more aggressive than allopatric populations, indicating the variation of aggressive behavior. In accordance with results of Lindholm and Thomas (2000), who found a weaker response and no specific discrimination in an unparasitized British reed warbler (*Acrocephalus scirpaceus*) population, our study suggests that host populations which are exposed to frequent interactions with the common cuckoo have evolved finer-tuned discrimination than those with moderate levels of parasitism.

Plumage dimorphism in cuckoo females

The hosts discriminated the rufous morph better than the gray morph at Apaj (prediction 2). In Lužice, no differences in discrimination of the cuckoo morphs were found, probably because of low overall parasitism rate. Our findings thus support the prediction that the recognition also depends (in addition to parasitism rate) on the ratio of the color morphs in the population of females. Moreover, specific aggression was higher at Apaj than at Lužice, but only for the rufous morph (prediction 3). Between-site difference of hosts' exposure to the rufous female morph, resulting simply from the local parasitism rates, was even more enhanced by its higher local ratio at Apaj (whereas this difference was thereby lowered for the gray morph). Therefore, this between-site comparison in specific aggression to the two morphs supports our prediction that recognition depends on color morph ratio.

Thus, if the color can be subject to selection, the ratio should fluctuate in co-evolution, varying in time with the level of evolved recognition of each morph due to its relative abundance in the female population. This is in accordance with the hypothesis of apostatic selection, a frequency-dependent type of selection, according to which it is advantageous for a given morph of predator to differ from the majority of other morphs in a given area such that it will be less familiar to the potential prey (Paulson 1973). This could also apply to brood parasites (Payne 1967), which can be under selection pressure not to be recognized as parasites by the hosts. When one looks at the plumage coloration in the family Cuculidae, it will be found that, in the total of 136 cuckoo species, plumage color polymorphism confined to females occurs in 10 species, all of which are parasitic (Payne 1997). If host species form a "brood-parasite image" for the more common color morph, we can expect the defenses against the rarer morph to be lower than to a more numerous morph, resulting in their relative abundance fluctuation, as described above.

Possible explanations of interpopulation differences in host responses

This study revealed differences in the reactions towards the two cuckoo morphs between Apaj and Lužice (prediction 1). Moreover, at Apaj, compared with Lužice, we found higher specific aggression towards the rufous morph, but not towards the gray morph (prediction 3). This variation seems to reflect

differences in frequencies of occurrence of the two morphs between the study sites. The differences in responses can be explained by the phenotypic plasticity hypothesis (Via et al. 1995; Lindholm 2000; Lindholm and Thomas 2000), which states that plasticity in defenses would be favored in environments where the risk of parasitism fluctuates. According to this hypothesis, individual hosts may assess their risk of being parasitized then adjust their rejection or defense behavior accordingly (Davies et al. 1996). Thus, the hosts in our studied populations can change the intensity of their nest defense towards the morph according to its occurrence, without need of long-term genetic change.

Alternatively, that lack of difference in the reactions towards the two morphs in the locality with low occurrence of the rufous morph could suggest a genetic basis for such behavior (the host discrimination of a morph lags behind its changing proportion in cuckoo population). According to the metapopulation theory (Gandon et al. 1996; Grenfell and Harwood 1997; Barabás et al. 2004), host populations under different selection pressures can be connected by gene flow opposing their adaptation differentiation. According to the spatial habitat structure hypothesis (Røskaft et al. 2002a), a species, where the mosaic character of habitats leads to the existence of both non-parasitized and parasitized populations, will have a lower level of cuckoo egg rejection in the parasitized population due to gene flow than in the parasitized population without such gene flow. The same may apply to the morph recognition and consequent nest defense. Due to the short distance dispersal of Czech great reed warblers (mean juvenile and breeding dispersal 44.7 km and 41.1 km, respectively; Procházka and Reif 2000), it is plausible that the two study sites are distant enough that the limited gene flow at either site cannot influence responses towards the cuckoo.

Conclusion and future research

This is the first experimental study investigating host responses against a color-dimorphic brood parasite. We suggest that color polymorphism might be adaptive for brood parasitic birds by helping females to escape the chance of being detected as brood parasites. We recommend widening the questions raised in this study to other common cuckoo host populations and to other polymorphic parasitic cuckoos. Such studies would certainly deepen our knowledge of the adaptive significance of plumage polymorphism in parasitic birds.

Zusammenfassung

Verteidigung des Nestes durch den Wirt eines farbdimorphen Brutparasiten: Drosselrohrsänger (*Acrocephalus arundinaceus*) *versus* Kuckuck (*Cuculus canorus*)

Wir untersuchten Drosselrohrsänger hinsichtlich ihres Unterscheidungsvermögen zweier verbreiteter Farbmorphe (grau und rot) bei weiblichen Kuckucken (*Cuculus canorus*) in zwei Gebieten mit unterschiedlicher Parasitismusrate und unterschiedlichen Anteilen der Farbmorphe. Die Wirte unterschieden die zwei Kuckuckmorphe von einer Kontrolle, der Felstaube (*Columba livia*) in Arpaj, Ungarn (wo der Brutparasitismus hoch war), wogegen kein signifikanter Unterschied zwischen den Modellen festgestellt wurde in Lužice, Tschechische Republik (wo der Parasitismus gemäßigt war). In Apaj unterschieden die Wirte die rote Morphe, die hier etwas häufiger vorkommt, besser von der Kontrolle als die graue Morphe. Ein Vergleich zwischen den Untersuchungsgebieten (nach Kontrolle für Hintergrundaggression) ergab, dass Drosselrohrsänger in Arpaj größere Aggression gegen die rote Morphe zeigten als diejenigen in Lužice, während ihre Reaktion auf die graue Morphe ähnlich war, was gut zu dem zu dem großen Unterschied der Gebiete in der relativen Häufigkeit der der roten Morphe passt. Unsere Ergebnisse legen nahe, dass sowohl der lokale Druck durch Parasitismus als auch die relative Abundanz zweier weiblicher Farbmorphen eines Brutparasiten die Verteidigung des Nestes durch den Wirt signifikant beeinflussen kann.

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