First records of conspecific brood parasitism in two species of small passerines: lesser whitethroat and common linnet

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ABSTRACT

We provide the first records of possible conspecific brood parasitism in the lesser whitethroat *Sylvia curruca* and the common linnet *Linaria cannabina*, two species of small passerines. In 2018 we found two unusually large clutches, one for each species (8 and 9 eggs, respectively), both containing two distinct egg morphs differing in coloration. Further detailed analysis of egg morphology and brood phenology (in the whitethroat) suggested that the eggs in each nest had been laid by different females. Surprisingly, two seemingly full sized clutches were laid in both nests, a pattern that is unusual in conspecific brood parasitism in passerines, whose nests are typically parasitized with single eggs. Alternatives to conspecific brood parasitism are therefore discussed. We argue that traditional field-based methods, when carefully used, may be sufficient to document brood parasitism recorded during occasional observations. We finally conclude that enlarged broods, resulting from conspecific brood parasitism, are probably more frequent than expected, but they may be often overlooked.

INTRODUCTION

Parental care is costly (Trivers 1972, Harshman and Zera 2007) and hence many animals developed stratagems enabling them to raise their young at lower costs or to increase their reproductive success. One of them is conspecific brood parasitism (thereafter CBP), wherein a female deposits eggs in the nests of other females of the same species (Lyon and Eadie 2008). At first CBP was perceived as a very rare phenomenon (Yom-Tov 1980), but the development of molecular techniques and detailed field studies brought evidence of its greater prevalence in birds. According to a recent review by Yom-Tov and Geffen (2017), CBP has been recognized in at least 256 species, mostly grebes *Podicipedidae*, waterfowl *Anatidae*, grouse *Phasianidae* and allies, rails *Rallidae*, estrildid finches *Estrildidae*, swallows *Hirundinidae*, starlings *Sturnidae*, and weaverbirds *Ploceidae*.

The widespread occurrence of CBP indicates that it is not simply an aberrant or accidental behavior. It should be rather perceived as an alternative female reproductive strategy, affecting population and evolutionary dynamics. Lyon and Eadie (2008, 2017) summarized adaptive hypotheses for CBP and reviewed empirical studies investigating life history aspects of CBP. Based on 56 species from 19 families of birds Lyon and Eadie (2017) showed that the ‘best of a bad job’ hypothesis (BOBJ) can often be used as the primary explanation for CBP for non-nesting females. In case of nesting females reproductive (fecundity) enhancement (RE) seems to be the mostly likely explanation for parasitism, as nesting parasites usually lay more eggs during the breeding season than non-parasitic birds. The hypotheses other than BOBJ and RE (breeding interruption, nest competition, risk spreading) received less support in the reviewed work. However, there is a considerable body of evidence suggesting that conspecific brood parasitism represents a flexible life history tactic, *i.e.* mechanism that allows females to adjust reproductive investment according to varying ecological and physiological conditions. Overall, despite decades of research, there is still no clear answer to the question of why females take risk and lay eggs in conspecific nests.

Conspecific brood parasitism has been relatively rarely reported in passerine birds, considering the size of the group. Apart from weavers, where CBP is common, the phenomenon has been found mainly in well-studied species, such as tits, flycatchers, sparrows, house wrens, and starlings (Vedder *et al.* 2007, Tomás *et al.* 2017, Yom-Tov and Geffen 2017). Surprisingly, the phenomenon has not been reliably confirmed in the widespread, species-rich family of *Sylvidae*, though large clutches have been occasionally observed among *Sylvia* warblers (Glutz v. Blotzheim and Bauer 1991). Similarly, CBP has been described in merely three species from the family Fringillidae (Yom-Tov and Geffen 2017).

In this paper we provide the first evidence for the presence of CBP in the lesser whitethroat *Sylvia curruca* and common linnet *Linaria cannabina*. Due to the rarity of this phenomenon we also stress the value of observational criteria, especially detailed egg morphology, in detecting parasitized nests.

METHODS

Study species and nest sites

The lesser whitethroat and common linnet are small passerines widespread in temperate Europe, mostly in lowlands. Both species occupy various habitats that contain well-spaced tall bushes, including rural and suburban gardens. Breeding densities vary in response to the availability of preferred habitats. For example, in heterogeneous agricultural landscapes of SW Poland neighboring the village with the observed lesser whitethroat's nest (see below for exact location), the densities were 1.22 and 0.25 pairs per km^2, respectively (Wuczyński 2016). Despite the sympatric occurrence, lesser whitethroat and common linnet have different life histories and breeding biology (Appendix 1).

Enlarged clutches of the lesser whitethroat and common linnet were recorded during occasional observations combined with ringing of birds in rural areas of SW Poland, in the breeding season of 2018. Each of these clutches contained two egg morphs, differing markedly in a pattern and coloration. The nest of the lesser whitethroat was found in a residential garden in the village of Sieniawka (50°46′37″N; 16°46′11″E; elevation 214 m) (Fig. 1). It was built in the common barberry (*Berberis vulgaris*), at the height of 119 cm. The enlarged clutch of the common linnet was recorded about a month later, also in a residential garden in Nadolice Wielkie, (51°04'60"N; 17°15'29" E; elevation 123 m). The nest was located in the dwarf ornamental black pine (*Pinus nigra*) cultivar Brepo, at the height of 101 cm.

After the clutches had been detected, the nests were checked on a daily basis (Appendix 1). Eggs were numbered with a fine-tipped non-toxic marker and measurements of the length and width of each egg were taken to the nearest 0.01 mm using a digital caliper. The egg volume was calculated using the equation: $V = 2/3 * \pi * (W/2)^2 * L$, where: W and L are width and length (www.rechneronline.de/pi/egg-shape.php). The eggs were easily classified into two morphs on the basis of their coloration (Fig. 2 A, B). To assess the differences in the shape and size between egg morphs we followed Lyon's (1997) approach, *i.e.* eggs were plotted in length-width space and the Euclidean distances between all possible pairs of eggs were calculated. Euclidean distance between two eggs, egg i and egg j, is

$$\sqrt{\left(L_i - L_j\right)^2 + \left(W_i - W_j\right)^2}$$

where: L and W are length and width. We expected that the eggs of the same color morph would be more similar in dimensions than

Fig. 1. Overview on the nesting habitats and mixed clutches of the lesser whitethroat *Sylvia curruca* (top images) and common linnet *Linaria cannabina* (bottom images). The arrows show the locations of the nests.

eggs belonging to the other morph (female), meaning they should cluster on a graph. The results of our observations and measurements were presented in a graphical and tabular form, but we abandoned statistical testing due to small sample sizes and the risk of pseudoreplication.

RESULTS

Breeding performance

A singing lesser whitethroat male has been frequently observed in the garden since its spring arrival (9th April). An empty nest was found on 28th May and the first egg was laid on 29th May (Appendix 1). During several next inspections an adult bird was observed incubating persistently, not being flushed out of the nest. It was only on 5th June that a surprisingly large brood of 8 eggs was found. According to the species biology, the incubation should have started on 4th or 5th June and lasted for 11–14 days. However, the hatching occurred earlier (between 13th and 15th June) than expected, suggesting that the egg-laying stage lasted for fewer than 8 days. This indicates that the last egg was laid on 2nd June or earlier, and hence laying of more than 1 egg per day must have occurred. The breeding attempt was successful, 7 eggs hatched, and 6 young fledged. Both parental birds and the nestlings were ringed and their blood samples were taken, but DNA analyzes could not be performed for logistical reasons. We never observed more than two adults near the nest. However, in the next breeding season (2019), the lesser whitethroats built a nest in almost the same place (20 cm away) and none of the mates had rings, suggesting an indirect evidence for possible intraspecific interactions.

The nest of the common linnet was found between 19th and 21st June but it was not inspected at the early stages. It was not until 3rd July that the presence of 9 incubated eggs, including well developed embryos (based on flotation method; Dunn et al. 1979, Brua and Machin 2000), was confirmed (Appendix 1). Three eggs hatched on 6th-7th July and finally 3 chicks fledged, however, the low hatching success and the unusual course of egg losses

Table 1. Size of the lesser whitethroat eggs divided into brown and grey morphs.

No of egg	Color	Width (mm)	Length (mm)	Volume (cm^3)
1	brown	12.48	17.38	1.417
2	brown	12.78	17.93	1.533
3	brown	12.34	17.62	1.405
4	brown	12.27	16.19	1.276
5	grey	12.76	16.86	1.437
6	grey	12.80	17.02	1.460
7	grey	12.79	16.91	1.448
8	grey	12.43	16.63	1.345
Median	all eggs	12.620	16.965	1.427
Median	brown	12.410	17.500	1.411
Median	grey	12.775	16.885	1.443

drew our attention. Six out of 9 eggs were lost and the losses were spread over time. Two broken eggs (no. 5 and 4 in Fig. 2B) with dead embryos remained in the nest for some time, while another broken egg (no. 8) was found nearby. This may indicate the hosts' attempts to get rid of defective or redundant eggs rather than the activity of predators.

Egg morphs

In both species, the clutches consisted of eggs of two color morphs, also differing in shape, putatively laid by different females. Eggs of the lesser whitethroat could be visually divided into brown and grey morphs (4 + 4 eggs, Fig. 2A). Although the morphs were not clearly different in width, length and resulting volume (Table 1), the difference was visible on the basis of egg clustering presented in the width-length space. The grey eggs were noticeably more clustered than the brown ones (Fig. 2C). As a result, the median Euclidean distances between pairs of grey eggs were about three times smaller than distances between pairs of brown eggs and between pairs of brown-grey eggs (Fig. 2E, Appendix 2).

Similarly, eggs of the common linnet were visually matched into two color morphs, blue and beige (5+4 eggs, Fig. 2B). The morphs seemed to differ slightly in dimensions since medians of the width, length and volume were consistently greater in blue eggs (Table 2). The differences between egg morphs were more clearly revealed when plotted as a function of their length and width (Fig. 2D). Again, blue eggs clustered more than beige eggs, and the median Euclidean distances between pairs of blue eggs turned out to be twice as small as the distances between pairs of beige eggs and between pairs of blue-beige eggs (Fig. 2F, Appendix 2).

DISCUSSION

Occasional observations of breeding attempts performed in a short time and in nearby locations, revealed the presence of large clutches consisting of two egg morphs in two passerine species. Differences in egg coloration, pattern and dimensions, as well as brood phenology clearly indicate that the eggs in each nest belonged to different females. It is widely assumed that any nest containing eggs of more than one female is considered as brood parasitism in the narrow sense (a strategy to avoid parental care) (Yom-Tov and Geffen 2017). Therefore we can also classify the enlarged clutches of the lesser whitethroat and common linnet as CBP. Nevertheless, below we also provide alternative explanations for this phenomenon to draw attention to the fact that a clutch containing eggs of different

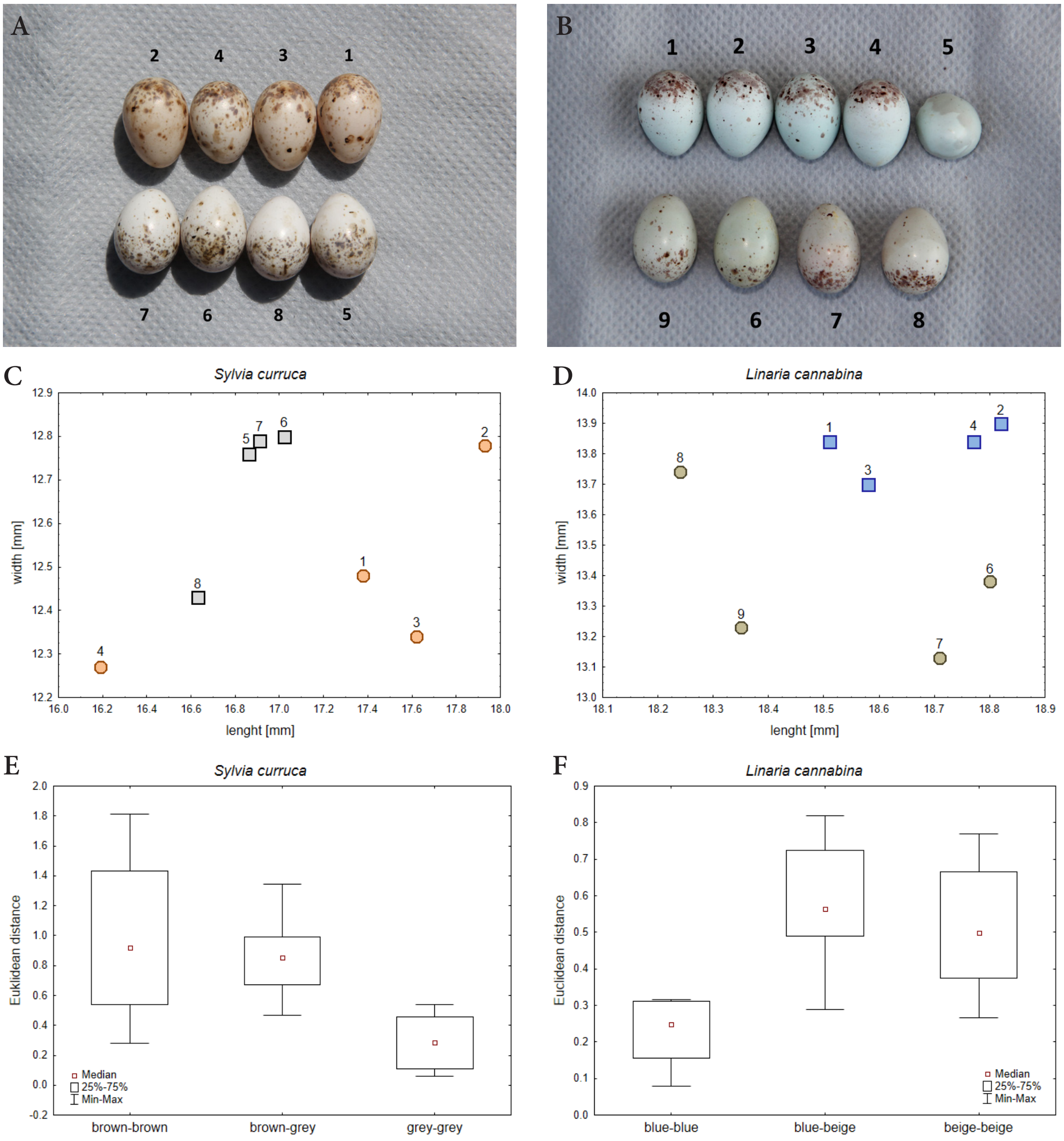

Fig. 2. Mixed clutches of the lesser whitethroat (left panel) and the common linnet (right panel). A, B – appearance of eggs divided into groups visually matched into two color morphs: left side A, 1–4 brown and 5–8 grey; right side B, 1–5 blue and 6–9 beige; C, D – egg morphs plotted against their width and length; the numbers in the graphs correspond to the numbers in the pictures; E, F – median Euclidean distances between pairs of eggs grouped in different color morphs.

females is not necessarily a result of brood parasitism (B. Lyon, corresp.).

Although abnormally large clutches were occasionally noted in both the lesser whitethroat and common linnet (Mason 1976, Glutz v. Blotzheim and Bauer 1991), our observations provide the first convincing evidence that at least two females laid eggs in the same nest. The most intriguing aspect of our observations is the fact that a large number of eggs in each color morph were noted in both species. It suggests that two apparently full sized clutches were laid in both nests, a pattern that is quite unusual in CBP. Typically, in passerines the host nest is parasitized with single eggs, occasionally more (*e.g.* 2–3 in *Cyanistes caeruleus*, Vedder *et al.* 2007). Lyon and Eadie (2017) also showed that the frequency of parasitic eggs is particularly low in non-waterfowl species, including passer-

Table 2. Size of the common linnet eggs divided into blue and beige morphs.

No of egg	Color	Width (mm)	Length (mm)	Volume (cm^3)
1	blue	13.84	18.51	1.856
2	blue	13.90	18.82	1.904
3	blue	13.70	18.58	1.826
4	blue	13.84	18.77	1.883
5	blue	damaged prior to measurements		
6	beige	13.38	18.80	1.762
7	beige	13.13	18.71	1.689
8	beige	13.74	18.24	1.803
9	beige	13.23	18.35	1.682
Median	all eggs	13.720	18.645	1.814
Median	blue	13.840	18.675	1.869
Median	beige	13.305	18.530	1.726

ines. Therefore, other explanations should be considered, and at least two mechanisms, other than CBP, might explain our unusual findings. First, it is possible that one female took over another nest containing the eggs of the first owner (Waldeck and Andersson 2006). The second possibility is that the two females nested jointly (Vehrencamp and Quinn 2004). Theoretically, such tactics are to be expected rather in the common linnet than in the lesser whitethroat, due to its poor discrimination against alien eggs (Davies and Brooke 1989), more gregarious behavior, semi-colonial nesting and occasional polygyny (Appendix 1) (Cramp and Simmons 2004). Yet, despite extensive literature survey (Glutz v. Blotzheim and Bauer 1991, Shirihai *et al.* 2001, Cramp and Simmons 2004) we have not been able to find the information on any confirmed cases of egg adoption or joint nesting in either species. Both passerine species belong to hosts of the common cuckoo *Cuculus canorus* (an obligate brood parasite), but not the common ones. Therefore they should be able to recognize their own eggs, but rejection decisions may be very rare among them (such a behavior pays off only when parasitism rate is high; Davies 2000).

A variety of methods have been used to detect parasitic eggs (Yom-Tov 1980, Eadie *et al.* 2010, Lyon and Eadie 2017), including the analysis of egg laying rates, the presence of eggs laid well after a clutch is complete, intervals in egg-laying, abnormally large clutch size, egg features, late hatchlings and finally several molecular methods. In the ongoing discussions on methods of detecting CBP, the traditional non-molecular methods, especially those relying only on comparisons of egg dimensions, are being criticized for an insufficient accuracy in the identification of foreign eggs (Grønstøl *et al.* 2006, Lemons *et al.* 2011, Petrželková *et al.* 2017). On the other hand they are believed to be very powerful when used carefully and properly (*Pöysä et al.* 2009, *Eadie et al.* 2010, Lyon and Eadie 2017). In particular, the analysis of multiple criteria are advocated (Cheng *et al.* 2016), an approach adopted also in our study. First, the comparison of egg pattern and coloration within the lesser whitethroat and common linnet clutches, combined with egg measurements, revealed a prominent egg clustering confirmed by differences in Euclidean distances. Second, a large number of eggs in color morphs is again noteworthy and helpful. Many bird species have evolved within-clutch uniformity of egg appearance as well as individual distinctiveness in egg color and spotting, a combination that facilitates distinguishing between an individual's own eggs and those of conspecific or intra-specific brood parasite (Davies and Brooke 1989, Moskát *et al.* 2008, Brulez *et al.* 2015). Eggshell patterning is genetically sex-linked and inherited, and allows for the individual-specific eggshell patterning in birds with maculated eggs (Gosler *et al*. 2000, Brulez *et al*. 2015). Likewise, dimensions of subsequent eggs of one female are usually highly repeatable and vary considerably from eggs of other females of the species (Christians 2002, Stępniewski *et al*. 2021), although egg size varies with the laying order (Ojanen 1983, Orłowski *et al.* 2016). Because in both nests we observed two egg morphs, differing in coloration and size, this indicates a different maternity. Third, brood phenology showed that laying of more than one egg per day must have occurred in the lesser whitethroat (Appendix 1), and this is a widely accepted criterion of CBP. We did not record laying order in the common linnet, but the low hatching success of the beige egg morphs may indirectly indicate that they were laid by a parasitic female, as eggs from CBP have typically lower hatching success (Lyon and Eadie 2017). In summary, the evaluation of the multiple criteria yielded convincing evidence of CBP in the lesser whitethroat and common linnet and supported a value of observational studies.

Finally, both events occurred in one year (2018) in single nests located in gardens in one region of Poland, and were noticed during occasional observations, and not as a result of systematic research. This suggests that conspecific brood parasitism may be more common than previously thought, but have not received much attention so far. Therefore we conclude that more studies looking into differences in egg coloration and dimensions within a nest, are needed.

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APPENDIX 1. Biological and ecological characteristics of the lesser whitethroat and common linnet (all data after Cramp and Simmons 2004), and timing of the broods with enlarged clutches recorded in 2018.

Feature	lesser whitethroat	common linnet
Order/Family	Passeriformes/Sylviidae	Passeriformes/Fringillidae
Mass, sexual dimorphism	10–14 g, sexes alike	15–22 g, prominent dimorphism
Movements	migratory, wintering in Africa	partially migratory, wintering slightly south of breeding range
Mating system	monogamous, solitary and territorial, sexes share incubation, brooding and feeding	mainly monogamous, occasional polygyny, frequent breeding in loose neighborhood groups of many pairs, incubation by female, brooding and feeding shared
No of broods	single-brooder, frequent replacement broods	2 broods, 3 in favorable conditions
Clutch size	4–6 (2–7), eggs laid daily	4–6 (3–7), eggs laid daily
Incubation	11–14 days, begins with penultimate or last egg	12–14 days, usually begins with penultimate or last egg
Fledging period	10–13 days	10–17 days
Timing of the broods		
Finding the nest (contents)	28.05 (empty nest)	~20.06, not checked
First egg laid	29.05	undetermined
Further nest checking	03.06 (incubation, adult not flushed) 05.06 (8 eggs, incubated)	1.07 (at least 7 eggs, incubated) 3.07 (9 eggs, incubated) 4.07 (morning, 9 eggs, incubated) 4.07 (evening, 8 eggs + 1 egg crushed, incubated)
Egg measurements	07.06	4.07
Hatching	13.06 (eggs 4, 5, 6, 7) 14.06 (eggs 3, 8) 15.06 (egg 2)	6.07 (eggs 1, 2) 7.07 (egg 3)
Partial failures	17.06 – remaining egg (no 1) fractured and light, removed 19.06 – one nestling lost	4.07 (1 egg, ~half shell in nest) 5.07 (3 eggs lost, no 4, 6, 8) Eggs 7 and 9 not hatched, disappeared only 17.07
Fledging	26.06 – 6 fledglings, 4 observed nearby (6 present in the nest the evening before)	17.07 – 2 fledglings 18.07 – 1 fledgling
Outcome of breeding attempt	8 eggs laid, 1 egg lost, 1 nestling lost, 6 young left	9 eggs laid, 6 eggs lost, 3 young left

APPENDIX 2. The Euclidean distances between all possible pairs of eggs of the lesser whitethroat and common linnet. Pair of eggs are arranged according to their color morphs. Egg numbers correspond to the numbers in Fig. 2. Egg no. 5 of the common linnet was damaged prior to measurements.

lesser whitethroat			common linnet		
Pair of eggs	Color	Euclidean distance	Pair of eggs	Color	Euclidean distance
1vs2	brown-brown	0.6265	1vs2	blue-blue	0.3158
1vs3	brown-brown	0.2778	1vs3	blue-blue	0.1565
1vs4	brown-brown	1.2084	1vs4	blue-blue	0.2600
2vs3	brown-brown	0.5382	2vs3	blue-blue	0.3124
2vs4	brown-brown	1.8132	2vs4	blue-blue	0.0781
3vs4	brown-brown	1.4317	3vs4	blue-blue	0.2360
1vs5	brown-grey	0.5906	1vs6	blue-beige	0.5438
1vs6	brown-grey	0.4817	1vs7	blue-beige	0.7376
1vs7	brown-grey	0.5630	1vs8	blue-beige	0.2879
1vs8	brown-grey	0.7517	1vs9	blue-beige	0.6306
2vs5	brown-grey	1.0702	2vs6	blue-beige	0.5204
2vs6	brown-grey	0.9102	2vs7	blue-beige	0.7778
2vs7	brown-grey	1.0200	2vs8	blue-beige	0.6017
2vs8	brown-grey	1.3463	2vs9	blue-beige	0.8184
3vs5	brown-grey	0.8683	3vs6	blue-beige	0.3883
3vs6	brown-grey	0.7560	3vs7	blue-beige	0.5846
3vs7	brown-grey	0.8406	3vs8	blue-beige	0.3423
3vs8	brown-grey	0.9941	3vs9	blue-beige	0.5233
4vs5	brown-grey	0.8301	4vs6	blue-beige	0.4610
4vs6	brown-grey	0.9848	4vs7	blue-beige	0.7125
4vs7	brown-grey	0.8881	4vs8	blue-beige	0.5394
4vs8	brown-grey	0.4682	4vs9	blue-beige	0.7406
5vs6	grey-grey	0.1649	6vs7	beige-beige	0.2657
5vs7	grey-grey	0.0583	6vs8	beige-beige	0.6657
5vs8	grey-grey	0.4022	6vs9	beige-beige	0.4743
6vs7	grey-grey	0.1105	7vs8	beige-beige	0.7701
6vs8	grey-grey	0.5376	7vs9	beige-beige	0.3736
7vs8	grey-grey	0.4561	8vs9	beige-beige	0.5217
Median	all pairs	0.7539	Median	all pairs	0.5211
Median	brown-brown	0.9174	Median	blue-blue	0.2480
Median	brown-grey	0.8545	Median	blue-beige	0.5642
Median	grey-grey	0.2836	Median	beige-beige	0.4980