Host sexual selection and cuckoo parasitism: an analysis of nest size in sympatric and allopatric magpie *Pica pica* populations parasitized by the great spotted cuckoo *Clamator glandarius*

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Magpies (*Pica pica*) build large nests that are the target of sexual selection, since males of early breeding pairs provide many sticks for nests and females mated to such males enjoy a material fitness benefit in terms of better quality territory and parental care of superior quality. Great spotted cuckoos (*Clamator glandarius*) preferentially parasitize large magpie nests and sexual selection for large nests is thus opposed by natural selection due to brood parasitism. Consistent with the hypothesized opposing selection pressures, in a comparative analysis of 14 magpie populations in Europe we found that nest volume was consistently smaller in sympatry than in allopatry with the great spotted cuckoo, in particular in areas with a high parasitism rate and high rates of rejection of mimetic model cuckoo eggs. These observations are consistent with the suggestion that magpies have evolved a smaller nest size in areas where cuckoos have exerted strong selection pressures on them in the recent past.

Keywords: autocorrelation; brood parasitism; cost of sexual selection; comparative analysis; nest building behaviour

1. INTRODUCTION

Secondary sexual characters and displays have evolved in the context of sexual selection because they provide signallers with exaggerated traits with a mating advantage (Andersson 1994). Independent of the specific mechanism of sexual selection involved, the level of display will be limited by production or maintenance costs (see the review in Andersson (1994)) or by the character going to fixation (Fisher 1930). Theory on signalling evolution, mostly that considering sexually selected traits, is mainly based on conspecific communication. Selection favours individuals whose displays are more efficient in eliciting beneficial responses from the receivers (Johnstone 1997). However, it is known that signals can also be detected by undesired receivers, such as predators and parasites (Cade 1979; Endler 1980; Tuttle & Ryan 1981; Thornhill & Alcock 1983; Sakaluk & Belwood 1984; Magnhagen 1991; Petrie 1992; Götmark 1993; Andersson 1994; Møller & Nielsen 1997). Such costs may prevent the continuous evolution of exaggerated signals. Therefore, signals observed in nature should strike the optimal balance between conflicting pressures for greater efficiency and lower fitness costs (Wiley 1983, 1994; Endler 1992, 1993).

Several intraspecific studies have investigated the cost of sexual displays in relation to parasitism. For example, pheromone signalling by male stink bugs attracted parasites that used the pheromone to cue in on potential hosts (Mitchell & Mau 1971). Similarly, a study of a cicada demonstrated that calling males attracted parasitic Diptera (Soper *et al.* 1976). Cade (1979) studied the relationship between parasitism by a Diptera of calling male field crickets and found that male crickets attracted parasitic flies by emitting calls. Several other examples of this kind are reported in Thornhill & Alcock (1983). Although there are costs of parasitism associated with sexual display, it remains unknown to what extent parasites are able to affect the expression of sexual displays.

Nest size in monogamous passerines has recently been hypothesized to be a sexually selected signal of parental quality, because females may be able to assess male parental quality from male participation in nest building or from nest characteristics and then adjust clutch size to male parental quality or male willingness to invest in reproduction (J. J. Soler *et al.* 1998a). Empirical data have supported this hypothesis in several species. In the black wheatear (*Oenanthe leucura*), nest size was related to parental quality (Moreno *et al.* 1994). In the barn swallow (*Hirundo rustica*), nest size was related to male contribution to nest building and nest size was related to the number of eggs laid by a female during the breeding season

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(J. J. Soler *et al.* 1998b). In the rufous bush robin (*Cercotrichas galactotes*), nest size was positively related to the size of prey carried by males to the nest to feed the young (Palomino *et al.* 1999). Furthermore, two experimental tests of this hypothesis exist. Female black wheatears (*Oenanthe leucura*) paired with males that carried a larger number of stones to the nest laid earlier and, hence, had greater reproductive success than females paired with other males (Soler *et al.* 1996a). In the magpie (*Pica pica*), nest size is negatively related to laying date and an experimental increase in nest size resulted in an increase in clutch size (Soler *et al.* 1999a). Therefore, nest size is a good candidate for a sexually selected signal in magpies.

Here we investigate the relationship between sexual selection in a host (the magpie) and parasitism by the brood-parasitic great spotted cuckoo *Clamator glandarius*. Great spotted cuckoos are known to use the size of the nest of their magpie host in host choice (Soler *et al.* 1995). Soler *et al.* (1995) showed that host nests parasitized by the great spotted cuckoo are larger than the nearest neighbouring nest not parasitized by the cuckoo. Furthermore, such hosts are able to rear a cuckoo nestling better than a randomly chosen host because experimental parasitism of large and small magpie nests will more probably result in a fledged cuckoo nestling for the magpie pair with the largest nest (Soler *et al.* 1995). Hence, we predicted that great spotted cuckoos should cause a reduction in nest size in sympatric magpie populations due to the costs of this sexual display. Furthermore, if magpie nest size has been reduced in response to natural selection pressure from the cuckoo, we should expect that nest size will be negatively related to estimates of past and present selection pressures from the cuckoo. In other words, we should predict a negative relationship between the nest size of magpies and parasitism rate by the cuckoo and rejection rate of mimetic and non-mimetic model cuckoo eggs by the magpie, respectively (see §2). These predictions were tested by comparing the nest size of 14 European populations of magpies that were either sympatric or allopatric with the great spotted cuckoo.

2. METHODS

(a) *Study species*

We have described the coevolutionary interactions between the great spotted cuckoo and the magpie in detail elsewhere (Soler 1990; M. Soler *et al.* 1994a, 1998a). Magpies are single-brooded corvids that occur throughout large parts of the Holarctic region. They are territorial, sedentary and relatively long lived for passerine birds, with a well-described biology (extensively reviewed in Birkhead (1991)). A single clutch is laid in spring from March to May in their Western European range and clutch size ranges from three to ten eggs (Birkhead 1991). The monogamous magpie normally builds a domed, almost spherical nest with a stick framework. After the framework is finished, a bowl of mud is built inside and lined with fibrous roots, hair and grass (nest cup) (Birkhead 1991). Both members of the pair participate in nest building, but the male makes significantly more trips to collect mud and large twigs, generally collecting more sticks than does the female (Birkhead 1991). The size of the nest structure has been suggested to be a reliable signal of territory quality and/or pair quality (Soler *et al.* 1995).

Moreover, nest volume in magpies is a post-mating sexually selected trait, because an experimental increase in nest size resulted in an increase in clutch size (Soler *et al.* 1999a).

The great spotted cuckoo is a migratory brood parasite which in Europe occurs commonly in the Iberian Peninsula, Southern France and Bulgaria (Cramp 1985). One or more cuckoos may parasitize magpie nests and parasitism severely reduces host reproductive success through early hatching and effective competition for parental food delivery (Soler 1990; Soler & Soler 1991; Soler *et al.* 1996b). Magpie hosts provide parental care for cuckoo chicks for an extended period of almost five weeks after fledging compared to the usual duration of parental care of three weeks for their own offspring (Soler *et al.* 1994b). Thus, it is probable that parasitism will severely delay the annual moult and, hence, impose a mortality cost on adult hosts. Moreover, it is known that great spotted cuckoos select magpie hosts based on magpie nest size (Soler *et al.* 1995).

(b) *Sampling and study areas*

The study was conducted in 1993–1996 in 14 European magpie populations (see Martínez *et al.* (1999) for the location of these populations). Eight populations were sympatric with the great spotted cuckoo, while the remaining six were allopatric.

Nest volumes were estimated from field measurements of the largest and smallest radii of the nests, measured to the nearest centimetre with a measurement tape. Nest volumes were calculated assuming that the shape of the nests approached that of an ellipsoid, which is a good approximation (see Soler *et al.* (1995) for further details). We did not use magpie nests built for replacement clutches. The mean population values of nest volumes as well as other variables used in the analyses are shown in table 1.

We tested magpies for their ability to recognize and successfully reject mimetic and non-mimetic model eggs introduced into magpie nests during their laying period. We used both kinds of eggs because the rejection rate of non-mimetic model eggs has a strong genetic component, whereas the main component of the rejection rate of mimetic model eggs is geographical distance rather than genetic distance (Soler *et al.* 1999b). Thus, while differences in the rejection rate of non-mimetic model eggs provide information on genetic differences between populations of magpies, differences in the rejection rate of mimetic model eggs provide information on the adult migration rates between populations (Soler *et al.* 1999b). In other words, the rejection rates of non-mimetic model eggs could be used as an index of genetic differences between populations in relation to the ability of magpies to recognize dissimilar eggs in their nests, but it could not be directly related to the current impact of brood parasitism on host populations because the rejection rates of non-mimetic model eggs will probably be related to gene flow due to recognizer individuals from areas of sympatry or allopatry with the great spotted cuckoo (Soler *et al.* 1999b). On the other hand, the rejection rate of mimetic model eggs could be used as an index of recent selection pressure from brood parasitism, because it is probably related to gene flow due to recognizer individuals from populations sympatric with the brood parasite (Soler *et al.* 1999b). These estimates of selection pressure due to parasitism have the advantage of being more repeatable than estimates of the parasitism rate based on a single study year. While the rate of parasitism fluctuates greatly between years, the rejection rates are relatively constant between years, increasing rapidly at the beginning of cuckoo colonization of a host population, but remaining stable once the

Table 1. Mean nest volume (cm³), laying date (1 April), latitude, parasitism rate, rejection rate of mimetic and non-mimetic model eggs and information on sympatry or allopatry of the 14 European magpie populations (including the study year)

(Values are means, standard errors (s.e.) and numbers (n))

area of Europe (study year)	nest volume (cm ³)			laying date			latitude
	mean	s.e.	n	mean	s.e.	n	
Doñana (1995)	119 642.3	12 237.7	20	−1.69	1.15	39	37.13
Santa Fe (1993)	96 807.6	6163.9	14	13.79	3.26	14	37.18
Guadix (1995)	37 280.2	1350.8	64	18.38	1.01	37	37.30
Badajoz (1993)	92 312.9	9964.4	23	9.96	1.44	24	38.87
Calahorra (1994)	101 469.8	8044.6	28	15.33	2.40	27	42.30
Torres del Segre (1994)	70 361.0	9014.0	37	19.54	1.43	37	41.53
Les Camargues (1994)	79 568.6	6732.2	27	9.10	1.73	29	43.67
Milano (1994)	108 385.9	16 867.0	33	−5.64	0.53	14	45.47
Bern (1995)	168 566.9	13 851.1	43	15.13	2.00	23	46.93
Freneuse (1995)	127 761.5	10 024.1	33	7.91	1.10	32	49.00
Sheffield (1995)	67 248.3	5403.7	28	45.15	3.18	26	53.38
Eljovo (1996)	94 927.0	7811.7	24	14.67	4.81	3	42.15
Jyväskylä (1996)	135 119.7	13 688.3	21	19.83	0.61	18	62.25
Trondheim (1996)	187 031.0	19 329.2	37	—	—	—	63.40

area of Europe (study year)	parasite rate		rejection rate of mimetic eggs		rejection rate of non-mimetic eggs		population
	%	n	%	n	%	n	
Doñana (1995)	11.5	52	43.5	23	84.0	25	sympatric
Santa Fe (1993)	85.7	21	33.3	12	100.0	10	sympatric
Guadix (1995)	51.8	85	63.6	44	89.7	39	sympatric
Badajoz (1993)	0.0	32	43.8	16	78.6	14	sympatric
Calahorra (1994)	0.0	33	62.5	16	69.2	13	sympatric
Torres del Segre (1994)	2.3	43	38.1	21	71.4	21	sympatric
Les Camargues (1994)	0.0	32	18.8	16	62.5	16	sympatric
Milano (1994)	0.0	33	25.0	16	56.3	16	allopatric
Bern (1995)	0.0	49	26.3	19	57.9	19	allopatric
Freneuse (1995)	0.0	38	22.2	18	52.9	17	allopatric
Sheffield (1995)	0.0	28	21.4	14	57.1	14	allopatric
Eljovo (1996)	0.0	34	11.1	9	25.0	4	sympatric
Jyväskylä (1996)	0.0	24	7.1	14	87.5	16	allopatric
Trondheim (1996)	0.0	45	16.7	6	100.0	6	allopatric

asymptotic rejection rate has been reached (M. Soler *et al.* 1998b).

Mimetic eggs were made by filling moulds of great spotted cuckoo eggs with plaster of Paris and, once dry, these models were painted with a colour similar to the background colour of cuckoo eggs. In a second step, brown spots were added with a distribution and size similar to those of real cuckoo eggs. Finally, the model eggs were covered with a thin layer of lacquer that simulates the sheen of real cuckoo eggs. The mass of these model eggs is similar to that of real cuckoo eggs (Soler & Møller 1990). Quail, *Coturnix coturnix*, eggs painted with red acrylic paint were used as non-mimetic eggs, since these differed from magpie and cuckoo eggs in size, background colour and spot size and distribution (Soler *et al.* 1999b). Each model was used only once. An experiment in a magpie population in southern Spain demonstrated that magpies responded identically to red non-mimetic model eggs made from plaster of Paris and red quail eggs (rejection rate of plaster of Paris eggs 91.7% of 12 eggs and rejection rate of red quail eggs 90% of ten eggs; Fisher exact test, $p=1.00$; M. Soler *et al.* 1998b). Nests were revisited four to seven days after the introduction of the model egg

(which is sufficient to record the response of a magpie to a parasitic egg reliably; Soler & Møller 1990) and magpies were then scored as 'acceptors' if the model egg was still in the nest, 'ejectors' if the model egg was no longer present or 'deserters' if the nest was abandoned with the eggs remaining in the nest. Deserters are relatively uncommon in all magpie populations, comprising 3.1% of all cases. Soler *et al.* (1999b) provided evidence for why ejection and desertion can be considered an estimate of the ability of magpies to recognize and discriminate against foreign eggs. We followed this procedure in the present study by classifying magpies as acceptors or rejectors (ejectors and deserters combined). The conclusions of the present study do not change if the analyses are based on ejection rates instead. Estimates of the rejection rates are given in Soler *et al.* (1999b).

(c) Statistical methods

The magpie nest volume was normally distributed once it had been logarithmically transformed (Kolmogorov–Smirnov test for continuous variables, $d=0.036$, $p>0.2$).

We investigated the relationship between the nest size of magpies and parasitism by the great spotted cuckoo using two

different methods. First, we used nested analyses of covariance with nest size as the dependent variable and magpie populations nested in sympatric or allopatric populations as an independent factor. In these analyses we were unable to use latitude as a covariate since the variation within populations is non-existent. However, laying date is related to latitude in magpies (weighted regression analysis, $r = 0.45$, $F_{1,321} = 79.17$, $p < 0.000\,000\,1$) and, thus, we used laying date instead of latitude as a covariate in the analyses. Moreover, since nest size in magpies is negatively related to laying date within a population (Soler *et al.* 1995), the use of laying date as a covariate has the advantage of controlling for variation within populations. In this analysis we used each observation of a magpie pair nested within populations as an independent observation. These analyses provide an appropriate weighting of the estimates for each population by the number of observations.

Second, we calculated correlations between nest size and cuckoo parasitism rate and the rate of rejection of experimental cuckoo eggs, respectively, by means of spatial autocorrelation analyses. Geographical distances between populations were measured in terms of degrees of latitude, since the difference in latitude reflects the importance of nest size for efficient insulation (Kern & Riper 1984). In a previous study, we calculated the genetic distances between the 14 European magpie populations based on the frequencies of alleles at three microsatellite loci (Martínez *et al.* 1999). We constructed a genetic distance matrix (Martínez *et al.* 1999), a latitudinal distance matrix, a matrix of differences in the parasitism rate between populations, a matrix of differences in the rejection rate of mimetic and non-mimetic model eggs between populations and a matrix of differences in nest volume between populations, respectively. We controlled for phylogenetic effects by conducting autocorrelation analyses (Gittleman & Luh 1992; Edwards & Kot 1995; Foster & Cameron 1996), since the use of population phylogenies is not recommended for comparative analyses when gene flow is high among populations (Foster & Cameron 1996), as is the case for the magpie (Martínez *et al.* 1999). The spatial autocorrelation analyses were made with the computer program Le Proiciel R (Legendre & Vaudor 1991). The import-export section was used to transform the distance matrix into binary files, which were used for multiple autoregression analysis using the Mantel section of the program. Partial correlation coefficients were calculated as suggested by Smouse *et al.* (1986) by making a matrix with residuals (A') of the relationship between the dependent matrices (A) and one of the independents (B) and another matrix with the residuals (B') of both independent variables (B and C). The Mantel (1967) test was subsequently run for the two residual matrices (A' and B'), with the estimated r being the partial correlation coefficient between A and B while controlling for the effect of matrix C . We report (i) the Mantel statistic (R) which is the correlation coefficient and (ii) the standardization of R proposed by Hubert (1985), which varies between $+1$ and -1 and consists of a real value of R produced by the extremes (maximum and minimum) obtained from the permutations (Legendre & Vaudor 1991). We tested the statistical significance of the autocorrelation coefficients using permutation tests with 1000 permutations. By using partial autocorrelation analyses we were able to distinguish between genetic and purely geographic effects on differences in nest volume in different magpie populations.

3. RESULTS

The nest size of magpies is related to territory quality, breeding success and risk of brood parasitism. We have

previously found that nest size is negatively related to laying date (Soler *et al.* 1995) and, thus, we controlled for laying date in the analyses. The nest volume of unparasitized nests was significantly smaller in areas of sympatry than in allopatry when statistically controlling for laying date, either including or excluding parasitized nests (table 1). Nest volume was on average reduced by 33.2% in sympatry as compared to allopatry when including parasitized nests and by 37.6% when excluding parasitized nests (table 2). In the subsequent analyses, we used all available magpie nests.

The relationship between the nest volume of magpies and the prevalence of parasitism was investigated in a multiple autocorrelation. We found no relationship between nest volume and rate of parasitism while controlling for differences in latitude between populations (Mantel's test, $r = -0.12$, $r_{\text{std}} = -0.31$, $p = 0.14$). However, a second autocorrelation, controlling for genetic distances between populations, showed a significant correlation (Mantel's test, $r = -0.30$, $r_{\text{std}} = -0.94$, $p = 0.004$).

While parasitism rates in sympatric populations may vary between years (M. Soler *et al.* 1998b) and, thus, not reflect the long-term selection pressures on the host imposed by the brood parasite, the rejection rates of experimental mimetic cuckoo eggs would be a more appropriate estimate of the selection pressures imposed by the cuckoo during the recent past (Soler *et al.* 1999b). On the other hand, the rejection rates of non-mimetic cuckoo eggs could be used as an index of genetic similarity due to their association with genetic distances, but not as an index of the selection pressures imposed by cuckoos (see §2 for further explanation). For mimetic experimental eggs, we found a negative relationship between nest volume and the rejection rate (figure 1) while controlling for differences in latitude between populations (Mantel's test, $r = -0.25$, $r_{\text{std}} = -0.68$, $p = 0.009$). A second autocorrelation analysis between nest volume and the rejection rate of mimetic eggs while controlling for genetic distances between populations also showed a highly significant correlation (Mantel's test, $r = -0.46$, $r_{\text{std}} = -1.00$, $p = 0.001$). However, an analysis of non-mimetic eggs revealed a non-relationship between nest volume and the rejection rate (figure 1) while controlling for differences in latitude between populations (Mantel's test, $r = -0.01$, $r_{\text{std}} = -0.03$, $p = 0.49$) and also while controlling for genetic distances between populations (Mantel's test, $r = 0.04$, $r_{\text{std}} = 0.10$ and $p = 0.35$).

4. DISCUSSION

Sexual selection causes exaggeration of traits that confer an advantage to certain individuals in terms of mating success (Darwin 1871). The extent of exaggeration of secondary sexual characters depends on the balance between the sexual selection benefits of such traits and their costs in terms of natural selection (see the review in Andersson (1994)). The balance between natural and sexual selection may differ between sites due to differences in the intensity of natural and sexual selection, as exemplified by particular predator communities causing a reduction in male coloration in the guppy *Poecilia reticulata* as compared to populations without these predators

Table 2. Nested analyses of covariance (nested analysis of variance for laying date) with mean nest volume of magpies as the dependent variable, laying date as a covariate and individual nests nested within areas

(Means (s.e.) are also reported for sympatric and allopatric host populations, respectively. MS, mean squares.)

variable	MS	d.f.	F	p	mean (s.e.) volume in sympatry (cm ³)	mean (s.e.) volume in allopatry (cm ³)
using parasitized nests						
cuckoo presence	6.08	1	24.87	0.000 001	81 729.2 (4014.9)	122 260.2 (7230.9)
error	75.34	308	—	—	—	—
not using parasitized nests						
cuckoo presence	5.25	1	19.67	0.000 013	76 343.5 (3409.6)	122 260.2 (7230.9)
error	71.54	268	—	—	—	—

Figure 1. Mean nest size (cm³) in European magpie populations in relation to (a) the rate of parasitism by the great spotted cuckoo (regression line $\log(y) = 11.45 - 0.012x$), (b) the magpie rejection rate of mimetic model eggs (regression line $\log(y) = 11.86 - 0.017x$) and (c) non-mimetic model eggs. Each observation represents the mean value for a population. Open and filled circles represent allopatric and sympatric populations, respectively.

(Endler 1980). Several studies have suggested that parasitism can be a cost of sexual selection because parasites use secondary sexual characters or displays as cues to locate a host (Mitchell & Mau 1971; Soper *et al.* 1976; Cade 1979; Thornhill & Alcock 1983). However, there are, to the

best of our knowledge, no studies showing differences in the parasitism rate affecting the equilibrium expression of secondary sexual characters between different populations of hosts.

Magpies build very large nests for their body size (J. J. Soler *et al.* 1998a) and a hypothesis explaining this extravagant nest size is sexual selection: male magpies bring sticks and other nest material to the nest and females may evaluate the working ability of their mate and, hence, potentially their parenting ability from this activity (J. J. Soler *et al.* 1998a). There is experimental evidence for magpies that nest size directly affects female reproductive decisions such as clutch size, the start of incubation and, hence, the degree of hatching asynchrony, suggesting that nest size plays a direct role in sexual selection (Soler *et al.* 1999a). Great spotted cuckoos preferentially parasitize large magpie nests as indicated by a significant correlation between nest size and risk of parasitism in the Guadix magpie population in southern Spain (Soler *et al.* 1995). The functional basis for this preference appears to be the high-quality parental care provided by magpies with large nests: experimental parasitism of magpie clutches in relation to nest size has revealed a significantly higher probability of successful fledging for cuckoo offspring in large nests (Soler *et al.* 1995). Thus, there is natural and sexual selection pressures of opposite direction on magpie nest size: sexual selection for a larger nest size and natural selection imposed by cuckoos for a smaller nest size. The evolutionary equilibrium nest size in different magpie populations should thus depend on the net selection pressure on nest size. Consistent with this expectation we found that nest size was 33–37% smaller in sympatric than in allopatric magpie populations (table 1).

Following the hypothesis that nest size is related to clutch size, which has been detected in several species (e.g. Slagsvold 1982, 1989a,b; J. J. Soler *et al.* 1998b), we should find that magpies build larger nests in areas with larger clutch size. However, although this pattern has been detected within a magpie population (Soler *et al.* 1999a), when studying different magpie populations we showed an opposite trend (Soler *et al.* 1999c). Magpies in sympatric areas with the great spotted cuckoo laid clutches that were around 10% larger than magpies in allopatric areas. It implies that, not only has the equilibrium nest size been reduced due to natural selection imposed by the cuckoo, but the female response to nest size (i.e. number of eggs laid) has also been altered.

In accordance with the hypothesized opposed natural and sexual selection pressures, spatial autocorrelation analyses revealed a negative relationship between nest size and the prevalence of parasitism and other variables related to parasitism pressure, after controlling for latitude. The magnitudes of the correlation coefficients were slightly larger for parasitism and rejection of mimetic eggs for analyses controlling for genetic distances between populations as compared to analyses controlling for differences in latitude between populations. However, the autocorrelation coefficients for nest volume in relation to rejection of non-mimetic eggs were non-significant when controlling for latitude or genetic distances. These findings are consistent with responses to parasitism and mimetic model eggs, mainly reflecting phenotypic differences between magpie populations, with responses to non-mimetic model eggs being strongly influenced by genetic distances between populations and, hence, genetic differentiation (Soler *et al.* 1999b).

In conclusion, the brood-parasitic great spotted cuckoo has affected the evolution of the nest size of its magpie host, as evidenced by differences between sympatric and allopatric populations. This difference is consistent with the hypothesis that a balance between the effects of natural and sexual selection maintains sexual displays.

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