Can social interactions rescue "lost" behavioural defences in an allopatric cuckoo host?

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ABSTRACT

Social information use by cuckoo-hosts provides an excellent example of how social interactions within species can influence selection on another. Neighbours observe each other's mobbing behaviour towards cuckoos, and then adjust costly defences back at their own nest in response. This may even allow naïve juveniles to 'learn' to recognise cuckoos, suggesting that 'social responsiveness' must play a key part in determining how hosts respond to changing rates of brood parasitism. However, if the 'cultural memory' of cuckoos is lost, can this plasticity in defences be rescued? This is fundamental for cuckoo-host coevolution, as the rates at which host defences are lost, gained, or retained determines evolutionary dynamics. Using populations of reed warblers at the northern- and southernmost extents of their range, we designed a field experiment to test whether populations allopatric to cuckoos (i) still recognise cuckoos as a threat, (ii) respond to social cues to upregulate defences, and (iii) vary in their strength of social responsiveness. We found defences and social responsiveness to be weaker in the south, where there is a much longer history of allopatry. In the north, only birds that retained recognition of cuckoos showed social responsiveness: social information about cuckoos did not increase hosts' propensity to attack (whereas it doubled in the range core), but it did increase the strength of mobbing in the 30% of birds that recognised the cuckoo at the northern range front. Most importantly, however, experimental cuckoo eggs remained in the nest, whereas in previous experiments elsewhere the same social information increased egg rejection ten-fold. This suggests that social responsiveness is more limited at the range edges, under relaxed selection, and this would incur little immediate cost to cuckoos' fitness if they (re)invade. Our study provides a rare example of geographic variation in social information use and highlights how current range expansions may influence the outcome of future species interactions.

INTRODUCTION

When their distributions change, species are likely to experience new selection pressures, but they may also be released from existing ones (Lahti et al., 2009). Relaxed selection can lead to the reduction or loss of previously adaptive traits (Lahti et al., 2009), contributing prominently to patterns of evolutionary change (Fong et al., 1995; Porter and Crandall, 2003; Rayner et al., 2022). In a changing world, past selection pressures can re-emerge, making long unexpressed traits adaptive again. Social learning and information-use could play a key role in determining whether behaviours are lost or retained (Foster, 2013). For example, social information is used by prey and hosts to assess their predation and parasitism risks (Gil et al., 2018) and predators also use information transmitted by other predators to find suitable prey, feeding back to alter prey defences (Hämäläinen et al., 2022). If and how individuals and populations respond to social information (their 'social responsiveness') therefore affects their own fitness and the strength of selection on interacting parties (Dall et al., 2005). Social behaviour may also determine whether populations are resilient to change, as information from others can rescue populations from extinction (Thorogood et al., 2018; Gil et al., 2019). However, behaviour and behavioural plasticity are relatively understudied in the context of relaxed selection, despite the expectation that they persist longer than morphological traits after selection for them ceases (Rayner et al., 2022).

Social information use by hosts of brood parasitic cuckoos provides an excellent example of how social interactions within a species can influence selection on another. After observing their neighbours mobbing a common cuckoo (*Cuculus canorus*), reed warblers (*Acrocephalus scirpaceus*) increase mobbing at their own nests (Davies and Welbergen, 2009). This eavesdropping may even allow naïve juveniles to 'learn' to recognise cuckoos (Feeney and Langmore, 2013), suggesting that social responsiveness must play a key part in determining how hosts respond to changing rates of brood parasitism. This is likely a specific response to information about cuckoos, rather than nest predators or novel stimuli, because hosts must discriminate between cuckoos and the deadly hawks they mimic (Welbergen and Davies, 2011). In optimising their discrimination thresholds, social interactions of hosts cause frequency-dependent selection of a plumage polymorphism in cuckoos, where the less common colour morph benefits from being less detectable (Thorogood and Davies, 2012). However, learning from your neighbours requires that your neighbours have experience, so what happens when this social memory of cuckoos is lost?

Host populations may be currently parasitised, previously but no longer parasitised, or naïve to parasitism. It is thought that gene flow from populations under varying degrees of coevolutionary

pressure determines how quickly a population responds to parasitism and thus the strength of selection on the parasite (Nuismer et al., 2003; Thompson, 2005). The movement of experienced individuals between populations creates an analogous information landscape (Bergman and Beehner, 2023), though population-scale changes in behaviour can be seen rapidly, even within the same generation, through social learning. Behaviour therefore varies geographically according to the local information and adaptive landscapes, but "cold spots" where selection is relaxed have received relatively less research attention (Lahti et al., 2009).

Defences are costly, so host populations that find themselves allopatric from cuckoos, such as through range expansion, tend to plastically reduce their expression of anti-parasite adaptations (Brooke et al., 1998; Lindholm and Thomas, 2000), or lose them altogether (Lahti, 2006; Lawson et al., 2020). Parasitised reed warblers in England, for instance, have reduced their defences proportional to the decline of cuckoos in the country (Thorogood and Davies, 2013), and hosts introduced to New Zealand do not mob cuckoo mounts (Hale and V. Briskie, 2007). Naïve populations may represent opportunities for rapid invasion or host switching by cuckoos. However, some hosts have also been seen to increase defences very rapidly upon the (re)invasion of brood parasites. When common cuckoos expanded their range in Japan and began parasitising new populations of azure-winged magpies, the magpies increased their rejection rates by 2-3% per year (Nakamura, 1991). Such rapid behavioural changes in a population implicate plasticity and social learning as their mechanisms rather than genotypic changes. It is unknown whether a host population allopatric to cuckoos can (re-)learn defences immediately from a few informed individuals, or if the mechanisms to do so are lost altogether. In fact, these outcomes may not be mutually exclusive and a population's ability to use social information may depend on how long ago it was parasitised, as an evolutionary loss of these mechanisms may occur over a long enough time.

Here we use allopatric populations of reed warblers from the northern- and southernmost limits of their range to test by experiment how social responsiveness varies with geography and time since last being parasitised. Reed warblers colonised Finland only about 100 years ago (Järvinen and Ulfstrand, 1980), escaping parasitism by their cuckoo gens which has yet to expand as far north. At the southern range limit in Sicily, reed warblers are unlikely to have been parasitised – their nearest known parasitised conspecifics are > 850 km away (Quaglierini, 2004) and reed warblers tend to disperse < 100 km (Ceresa et al., 2016) (but adults are highly philopatric (Ceresa et al., 2016; Halupka et al., 2017), limiting the influence of experienced individuals from parasitised populations on allopatric populations). There is further evidence of isolation in the Sicilian population in that they differ in

body size from Sardinian and mainland populations (Ientile et al., 2023). Cuckoos are present in Sicily only on mountainsides, while reed warblers are restricted to the island's coast and singular inland lake. This separation between the two species is likely to have existed since antiquity as cuckoos and reed warblers are mentioned in historical records but not in association with each other (Arnott, 2007).

First, we test whether reed warblers in these range-edge populations already recognise and respond to cuckoos. Second, whether they upregulate their defences in response to social information about cuckoos, as in core populations. Finally, we test if reed warblers in Finland, with a more recent history of parasitism, respond more to social information about cuckoos than those in Sicily.

METHODS

Study areas and host populations

We studied reed warblers at 30 reed-line bays near Helsinki, along 100km of southern coast of Finland, from 60.19848N 24.07305E to 60.34039N 25.71162E, and in the Fiume Ciane nature reserve, Sicily, Italy 37.04285N, 15.24273E, EPSG:3857. These represent the northern- and southernmost extents of the reed warbler's range. Throughout this range, they nest almost exclusively in *Phragmites* reeds. On the coast of Finland, reed beds are often expansive, and reed warblers nest in relatively low densities (distances to closest nest measured using GPS coordinates, median (lower quartile, upper quartile) 2019: 57 m (33, 95), 2020: 49 m (27, 77); range, 2019: 15–573, 2020: 9–398). In Fiume Ciane, reeds are concentrated along the river, its floodplains, and irrigation ditches, as well as a disused salt work (Saline di Siracusa). Reed warblers here nest more densely (median distance to closest nest: 36 m (24, 53)). Neither of the reed warbler populations, in Finland nor Sicily, are parasitised by cuckoos (see Introduction).

Measuring host mobbing of cuckoos before and after social information

In Finland, we conducted experiments at reed warbler nests in May-July in 2019 and 2020 and in Sicily in May-July 2022. We began on the day the fourth egg was laid, the usual day of clutch completion for this species. However, reed warblers typically lay 3-5 eggs, so some nests were tested either the day before or the day after clutch completion. Since incubation usually begins with the penultimate egg (Cramp and Brooks, 1992), any differences in nest attendance were expected to be minimal. The experimental design was essentially the same between the two locations: at each focal nest we first measured the base-line mobbing response to a model cuckoo, then presented social information of either a cuckoo or control model, and finally measured their mobbing response to a

cuckoo again at their nest. We waited at least 1.5 h between presentations and limited them to between the hours of 10:00 and 18:00 local time as cuckoos tend to lay in the afternoon. As such, presentations were split over 2 days for each nest.

The models used as controls were different in Finland and Sicily, as was the number of control model presentations at the nest. In Finland, there were 3 presentations of models at the nest and 1 social presentation: the first and last nest presentations were always a cuckoo, and the social presentation was either a cuckoo or a magpie, while the second presentation at the nest was either a cuckoo or magpie depending on treatment so that each nest saw the same models the same number of times. In Sicily, each nest had 4 presentations of models at the nest - one cuckoo and one teal both before and after a social presentation of either cuckoo or teal – with model order being randomised to control for order effects. This slight difference in design was so that we could test an additional question: would any threat to the nest elicit the same increase in nest defence or is this behaviour specific to cuckoos? Previous studies have not experimentally considered this. Hypothesising that reed warblers in Sicily would express a reduced response to cuckoos, we decided to replicate the methods of previous studies (e.g. Davies and Welbergen, 2009) that used a novel, harmless intruder, so that we could even more directly compare social responsiveness to populations in the range core. To compare how reed warblers at each range edge responded to a benign intruder, we additionally presented teal models to 56 nests in Finland in 2018-2020. These were not the same nests used in the social information experiment in Finland, and all teal models used were of females.

We used 3D-printed ABS plastic cuckoo models (3D QuickPrinting United Kingdom) painted with acrylics by an artist, and the magpie and teal models were commercially available hunting decoys (Live Decoys and Flambeau Outdoors, respectively). A similar range of mobbing behaviours were elicited by our cuckoo models as studies using taxidermy models (e.g. Welbergen and Davies, 2008) and they were produced with the same 3D templates as other, independent researchers (e.g. Marton et al., 2019).

To measure mobbing at the nest, we placed models adjacent to the rim of the focal nest and upon the arrival of the first bird within 3 m, we counted bill snaps and rasp vocalisations for 5 min (intensity). Bill snaps and rasp calls are correlated with close approach, threat postures and direct attack of cuckoo models (Welbergen and Davies, 2008), and differ according to the threat posed by the model (Duckworth, 1991; Welbergen and Davies, 2008; Campobello and Sealy, 2010). Bill snaps and rasp calls were summed together for data analysis and to reduce the risk of misidentifying the sound of

drying and cracking reed as bill snaps, or some "churr" warning calls as rasp calls, we conservatively set the threshold for mobbing (propensity and intensity) at 20 combined rasps and bill snaps as per previous studies (Welbergen and Davies, 2009; Thorogood and Davies, 2012, 2013). Three observers carried out the experiments in Finland, each with a different set of models. We filmed each trial with a small action camera on a pole 1 m from the nest and after the field season each observer independently counted mobbing signals from 10 videos, blind to the field-collected data. There was high consistency among observers' counts of bill snaps [ICC: 0.92 (95%CI 0.80–0.98), $p < 0.001$] and rasps ICC: 0.98 (95%CI 0.95–1.0), $p < 0.001$], as assessed using the Intraclass Correlation Coefficient (ICC) in the *irr* package in R (see Statistical analyses below). One of these same observers also did trials in Sicily, plus two others. All field mobbing data in Sicily were confirmed by video analysis.

To provide social information, we placed either a model cuckoo or model magpie/teal (Finland/Sicily; treatments randomly assigned) in the reeds adjacent to a disused warbler nest, collected in previous years, 10-15 m from the focal nest. We then played recordings of reed warblers mobbing a model cuckoo for 10 min to simulate a close neighbour mobbing a cuckoo or teal at their nest, providing social information for the focal pair of cuckoo activity (or magpie/teal as a nest predator/harmless control) in the area. We used 5 mobbing audio tracks, recorded at different nests in Wicken Fen, England, by Welbergen and Davies (2008) (also used by (Thorogood and Davies, 2016). We only did trials at nests at least 50m from other social presentations, to avoid contamination of information. We additionally presented social information from 4 active neighbouring nests (3 cuckoo and 1 teal; < 20m from the focal nest) instead of disused nests in Sicily, for which none of the focal nests mobbed a cuckoo and hence were combined with the rest of the data.

Upon visualising the mobbing data from Finland, there seemed to be greater mobbing propensities and intensities by reed warblers towards cuckoos in bays where we had conducted this experiment the previous year. We therefore conservatively excluded the data from these 18 bays in 2020. Excluding these data did not qualitatively change our results and only weakened the effects we report in this study. We also excluded 4 focal nests (1 in Finland and 3 in Sicily) where birds failed to appear at one or both cuckoo presentations at their nest (field observations confirmed by video). In total, 81 Finnish nests (Cuckoo treatment $N = 41$; Magpie treatment $N = 40$) and 39 Sicilian nests (Cuckoo treatment $N = 22$; Teal treatment $N = 17$) were analysed from the social information experiment.

To measure rejection rates of mimetic eggs, after the final model presentation, we chose a warbler egg at random from the focal nest and coloured it with forty equally spaced brown dots using a Staedtler permanent felt tip pen (Lumocolor® 314-7 (Thorogood and Davies, 2016)). In Sicily we got rejection data from 40 nests (Cuckoo treatment $N = 21$; Teal treatment $N = 19$) and in 2019 in Finland from 49 nests (Cuckoo treatment $N = 24$, Magpie treatment $N = 25$). In 2020 in Finland, we instead used 3D-printed eggs with the same dimensions as redstart-gens cuckoo eggs and painted blue (Citadel© acrylic paints, custom mixed) to simulate a non-mimetic foreign egg in 46 nests (Cuckoo treatment $N = 29$, Magpie treatment $N = 27$). Nests were checked for rejection at least 3 days after colouring or placement as reed warblers most often reject within 3 days (Davies and Brooke, 1988). However, video analysis later showed that, despite vigorous pecking (4/25 nests in 2021, not included in this experiment), reed warblers were not able to pierce and remove the 3-D printed eggs from the nest. Therefore, we considered model eggs rejected when clear attempts had been made to reject them or at least one own egg broken (i.e. not considered a rejection cost in this study). Finally, in Sicily we also assessed non-mimetic egg rejection without any information of cuckoo presence ($N = 11$) and after a cuckoo model was presented at the nest (personal information; $N = 12$) by colouring one egg in the nest with a blue Copic felt tip pen (Copic Ciao B).

Statistical analyses

All analyses were conducted in R (v. 4.3.2; R Core Team, 2023). We used the package *glmmTMB* (Brooks et al., 2017) for generalised linear mixed models (GLMMs) and generalised linear models (GLMs). We present the estimated effect sizes, with their standard error, and *p*-values. We checked for the most appropriate model error structure for each model of mobbing intensity by using QQ-normality plots, residuals vs. predicted plots, and dispersion and outlier tests with the *DHARMa* package (Hartig, 2022). All the models of mobbing intensity were best suited to a quasi-poisson distribution (*nbinom1* in *glmmTMB*). Analyses of change in mobbing behaviour contained a random effect term of nest identity to account for each nest being measured twice (before and after social information), as did models comparing mobbing to different stimuli in Sicily to account for intruders being presented at each nest twice. A binomial error structure and logit-link function were used for most models of mobbing propensity, but due to the small number of nests at which mobbing occurred in Sicily, for these data we compared mobbing propensity between treatments using Fisher's exact tests. Reed warblers are known to assess parasitism risk using indirect cues, including distance from nearest potential cuckoo perch (Oien et al., 1996; Welbergen and Davies, 2009). We confirmed an even distribution of distances to possible cuckoo perches among treatments before further analysis (gamma GLM: estimate = -0.001 ± 0.003, $z = -0.335$, $p = 0.74$). Despite data being collected across

30 different bays in Finland, including bay as a random effect did not improve model fit (Akaike Information Criterion (AIC) > 2) so it was not part of our final models.

RESULTS

Before our social presentations, there was no difference among our treatment groups in the likelihood that focal pairs would mob a cuckoo presented at the nest (Finland, binomial GLM: estimate = -0.0792 ± 0.481, z = -0.165, $p = 0.87$; Sicily, Fisher's exact test: $p = 1.0$). There was also no difference among the two years in which the experiment was conducted in Finland (binomial GLM: estimate = 0.113 ± 0.532, z = 0.213, $p = 0.83$).

We found no significant difference in reed warblers' propensity to mob cuckoos before and after social information in Finland (binomial GLM: estimate = -1.31 ± 1.24, $z = -1.06$, $p = 0.29$), nor between treatments (estimate = -0.993 ± 1.793, $z = -0.554$, $p = 0.58$). There was also no significant interaction between presentation order and treatment for propensity to mob a cuckoo at the nest (Finland: estimate = 2.93 ± 1.765, $z = 1.659$, $p = 0.097$) and therefore neither treatment independently affected the likelihood of a cuckoo being mobbed. In Sicily, a smaller sample size combined with a low mobbing propensity necessitated the use of a Fisher's Exact test, which suggested no association between social treatment and the likelihood of mobbing a cuckoo ($p = 1.0$).

Of those Finnish pairs that did mob cuckoo models ($N = 32$), their rate of mobbing calls (intensity) increased when presented with social information about cuckoos (Fig. 1A), but not magpies (Fig. 1B), i.e. there was a significant interaction between presentation (before/after social information) and treatment (GLMM: estimate = 0.944 ± 0.458, $z = 2.05$, $p = 0.039$) but no significant differences among presentation orders (estimate = -0.104 ± 0.340, $z = -0.301$, $p = 0.76$) or treatments (estimate = -0.717 ± 0.482, $z = -1.49$, $p = 0.14$) separately. An increase in mobbing intensity but not propensity in Finland suggests only reed warblers that retained recognition of cuckoos were responsive to social information. In Sicily, there were too few nests at which birds mobbed for us to compare just "mobbers", but there was no difference in mobbing intensity when all nests were compared between cuckoo and teal social information (GLMM Presentation order x Treatment interaction: estimate = 0.761 ± 0.951, $z = 0.800$, $p = 0.423$; Fig. 1C & 1D).

Although only 23% (5/22) of pairs tested in Sicily mobbed model cuckoos above a threshold of 20 rasp calls and bill snaps, compared to 39% (16/41) in Finland, we did not detect a statistically significant difference in propensity between the two countries (binomal GLM Presentation order x

Country: estimate = 5.91 ± 3.42, z = 1.726, p = 0.084). However, mobbing intensity toward cuckoos was significantly greater in Finland than Sicily after social information (GLMM: estimate = 1.90 ± 0.67, z = -3.13, p = 0.0017). This difference between the northern and southern range edges was specific to cuckoos, and not a general difference in nest defence, because teal, a harmless intruder that does not require special recognition (unlike cuckoos, which mimic hawks), were mobbed at a similar intensity between the two countries (estimate = -0.364 ± 0.400, z = -0.915, p = 0.36).

Mimetic eggs were not rejected at all in either Finland (Cuckoo treatment = 0/24; Magpie treatment = 0/25) or Sicily (Cuckoo treatment = 0/21; Teal treatment = 0/19). Non-mimetic eggs were rejected at low rates in Finland, but these were not influenced by social information (binomial GLM: estimate = 0.108 ± 0.635, z = 0.170, p = 0.86): 24% (7/29) of pairs rejected a non-mimetic egg after being presented with cuckoo social information, and 22% (6/27) with magpie social information. Although we did not test the effect of social information on the rejection of non-mimetic eggs in Sicily, there was no rejection of blue eggs here with either no manipulation of information (0/11) or after presenting a cuckoo model at their nest (0/12).

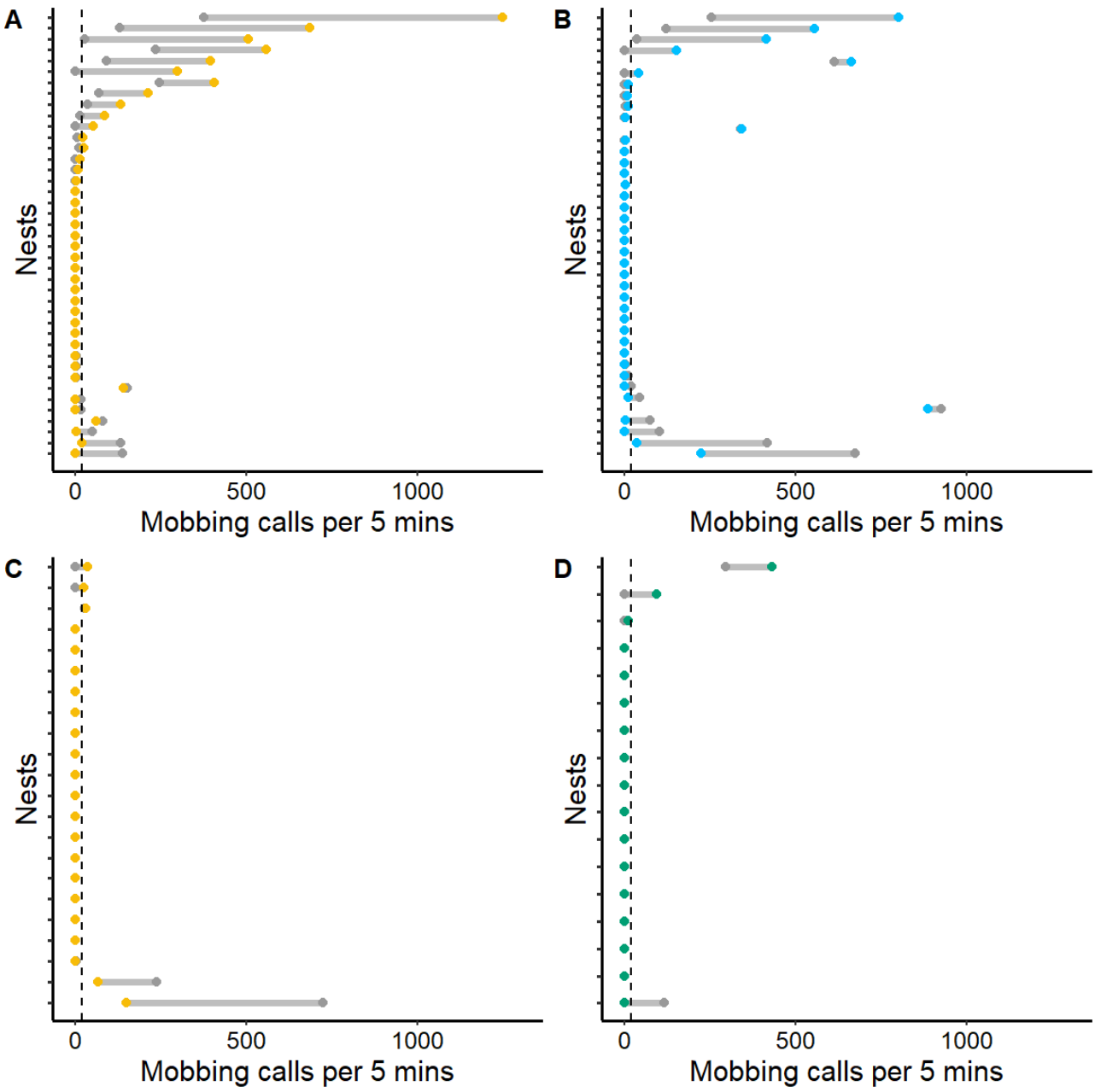

Fig. 1. At Finnish sites, (A) social information about cuckoo activity increases mobbing intensity towards cuckoos (*N* = 41 nests), but (B) social information about a nest predator (magpie) does not (*N* = 40). In Sicily, neither social information about (C) cuckoos (*N* = 22) nor (D) benign teal (*N* = 17) altered mobbing responses. Grey and coloured dots represent mobbing intensity prior to (grey) and after (coloured) social information (yellow = cuckoo, blue = magpie control, green = teal control). Any mobbing response < 20 (vertical dashed line) was considered as no response.

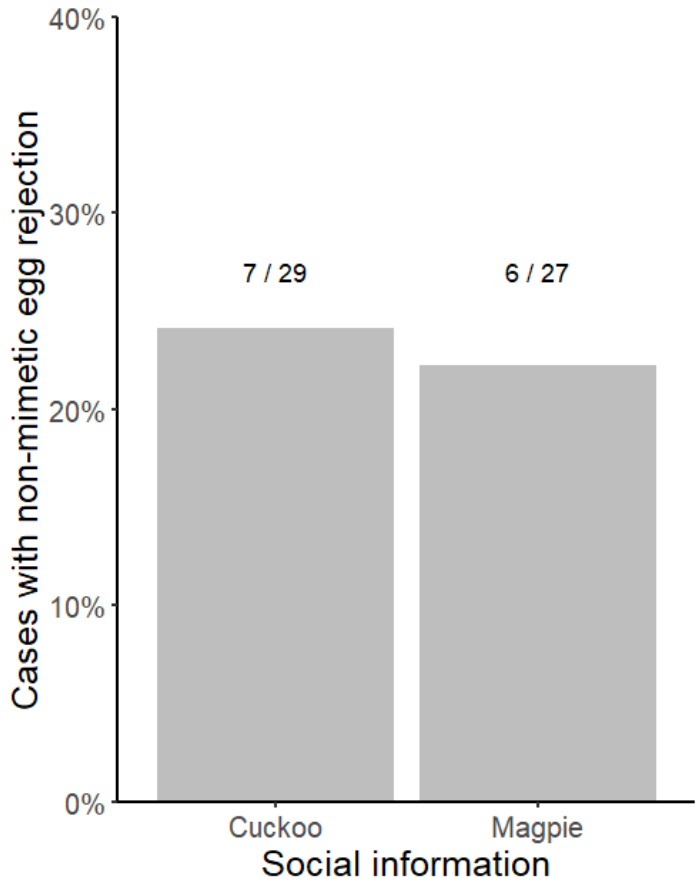

Fig. 2. Blue non-mimetic eggs were rejected at the same rate in Finland regardless of whether social information was provided about cuckoos or magpies. Mimetic eggs were not rejected in either country, regardless of social information.

DISCUSSION

Our results show that for some host populations at their range edges, who have escaped cuckoo parasitism, eavesdropping on neighbours has some potential to rescue waning behavioural defences should cuckoos invade. However, social responsiveness was contingent on birds already recognising cuckoos: reed warbler pairs that initially mobbed cuckoos subsequently increased their mobbing intensity after receiving social information, whereas quiet birds largely remained quiet. At the southern range edge, reed warblers hardly mobbed cuckoos, even after witnessing the mobbing of a cuckoo at a "neighbour's" nest. We also found that social information of a benign intruder or a nest predator did not affect mobbing of cuckoos, suggesting that social responsiveness is a specific strategy against cuckoos even in a population without cuckoo parasitism. Importantly, mimetic experimental eggs all remained in nests, whereas in previous experiments elsewhere, the same social information increased mimetic egg rejection ten-fold (Thorogood and Davies, 2016). Social

information also had no influence on the rate at which non-mimetic eggs were rejected, though 23% were rejected in Finland after seeing a cuckoo at their nest.

Why do reed warblers hardly respond to cuckoos in Sicily, even after social information?

Small-scale geographical variation in host defences can be explained by plasticity (Lindholm, 2000; Langmore et al., 2012), with rates of defence expression being close to optimal according to local parasitism risk (Davies et al., 1997; Welbergen and Davies, 2009). However, by comparing populations at a much larger geographical scale (and far from their parasitised conspecifics), we saw that not only do defences vary, but so does their plasticity. The lack of social responsiveness we measured in Sicily may be due to a longer (or total) absence of cuckoo parasitism, suggesting the effects of both plasticity and adaptation. The Finnish population not only has a more recent ancestral history of parasitism, having expanded recently from parasitised populations, but likely receives considerable gene flow from nearby parasitised populations in the range core (Sætre et al., 2022). This explanation – that relaxed selection has gradually lessened the expression of defences – is supported by recent experimental evolution work on burying beetles showing that social behaviours are less likely to be induced when the opportunity to express them is removed for multiple generations (Bladon et al., 2023).

Evolutionary changes can also be rapid in the sudden absence of brood parasites. In as little as a century, the eggs of African village weavers introduced to Mauritius had less between-individual variation and within-clutch consistency of appearance, as well as less spotting, all of which are adaptations to egg-mimicking brood parasitism (Lahti, 2005). A population of the same species introduced a century earlier to Hispaniola, also free from cuckoos, had even more pronounced reductions in these same egg traits (Lahti, 2005). This mirrors our results in that social responsiveness is more reduced in the population less recently in contact with cuckoos. However, in contrast to our results, alarm calls produced by yellow warblers that specifically warn of brood parasitic brown-headed cowbirds seem to have persisted similarly among sites in long-term allopatry and those close to parasitised ones (Kuehn et al., 2016), although differences in plasticity were not tested for. Similarly, some frontline defences are retained by Australian reed warblers, which are not hosts of its sympatric cuckoos (Chaumont et al., 2021).

Changes in introduced weaverbird egg appearance were subsequently found to prevent egg recognition, despite recognition and rejection themselves being maintained (Lahti, 2006). Like Lahti (2006), we saw an increase in egg rejection probability of non-mimetic eggs relative to mimetic eggs.

This implies potential changes in egg patterning rather than total loss of egg recognition, but we did not assess egg appearance. Many species that are likely to be ex-hosts also maintain egg recognition in the absence of parasitism (Medina and Langmore, 2015). Unlike Lahti's results, however, egg rejection by Finnish reed warblers was still considerably less prevalent than in parasitised populations (Stokke et al., 2008), and non-existent in Sicily, whereas the transplanted weaverbirds could reject at the same rates as source populations when controlling for egg appearance. The costs of maintaining phenotypic plasticity of defences may therefore be greater for some species than others (Murren et al., 2015). Indeed, there is evidence that hosts maintaining egg rejection without selection rarely make recognition errors when rejecting foreign eggs (Stokke et al., 2002).

Why do some pairs respond while many do not?

Reed warblers responded remarkably more to social information in previous studies in England and mainland Italy (Campobello and Sealy, 2011), where almost identical methods were followed. At Wicken Fen in S England, propensity to mob cuckoos increased from 46% to 75% (Davies and Welbergen, 2009) upon experimentally learning of local cuckoo activity. A similar proportion of reed warblers mob magpies, a nest predator, in Modena as in Finland, but in Finland cuckoos are not treated as a greater threat to the nest than magpies like they are in Modena (Tolman et al., 2021). Why in Finland do so few birds respond to both personal and social information of cuckoo presence? Perhaps the Finnish population is in the process of losing defences, locally adapting to a lack of selection by cuckoos. If we were to revisit this population many years later, would its response diminish further and look more like that in Sicily? Genomic analyses of mobbing and non-mobbing birds could yield some insights - perhaps mobbers are more recent immigrants from parasitised locales. There is already some genomic evidence that reed warblers are locally adapting to the climatic conditions at this range front (Sætre et al., 2022). However, even in parasitised populations not all individuals exhibit defences, although it is not clear why. An alternative explanation for why some pairs respond to social information while others do not is that the likelihood and/or costs of recognition errors are greater for some than others (and varied between northern and southern range edges) due to environmental and ecological differences. For example, mobbing can attract predators (Krams et al., 2007; Marton et al., 2019) and birds with more vulnerable nests may be more reluctant to make noise. We favour the explanation that there is local adaptation to the lack of brood parasitism, as egg rejection behaviour also appears to be greatly diminished in both of our study locations, yet mobbing and rejection behaviours are inherently different in their costs.

Conclusions

Overall, our results provide evidence for the degradation of socially mediated phenotypic plasticity under relaxed selection in the wild. A few experienced individuals are not sufficient to revive "ghosts of adaptation past" in the rest of the population if the tendency to use social information is reduced alongside the lack of expression of that trait. Whether we are witnessing microevolution in action (Lotem and Rothstein, 1995), or whether this reduction in responsiveness to social information is due to varied costs of plasticity, remains to be proven and warrants further research. Nevertheless, since the phenotypic traits we found to be geographically varied are defences in a coevolutionary arms race, our results also demonstrate how contemporary range expansions may influence the evolutionary outcomes of future species interactions.

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