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

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ABSTRACT

Behavioural adaptations are a key defence but whether they decay when selection pressures relax, or how quickly they can be restored if selection resumes, is poorly understood. Defences against a reinvading enemy could be reignited if individuals learn from their neighbours, but how effective is social information when the 'cultural memory' of a threat is lost? We tested by field experiment whether reed warblers allopatric from cuckoos retain defences and social responsiveness. In Finland, only birds that already recognised cuckoos responded to our manipulation of social information. Mobbing was even rarer and did not change in Sicily, where there is a longer history of allopatry. Experimental cuckoo eggs remained in nests, whereas the same social information has increased egg rejection ten-fold in sympatric populations. This suggests defences and social responsiveness can degrade under relaxed selection, and cuckoos would incur few immediate costs if they invaded. Our study highlights how information can be manipulated to assess behavioural reaction norms in situ, and how range expansions may influence the outcome of species interactions.

INTRODUCTION

As species' ranges expand or contract, their exposure to enemies and selection pressures can also change (1). Where selection relaxes (i.e. with allopatry), traits that were previously adaptive are expected to reduce (e.g. due to drift), particularly if maintaining the trait is costly (2). However, while behavioural defences are common across the animal kingdom (3), whether these respond to relaxed selection is rarely tested (2, 4). Behaviours are assumed unlikely to be lost due to complex genetic architectures (pleiotropy) and underlying trait variation that can be co-opted in response to other selective pressures (2). However, another key issue is that loss of behaviour can be challenging to measure. Behavioural responses depend on prior experience and availability of information about the relative costs or benefits of taking action [i.e. information ecology (5)]. Therefore, the absence of a response does not necessarily indicate a lack of enemy recognition but rather cryptic plasticity (4). Taking an informational approach (6, 7) and manipulating cues in allopatry, however, makes it possible to approximate the retention of behavioural reaction norms in the wild.

Social 'memory' could play a key role in determining whether behaviours are lost or retained. For example, prey and hosts observe the behaviour of others to learn about novel threats [e.g. social learning (8–10)] and assess risk of predation or parasitism (6), while predators use social information to find suitable prey (11). Therefore, how individuals adjust their behaviour in response to social information [i.e. social responsiveness; (12)] is likely to affect both their own fitness and the strength of selection on interacting parties (13, 14). Social responsiveness may also determine whether populations are resilient to environmental change (15, 16), especially as the utility of social information depends on the availability of more-informed 'demonstrators'. For example, gene flow among populations experiencing variable selection pressures (i.e. trait re-mixing) is thought to determine how quickly a host population responds to shifts in the strength of selection by parasites [Geographic Mosaic Theory of Coevolution; (17)]. If experienced individuals from 'hotspots' of

current selection also introduce social information to naïve ‘cold spots’ of relaxed selection, social learning could speed up the recovery of defences in host populations that are later reinvaded by a previous enemy. However, while recent experimental evolution studies show that social behaviours can diminish very rapidly after selection is removed (18), the role of social cues in maintaining behaviours in ‘cold spots’ is still largely unknown (2, 9).

Avian brood parasitism provides an ideal system to test if behavioural defences and social responsiveness decline in allopatry, altering the potential for hosts to respond to future (re)invasion. Virulent brood parasites lay eggs in the nests of host species and can exert strong selection for defensive behaviours such as mobbing or rejecting suspicious eggs. However, many brood parasites use aggressive or Batesian mimicry of dangerous predators (19, 20), selecting for hosts to adjust defences according to local risk and minimise costly mistakes (21, 22). Parasitism can also vary in time and space with some host populations or species escaping parasitism for many generations (23). Over time in allopatry, plasticity is expected to be lost with hosts either becoming resistant to reinvasion (i.e. fixation of defences) or susceptible to extinction if defences wane (24) but it is unclear which trajectory will occur. Some species long-separated from brood parasites (i.e. hundreds of thousands to millions of years) show persistent (experimentally-induced) egg rejection (25–29), but this common defence appears to reduce in others (26, 30–33). Until recently, mobbing of adult brood parasites has received less attention (34), but this frontline defence also appears to degrade (26, 35) or be preserved (26, 28, 36) under recent [e.g. lost in < 100 years; (37, 38)] or longer allopatry. Conversely, apparently naïve species can also obtain host defences very rapidly upon invasion (39) but whether these changes represent the cryptic persistence of defences in the population, gene flow from parasitised areas, or novel learning is unknown.

Here we use allopatric populations of Common reed warblers (*Acrocephalus scirpaceus*) at the northern- and southernmost extents of their European breeding range to test for the retention of behavioural defences and social responsiveness to brood-parasitic Common cuckoos (*Cuculus canorus*). Reed warblers colonised Finland ca.100 years ago (40), most likely expanding from the southwest (41) and away from regularly parasitised areas in the range core (42). Cuckoos in Finland use different host species, away from reedbeds. In Sicily, reed warblers are likely to have escaped parasitism by cuckoos for much longer – cuckoos only occur on mountainsides while reed warblers are largely restricted to coastal areas, and mentions of both species in historical records are not in association with each other (43). At parasitised sites in their range-core, reed warblers upregulate mobbing (44, 45) and egg rejection (46) defences after observing their neighbours attack cuckoos. Among populations not currently exposed to parasitism, however, egg rejection rates vary widely [e.g. from 0–40%, (22)] and mobbing responses are reduced [e.g. 25% of pairs; (47)]. However, as in other studies of brood-parasite host defences in allopatry (see also ref. 29), perceived parasitism risk has not yet been manipulated (e.g. via social information) so the extent to which host defences reduce under relaxed selection remains unclear.

Therefore, we used field experiments to manipulate social information and simulate parasitism to test if defences and/or social responsiveness decay in allopatry. We predicted that if defences are retained, then providing social information should induce plasticity (i.e. social responsiveness) and lead to an increase in mobbing (propensity and intensity) and egg rejection, as previously shown in range-core populations. However, if defences are not upregulated in response to our manipulated cues, then this would provide evidence that these behaviours are being lost under relaxed selection. Additionally, we expected any loss of defences or weakening of social responsiveness to be more pronounced in Sicily as reed warblers there are likely to have been in allopatry for longer.

METHODS

Study areas and host populations

We studied unparasitized populations of Common reed warblers breeding in May-July around Helsinki, southern Finland (30 discrete reed-lined bays along 100km of coastline, 60.19848N 24.07305E to 60.34039N 25.71162E, in 2019 and 2020) and in the Fiume Ciane nature reserve near Siracusa, Sicily, Italy (37.04285N 15.24273E, in 2022), avoiding re-use of areas across years in Finland to avoid contamination of experience or pseudoreplication. Reed warblers nest at relatively low densities in Helsinki (48) but are more numerous in Fiume Ciane (median distance to closest nest = 36 m, inter-quartile range = 24-53 m). We found nests by cold-searching or monitoring singing males and recorded location and distance to the nearest potential cuckoo vantage point [tree >3 m in height, a possible indirect cue of parasitism risk; (49, 50)] using handheld GPS (accuracy ± 1 m).

Experimental protocols

To compare results to previously-studied parasitised populations in the range-core, we adopted published protocols (45, 46) as follows. Experiments started on the day the fourth egg was laid [clutch sizes = 3-5 eggs, incubation begins with the penultimate egg; (51)]. At each nest we measured the change in mobbing response to a cuckoo after presentation of social information of either a cuckoo or control. We used the same 3D-printed model cuckoos (painted by an artist, see ref. 48 for details) in Finland and Sicily but controls differed. In Finland we used a commercially-available plastic magpie (Live Decoys) to assess whether changes in mobbing may be due to nest predators or specific to cuckoos, and in Sicily we used plastic female teal hunting decoys (Flambeau Outdoors), similar to previous range-core experiments using innocuous controls (45). Although this difference precludes comparisons of responses to controls, our focus was on probing the generality of previous findings in the context of relaxed selection, and at parasitised sites there has been similar variation in controls and presentation orders (13, 44–46). To also compare how reed warblers at each site responded to a

benign control, we presented teal models at 48 additional nests in Finland in 2018-2020. Model cuckoos elicit similar responses as taxidermy specimens (52, 53) and ours were printed using the same 3D template as independent work (e.g. ref. 54).

To assay mobbing behaviour [bill snaps and rasping calls (53)], we placed a model adjacent to the nest rim and recorded latency of the first bird to arrive within 3 m (using a stopwatch, seconds). We filmed each trial with a small action camera on a pole 1 m from the nest while observing from 3-5 m away, depending on visibility, and counted mobbing vocalisations for 5 min (mobbing intensity). Three observers carried out experiments in Finland, each with a different set of models. One observer also performed trials in Sicily. 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) from data collected later using 10 videos and blind to field-collected data.

We used simulated neighbour presentations to provide social information 10 m from the focal nest (cf. active neighbours < 40 m in ref. 45). A previously-collected reed warbler nest was attached to reeds at a similar height to the focal nest, with either a model cuckoo or control adjacent to it (treatments assigned alternately). We then broadcast one of 5 playback tracks of reed warblers mobbing a model cuckoo [recorded for range-core experiments; (45, 46)] for 10 min from a speaker placed under the dummy nest. Focal nests were at least 40 m from other nests or experimental neighbour playbacks to avoid contamination of information. Live mobbing by neighbours does not influence social responsiveness to playbacks (13, 45) and simulated vs. active nests elicited similar responses to social information treatments in previous experiments (44, 46). In Sicily, where densities were higher, we used active neighbouring nests for social information presentations in 4 trials (3 cuckoo and 1 teal; < 20m from the focal nest) but none of these focal pairs mobbed a cuckoo.

In Finland, we always presented the cuckoo model at the start of the experiment (P1) and after (P3) presentation of social information (SI) of either a magpie control or a cuckoo (Fig. 1A). To avoid pairs in the cuckoo SI treatment being exposed to cuckoos more (i.e. P1, SI, P3) than in the magpie SI treatment (P1 & P3 only), we included a second presentation (P2) of either a cuckoo (magpie SI treatment) or magpie (cuckoo SI treatment) before SI (Fig. 1A). This design also allowed us to compare whether any changes in behaviour were due to repeated exposure rather than the SI treatment. To rule out order effects, in Sicily (Fig. 1D) we followed the same design as Davies & Welbergen (45): here each nest was presented with a cuckoo and control (teal) in random order before (P1 & P2) and after (P3 & P4) social information (SI). We waited at least 1.5 h between presentations at both sites and conducted trials between 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.

In trials where mobbing responses were very weak (i.e. fewer than 20 vocalisations), we later confirmed sounds from video recordings of the trial and excluded five cases where three observers could not discern or agree on sound categorisation. We also excluded 4 nests (1 in Finland and 3 in Sicily) where birds failed to appear at one or more cuckoo presentations at their nest (field observations confirmed by video). In total, we analysed mobbing from 83 Finnish nests (Cuckoo treatment n = 42; Magpie treatment n = 41) and 40 Sicilian nests (Cuckoo treatment n = 22; Teal treatment n = 18).

Measuring egg rejection defences

After the final model presentation, we coloured one egg at random from the focal nest with 40 equally-spaced brown dots using a Staedtler permanent felt tip pen (Lumocolor® 314-7) to measure rejection (as in ref. 46) of a pseudo reed warbler-gens ‘cuckoo egg’ (Finland: Cuckoo treatment n =

24, Magpie treatment n = 25; Sicily: Cuckoo treatment n = 22, Teal treatment n = 18). Due to a low response (see Results), for trials conducted in Finland in 2020 we then used custom 3D-printed eggs with the same dimensions and colour (Citadel© blue acrylic paints, custom mixed) as a highly non-mimetic redstart-gens cuckoo egg (Cuckoo treatment n = 29, Magpie treatment n = 27). In all trials, nests were checked 3-6 days later for removal of the 'cuckoo egg' (reed warblers most often reject within 3 days; Davies & Brooke 1988) or evidence of damage (reed warblers were not able to pierce and remove 3D-printed models despite vigorous pecking: 4/25 rejection trials filmed in a subsequent year, unpublished data). Finally, in Sicily we also assessed non-mimetic egg rejection without any information of cuckoo presence (n = 11) and with personal information of parasitism risk (i.e. by presenting a cuckoo model at the nest; n = 12) by colouring one egg in the nest entirely with a blue felt-tip pen (Copic Ciao B).

Statistical analyses

All analyses were conducted in R v.4.3.2 (56). First, we used GLMs to check for bias of potential indirect cues (i.e. distance to potential cuckoo vantage points, see Supporting Information S1) and to confirm that initial responses to cuckoos (i.e. P1 in Finland, or P1|P2 in Sicily) were similar in the treatment groups and among years of the study (in Finland). We then used GLMMs with a random effect for nest identity when modelling change in response across multiple presentations (i.e. P1 vs. P3, or P1 vs. P2) as implemented in the package *glmmTMB* (57). To investigate whether social information led to a change in mobbing propensity or intensity, we only included responses to the first and last presentation of a cuckoo at the nest (i.e. P1 and P3 in Finland). However, due to a large proportion of zeroes and lack of suitable fit for a zero-inflated model structure, we adopted a hurdle approach to model mobbing propensity (i.e. binary variable, binomial error structure and logit-link function) and intensity (i.e. number of calls in at least one presentation > 0, quasi-poisson (*nbinom1*) distribution) separately in Finland. For mobbing data from Sicily, we used Fisher's Exact tests to

compare treatment effects on mobbing propensity and quasi-binomial GLMMs to investigate changes in mobbing intensity across all pairs, due to the smaller sample size. To investigate whether social information affected egg rejection decisions, we used a GLM (binomial error structure, logit-link function) which included clutch size as a covariate predictor. Despite data being collected across 30 discrete sites in Finland, including location as a random effect did not improve model fit (Akaike Information Criterion > 2) so it was not part of our final models.

Finally, we investigated latency to approach the nest during experiments to assess more subtle differences in reaction to cuckoos (i.e. cryptic recognition without a mobbing response). We used separate GLMMs with Tweedie distributions to test if change in latency to approach across presentations differed (i) between treatments and (ii) between mobbing versus non-mobbing pairs as we lacked power to test a Presentation order*SI treatment*Mobbing status 3-way interaction. We used QQ-normality plots, residuals vs. predicted plots, and dispersion and outlier tests using package *DHARMa* (58) to assess assumptions and fits of all models, and we present estimated mean effect sizes (± standard error), *z*-statistics, and *p*-values. Summary tables of all models are available in Supporting Information S2.

RESULTS

Mobbing defences

When first presented with a cuckoo at the nest, 36% (30/83) of pairs in Finland and 13% (5/40) of pairs in Sicily showed a mobbing response (Fig. 1). This propensity to mob did not differ between SI treatment groups (Finland, GLM: estimate = 0.16 ± 0.46, z = -0.35, p = 0.73; Sicily, Fisher's Exact test: p = 1.0; Table S2.1 in Supporting Information) or among years of the study in Finland (GLM: estimate = 0.25 ± 0.48, z = 0.52, p = 0.60; Table S2.1).

In Finland, providing social information about the risk of parasitism in the local area did not induce significantly more reed warblers to mob cuckoos than pairs exposed to information about magpies (GLMM Presentation order * SI treatment: estimate = 3.99 ± 2.39, z = 1.67, p = 0.099, Fig. 1B, Fig. 2A; Table S2.2) and this lack of interaction was not because social information about magpies also induced increased mobbing propensity (Fig. 1C, Fig. 2A). Social information about cuckoos did, however, increase mobbing intensity (i.e. number of signals) of pairs who responded (across treatments n = 36 pairs with calls >0, Fig. 1B,C; GLMM Presentation order * SI treatment: estimate = 0.97 ± 0.45, z = 2.14, p = 0.032, Fig. 2B; Table S2.2) compared to those who received social information about magpies where there was no significant change among presentations (GLMM estimate = -0.28 ± 0.33, z = -0.84, p = 0.40, Fig. 2B; Table S2.2). Instead, these pairs were just as likely to increase or reduce mobbing intensity by P3 (Fig. 1C). In Sicily, social information about cuckoos had no effect on either mobbing propensity (across treatments n = 10 pairs with calls >0, Fisher's exact test: p = 1.0, Fig. 2A) or intensity (GLMM Presentation order * SI treatment: estimate = -1.20 ± 0.88, z = -1.36, p = 0.17, Fig. 2B; Fig. 1E, F; Table S2.3). This meant that, overall, reed warblers in Finland were more likely to mob cuckoos presented during our experiments (19/42, 45%) than pairs in Sicily (5/22, 23%; GLM: estimate = -1.03 ± 0.42, z = -2.45, p = 0.014; Table S2.4), and at a greater intensity (n = 24, GLM: estimate = 1.44 ± 0.72, z = -2.01, p = 0.044; Table S2.4). These differences between the northern and southern areas are likely to be specific to cuckoos, as teal were mobbed at similar intensities between both populations (n = 96, GLM: estimate = -0.39 ± 0.31, z = -1.27, p = 0.21; Table S2.5).

Egg rejection defences

Reed warblers did not reject 'mimetic' brown-spotted eggs in either Finland (Cuckoo treatment = 0/24; Magpie treatment = 0/25; Fig. 3) or Sicily (Cuckoo treatment = 0/21; Teal treatment = 0/19), and there was no rejection of non-mimetic blue eggs in Sicily (no cuckoo presentation = 0/11, after

cuckoo presentation at nest = 0/12). Blue eggs were however rejected at low rates in Finland, although this did not differ between social information treatments (GLM: estimate = 0.11 ± 0.64, z = 0.17, p = 0.97; Fig. 3; Table S2.6).

Recognition of cuckoos vs. response

In Finland, reed warblers became faster to approach their nests across subsequent presentations of cuckoos (i.e. P1 vs P3; GLMM estimate = -0.45 ± 0.19, z = -2.37, p = 0.018; Fig. 4; Table S2.7), regardless of social information (i.e. difference in SI treatment at P3; GLMM estimate = 0.30 ± 0.27, z = 1.12, p = 0.26; Fig. 4; Table S2.7). Birds were, however, slower to approach a magpie than a cuckoo at P2 (i.e. difference in SI treatment at P2; GLMM estimate = 0.72 ± 0.26, z = 2.81, p = 0.005; Fig. 4; Table S2.8) even if they never mobbed (P2 data only, GLM mobbing status * SI treatment: estimate = 0.11 ± 0.38, z = 0.29, p = 0.78; Fig. 4; Table S2.8) suggesting that latency was specific to the threat at the nest. Mobbing birds were quicker to approach cuckoos at first (P1 data only, GLM estimate = -0.42 ± 0.19, z = -2.29, p = 0.022; Table S2.9), but non-mobbing birds reduced their latencies more across presentations (GLMM Presentation order * mobbing status interaction: estimate = 0.54 ± 0.28, z = 1.96, p = 0.049; Table S2.10) so that there was no difference by the end of the experiment (GLM estimate = -0.12 ± 0.21, z = 0.58, p = 0.56; Table S2.9). Reed warblers in Sicily approached cuckoos at the nest more quickly than in Finland (GLM estimate = -0.47 ± 0.20, z = -2.37, p = 0.018; Table S2.11), but latencies did not change over the experiment, either overall (GLMM Presentation order: estimate = 0.20 ± 0.21, z = 0.95, p = 0.34; Table S2.11) or differently according to social information treatments (GLMM Presentation order * SI treatment: estimate = 0.67 ± 0.42, z = 1.58, p = 0.12; Table S2.12). They also approached teal as quickly as they did cuckoos (estimate = 0.065 ± 0.168, z = 0.39, p = 0.67; Table S2.13).

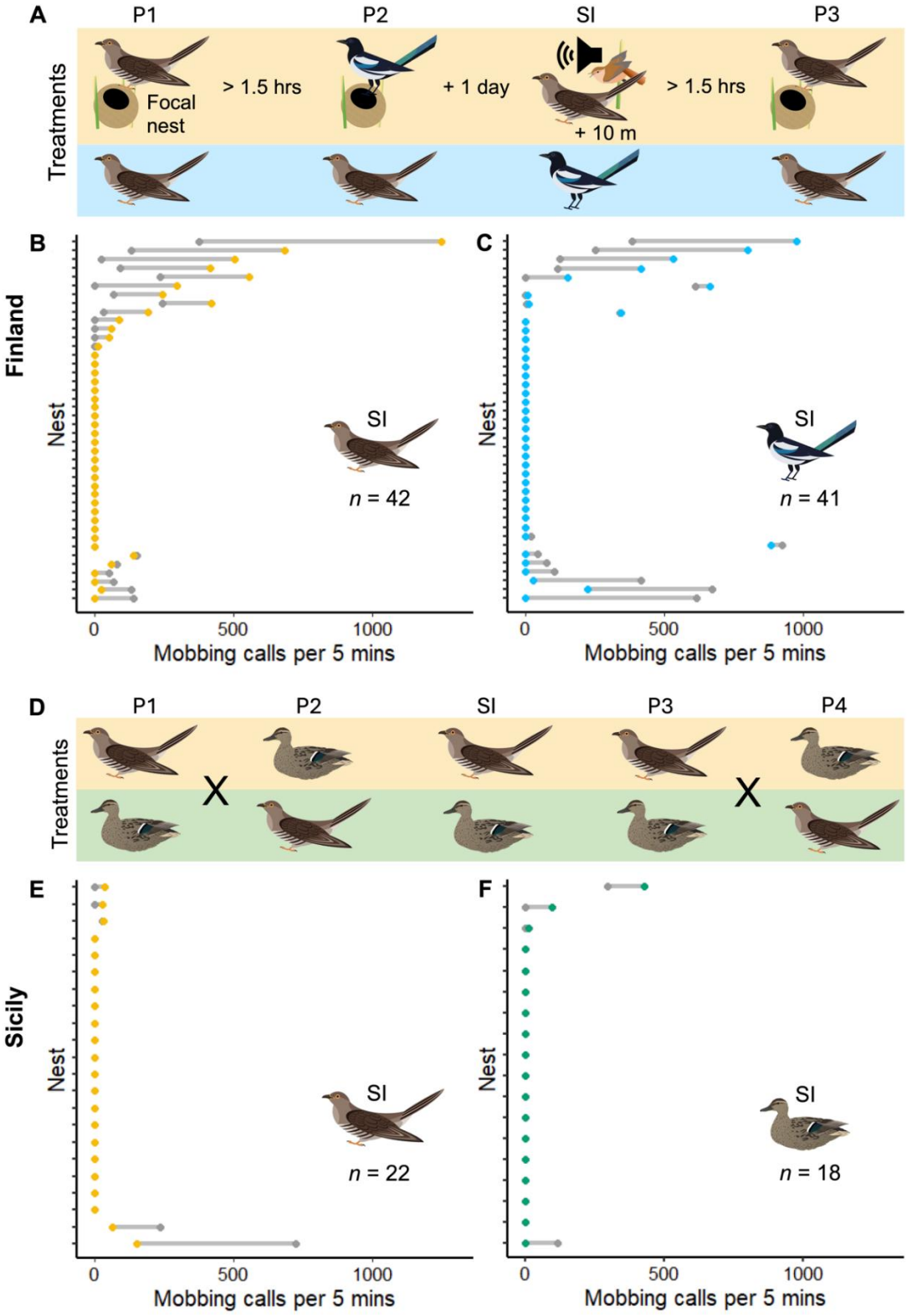

FIGURE 1. Reed warbler mobbing defences (calls per 5 minutes) in allopatry (Finland: A-C, Sicily: D-F) before (grey dots) and after (coloured dots) experimental manipulation of social information ('SI') about cuckoos (B, E) versus a control (C – magpie, F – teal). Details of experimental design are shown in A, presentation order ('P') of models was alternated in D.

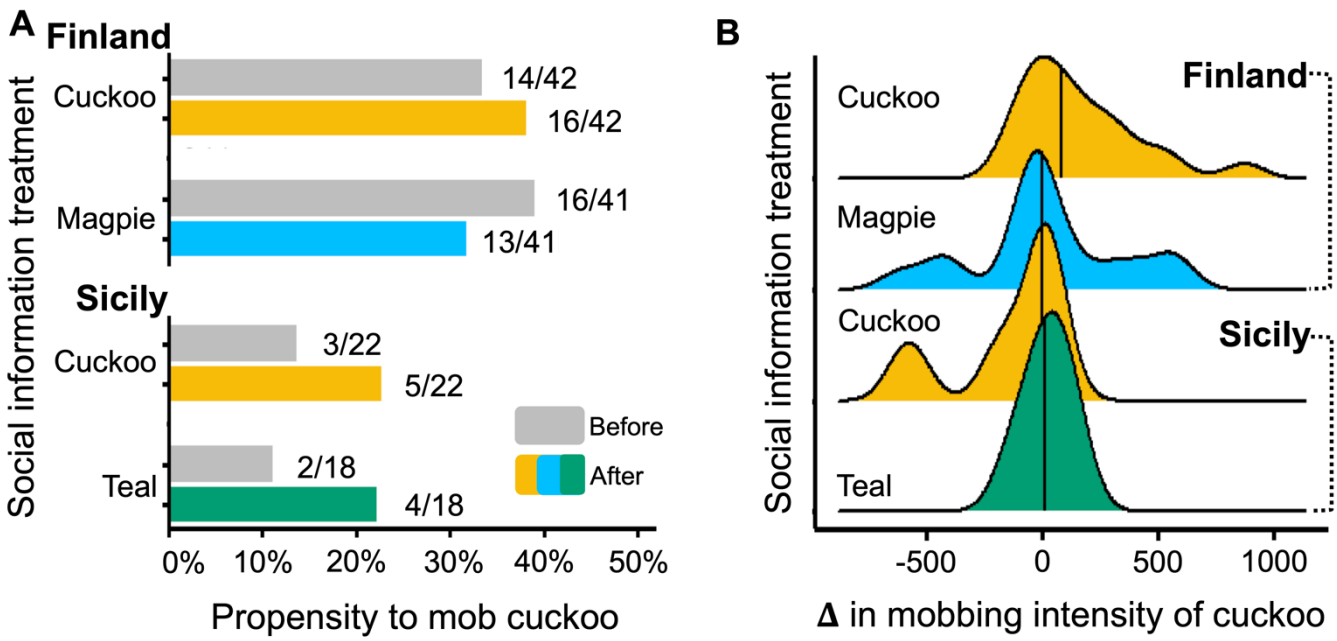

FIGURE 2. (A) Propensity to mob cuckoos did not change after social information about cuckoos or a control in Finland or Sicily. (B) Mobbing pairs showed social responsiveness (i.e. increased intensity) to cuckoos, but only in Finland (distributions of changes in mobbing intensity, vertical lines = medians).

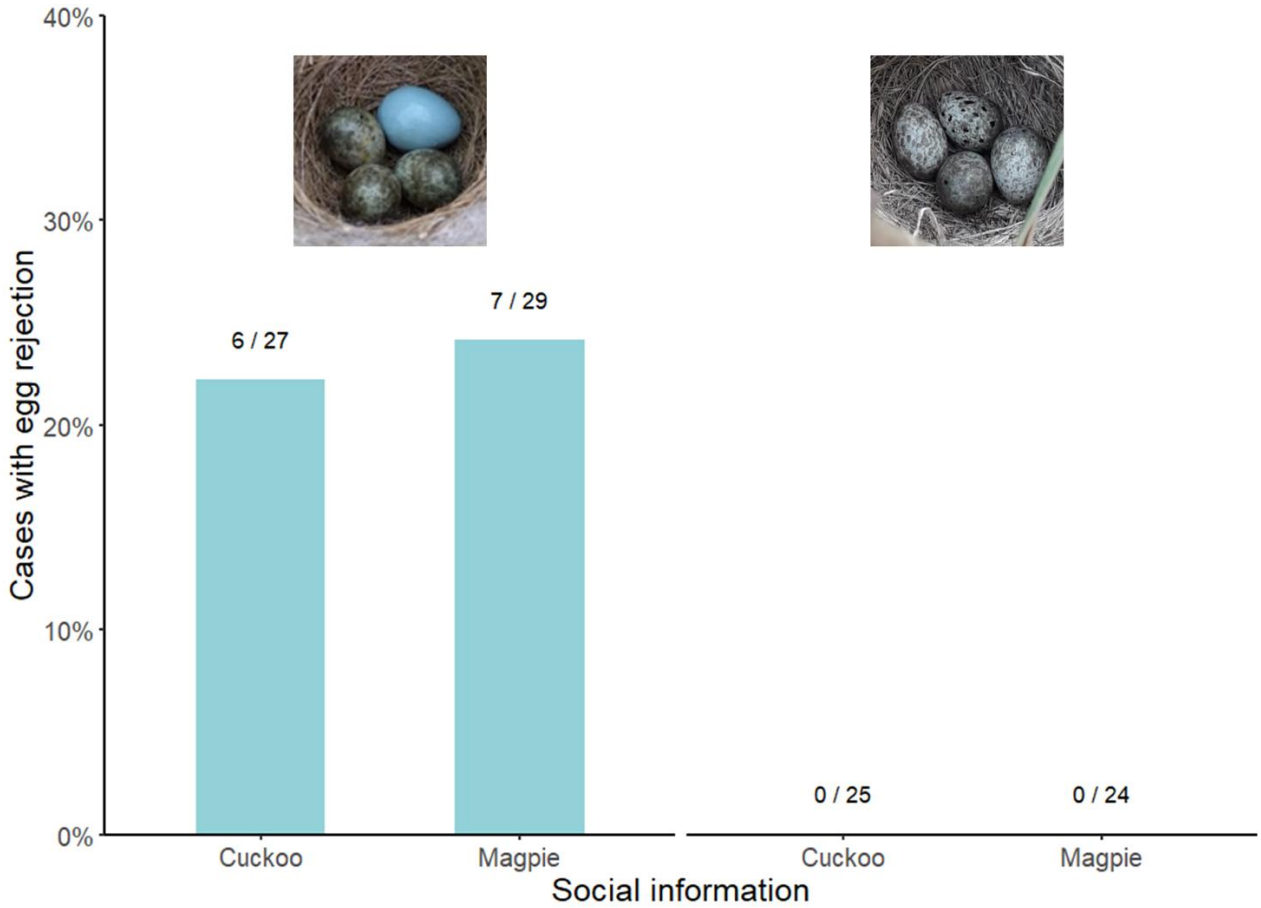

FIGURE 3. Rejection rates of experimental eggs in Finland (inset photos). Blue non-mimetic eggs (left) were rejected at the same rate regardless of whether social information was provided about cuckoos (24%) or magpies (22%). Mimetic brown-spotted eggs (right) were not rejected.

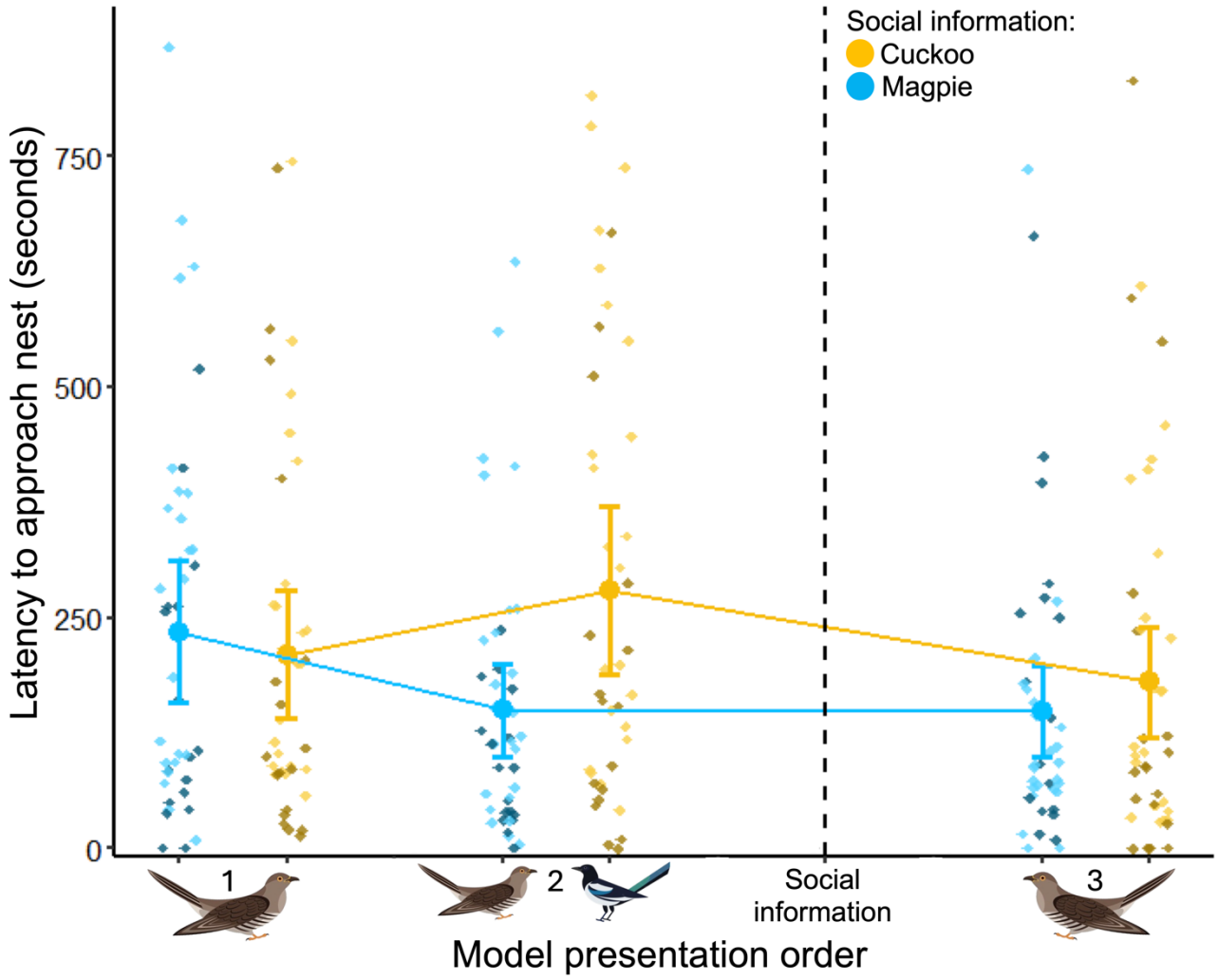

FIGURE 4. Latency of birds to approach presentations of models at their nest (indicated by icons) before and after social information (dashed line) about cuckoos (yellow) or a magpie control (blue) in Finland. Raw data are plotted as diamonds, with darker symbols indicating pairs that mobbed cuckoos. Predicted mean values (± standard error) from a GLMM are plotted as circles and bars, with connecting lines indicating change across model presentation order (P1-P3).

DISCUSSION

Behaviours are assumed hard to lose under relaxed selection. However, by using social information to simulate increased brood parasitism risk, we found that defences and social responsiveness of a common host of cuckoos are degrading in areas of allopatry. At the recent range front in Finland, only pairs that mobbed a cuckoo increased their mobbing intensity after receiving social information. The other two-thirds of birds largely remained quiet, although they differentiated cuckoos from magpies by approaching the nest more quickly, suggesting some recognition was retained. Our findings in Finland are enhanced by our results from the Sicilian population, where reed warblers have been in allopatry for longer. There, they showed an even greater reduction in defences and no evidence of social information use. Importantly, mimetic 'cuckoo' eggs remained in nests, and although non-mimetic eggs were rejected at low rates in Finland, social information had no influence on this defence either. This suggests that both allopatric populations would be unlikely to express plasticity or mount significant resistance should cuckoos invade.

Our results are likely evidence for the decay of ancestral defences rather than a methodological failure to detect responses, for three reasons. First, providing social information experimentally led to an increase in mobbing intensity in Finland, even if not in Sicily. Second, we followed very similar methods to previous studies conducted with reed warblers at parasitised sites, where social information heightened near-absent egg rejection of similarly manipulated eggs ten-fold (46) and induced mobbing of cuckoos (13, 44, 45), including for pairs that showed no initial response [e.g. 54% of quiet pairs mobbed cuckoos after social information: (45)]. Third, the differences we detected were specific to cuckoos as responses to a control teal and nest predator (magpie) were similar at our sites and to parasitized areas (53, 59, 48, 47) despite large ecological differences (i.e. climate, nesting density). By using consistent experimental designs to previous studies, testing a large number of reed warblers nesting across a broad range of environmental variation, and considering social

responsiveness explicitly, we can therefore be confident that the weak defences in our allopatric study populations are not the result of cryptic plasticity (60). Instead, they provide compelling evidence that behavioural defences may sometimes be lost in allopatry from cuckoos.

Given that studies of animal culture across a wide range of taxa demonstrate that the spread of even arbitrary behaviours is possible (61), it is surprising that we did not detect evidence for social learning among 'naïve' reed warblers (i.e. those that did not mob cuckoos). For example, juvenile superb fairy wrens begin to mob cuckoos after observing adults do so (8) and naïve individuals of several species can be trained to recognize novel predators (e.g. introduced species, (10) when paired with mobbing calls. Often social learning of threats requires only one exposure (i.e. similar to our experimental design; reviewed in ref. 62) and can even be effective when using arbitrary cues (11). Why did so many birds not mob cuckoos or reject eggs? One possible explanation is that ontogenetic experience or repeated exposure may be necessary before behaviours are expressed, as in the antipredator responses of several fish and mammals (63, 64) and personal encounters with avian or piscine brood parasites (65–68). While we cannot exclude this possibility it seems unlikely to explain the lack of response we detected here: we provided three encounters with cuckoos at or near their nests, yet most birds still did not respond. Perhaps with relaxed selection, there is an initial loss of recognition that then limits hosts' potential for observational learning.

Temporal and geographical variation in host defences has typically been explained by plasticity (9, 47, 69), particularly in reed warblers where individuals track local parasitism risk during egg-laying and adjust defences accordingly (22). However, here we found only limited evidence for plasticity in our allopatric populations in response to either indirect environmental or experimentally-manipulated cues of heightened parasitism risk. This is surprising given that in a previous study at an unparasitised site closer to the range core (Llangorse lake, Wales) and presumed to have been allopatric for at least

130 years [i.e. similar to Finland; (70)], reed warblers responded more aggressively to cuckoo models if nesting closer to vantage points for cuckoos, if they were present (47). We found no evidence for this indirect cue use: instead, birds nesting further from vantage points in Finland were *more* likely to mob, while mobbing in Sicily was unaffected (Supporting Information S1). Nevertheless, of the birds that mobbed, their initial intensities were similar across all three allopatric sites [Finland: 225 ± 43 calls per 5-min, Sicily: 280 ± 120, Llangorse: 281 ± 64; (47)], suggesting that while the frequency of birds retaining recognition may vary across allopatric populations, they can respond similarly (see ref. 47). In Sicily, a site we assume to have been in allopatry for much longer, there was no social responsiveness, suggesting that individual reaction norms may weaken in allopatry, and potentially lead to the eventual loss of defences in the absence of cuckoo parasitism (24). If we were to revisit the Llangorse or Finnish populations in future, would their responses have diminished further and look more like those in Sicily? There is already some genomic evidence from reed warblers to suggest local adaptation to the strength of parasitism (71), but whether the decay in defences we detected is accompanied by genetic change is yet to be determined.

Overall, our results suggest that it may be possible for host populations freed from parasitism to lose expression of defences, rendering them vulnerable to future reinvasion. The recovery of resistance is unlikely to be enhanced through social transmission, because even if there are individuals who retain recognition of cuckoos, our results show that social responsiveness may also be lost. Such a reduction of defences under relaxed selection is one of the key components of geographic mosaic theory explaining the maintenance of coevolution across time and space: rather than the arms race continually escalating, parasites are hypothesized to recurrently invade host populations, or host species, whose defences have waned in their absence. These so-called coevolutionary cycles (29) are thought to only exist during ‘intermediate phases’ of host-parasite interactions, before defences reach fixation (24), but the rapidity with which a brood parasite host species can acquire (or lose) successful

resistance has received little attention. Our results suggest that range expansions and a geographic mosaic of coevolution may moderate the arms race, with defences decaying within even relatively short time frames [e.g. approximately 35 generations in Finland (72)], allowing the longer-term persistence of parasites until host switching becomes more favourable (73, 74). As both social information use and behavioural defences against enemies are common across the animal kingdom, and species' ranges are changing rapidly, it is now crucial to determine how socially-mediated plasticity degrades under relaxed selection in the wild.

ETHICS STATEMENT

This study was reviewed and approved in Finland by the Project Authorization Board of the Regional State Administrative Agency (ESAVI/7857/2018) and conducted under permission of Centre for Economic Development, Transport and the Environment (VARELY/758/2018, VARELY/799/2019), and in Sicily by the Instituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA) and the Regione Siciliana.

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