Mobbing and sitting tight at the nest as methods of avoiding brood parasitism

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The arms race between brood parasites and their hosts has led to many different host behaviours for avoiding parasitism. Some of these behaviours are social, and require the presence of conspecifics to work effectively: in response to alarm calls, some species engage in mobbing behaviour where neighbours join nest tenants in attacking and repelling an invading brood parasite. There are risks involved for the neighbours, but it has been demonstrated that social mobbing allows individuals to learn about the presence of brood parasites in the environment, suggesting that social learning is occurring. Here, I consider whether using social signals to alert naive individuals to the presence of brood parasites is a suitable strategy, compared with sitting tight on the nest in response to the signal (which should reduce the chances of being parasitized). I also compare the efficiency of these strategies with the case where individuals fail to change behaviour in response to a brood parasite. Using an individual-based simulation model, I demonstrate that both mobbing and sitting tight are effective strategies in response to a signal, and that mobbing is more effective when the chances of being parasitized increase. These results are discussed and compared with known host–brood parasite relationships.

Keywords: cuckoo; reed warbler; group behaviour; individual-based model; alarm signals; mobbing

1. INTRODUCTION

During their extended period of parental care, birds typically lay and care for a clutch of nestlings in or near a fixed nesting location, until the nestlings are able to tend to themselves. During this period, the parents provide food and a stable environment for development [1,2], and defend their weak or naive offspring from predators [3,4]. However, cuckoos and other brood parasites can take advantage of this period of care in many species [5], by laying an alien egg in the nest that produces a nestling that the parents then raise as their own. The host parents consequently suffer a reduction in fitness owing to their own clutch being compromised or destroyed by the brood parasite. A well-documented arms race exists between brood parasites and their hosts, which has led to the vast range of tactics we see today in both parties [5–7].

As well as the many types of individual behaviour shown by nesting birds for recognizing and destroying parasite eggs and nestling [6], there is also a range of social behaviours that have been identified as reducing the risks and amount of brood parasitism seen in local populations of birds. Attacking and group mobbing behaviours are often seen in response to the presence of a parasite [8–10], and Welbergen & Davies [11] demonstrated that mobbing is an effective form of defence by reed warblers (Acrocephalus scirpaceus) against common cuckoos (Cuculus canorus). Alarm signals also exist that are specific to the presence of brood parasites [12,13], which bring both mates and neighbours into an area to jointly mob a parasite.

Why should neighbours mob? When used against predators, mobbing attacks are a risky behaviour [14–17], and their success may be partially dependent upon the size of the defending group [18]. Although there is perhaps less immediate danger to the parent of attacking a brood parasite (compared with the potentially fatal damage that could be incurred when attacking a predator), attacking and mobbing could inadvertently attract additional nest predators or brood parasites to the nest [19,20], and may offer opportunities for cuckoldry to occur [14,21]. There are some benefits of mobbing for the targeted individual, but why should unthreatened neighbours become involved, given the possible costs of mobbing? Curio et al. [22] suggested that mobbing acts as a form of cultural transmission, where naive individuals learn what an enemy looks like. Given that there is much evidence for social learning in birds [23], this suggestion is feasible. Davies & Welbergen [24] demonstrated that reed warblers responding to alarm calls from neighbours...
when they are mobbing common cuckoos are gaining information about the cuckoos, and that this socially transmitted information affects their subsequent response to the brood parasites. Campobello & Sealy [25] demonstrated that reed warblers are more likely to change their response to cuckoos based on the social cues they receive, rather than personal experience alone. Furthermore, aggressiveness may increase with repeated encounters of a brood parasite [26], demonstrating that the response to a potential host can be refined after the target parasite has been encountered. There may therefore be advantages to engaging in social mobbing in response to an alarm call.

However, if an individual is alerted to the presence of a brood parasite, responses other than leaving the nest to attack an unseen brood parasite may be a safer option for a parent with a clutch of eggs or vulnerable nestlings. Given that a brood parasite is unlikely to strike when the nest is occupied (but see [27]), returning to the nest and sitting tight until the threat has passed could protect the current clutch. Evidence exists that some species respond to the presence of brood parasites by increasing the time they spend at or near the nest ([21,28–30], but see [31]). Yellow warblers (Dendroica petechia) give a brood parasite-specific alarm call when they detect brown-headed cowbirds (Molothrus ater) [29], and hearing these calls induces sitting behaviour when it is heard by nesting females [32]. By sitting at the nest when danger is apparent, an individual can reduce its chances of being parasitized, but is less likely to learn what a parasite looks like, or know when the parasite has departed.

Mobbing and sitting tight are therefore alternative anti-parasite behaviours with different costs and benefits [33]. Here, I present an individual-based model that examines the efficiency of these two behaviours in reducing the likelihood that a small population of nesting individuals are parasitized by a visiting brood parasite. The model could feasibly be extended to consider different forms of nest predation too, but is constrained in this example to consider a host–brood parasite system. Given that there are risks incurred by individuals when conducting the two behaviours (exposing the nest when mobbing, and failing to learn what a parasite looks like when sitting tight), I use these models to identify the conditions where these two alternative strategies are more effective than failing to change behaviour in response to the presence of a parasite, and explore whether one of these strategies is more appropriate than the other.

2. METHODS

2.1. Outline of model

A population of nesting hosts was simulated within a two-dimensional environment, and simulations were run using NetLogo v. 4.1.2 and v. 4.1.3 [34], which has been demonstrated elsewhere to be an effective tool for exploring group-level behaviour [35,36]. Each member of a population of \( n \) hosts had a nest randomly positioned on an unoccupied square within a \( 101 \times 101 \) unit square grid, connected at opposite edges to form a torus. Each nest was tended by a single host. Within each simulation, the behaviour of the population was simulated for 10 000 consecutive periods. At the beginning of the first period, each individual started at its nest, and faced in a randomly generated direction.

At the beginning of every period, each individual host was in one of four behavioural states: ‘on nest’, ‘patrolling’, ‘returning’ or ‘mobbing’ (at the beginning of the first period, each host was randomly allocated one of the first three states). All individual hosts started the simulation in a brood parasite-naive state, but could subsequently learn to recognize a brood parasite as defined later. Once an individual had learnt to recognize a brood parasite, it was assumed to retain this ability throughout the simulation. Knowledgeable hosts who were within a distance \( d_{\text{detect}} \) of a brood parasite at the beginning of a period were assumed to be ‘alarmed’ during the period; otherwise, all naive hosts and knowledgeable hosts that were not within \( d_{\text{detect}} \) units of a brood parasite were assumed to be ‘not alarmed’. The population as a whole could either be ‘alert’ or ‘not alert’, depending on the presence and recognition of a brood parasite.

At the beginning of each period, before individual behaviours were calculated, it was decided whether a single brood parasite should appear if there was not one already present. If there was no parasite present at the beginning of the period, one appeared at a random location (facing in a randomly chosen direction) within the environment with probability \( p_{\text{appear}} \). Therefore, an environment that was initially free of a parasite at the beginning of a period remained free throughout the time period with a probability \( (1 - p_{\text{appear}}) \).

After the computational decision had been made about whether a brood parasite was present or not in the environment, the state of alarm of the population was assessed, as the behaviours of the hosts in the population during each period of the simulation were dependent upon the state of alertness of the population. By default, a population was not alert, but if at least one knowledgeable host was within \( d_{\text{detect}} \) of a parasite at the beginning of the period (and therefore ‘alarmed’), it was assumed to make an alarm call that raised the entire population to an alert state. If no brood parasite was present at the beginning of the period, or if the brood parasite was outside the detection range of any of the knowledgeable individuals, the population was not alert.

Having identified the state of alertness of the host population, the individual behaviours of the hosts and the brood parasite (if present) were then calculated for the period. Each individual host and brood parasite made a single decision about its behaviour during the period, following the criteria described later. Behavioural decisions by each individual were made consecutively, but the order in which each of the individual hosts and the brood parasite made their single decision was randomized within each period, to avoid any artefacts that could be caused by imposing an order on the decision-making process. Only when all individuals had made their behavioural choices (and had conducted the actions involved) was the next period started.
2.2. Host behaviour during a period

If the population started a period as not being alert, each host conducted one of four behaviours, dependent upon its state at the beginning of the period:

(i) If the host was ‘on nest’, it remained in that state (doing nothing) at probability $p_{\text{stay}}$, and left the nest at probability $(1 - p_{\text{stay}})$. If it left the nest, it initially ‘rotated’ to face an angle randomly chosen from a uniform distribution between $-90^\circ$ and $+90^\circ$ of its current heading, then moved forwards one unit and finally changed its state to patrolling.

(ii) If the host started the period patrolling, it started to return to the nest at probability $p_{\text{return}}$, and continued patrolling at probability $(1 - p_{\text{return}})$. If it continued patrolling, it ‘rotated’ (as described earlier). After turning, if moving one unit forwards kept it within a territory distance $d_{\text{territory}}$ from its nest, it moved forwards one unit; otherwise, it turned $180^\circ$ and then moved forwards one unit, leaving its behavioural state unchanged. If, on the other hand, the bird started to return to the nest, it turned to face towards the nest, moved forwards one unit and altered its state to returning.

(iii) If the host started the period as ‘returning to the nest’ and was positioned within the unit square that contained the nest, it remained in position and changed its state to ‘on nest’. If the individual was not in the nest square at the beginning of the period, it instead turned so that it faced towards its nest, and moved forwards one unit, leaving its behavioural state unchanged. If, on the other hand, the bird started to return to the nest, it turned to face towards the nest, moved forwards one unit and altered its state to returning.

(iv) If the host started the period as ‘mobbing’ within a non-alarmed population, it conducted exactly the same behaviour as an individual in the ‘return to the nest’ state (therefore changing its state to ‘on nest’ if it was in the nest at the beginning of the period).

If the host population started a period as being alert, and the default response was to return to the nest, all individuals had their states changed to ‘return to nest’, and the behaviour described in (iii) was conducted. (Note that hosts therefore did not return instantaneously to the nest, but rather travelled at the standard speed they used during non-alarmed patrolling. This model does not consider what could happen if the host is able return at an accelerated rate, which may more accurately describe what happens in some species.) If, at the end of the movement, an individual host was within a distance $d_{\text{detect}}$ of the brood parasite, it was assumed to have learnt how to recognize a brood parasite for all consecutive periods of the simulation.

If the host population was ‘alert’ and the default response was to mob the brood parasite, the action of an individual host during the period was dependent upon the location of the parasite. If the host was knowledgeable and within $d_{\text{detect}}$ of a brood parasite (and therefore in an ‘alarmed’ state as described above), it oriented itself towards the parasite, and moved forwards one unit if it was more than a unit away for the parasite. If the individual was either naïve or further than $d_{\text{detect}}$ away from the brood parasite (and therefore ‘not alarmed’ as described above), it turned itself towards the nearest ‘alarmed’ individual, and moved forwards one unit. If, at the end of the movement, a naïve individual was within a distance $d_{\text{detect}}$ of the brood parasite, it was assumed to have learnt how to recognize a brood parasite for all consecutive periods of the simulation.

2.3. Brood parasite behaviour during a period

As described earlier, the arrival of a brood parasite in the habitat was simulated at the beginning of a period, but the point at which it made its behavioural decision within the period was randomly allocated within the roster of consecutive decisions made by the individual host. If the host population was alert (as defined earlier), the brood parasite vanished with probability $p_{\text{disappear}}$, and remained with probability $(1 - p_{\text{disappear}})$. If the brood parasite remained, or if it had not been detected, it behaved according to the status of the grid square it currently occupied, and whether it had already successfully laid an egg in a nest since it arrived in the environment (as newly arrived brood parasites were assumed to have not laid an egg). If a brood parasite that had not already laid occupied a grid square containing an unoccupied nest (where the nest owner occupied a cell that was not its nest), it remained laying on the nest for the rest of the period with probability $p_{\text{laying}}$. It was assumed to have successfully laid with probability $(1 - p_{\text{laying}})$; if this was the case, it rotated (following the same process as described for the hosts) and moved forward one unit. Being able to vary the length of time that the brood parasite takes to lay allows us to relax the assumption that brood parasites usually approach the nest, stay, and then leave all within a few seconds [37], as there are recorded cases where laying takes longer [27].

Brood parasites that had laid an egg since appearing in the environment were not able to lay a second. Instead, they would then disappear from the environment with probability $p_{\text{disappear}}$. If they did not disappear during the period, they instead rotated and moved forward one unit.

Brood parasites that had not laid an egg, but occupied a square either that did not contain a nest or that contained at least one host, rotated and moved forward one unit during the turn. Therefore, brood parasites were unable to lay eggs in nests that were occupied (a feasible assumption, although there are recorded cases where this occurs [27]).

2.4. Details of simulations, and analysis conducted

To test whether mobbing led to a reduction in nest parasitism, 1000 sets of the nine parameters described earlier were randomly generated, with values drawn from uniform distributions with the limits given in table 1. For
Table 1. Description of the parameters used in the model, with limits to values considered. ANOVA results are shown for the systematic explorations of parameter effects.

<table>
<thead>
<tr>
<th>parameter</th>
<th>description</th>
<th>limits considered when randomized within simulations</th>
<th>values of parameter considered during systematic exploration</th>
<th>strategy (mob or return home)</th>
<th>parameter</th>
<th>interaction (between strategy and parameter)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$d_{\text{detect}}$</td>
<td>distance over which host can detect a brood parasite</td>
<td>1–10 units</td>
<td>1, 2, ..., 10 units</td>
<td>$F_{1,999} = 0.69, p = 0.405$</td>
<td>$F_{9,899} = 481.84, p &lt; 0.001$</td>
<td>$F_{9,899} = 9.94, p &lt; 0.001$</td>
</tr>
<tr>
<td>$d_{\text{territory}}$</td>
<td>radius of territory around nest</td>
<td>5–20 units</td>
<td>5, 7, ..., 15 units</td>
<td>$F_{1,999} = 0.85, p = 0.356$</td>
<td>$F_{5,499} = 9.74, p &lt; 0.001$</td>
<td>$F_{9,899} = 481.84, p &lt; 0.001$</td>
</tr>
<tr>
<td>$n$</td>
<td>host population size</td>
<td>10–50 nests</td>
<td>10, 15, ..., 50 nests</td>
<td>$F_{1,999} = 3.81, p = 0.051$</td>
<td>$F_{5,499} = 465.13, p &lt; 0.001$</td>
<td>$F_{9,899} = 11.50, p &lt; 0.001$</td>
</tr>
<tr>
<td>$p_{\text{appear}}$</td>
<td>probability that a brood parasite appears at the beginning of a period</td>
<td>0–0.05</td>
<td>0.005, 0.01, ..., 0.05</td>
<td>$F_{1,999} = 4.69, p = 0.031$</td>
<td>$F_{9,899} = 84.12, p &lt; 0.001$</td>
<td>$F_{9,899} = 11.48, p &lt; 0.001$</td>
</tr>
<tr>
<td>$p_{\text{detected}}$</td>
<td>probability that a brood parasite vanishes if it is detected at the beginning of a period</td>
<td>0.01–0.20</td>
<td>0.01, 0.04, ..., 0.19</td>
<td>$F_{1,999} = 1.11, p = 0.292$</td>
<td>$F_{6,599} = 5.49, p &lt; 0.001$</td>
<td>$F_{6,599} = 1.67, p = 0.376$</td>
</tr>
<tr>
<td>$p_{\text{disappear}}$</td>
<td>probability that a brood parasite that has previously laid an egg vanishes during a period</td>
<td>0–$p_{\text{detected}}$</td>
<td>0.2, 0.4, ..., 1.0</td>
<td>$F_{1,999} = 0.54, p = 0.465$</td>
<td>$F_{4,399} = 2.52, p = 0.039$</td>
<td>$F_{4,399} = 1.02, p = 0.395$</td>
</tr>
<tr>
<td>$p_{\text{laying}}$</td>
<td>probability that a brood parasite on an unoccupied nest has finished laying during a period</td>
<td>0–1.0</td>
<td>0, 0.1, ..., 0.9</td>
<td>$F_{1,999} &lt; 0.01, p = 0.993$</td>
<td>$F_{9,899} = 1170.70, p &lt; 0.001$</td>
<td>$F_{9,899} = 0.89, p = 0.530$</td>
</tr>
<tr>
<td>$p_{\text{return}}$</td>
<td>probability that a host switches behaviour from patrolling to returning during a period</td>
<td>0–0.5</td>
<td>0.05, 0.1, ..., 0.5</td>
<td>$F_{1,999} = 0.08, p = 0.773$</td>
<td>$F_{9,899} = 369.85, p &lt; 0.001$</td>
<td>$F_{9,899} = 32.34, p &lt; 0.001$</td>
</tr>
<tr>
<td>$p_{\text{stay}}$</td>
<td>probability that a host decides to remain on its nest during a period</td>
<td>0.1–1.0</td>
<td>0, 0.1, ..., 0.9</td>
<td>$F_{1,999} = 3.26, p = 0.071$</td>
<td>$F_{9,899} = 123.87, p &lt; 0.001$</td>
<td>$F_{9,899} = 6.57, p &lt; 0.001$</td>
</tr>
</tbody>
</table>
each of these parameter sets, one simulation was conducted as described earlier where the population engaged in mobbing behaviour when alert, and another simulation was conducted where the population did not conduct this behaviour (which was implemented by setting the detection distance $d_{detect}$ to zero before the simulation began). Initial positions of the nests were not replicated between the two pair simulations. After 10 000 periods, the number of nests that were parasitized was recorded. A paired two-tailed t-test was then used to compare the number recorded for mobbing and non-mobbing strategies across the 1000 pairs of results. A separate 1000 pairs of simulations were conducted and compared for populations that either returned to their nest when alarmed or did not respond to an alarm signal.

The nine parameters described in table 1 were also systematically altered to explore their effect on the success of the two defence strategies. For each, 1000 parameter sets were randomly generated when the additional eight parameters not being investigated were drawn from the uniform distributions described by the limits given in table 1. The parameter set of interest was then altered systematically, with a new simulation for each of the strategies being conducted for each of the systematic changes: table 1 outlines the values used for the systematic changes in parameters. Both the defence strategies (mobbing or returning to the nest when alarmed) were tested for each parameter combination (noting that the initial position of the nests was randomized separately before each trial). Within each simulation, the success of the behavioural strategy was assessed by recording the number of nests that had been parasitized (nests parasitized) at the end of 10 000 periods. I assumed that, once a brood parasite has laid in a nest, the host takes no further action, regardless of whether it was able to recognize the parasite during the laying event. It should be noted that there are many records of egg rejection [27,37–39] or nest desertion [40] if the host species observes the parasite at its nest.

Summary statistics were extracted from these data using R v. 2.13.0 [41], and analysis of variance (ANOVA) was conducted for the nine sets of parameter explorations outlined in table 1. Each exploration calculated a value for both of the strategies (strategy) described for each value of the parameter being explored, which in turn was conducted for 1000 independent sets (set) of the other parameters. Consequently, the data were analysed using ANOVA, using the model described by the word formula nests parasitized ~ parameter × strategy + error(set/(parameter × strategy)). It should be noted that the variances considered were not normally distributed, but the very large size of the samples and the fact that equal numbers of samples were considered for each of the levels means that the ANOVA assumption of normality can be dropped [42]—see [43] for an example where resampling analyses for large samples gave estimated F-values that were near-identical to true values taken from the F distribution.

![Figure 1](http://rsfs.royalsocietypublishing.org/)

### 3. RESULTS

Mobbing led to fewer nests being parasitized than if the birds did not respond to an alarm (mobbing: $2.84 \pm 0.09$ nests (mean ± s.e.); no response: $5.13 \pm 0.14$ nests; $b_{g09} = 20.61$, $p < 0.001$). Similarly, returning to the nest when alarmed also reduced the level of parasitism (returning: $2.82 \pm 0.10$ nests; no response: $5.11 \pm 0.14$ nests; $b_{g09} = 22.45$, $p < 0.001$).

There was little difference in the success of the two strategies however: over the systematic investigation of the nine parameters considered, the only significant difference in the success of the two strategies occurred when $p_{appear}$ was being systematically altered (table 1), which is discussed in further detail later. All of the parameters themselves had an effect upon the number of nests parasitized, and some of the parameters had interacting effects with the strategy used.

As would be expected, increasing the number of nests (n) available in the population increased the ultimate number of nests parasitized (figure 1a and table 1). There was a slight interaction between nest number and strategy used, where returning to the nest appeared...
individuals sat tight on the nest (higher values of $p$ likely to spontaneously return to the nest when foraging affected the rate of parasitism. Birds that were more likely to return when mobbing was a better strategy for the smaller nests to defend space from a brood parasite (figure 1), while larger detection distances ($d_{detect}$) led to a reduction in parasitism (figure 1a and table 1). Increasing the probability that it remained on the nest during the following period $p_{stay}$ led to a reduction in the number of nests parasitized (figure 3d and table 1).

Figure 2. Effects of systematically altering host behaviour parameters on population parasitism levels, altering: (a) the probability that a foraging host switches to returning to its nest during a period, $p_{return}$; (b) the probability that a host that is already sitting on its nest decides to remain at the nest during a period, $p_{stay}$. Circles connected by a solid line give results when mobbing occurs, and squares connected by a dotted line give results when hosts return to the nest and sit tight.

to lead to a slight increase in parasitism for intermediate nest numbers.

Smaller territories ($d_{territory}$) meant that it was easier to defend space from a brood parasite (figure 1b and table 1), while larger detection distances ($d_{detect}$) led to a reduction in parasitism (figure 1c and table 1), where mobbing was a better strategy for the smaller or larger detection ranges.

The behaviour of the bird within its territory also affected the rate of parasitism. Birds that were more likely to spontaneously return to the nest when foraging (higher values of $p_{return}$) were parasitized less often, although the best strategy to conduct was dependent on their likelihood to return, with mobbing working better when they were more likely to stay away from the nest (figure 2a and table 1). Increasing the likelihood that an individual sat tight on the nest ($p_{stay}$) also led to a reduction in parasitism, where mobbing was a better strategy when individuals tended to switch to foraging more frequently (figure 2b and table 1), but returning to the nest was more successful when the birds were most likely to be staying on their nests in consecutive periods.

The behaviour of the brood parasite also affected nest parasitism rates. Increasing the likelihood of the brood parasite appearing ($p_{appear}$) unsurprisingly increased the rate of parasitism (figure 3a and table 1). As the rate of brood parasite appearance increased, mobbing became an increasingly successful strategy compared with returning to defend the nest, which was more successful when brood parasites were rare. Increasing the probability that the brood parasite disappeared once it had been detected ($p_{detect}$) led to a reduction in parasitism (figure 3b and table 1), but changing the probability that it disappeared once it had laid ($p_{disappear}$) made no difference to the amount of parasitism seen (figure 3c and table 1). Increasing the average length of time the brood parasite had to stay on the nest while laying by increasing the probability that it remained on the nest during the following period $p_{laying}$ led to a reduction in the number of nests parasitized (figure 3d and table 1).

4. DISCUSSION

Responding to brood parasites by either mobbing or sitting tight at the nest led to a reduction in the overall chance that a parent was parasitized, and both strategies appear to be equally effective in most of the cases examined. However, mobbing was more effective than sitting tight when the chance of a brood parasite appearing within the population increased. Given the social learning inherent to the model, this therefore gives some support to the suggestion that mobbing may increase protection by enhancing individuals’ abilities to learn and recognize threats [22,24,25], although there could feasibly be a switch in the anti-parasite behaviour seen dependent upon the level of parasitism experienced at the population level (as suggested in Bártol et al. [38] and Takasu & Moskát [44]). It would be interesting to explore whether parasitized populations or species spend more time mobbing or sitting tight on the nest than unparasitized ones. Sex differences between the parents could also mean that different parents could respond in different ways to the presence of the brood parasite (as is seen in the great reed warbler, Acrocephalus arundinaceus [45]), which could be incorporated into the model by considering two host parents rather than just one.

By considering individuals as making transitions from being naive to being able to recognize parasites, I assumed that they can demonstrate a change in their informational state, which in turn informs their behaviour. Allowing naive individuals to respond to alarm signals has a similar effect; so an individual’s intentional signalling concerning the presence of a brood parasite alters the information received by all the individuals within a population. The information that individuals possess, both through learning and from signals within the population, is handled in a very simple way within the current model. It is likely that the passage of time since these pieces of information were received, coupled with other information from the physical and social environment, could affect the behaviour of an individual [46,47]. Furthermore, directly observing a brood parasite gives an individual very different information if it was informed that there might be a parasite present somewhere in the environment, which could in turn strongly influence the behaviour it shows (see Rands & Cuthill [48], for discussion of this issue in response to anti-predator alarm calls).

The model also gives us an indication where brood parasites may be more successful. Visiting the population more often increases the number of nests parasitized (although mobbing works much better as

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a strategy against parasitism), while being more likely to flee when mobbed or taking longer when laying reduces the success of the cuckoo, which demonstrates why brood parasites usually spend a matter of seconds on the host’s nest when laying [37].

The model made a number of assumptions about individual brood parasite behaviour, which need to be explored in more depth. In the model, the brood parasite was assumed to move without targeting individual nests, but brood parasites are unlikely to move randomly within the environment. Also, the model does not account for heterogeneity in the nesting environment. The visibility and accessibility of nests may be an important contributor to the likelihood of being parasitized in many species [29,49,50].

If signalling is an important anti-parasite behaviour, then signal decay within a complex environment could affect the information that an individual receives [51,52]. Incorporating signal deterioration with distance may give us further insights into the effectiveness of mobbing signals. Also, different individuals may be experiencing different and conflicting information about the presence of parasites within the environment, and a group mobbing response may reflect a population consensus about how to respond to the possible presence of a parasite [53].

The model also demonstrated that smaller territories and larger detection distances lead to lower rates of parasitism. Local population size has been shown to be related to parasitism: birds nesting in close proximity to each other may experience a reduction in the degree of brood parasitism experienced [54]. In the model, I assumed that all individuals would respond identically to a given stimulus. However, heterogeneity in the anti-parasite responses shown by individuals of the host species could alter the effectiveness of behaviours in a manner that was not explored in this model. I assumed that mobbing behaviour is effective for every individual, meaning that group behaviour is effective for all the members of the local population [55], rather than occurring between differently sized subgroups of the population. However, there could be differences between individuals in the way that they initiate and engage with mobbing behaviour, and the maintenance of this behaviour within a population may require reciprocity from neighbours [56,57]. There is therefore an evolutionary game in progress between both hosts and parasites, and between hosts that may require a degree of cooperation in order to coordinate their defences against the parasites. The modelling framework considered here used predetermined rules-of-thumb to simulate the known behaviours of individuals, and would therefore not be sufficient for exploring this as a game—input from appropriate techniques would be needed to first identify the rules that could be used [58,59].

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