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How to learn to recognize conspecific brood parasitic offspring

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Recognition systems evolve to reduce the risk and costs of making recognition errors. Two main sources of recognition error include perceptual error (error arising from inability to discriminate between objects) and template error (error arising from using the wrong recognition template). We focus on how template error shapes host defence against avian brood parasites. Prior experiments in American coots (*Fulica americana*), a conspecific brood parasite, demonstrated how hosts learn to recognize brood parasitic chicks using predictable patterns of hatching order of host and parasite eggs. Here, we use these results to quantify the benefit of chick rejection as well as the cost of template error, and we then use mathematical models to explore fitness pay-offs of chick recognition from different template acquisition mechanisms. We find that fitness differences between mechanisms do not fully explain aspects of the learning mechanism, such as why coots reacquire their recognition template each year. Other constraints arising from mating systems and genetic mechanisms likely influence which learning mechanism for parasitic chick recognition is optimal. Our approach highlights how mechanisms of template acquisition influence other recognition systems, including parasitic chick recognition in other brood parasite hosts.

This article is part of the theme issue ‘Signal detection theory in recognition systems: from evolving models to experimental tests’.

1. Introduction

The coevolutionary dynamics between avian brood parasites and their hosts largely hinge on cognitive mechanisms that enable hosts to recognize and reject parasites at various stages of the reproductive cycle [1,2]. Thus, host-brood parasite systems provide unique opportunities to integrate an evolutionary cost-benefit approach with the cognitive mechanisms the organisms use in recognition. Reeve [3] established a general framework—the acceptance threshold model—for how the evolution of discrimination decisions can be the result of not just phenotypic similarity but also risks and costs of recognition errors. Davies *et al.* [4] used a similar signal detection model to describe in detail how host response (accept versus reject) to cuckoo eggs depends on egg appearance, costs and benefits of egg rejection, and the probability of parasitism. Since then, host responses to the presence of brood parasites in the nest has proved to be an effective way to test predictions about mechanisms underlying recognition systems, particularly with respect to the potential costs of recognition error [5–8].

There are two primary sources of recognition error: *perceptual error* and *template error*. Perceptual errors occur because there are cognitive limits to an organism’s ability to accurately discriminate between objects. Perceptual errors can lead to false acceptance or false rejection as a result of phenotypic similarity between host and parasites (e.g. in eggs [4,9–11]), or the inability to detect the parasite (e.g. dark egg in dark nests [12]). The second source of recognition errors is mistakes during the process of acquiring a recognition ‘template’—i.e. a neural representation of the ‘correct’ cues of their own eggs or chicks. These errors can

occur when recognition cues are learned, and parasites are present during the time window of template acquisition.

A host defence strategy against brood parasites is effective only when the benefits outweigh the costs that stem from both perceptual and template error. For example, a parasitic cuckoo egg that perfectly matches a host egg will not be rejected even when no template error has occurred. Conversely, the costs of template errors have been proposed as one explanation for the rarity of chick recognition as host defence, even when the parasitic chicks are dramatically different from the host's own offspring [13]. Hosts that use an imprinting-like mechanism (i.e. learning restricted to a single time window in life) to learn recognition cues from chicks during their first breeding attempt could incorrectly learn recognition cues from parasitic chicks if parasitized in the first breeding season. For hosts of cuckoos that eject all of the hosts' own eggs, the cost of this type of template error—i.e. the 'cost of misimprinting'—will almost always exceed any benefits of chick recognition because hosts that misimprint on a cuckoo chick in their first year will then reject their own chicks in all subsequent years [13].

A corollary to this misimprinting hypothesis is that, in systems where the risks and costs of misimprinting do not outweigh the benefit of parasitic chick rejection, learned chick recognition would be a viable host defence mechanism. Indeed, in the years since Lotem [13], we have now learned that some hosts of brood parasites can indeed recognize and defend against parasitic chicks (reviewed in [14]), including cases where the brood parasite ejects host offspring [15–18]. In a few hosts of brood parasites, we now have experimental evidence for how they acquire the template for recognizing brood parasitic chicks (American coot, *Fulica americana* [8]; superb fairy-wren, *Malarus cyaneus* [19]; large-billed gerygone, *Gerygone magnirostris* [20]). This has presented new opportunities to test how reduction of template error contributes to the evolution of parasitic chick recognition.

The prediction that chick recognition involves the reduction of template error was explicitly tested and confirmed in an experimental study of a conspecific brood parasite, the American coot [8]. American coots opportunistically lay parasitic eggs in nests of conspecifics, and each successful parasitic chick is costly to the hosts because it comes at the demise of one of their own chicks [21,22]. Coot eggs hatch asynchronously over several days, and hosts use the first-hatched chicks of the brood as the template for recognizing own versus parasitic chicks. When provided with the wrong reference chicks (i.e. chicks from a foreign brood) on the first day of hatching, hosts mistakenly reject their own offspring that hatch later in the hatching sequence. However, coots are able to reduce the risk of learning mistakes by increasing the length of the incubation period of parasitic eggs by manipulating their position of eggs within the nest, thereby reducing the likelihood that parasitic chicks hatch during the first day of hatching [23]. Our previous study [8] clearly demonstrated that coots use first-hatched chicks as templates but was less clear about how often learning happens. The experimental results showed that parasitic chick recognition is likely largely re-learned each year, but there may also be some influence of innate or previously acquired templates. Briefly, this is because (i) most coots did learn to recognize and reject parasitic chicks when exposed to the correct template chicks, but (ii) coots can be induced to reject parasitic chicks more readily than their own chicks, suggesting some bias against committing template error.

Here, we combine empirical data and theoretical models to explore why certain template acquisition mechanisms may evolve. Specifically we compare the fitness consequences of four different template acquisition strategies: (i) no chick recognition (baseline), (ii) using all chicks in the first brood in life as the template, (iii) using the first-hatched chicks from the first breeding attempt as the template, and (iv) using the first-hatched chicks each year as the template. We use field data from both observational and experimental studies to estimate the benefit of parasitic chick recognition and the cost of template error to parameterize these models and explore the fitness effects of different learning modes. Finally, we consider the impact of additional constraints such as the mating system and genetic mechanisms of recognition cues that likely affect the evolution of recognition learning in parasitic chick recognition.

2. Material and methods

(a) Study system

American coots are wetland birds of the rail family (Rallidae) that build nests in exclusive territories, but also opportunistically lay eggs in other coot nests in neighbouring territories [21,24]. Conspecific brood parasitism is very common; 41% of nests were parasitized during a 4-year study [22]. Although coot chicks are precocial and leave the nest and move about on water shortly after hatching, they are critically dependent on parental provisioning and brooding for a period of time. Parasitic chicks usurp these critical resources from host chicks and can decrease the reproductive output of host parents [25].

(b) Field data collection

We studied the dynamics of brood parasitism in American coots in wetlands near Williams Lake, British Columbia in 1987–1990 (417 nests) and again from 2005 to 2008 (258 nests). We monitored nests every 1–4 days during egg laying, and new eggs were marked individually with indelible pen on each nest check. We detected brood parasitism when we found more than one egg laid in a nest per day and identified parasitic eggs using egg features like shape and colour. The accuracy of these methods has been previously validated using genetic techniques [25]. We monitored nests daily during the 3- to 9-day hatching period. For analyses of hatching patterns, we used 63 nests for which both laying sequence and hatching sequence of parasites relative to hosts were known. Calculations of relative survival of hosts and parasites in control broods (i.e. naturally parasitized broods that were unmanipulated except for chick tagging) were based on 35 nests for which detailed censuses were conducted until the end of the parental care period.

For both control and experimental nests, we hatched chicks in captivity to assure complete accuracy in matching each chick to the egg it hatched from. We took eggs from nests at first sign of pipping, typically 1 or 2 days before the chicks hatched. We then hatched each egg inside an individual mesh pouch in an incubator (Hovabator 1602 N, GQF Manufacturing, Savannah, GA). We returned the chicks to nests within 24 h of hatching, after attaching colour-coded nape tags that were individually unique at each brood [26]. Because of a high degree of hatching asynchrony, nests were never left with less than two eggs or chicks, and parents did not abandon the nest during this period.

We conducted censuses periodically for at least 20 days, and up to 35 days, after the last chick was returned to the nest. Brood censuses and behavioural observations were conducted at close range (10–40 m) from floating blinds equipped with camouflage coverings, where the individually distinct chick tags could be observed easily with binoculars. We determined survival by counting chicks that were seen in one of the last two censuses.

(c) Cross-fostering experiment design

We conducted cross-fostering experiments to investigate the learning mechanism used in chick recognition [8]. In the ‘Host First’ experiment, the hosts were provided with their own offspring during the learning period, i.e. first day of hatching. Conversely, in the ‘Foreign First’ experiment, we provided the experimental hosts with foreign chicks (i.e. experimental parasitic chicks) on the first hatching day. In both treatments, on all days after the first hatching day, we matched each host chick that hatched on a given day with a foreign chick of the same age. All foreign chicks used in a given experimental nest came from the same donor clutch so that all nests had chicks from only two sets of parents. Subsequent survival rates of chicks in experimental broods were assessed using the same protocol as control broods.

(d) Calculating benefits of rejection

To estimate the rate of rejection of parasitic chicks in American coots, we must first account for the extreme effect of brood reduction, in which about half of chicks die before independence owing to starvation [21,27]. In addition, the rate of mortality due to brood reduction is highly dependent on hatching order [21,27]. To quantify the benefit of chick recognition while taking these factors into account, we make the important assumption, based on prior evidence [25], that the overall number of chicks fledged (host and parasite combined) from a given nest is density dependent (there is a limit to how many chicks a pair can raise based on food availability), and that each successful parasite comes at the cost of a host chick. In the absence of chick recognition, the cost of parasitism is the incremental decrease in the survival of host offspring owing to the presence of extra competitors. Thus, the benefit of chick rejection is the decrease in survival of parasitic offspring, and consequently, the increase in survival of their own (host) offspring relative to random chance, given their position in the hatching order.

We estimated the benefit of rejection separately for two types of nests in which host parents had access to a correct recognition template: naturally parasitized broods where only host chicks hatched on the first day ($n = 35$ nests) or Host First broods ($n = 15$ nests). We first measured the total proportion of host chicks that survived for the i th position in the hatch order ($P_{H,i}$). To determine the ‘expected’ survival rates, we also calculated the overall survival of all chicks (i.e. regardless of host or parasite status) at each hatching sequence ($P_{A,i}$) for these broods. We then summed the differences between observed and expected host chick survival for each position in the hatching sequence (H_i) for all nests, and then divided by the number of nests (n) to get the per nest benefit of chick recognition, B :

$$B = \frac{\sum_i (P_{H,i} - P_{A,i})H_i}{n}$$

Because of reduction of sample size later in the hatching sequence, we pooled chicks hatching on day 5 and later for the calculations presented here.

(e) Calculating the cost of rejection error

The calculations for the cost of learning an incorrect cue, C , are identical to the calculations for the benefit of rejection but are calculated for broods that hatch only parasitic chicks on the first day, and the cost is estimated in terms of host chicks that are lost, not gained. We calculated the observed number of host chicks that survived relative to the number that would have survived if the bird were an acceptor. If there were any costs associated with learning incorrect information, then the hosts that were induced to make mistakes would produce fewer host offspring than expected if mortality was random. We could not calculate C from naturally parasitized broods because there were very few broods where

only parasitic chicks hatched on the first hatching day. Instead, we calculated C using our Foreign First broods ($N = 15$ broods), where learning errors were induced experimentally.

3. The models

We built four models to represent potential mechanisms of template acquisition for chick recognition based on both previous work on parasitic egg recognition [5,13] and our own work on parasitic chick recognition in coots [8]. The models are depicted graphically in figure 1 (see electronic supplementary material for codes).

(a) Model 1—acceptors

The null model is that hosts fail to recognize and reject parasitic chicks. The lifetime fitness of a universal acceptor, W_{model1} , is

$$\overline{W}_{\text{model1}} = N(PX_p + (1 - P)X),$$

where X is the average number of own fledglings at unparasitized nests, X_p is the average number of fledglings at parasitized nests, P is the probability that a nest contains a parasitic chick and N is the number of breeding seasons in an average lifetime.

(b) Model 2—imprinting on all of the chicks in the first brood of life

Experimental studies on hosts of cuckoos have shown that some hosts imprint on the first clutch of eggs they lay in the first breeding season [28]. We explore how such a mechanism would play out for learning to recognize chicks in a system where parasites do not evict their nest-mates (see also [29,30]). Hosts that are not parasitized in the first breeding season correctly imprint on their own chicks, and those that are subsequently parasitized in later years gain the benefit of chick rejection, B . Thus, a bird that is not parasitized in its first year will raise X offspring in subsequent years when it is not parasitized, and it will raise $X_p + B$ offspring in years when it is parasitized. Thus, its fitness will be

$$W_{\text{np2}} = X + (N - 1)(PX_p + B) + (1 - P)X.$$

Now consider a bird parasitized in its first year. This host would imprint on both host and parasitic chicks and become a universal acceptor in all $N - 1$ future breeding attempts (i.e. will not gain benefit of chick rejection). Its lifetime fitness would be therefore be

$$W_{\text{p2}} = X_p + (N - 1)(PX_p + (1 - P)X).$$

The average fitness for a strategy where individuals imprint on the first brood in their life is the sum of each fitness outcome multiplied by its probability of occurrence

$$\overline{W}_{\text{model2}} = (1 - P)W_{\text{np2}} + PW_{\text{p2}}.$$

(c) Model 3—imprinting on the first chicks of the first brood in life

Another potential mechanism for learned parasite recognition is to imprint on the first chicks that hatch during the first breeding season. This is similar to parasitic egg recognition in some cowbird hosts which apparently use the first

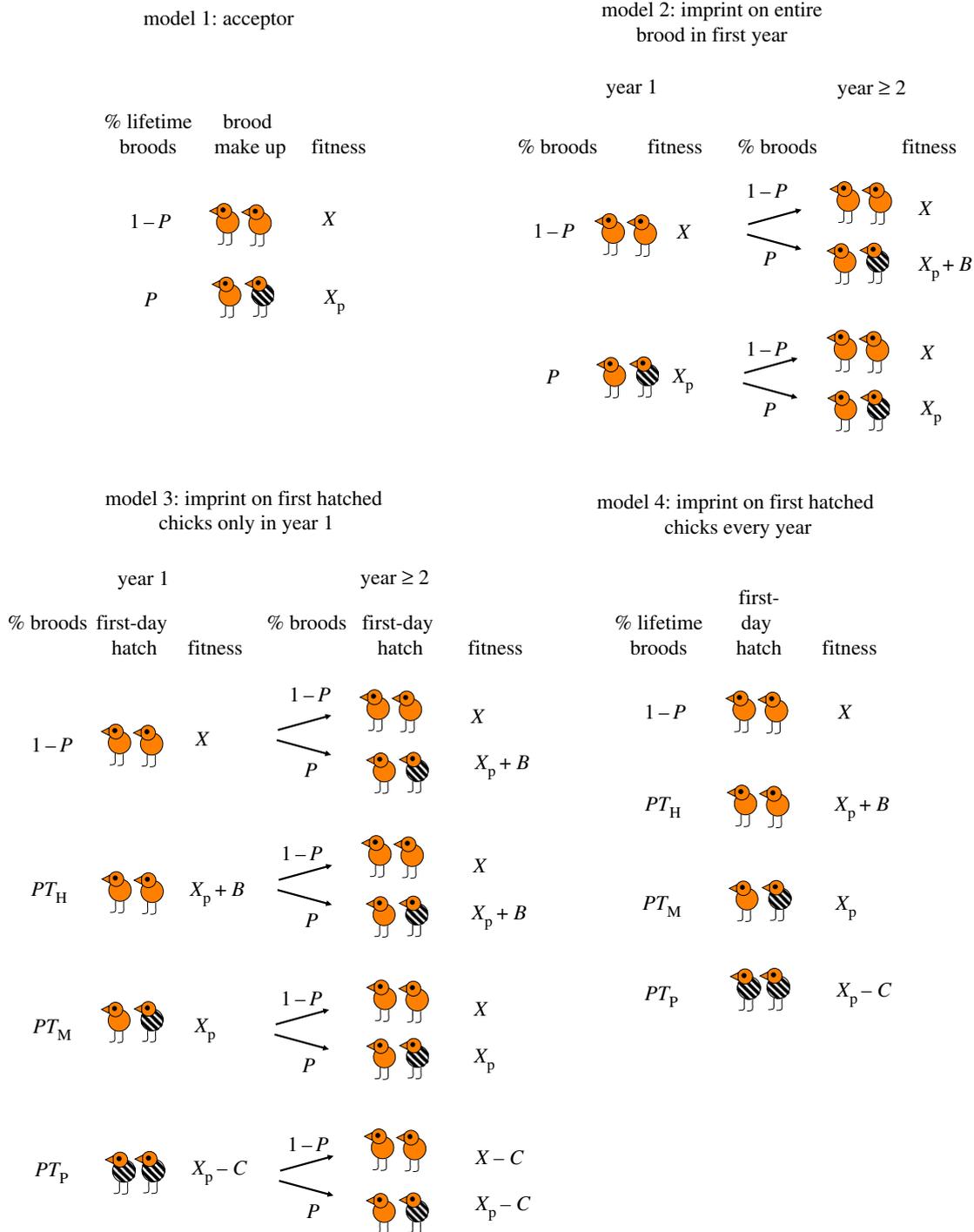


Figure 1. Graphical representations of the four models of template acquisition used in this study. In each model, we show the respective probabilities of template patterns % broods, the graphical representation of the template (orange chicks = host, striped chicks = parasite) and the fitness outcomes for each scenario. For models 2 and 3, template acquisition occurs during the first breeding attempt; thus the fitness outcome for the first breeding attempt (year 1) is shown separately from those in subsequent years. The parameters are as described in the text: probability of parasitism (P), expected number of chicks fledged from an unparasitized nest (X), number of chicks expected to fledge from a parasitized nest in the absence of chick recognition (X_p), benefit of chick recognition (B), cost of recognition error (C) and the probability of different template types at parasitized broods (T_H = host-only template, T_M = mixed template, T_P = parasite-only template). (Online version in colour.)

laid eggs of their first breeding attempt as the template for recognition [31]. For chick recognition, the relative hatching timing of host and parasitic eggs becomes a critical component of recognition. There are three possible patterns on the first hatching day: only host chicks hatch, a mix of host and parasitic chicks hatch, or only parasitic chicks hatch. The probabilities for each hatching pattern (host-only, mix and parasite-only) are T_H , T_M and T_P respectively.

A host not parasitized in its first breeding season imprints on its own chicks and gains the benefit of rejection (B)

whenever it is subsequently parasitized while paying no costs of misimprinting when it is not parasitized. Thus, its lifetime fitness would be

$$W_{np3} = X + (N - 1)(P(X_p + B) + (1 - P)X).$$

For individuals that are parasitized on their first breeding attempt, the three different hatching patterns affect the outcome of learned recognition. First, the hosts that hatch only their own chicks on the first hatching day will correctly

Table 1. Calculating the benefit of rejection from control broods.

hatch order	average survival	initial host chicks	expected host chicks alive	actual host chicks alive	host chicks saved	nests	benefit per nest
1	—	—	—	—	—	—	—
2	0.53	49	25.9	31	5.1	23	0.22
3	0.51	23	11.8	14	2.2	20	0.11
4	0.23	21	4.8	5	0.2	19	0.01
5+	0.20	38	7.5	9	1.5	14	0.11
							<i>total benefit: 0.45</i>

imprint on their own chicks and gain the benefit of rejection whenever they are parasitized later in life. Their lifetime fitness is

$$W_H = (X_p + B) + (N - 1)(P(X_p + B) + (1 - P)X).$$

Second, parasitized hosts that have both their own chicks and parasitic chicks hatch on the first day will imprint on both and will then accept all chicks for the rest of their lives. Their lifetime fitness is

$$W_M = X_p + (N - 1)(P X_p + (1 - P)X).$$

Last, hosts that have only parasitic chicks hatch on the first day of the first breeding season will misimprint on parasitic chicks and then pay the cost of misimprinting, C , for the rest of life, even when they are not parasitized in subsequent broods. Their lifetime fitness is

$$W_P = (X_p - C) + (N - 1)[P(X_p - C) + (1 - P)(X - C)].$$

With this, the average fitness for this learning mechanism (\bar{W}_{model3}) is

$$\bar{W}_{\text{model3}} = (1 - P)W_{np3} + P(T_H W_H + T_M W_M + T_P W_P).$$

(d) Model 4—Re-learning first-hatched chicks every year

Coots could also completely renew their recognition templates with the first-hatched chicks of each brood. In this model, the payoff for recognition for a parasitized host is completely dependent on the hatching patterns of chicks on the first day for each brood. If only host chicks hatch on the first day (T_H), the hosts gain the benefit of rejection (B). If both host and parasitic chicks hatch (T_M), hosts accept both chick types. If only parasitic chicks hatch on the first day (T_P), then hosts pay the cost of template error (C). Thus, the lifetime fitness under this scenario is

$$\bar{W}_{\text{model4}} = NP(T_H(X_p + B) + T_M X_p + T_P(X_p - C)) + N(1 - P)X.$$

(e) Model parameterization

We parameterized each of our four models using values estimated from our field studies. The probability of a nest containing a parasitic chick (P) was set at 0.266, based on previous finding that about 40% of nests contain a parasitic egg, and that about 33% of parasitic eggs are rejected before hatching [21,22]. We estimated the number of chicks fledged at

non-parasitized nests (X) as 5.0, based on our field data (from 35 non-parasitized control nests in 2005–2008 for which we had complete census data; mean \pm s.e.m. = 4.89 ± 0.25). We estimated the number of chicks fledged from parasitized broods in the absence of chick recognition as $X_p = 4$, based on the previous finding that 50% of chicks die before independence [24] and our long-term data, which show that nests with at least one parasitic chick contain 2.1 parasitic chicks on average. Reproductive lifespan (N) was set at 2 breeding attempts, calculated based on the published estimate of 49% annual survival of adults [32]. The probabilities of template type ($T_H = 0.81$, $T_M = 0.16$, $T_P = 0.03$) were based on previous estimates [8]. The benefit of chick recognition (B) and cost of template error (C) were estimated in this study (see above).

4. Results

(a) Benefit and cost of rejection

The total benefit of rejection as calculated from naturally parasitized broods was 0.45 chicks per parasitized nest (table 1). The benefit of rejection calculated using the Host First broods yielded a greater value, 1.06 host chicks saved per nest (tables 2 and 3). The discrepancy between the B values calculated from the two treatments is likely due to the difference in number of parasitic chicks introduced into the brood: naturally parasitized nests contained 2.1 parasitic chicks on average, whereas Host First experimental nests received 4.5 ‘parasitic’ (i.e. foreign) chicks. When this is taken into account, the results are similar—parasite recognition leads to approximately 20% increase in survival of host chicks relative to what would have been lost to parasitism. Given the previous estimate that each successful parasite chick comes at a cost of one host chick, this accounts for about 20% of the potential cost of parasitism that is recovered owing to chick recognition.

The total cost of learning errors, C , is 0.43 host chicks lost per nest where only parasites hatch on the first day. The average number of host chicks in these broods was 4.1 chicks, suggesting that learning the wrong template leads to 10% decrease in survival of host chicks hatched after the first day.

(b) Model comparisons

We explored how variation in parasitism rate, cost–benefit ratio and template error rate affect the relative fitness payoffs of each of four mechanisms of template acquisition (figure 2). Overall, learning to recognize is typically better than remaining an acceptor, except when the information gets very poor

Table 2. Calculating the benefit of rejection from Host First broods.

hatch order	average survival	initial host chicks	expected host chicks alive	actual host chicks alive	host chicks saved	nests	benefit per nest
1	—	—	—	—	—	—	—
2	0.54	19	10.3	16	5.7	14	0.41
3	0.56	18	10.0	13	3.0	14	0.21
4	0.23	11	2.5	5	2.5	10	0.25
5+	0.15	20	3.0	5	2.0	11	0.18
							<i>total benefit: 1.06</i>

Table 3. Calculating cost of learning error using Foreign First broods.

hatch order	average survival	initial host chicks	expected host chicks alive	actual host chicks alive	host chicks lost	nests	cost per nest
1	—	—	—	—	—	—	—
2	0.58	20	11.6	9	2.6	15	0.17
3	0.46	12	5.5	5	0.5	11	0.05
4	0.50	11	5.5	6	−0.5	11	−0.05
5+	0.31	18	5.6	3	2.6	10	0.26
							<i>total cost: 0.43</i>

(high frequency of nests with parasite-only on first day). Moreover, our models show that learning the entire first brood (model 2) is not as good as using the first-day rule (model 3 or 4), except for cases where the template error rate is very high. Learning the entire brood is relatively advantageous when template error rate is high because parents that learn the entire parasitized brood in the first breeding will accept parasitic chicks for life, but they do not mistakenly reject their own chicks (i.e. they do not pay the cost of misimprinting), even at extremely high parasitism rates. The number of breeding attempts has little effect on the relative fitness payoffs of different template acquisition strategies after $N = 2$ breeding attempts (figure 2*d*).

As parasitism rate increases, the benefit of learning chicks using the first-day rule increases (figure 2*a*). The relative advantage of learning chicks on the first day of hatching is not dependent on the cost of recognition error in American coots (figure 2*b*) because the probability of having a parasite-only template is very low. However, in cases where template error rate is large (e.g. hosts of interspecific brood parasites that tend to hatch ahead of host chicks), learning the first chicks is less advantageous than imprinting on the whole brood or accepting parasites, and this disadvantage becomes exacerbated with increasing costs of recognition error (figure 3).

There is generally very little difference between learning recognition templates from the first-hatched chicks one time versus re-learning each year, particularly at parameter values that reflect the natural history of the system (figure 2). However, as the template error rate increases (i.e. probability that only parasitic chicks hatch first), the lifetime fitness decreases faster for hosts that re-learn first chicks each year (model 4) compared with hosts that imprint on the first chicks in the first year (model 3: figure 2*c*). This is because hosts that correctly imprint on first chicks in the first year

(i.e. those that do not get parasitized or only host chicks hatch first) continue to gain the benefit of chick rejection over subsequent years, whereas hosts that re-learn the first-hatched chicks each year will potentially pay the costs of template error each year.

5. Discussion

The potential costs of recognition errors—cost of false acceptance and cost of false rejection—have often been recognized as an important constraint for recognition in general [3]. However, signal detection theory has primarily focused on ways recognition systems work to lower the costs of perceptual errors that arise when potential targets of an action (in this case, host and parasite chicks) have similar phenotypes. Here, we show that the template acquisition process (i.e. probability of template error) also has large effects on the costs and benefits of recognition, and that this may facilitate or constrain the evolution of parasitic chick recognition [5,13]. It has long been clear that phenotypic similarity alone cannot explain the existence or absence of host defence against brood parasitic offspring. In American coots, host and parasitic offspring share similar phenotypes because they are the same species, yet a learned recognition template allows them to reliably discriminate parasitic offspring. This stands in stark contrast to many hosts of common cuckoos, which do not reject parasitic offspring, even when the parasites look nothing like their own [13]. In some cases where hosts are now known to recognize and reject parasitic cuckoo chicks, the cuckoo chick has evolved to closely resemble the host offspring [18,20,33]. Thus, we must simultaneously consider the various sources of recognition error as well as the costs and benefits of rejection and acceptance to reconcile the often puzzling

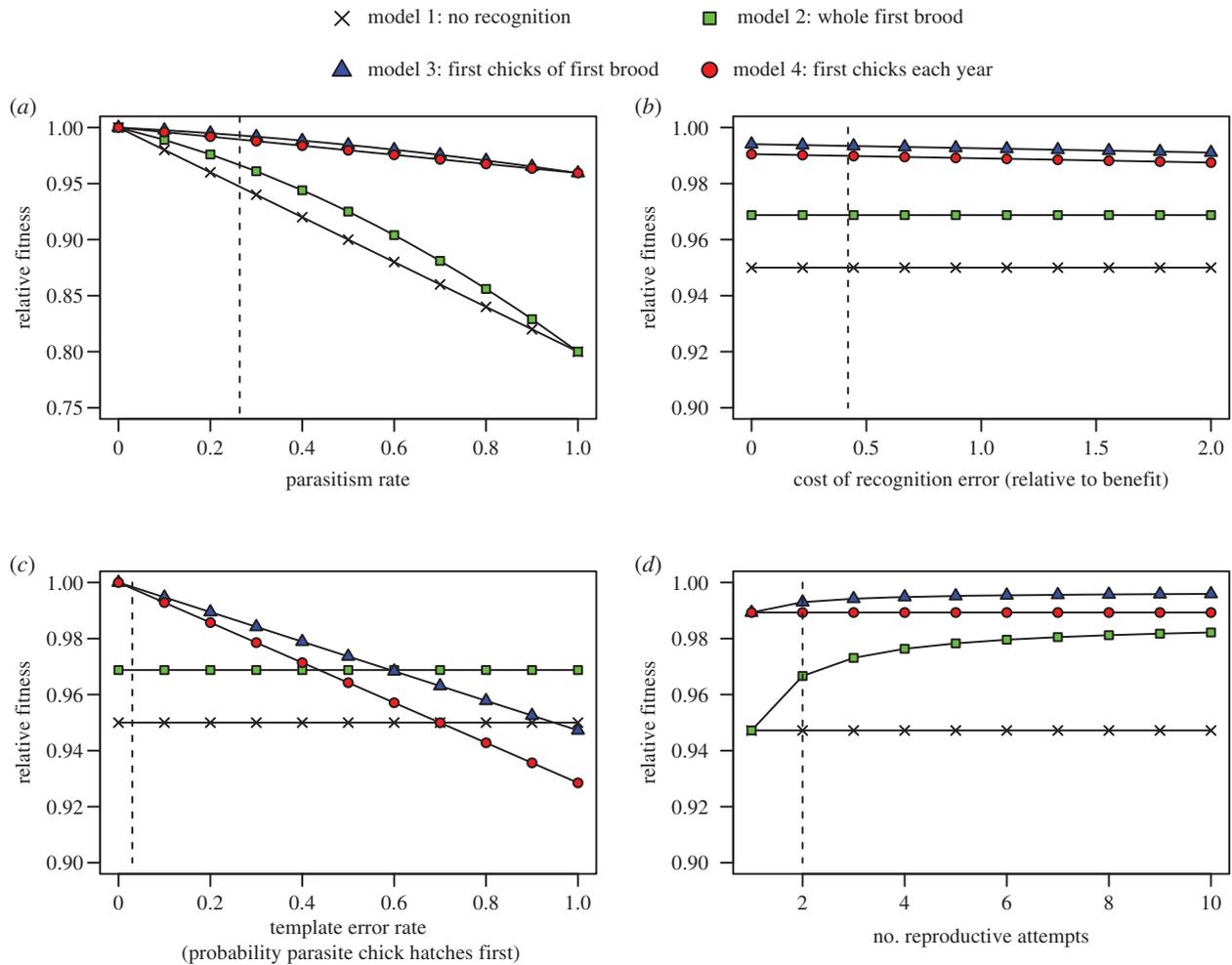


Figure 2. Results of models of template acquisition. Parameters are estimated based on long-term monitoring data and experimental results (see main text): $P = 0.266$, $X = 5$, $X_p = 4$, $N = 2$ years, $C = 0.45$, $B = 1.06$, $T_H = 0.81$, $T_M = 0.16$, $T_P = 0.03$. In (a)–(d), we vary the values of one parameter and compare their effects on lifetime fitness relative to the maximum possible. Dashed line in each panel represents the estimated value for the parameter based on field data. (a) Effect of variation in parasitism rate on relative lifetime fitness. (b) Effect of variation in the ratio of cost of template error and benefit of correct template. (c) Effect of variation in template error rate. In this scenario, we assume $T_P + T_H = 1$ (i.e. we disregard the probability of mixed template) for simplicity. (d) Effect of number of breeding attempts. (Online version in colour.)

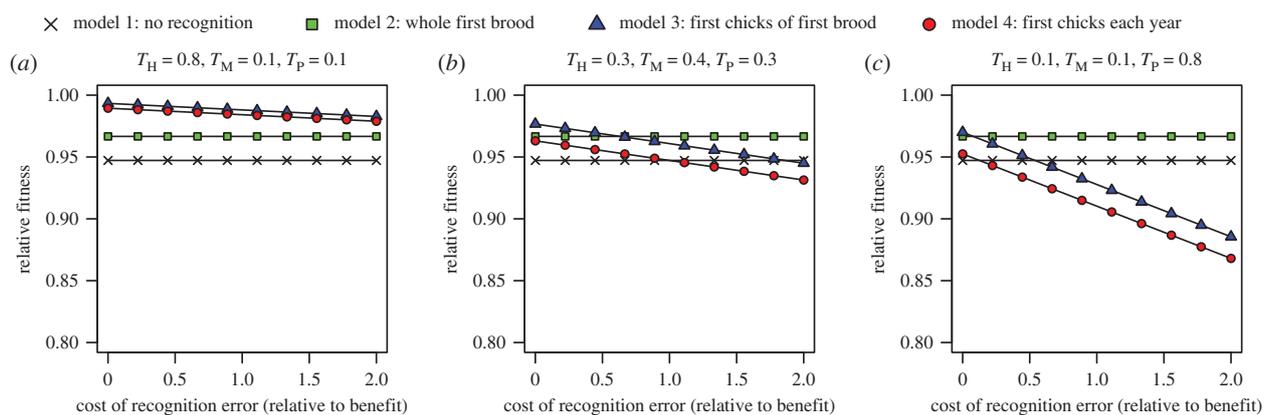


Figure 3. Increasing the rate of template error reduces the advantages of learning the first chicks of a brood as the template. With low levels of template error (a), learning the first chicks (either in first brood or each year) is advantageous over learning the whole brood or accepting parasites. At intermediate (b) or high levels of template error (c), learning the first chicks as the template becomes less advantageous, particularly at higher costs of recognition error. In such cases—as might arise in hosts of interspecific brood parasites that hatch earlier than host chicks—learning the first chicks as the template may be maladaptive. (Online version in colour.)

endpoints of antagonistic coevolution between brood parasites and their hosts.

We leveraged our field manipulation of the template acquisition process to estimate the benefits of chick recognition and

the cost of recognition error stemming from template error. We found that when hosts have access to correct templates, chick recognition allows them to save roughly 0.45–1.06 offspring per nest, or 0.2 host chicks per parasitic chick. Because

previous estimates suggest that each successful parasitic chick comes at the cost of one host chick, this represents a recovery of 20% of the cost of parasitism. Most hosts (81%) have access to the correct referents during the first hatching day each year and thus gain the benefit of correct rejection. Conversely, when parents incorrectly learn parasitic chicks as their own, they suffer a cost of 0.43 offspring per nest, or approximately a 10% increase in host chick mortality in addition to the costs of brood parasitism. However, hosts rarely pay this cost of learning error because the frequency of nests in which only parasitic chicks hatch on the first day is extremely low (3%).

Our model results show that, under a wide range of parameter values, using the first-hatched chicks of the brood as the recognition template (model 3 or 4) is better than imprinting on the entire first brood or no recognition (model 2 and 1, respectively: figure 2). The exception to this is when parasitic chicks hatch ahead of host chicks at high rates, as is the case for hosts of many interspecific brood parasites. Under such conditions, using the first chicks as the template can become maladaptive (figures 2c and 3). These results demonstrate how coots benefit from using first-hatched chicks as templates [8] and why hosts may actively lower the probability of template error by manipulating hatching patterns of parasitic eggs [23].

One important issue not resolved by the model results is how selection might shape the frequency of chick recognition learning: i.e. whether coots learn their recognition template from the first-hatched chicks of their first breeding only (model 3) or at each breeding attempt (model 4). Our model results show that, while imprinting on first chicks of the first brood in life (model 3) and annually re-learning first chicks (model 4) yield very similar lifetime fitness under a wide range of conditions, re-learning each year (model 4) becomes relatively more costly when parasitic chicks tend to hatch early. This is because hosts that imprint on the first chicks of the first brood can gain the benefit of a correct template for a lifetime whenever they are not parasitized on the first breeding attempt, but hosts that re-learn the first chicks each year continue to risk committing template errors each year. These model results conflict somewhat with our previous experimental results suggesting that imprinting on the first chicks of the first brood is unlikely to explain the observed patterns of chick rejection [8]. This suggests that other factors may make it easier to evolve host defence mechanisms that involve re-learning the recognition template each year despite the potential costs of template error.

Mating system and patterns of gene expression for the recognition cues could potentially explain why repeated learning each year (model 4) is favoured over single-time imprinting on the first chicks in the first brood of life (model 3). First, when birds change mates across breeding attempts, the single learning event imprinting mechanism would only work for female breeders. Conversely, annual re-learning of first-hatched chicks would be a viable mechanism for acquiring recognition templates for both sexes, even when mating partners switch across years. Second, even if recognition and culling of parasites is restricted to females, single-time imprinting would be viable only if her genes are able to control the expression of the recognition cue in offspring, e.g. through mechanisms such as genomic imprinting. The expression of recognition cues in offspring is potentially much more complex than the expression of features used for egg recognition, since egg features are maternal traits. Given this, unless she mates for life, a female may need to update her template annually

because of the genetic influence of her mate on the recognition cues of the pair's offspring. In reality, the learning process for chick recognition that optimizes host fitness is likely more complex than either single-time learning or complete re-learning each year, involving either (i) a population with a mix of individuals using imprinting or annual learning of first chicks, or (ii) all individuals using template updating at each breeding attempt [8].

Our study has implications for a broader understanding of the evolution of offspring recognition systems in general. First, we emphasize that there are two ways in which recognition systems can go awry—perception error and template error—and these two sources of errors interact in any recognition system. Classic work on recognition systems has often focused on perceptual errors induced by overlap in cues used for recognition (e.g. [3]). In this study, we focus on how template errors—mistakes in development of a recognition template—can come with large costs, and these costs could be a major constraint in the evolution of recognition systems [13]. This is particularly important in the context of antagonistic coevolution between brood parasites and hosts, because parasites may evolve strategies to exploit the template acquisition process of hosts to induce template error. For example, obligate interspecific brood parasites often evolve mechanisms to hatch earlier than the hosts' own offspring, and this would make the hatching order mechanism less useful as a mechanism for template acquisition. However, in facultative conspecific brood parasites, learning based on first-hatched chicks is a reliable template acquisition mechanism because the incubation periods of host and parasitic eggs do not differ substantially. In fact, in American coots, hosts manipulate incubation positions of eggs to delay the hatching of parasitic eggs by about 1 day, further decreasing the risk of template error [23].

Recent studies have shown that American coots are not the only species that can recognize and reject brood parasitic chicks from their nests, suggesting that there are other ways to ensure the reliability of template acquisition. For example, Colombelli-Negrel *et al.* [19] showed that offspring of superb fairy-wrens, *Malurus cyaneus*, learn their mother's incubation call while in the egg and incorporate these elements into their begging call. They further show that the chicks of the brood parasite Horsefield's bronze cuckoo, *Chalcites basilis*, are not able to learn these incubation calls, and thus this can act as a cue for parasitic chick recognition, which causes the hosts to abandon the nest [15]. A different example involves large-billed gerygones, *Gerygone magnirostris*, which recognize and reject chicks of the obligate brood parasite little bronze cuckoo, *Chalcites minutillus* [16,33]. Evidence suggests that gerygones likely use an innate template, based on the presence of down feathers, as one component of chick recognition [20]. The evolution of such reliable template acquisition processes (e.g. embryonic learning, genetically heritable template) may have been the key that enabled hosts to recognize and defend against brood parasitic chicks, spurring the evolution of chick mimicry [33] and chick polymorphism [18]. However, questions remain about why other potential mechanisms of template acquisition are not used by hosts of brood parasites to recognize and reject parasitic offspring [34]. In this context, it would be interesting to explore the potential template acquisition mechanisms by hosts in other brood parasite–host systems that exhibit the patterns of chick mimicry (e.g. brood parasitic pin-tailed whydah, *Vidua macroura*, and its host, common waxbill, *Estrilda astrild* [35]; brood

parasitic shining cuckoo, *Chrysococcyx lucidus*, and its host, grey warbler, *Gerygone igata* [36]; brood parasitic screaming cowbird, *Molothrus rufoaxillaris*, and its host, baywing, *Agelaioides badius* [37]). Brood parasite–host systems remain a rich area for exploring the fundamental factors, including various sources of recognition error, that limit or facilitate the evolution of recognition systems.

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Data accessibility. The data have been deposited in Dryad [38].

Competing interests. We declare we have no competing interests.

Authors' contributions. D.S. developed original models, analysed data and wrote the first draft. B.E.L. edited the manuscript and checked the logic and mathematics of models. D.S. and B.E.L. both collected data in the field.

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