

Chapter 2

Cuckoo eggs and IEDs: A game theoretic model for asymmetric arms races

A complex weapon makes the strong stronger, while a simple weapon—so long as there is no answer to it — gives claws to the weak. —George Orwell

Each spring in Wicken Fen, Reed Warblers begin building nests in anticipation of their annual brood and Cuckoos sit from nearby perches waiting to slip one of their own eggs in amongst the Warbler's clutch. If the Cuckoo's egg is allowed to hatch, it will bring forth a ruthless creature. Whenever the blind nestling bumps into another young bird, it will carefully balance its nestmate on its broad back, move to the edge of the nest, and with a swift push from its legs, eject the chick from the nest. The task is not easy for the blind and naked newborn. If the nestmates had not yet hatched, the eggs would have taken only a few minutes of efforts though still required frequent breaks. The squirming nestlings will take several attempts over days, but eventually they too will be cast into the water below (Dunn, 1985). Accordingly, Reed Warblers who can detect such threats enjoy a large gain in relative fitness as do Cuckoos who can avoid being so detected. Given that there are many possible distinctions and that mistakes will be made, strong evolutionary pressures influence what strategy a Reed Warbler employs to reliably raise its own chicks.

Two thousand miles away a group of American troops board their patrol vehicle, turn on their radio jammers and begin visually scanning the road ahead in search of any sign of a newly emplaced improvised explosive devices (IEDs). The scorching Iraqi desert seems worlds away from the placid marsh, yet Dawkins and Krebs (1979) famously asserted they have much in common. Both the soldier and the Reed Warbler are engaged in an ongoing struggle against an evolving threat and have adopted new behaviors as a result. Given the threats facing soldiers, military planners are constantly searching for reliable ways to protect them. Such similarities led to use of the term "arms race" to capture a class of biological phenomena and in particular "interspecific asymmetric arms race" to describe the relation

between the Cuckoo and the Warbler.¹ I will argue that this characterization is correct and that, in some deep sense, these are the same type of phenomena.

Because the evolution of strategies is observable in human populations, I will first explore the arms race between US troops and Iraqi insurgents during the occupation of Iraq. From a detailed examination of the emergence and refinement of IEDs I will draw out the characteristic features of military asymmetric arms races.² I will next explore the dynamic between the Cuckoo and the Reed Warbler and show that these characteristic features obtain in biological arms races. I suggest that these commonalities point to a deeper underlying structure. In section three, I introduce a game theoretic account that captures this shared dynamic. Within this formal framework we can see that reliability is just a generalized notion of biological fitness. I will conclude that while biological evolution (and often humans engaged in arms races) select strategies on the basis of their reliability, the proper standard to judge possible interventions is robustness.

2.1. The asymmetric war in Iraq: IEDs and MRAPS

Revolutionary warfare . . . represents an exceptional case not only because as we suspect, it has its special rules, different from those of the conventional war, but also because most of the rules applicable to one side do not work for the other. In a fight between a fly and a lion, the fly cannot deliver a knockout blow and the lion cannot fly. It is the same war for both camps in terms of space and time, yet there are two distinct warfares—the revolutionary's, and shall we say, the counterrevolutionary's. (Galula, 1964, p. xii.)

The fight against insurgents is commonly described as an asymmetric war without identifying what makes it so (e.g. Adamson, 2007). As is clear from the submarine/anti-submarine warfare

¹ All discussion of arms races in this chapter is directed at the dynamic in two separate populations with divergent goals and so is directed at this type of arms race.

² While I focus on the American/Iraqi arms race, the claim is general. Each aspect can also be seen in other asymmetric arms races, such as the submarine/anti-submarine warfare between the American and German forces during WWII (Meigs, 1990). While providing less detail on arms races per se, Nagl's (2003) study of the Malayan Emergency and the War in Vietnam is an interesting study of strategic evolution in asymmetric conflicts. While there are numerous other sources (e.g. Sarkesian, 1993), these references are particularly of value to this case as Lt. Con. Nagl subsequently cowrote (with Gen. Patreus) the US military handbook on counter-insurgency and Gen. Meigs ultimately lead the US organization within the defense department tasked with responding to the IEDs.

between the Americans and Germans in WWII, an asymmetric arms race is not necessarily between opponents of disparate resources (Meigs, 1990). What defines an asymmetric arms race is that, regardless of the reason, opponents are compelled to use disparate strategies, often in the form of measure/countermeasure. In 2.1 I will elucidate the consequences of such asymmetries using the term *strategy* to apply to the entire collection of actions that an agent takes (or does not take) and *measure* or *countermeasure* to refer to the individual components of a strategy.

Specifically, I will show that asymmetric arms races are inherently dynamic and thus the reliability of any given strategy is inextricably tied to the strategy employed by ones opponent. While this may be said of many different dynamic games, asymmetric arms races have the following unique set of features: (i) the reliability of any strategy (once it is employed) typically decreases over time; this is because both (ii) opponent responses often attenuate the efficacy of one's strategy; and (iii) opponents engage in a search process to identify and exploit weaknesses; however, (iv) because measures are costly it is often disadvantageous to adopt new strategies until they are necessitated by an opponent; and (v) the process results in the gradual accumulation of costly measures. These five features will serve to ground both the argument in section 2.2 that an asymmetric arms race is type of phenomena that spans the natural world and the argument in section 2.3 that the proposed game can serve as a canonical model for interspecific asymmetric arms races.

2.1.1 The end of major combat operations, the beginning of asymmetric conflict

On May 1st 2003, six weeks after the invasion began, President Bush announced an end to major combat operations in Iraq. In the early days after the fall of Baghdad, insurgents attacked, but posed little threat to American troops (Adamson, 2007). Frontal assaults on better trained and superiorly armed troops occurred, but were far more costly to insurgents. By late summer, patrolling forces in the "Sunni Triangle" began encountering more opportunistic attacks such as sniper fire and rocket propelled

grenades. While still within the operational capabilities of American forces, the canvas-doored Humvees driven on most patrols were not equipped for battle (Krepinevich & Wood, 2007).

Though identified as a problem as early as May, the impending scope of the IED emergency to come was not yet apparent. In August of 2003, roadside bombs were terrifying, but infrequent; six months of battle had left close to 300 soldiers dead, but only 11 were the result of IEDs (Anderson, Fainaru, & Finer, 2005). During the following year IEDs proliferated to the point of becoming the primary weapon of the insurgency. In June 2004, the Commander of U.S. Central Command, General John Abizaid wrote a personal letter to Secretary of defense Donald Rumsfeld calling for “a Manhattan Project-like effort” to deal with the emerging threat. From 2006 to 2011, the Joint IED Defeat Organization (JIEDDO) spent over \$18 billion on C-IED technology, not including the Pentagon’s Mine Resistant Ambush Protected (MRAP) vehicle program which drew an additional \$40 billion from federal coffers (GAO, 2012). To put this in context, the total cost (adjusted for inflation) of the actual Manhattan project was approximately \$20 billion (Schwartz, 1998).

In both military and academic circles, debates have raged about whether C-IED efforts were transformative and necessary (Gayl, 2008; Lamb, Schmidt, & Fitzsimmons, 2009; Carter and Gilmore, 2012) or massive boondoggles (Krepinevich & Wood 2007; Rohlfs & Sullivan, 2011; Cary & Youssef, 2011). Whereas the goal for the actual Manhattan project was technological and the criterion for success definite, an evolving enemy makes judging C-IED efforts extremely complicated. Whether or not C-IED efforts are judged to be reliable depends on how one evaluates statements like: IED casualties remain about the same [circa 2007] in spite of a four-fold increase in IED use in Iraq. On one hand the effectiveness of a single IED decreased steadily over the four year period. On the other, massive expenditures failed to reduce the probability that a soldier would die from an IED. Yet, the accumulation of costly measures without a substantial decline in casualties is not obviously indicative of failure. Both the increased number and complexity of IEDs as well as the accumulation of costly C-IED

technology on American vehicles may easily be seen as a standard consequence of participation in asymmetric arms race.

2.1.2.0 Make yourself hard to kill

The Army Corps of Engineers divides the conceptual terrain into the five categories: predict, prevent, detect, neutralize, and mitigate. While eventually all facets would be actioned, early efforts were directed at blast mitigation. In this section I will examine the evolution of armored vehicles from the “light-skinned” (i.e. unarmored) Humvee to the fourth generation MRAP. The MRAP is an important case-study because unlike some technology, MRAPs were available from the beginning of the war. Some warplanners advocated skipping the 2nd generation and 3rd generation of development and moving straight to 4th generation MRAPs, while others resisted such escalation. In section 2.1.3 I will show that the decision to upgrade vehicles only occurred when the effectiveness of the current generation had been degraded by new insurgent strategies (criteria i,ii, and iii). But beforehand, I will examine in 2.1.2.2 how the refusal to skip 2nd and 3rd generation vehicles illustrates the reluctance to get too far ahead of the enemy (criteria iv) and first set the stage for making these points in 2.1.2.1 by reviewing the increasing cost of American countermeasures (criterion v).

2.1.2.1 From Hillbilly armor to MRAPS: Accumulating costly measures (criterion v)

One of the consequences of not preparing for a post-Sadam Iraq was a lack of the right equipment for US Soldiers. This failure is clearest in the primary mode of transportation, the Humvee. Designed to be an agile form of transport behind front lines, the Humvee was ill-equipped for fighting an insurgency without any clear distinction between military zones (Krepinevich & Wood, 2007). The military’s unofficial policy was to use first generation “field expedient” armor (1st generation), a measure described bluntly by American serviceman Thomas Wilson to Secretary Rumsfeld on the latter’s tour of Iraq: “Our vehicles are not armored. We’re digging pieces of rusted scrap metal and compromised

ballistic glass that's already been shot up, dropped, busted, picking the best out of this scrap to put on our vehicles to take into combat" (Rumsfeld, 2004).

Though the problem of IEDs was identified in May of 2003, it was not until November that the threat became serious enough to justify the \$14,000 cost of armor kits designed to be added to the Humvees already in the field (2nd generation vehicles). Production of armor kits went from 35/month at the end of 2003 to 600/month by mid-2004 (Lamb, Schmidt, & Fitzsimmons, 2009).³ In October 2004, the army purchased 498 additional 3rd generation armored vehicles and began turning every Humvee into a 2nd generation up-armored Humvee (Gayl, 2008).

Following an Inspector General's trip to the theatre in early 2005, the US decided to expedite "bolt-on armor" kits for existing Humvees (2nd generation vehicles) in the short-term and as soon as possible, make a full transition to the 3rd generation M1114 at a cost of \$200,000/vehicle (Gayl, 2008; Lamb, Schmidt, & Fitzsimmons, 2009). Unlike the Humvee, the M1114 was designed to be armored from the ground up and was thus, far more durable. Adding 750-1000 lbs. of extra armor reduced a Humvee's payload, mobility, and reduced the operational life of the vehicle from 18 months to a year (Krepinevich & Wood, 2007; Gayl, 2008). The M1114 restored many of the original Humvee capabilities with significantly greater top, bottom, and side protection than a Humvee with bolt-on armor. By 2007, all of the estimated 21,000 Humvees in Iraq were equipped with some form of upgraded armor. Yet the decision in 2005 to field the M1114 was itself superseded less than two years later when the Joint Chiefs began the 4th generation MRAP program. In December of 2006, the procurement of 4,000 MRAP was approved at a cost of \$600,000-\$1,000,000/vehicle (Lamb, Schmidt, & Fitzsimmons, 2009). In June of

³ These add-on kits were largely the "Frag-5" add-ons. Except for some niche requirements, "Frag-6" kits were deemed to add unnecessary weight (Erwin, 2007). Armor kits had themselves went through a gradual evolution. First generation (Dec 03) armor kits included L-shaped doors and flank armor, 2nd generation (Mar 04) add-ons included armoring wheel-wells and underbodies and third generation (Nov 05) integrated add-ons such as the Marine Armor Kit (MAK) and the Frag 5 (USMC Vehicle Hardening Information Brief, 2005).

2007, the Pentagon approved a one-for-one replacement of up-armored Humvees for MRAPs (Eisler, Morrison, & Vanden Brook, 2007).

The MRAP was not just armored, it was built to allow soldiers to sustain mine blasts and then return fire. Whereas the low, flat-bottomed Humvee trapped the force of underbelly blasts, the hull of the MRAP was armored, raised, and v-shaped to mitigate and deflect the blast force. The weight and the shock absorbing rubber seats mitigated upward acceleration that could snap spines and throw lighter vehicles off the road. Fixed and sealed containers prevented cabin items from turning into projectiles. Side armor and ballistic glass was designed to mitigate road-side blasts and in some models soldiers were seated with their backs along the centerline of the vehicle to maximize situational awareness. Firing ports allowed for engaging the enemy from an armored position. Adding to the cost was a host of other C-IED features such as frequency jammers to prevent radio detonated IEDs (Sinclair, 1996). It was, in short, an embodiment of Gen James Mattis' (former Commander of U.S. Central Command) maxim: Make yourself hard to kill.

While in the beginning of the IED battle, nearly every explosion caused an injury or death, defense officials now stressed the increased protection of 4th generation vehicles. When sustaining a blast "nine times out of ten there are no injuries in an MRAP other than bumps, bruises and scrapes. And we're talking about sizable amounts of explosives" (Osborn, 2008, p. 11). Thus through every generation of vehicle, the military assumed greater costs as new vehicles carried over developments from earlier generations and made further costly additions.

2.1.2.2 For lack of a crystal ball: Avoiding "unnecessary" costs (criterion 4)

By designing a vehicle to protect against IEDs from the ground up, military engineers were able to mitigate or eliminate several of the unique threats of IEDs. But MRAPs were not built to respond to the IED attacks occurring in Iraq, they had been developed in the 1970s in response to the IED threat during

the Rhodesian bush wars. MRAPs had been available to American forces from the beginning and the failure to field them when the threat of IEDs became clear stands in need of explanation.

The argument for each generation of vehicle is plain: each upgrade is an improvement over the earlier generation that it replaced. The more complicated question is why the military didn't field the MRAP earlier. In February of 2005, a universal needs statement was issued by brigadier general Dennis Hejlik which asked "to utilize supplemental funding to replace 1st/2nd generation vehicles, by skipping a generation and procure 4th generation MRAP vehicles." In no uncertain terms, the commander of troops in MNF-W requested MRAPs, yet the Pentagon ultimately decided to expedite bolt-on armor (2nd generation) and field the 3rd generation M1114.

While a justification for expediting field armor might have been justifiable on the basis of speed, the reasoning behind forgoing MRAPs was far more complicated. The major drawback of the MRAP was the price tag. While Gayl (2008) notes that some of this cost would have been defrayed by the greater life-expectancy of the MRAP, there were several other areas that made the MRAP more expensive.

Because of the increased weight, only a few ships and aircraft were able to transport them, placing increased burdens on logistic infrastructure (Erwin, 2007). The heavy weight of the vehicles also resulted in increases in fuel costs (and associated infrastructure to refuel). All told the three-year operating costs (including transportation, maintenance, and fuel) for the MRAP (\$780,000) was over double the cost of the M1114 (\$345,000; Rohlf & Sullivan, 2011). At the time, side-blast IEDs were the predominate threat to soldiers and the military vehicle hardening study showed that the less expensive M1114 was nearly as reliable in dealing with this threat as the MRAP (Gayl, 2008). As a consequence the added costs of the MRAP seemed a needless expense. As long as side-blasts remained the predominant threat, it was disadvantageous to field the MRAP because the extra costs were unjustified.

2.1.3 What works today: Measures and countermeasures (Criteria i, ii and iii)

The main weakness of the M1114 was the hull. Though the hull was armored, it was flat and low to the ground. It is a simple matter of physics that raising the hull three extra feet off of the ground (as in the MRAP) exponentially reduces the force from an underbelly blast (a.k.a. deeply-buried IED (DBIED)). Predominantly used by Sunni insurgents, DBIEDs had occurred before the mass arrival of M1114, but there were only ten recorded between January and September 2005 (Gayl, 2008). By August 2006, there were an average of four DBIEDs per day in MNF-W alone and by the summer of 2007, DBIEDs were killing more soldiers than all other variants of IEDs combined (Atkinson, 2007). Marine Corps Commandant James Conway reported that the shift in tactics occurred “because there were more armored Humvees in Anbar.” (quoted in Vanden Brook, 2007).

DBIEDs were not the only reaction to the M1114, the Shi’a adapted to increased armor by employing explosively formed penetrators (EFPs). An EFP consists of the combination of a bomb with a metal disc that becomes a molten copper slug upon detonation, yet the creation of EFPs requires precise machine tools and adds significant costs to an IED (Wilson, 2006). Even if the vehicle was heavily armored, EFPs cut through the side of the vehicle and turned the armor into shrapnel. Though they emerged in March of 2004, EFP attacks remained relatively rare when far simpler and cheaper IEDs were effective. As second and third generation vehicles began to proliferate the battlefield between the spring and the summer of 2005, the use of EFPs more than tripled (Rohlf & Sullivan, 2011). Though M1114s reliably mitigated the predominant threat facing soldiers at the time they were fielded, that very success led to a proliferation of DBIEDs and EFPs. By 2007, DBIEDs and EFPs accounted for 70% of US casualties (Atkinson, 2007) and the inability of M1114s to deal with these devices prompted the Pentagon to approve a complete one-for one replacement with MRAPs.

This shift in tactics is not isolated to the introduction of M1114s. The IED is not just another weapon: “It is not a matter of IEDs on the battlefield, the IED is the battlefield.” (Barbero, 2012). IEDs allow small groups with minimal resources to engage in strategic competition effectively and

consistently with far more powerful entities. The flexibility of IEDs provided a continued ability to inflict damage against dramatically better equipped troops despite numerous attempts to nullify the threat. Further, the ability to detonate devices without direct confrontation decreased the risk to the insurgent and provided the opportunity to learn from failed attempts. All of these factors help explain why IEDs accounted for over half of the casualties sustained by American troops in Iraq (Krepinevich & Wood, 2007).

As noted in section 2.1.2.1, American vehicles have gotten progressively more sophisticated; however, soldiers have not become progressively less likely to be killed or injured by an IED. This is because of the corresponding evolution of countermeasures taken by insurgents. This dynamic was exquisitely captured by a US commanding officer: “What works today will not work tomorrow simply because it worked today.” (Kirin, quoted in Adamson, 2007, p. 52). First and second generation vehicles provided an initial increase in blast mitigation against “double bangers,” but increased armor quickly led to “five-bangers” capable of nullifying the added protection of an up-armored Humvee (Chisholm, 2005). Just as the Americans did not want to field more expensive vehicles than needed, prior to the arrival of the M1114, DBIEDs were uncommon as they required far more time to emplace, exposing the insurgent to greater risk of being detected by American forces (criterion iv). Yet increased vehicle armor required insurgents to take additional risks in order to reliably kill American soldiers. Though using DBIEDs led to a quicker depletion of caches of explosives and put the insurgent at greater risk of being detected, as insurgents began paying the higher cost associated with DBIEDs (criterion ii) the reliability of M1114s dropped precipitously (criterion i). This chapter explores just one aspect of the IED arms race, similar adaptations also occurred in trigger mechanisms, detection technology, surveillance, and intelligence.

Upon observing that costly innovations are quickly met with countermeasures that attenuate the reliability of US action (criteria i and ii), a tempting option is to avoid the process of escalation in the

first place. Indeed, there was a strong contingent in Rumsfeld's Pentagon that repeated the mantra: "We can't armor our way out of this." Whether the MRAP was worth the investment cannot be determined without access to classified data, but there have certainly been wasteful projects. The predetinator was a multimillion dollar venture that successfully caused a large majority of IEDs to explode safely ahead of the vehicle. While extremely reliable in the short-run, once insurgents identified the technology, a ten-cent counter measure completely negated its effect (Zorpette, 2007). Projects like these should surely be avoided. Yet it is also worth noting that arms races are not just reactive, they are proactive (criteria iii). It is not as if one side can stop the arms race by ceasing to innovate. Both the military and insurgents are constantly probing each other for ways to better exploit weaknesses. For example, insurgents studied American tactics and began placing IEDs in positions soldiers were likely to occupy after taking small arms fire (Barbero, 2012; c.f. Miegs, 1990). Criterion iii is a reminder that in such races a failure to continue innovating is a choice to fall increasingly behind.

In summary, the reliability of various forms of vehicle protection decreased over time. This occurred primarily because insurgents began building more expensive and complicated IEDs, but also because they refined their tactics to exploit American vulnerabilities. However, just as insurgents did not assume the costs of DBIEDs or EFPs while cheaper options were largely equivalent, American warplanners refused to field the more expensive MRAP until it was required by the nullification of cheaper options. For both sides, the dynamic has led to the gradual accumulation of costly measures with little change in the number of soldiers killed.

2.2 What to expect when you're expecting (and you're a Reed Warbler).

Once a pair of Reed Warblers has successfully incubated a cuckoo, they have surrendered the remainder of the breeding season to raise the creature that has killed their young. As a result there is intense pressure to prevent such a disaster. Though such obligate brood parasitism is relatively rare in the

animal kingdom, underlying the interaction is a deeper structure which is far more common. The interaction between the Cuckoo and the Reed Warbler is a continuously escalating contest between two species in which the success of one comes at the expense of the other. It is a co-evolutionary process that is typified by measures and countermeasures as each species evolve measures targeted to exploit or frustrate the other species' current strategy. As it is commonly accepted that the Cuckoo-Warbler dynamic is an example of a biological interspecific asymmetric arms race (e.g. Broom, Ruxton, & Kilner, 2008; Servedio & Hauber, 2006; Takasu, 1998), I will confine my discussion to briefly illustrating that the five features identified in military arms races occur in the biological world as well.

The cycle begins in mid-May when Cuckoos migrate from north Africa to western Europe in order to breed. Instead of building their own nests, Cuckoos must find nests of suitable hosts. Upon locating a number of such nests, the Cuckoo must keep a close eye on the behavior of the inhabitants. If the Cuckoo attempts to lay an egg before the Reed Warbler herself begins laying, it is virtually certain to be rejected. Similarly, an egg laid after the clutch is completed may receive insufficient incubation and fail to hatch at all (Davies & Brooke, 1988). While only laying during the this three to five day window dramatically increases the amount of surveillance required, given the Reed Warbler's strategy, the Cuckoo has no choice but to comply. Indeed, Cuckoos that miss the window of incubation may depredate a host's clutch to initiate a fresh laying cycle (Gehring, 1979, as cited by Davies, 2000).

Once a suitable host is located, the Cuckoo waits in a concealed location such as a nearby tree. When the Reed Warbler leaves to collect food, the Cuckoo descends and alights on the edge of the nest. Though egg laying in most birds takes between 20 and 60 minutes, the Cuckoo both snatches a host's egg and lays an egg of its own to replace it in less than ten seconds. This deft egg exchange is well motivated. Not only can a Reed Warbler occasionally kill a Cuckoo if they spot it, but a Cuckoo sighting also causes the Warbler to inspect their eggs more closely and increases the probability of rejecting the imposter egg (Davies and Brooke, 1988).

Yet it is the shells that are the *pièce de résistance* of the Cuckoo. Though the focus here is on the dynamic with the Reed Warbler, there are five other host species. Each host species lays a distinct looking egg and with one exception (the Dunnock), each host will reject non-mimetic eggs (Brooke and Davies, 1988). Amazingly, Cuckoos lay different looking mimetic eggs. It is only for the non-discriminating Dunnock that the Cuckoo's egg is noticeably distinct. In the five cases where the host species will eject non-mimetic eggs, the Cuckoo's eggs are nearly indistinguishable forgeries (see figure 1). If Cuckoo's laid indiscriminately most of their eggs would be detected. Instead, this pressure has led to the emergence of six different genets of Cuckoos. The female of each gens lays one kind of egg and prefers to lay her egg in the corresponding host's nest, while males mate indiscriminately and keep the population united as a single species (Davies, 2000).

Beyond the shell patterns, Cuckoo eggs are especially hard (Brooker & Brooker, 1991) and surprisingly small (Payne, 1974). The Cuckoo that parasitizes the Reed Warbler lays a 3.4g egg compared to the 10g egg laid by non-parasitic Cuckoos of the same size (Davies, 2000). The thick shell likely serves multiple purposes. It prevents breakage during the frantic laying process and makes it harder for some hosts to destroy by pecking. It may also increase the cost of ejection by being more likely to cause a breakage in the host eggs, should a Reed Warbler make such an attempt. The fact that birds without evolutionary exposure to brood parasites will both remain relatively calm in the presence of a stuffed Cuckoo (Moksnes *et al.*, 1991) and accept non-mimetic eggs in their nest underscores that such behavior is the vestige of a prolonged competition between host and parasite (Davies and Brooke, 1989; Moksnes *et al.*, 1995).

Thus the competition between the Reed Warbler and the Cuckoo is rightfully characterized as an asymmetric arms race. Each population must use disparate measures to maintain a relative fitness advantage over conspecifics. If we suppose that naïve populations of Reed Warblers, like contemporary

unparasitized populations, first showed no ejection behavior and Cuckoos did not lay mimetic eggs, then we can hypothesize a plausible trajectory of the evolutionary dynamic.

First, Reed Warblers became adept at identifying and ejecting non-mimetic eggs, keeping in mind that because Reed Warblers lose about $1/6^{\text{th}}$ of their clutch to breakage during ejection, this action is costly.⁴ Yet Reed Warblers who reject eggs with non-mimetic shell patterns eliminate roughly 70% of Cuckoo eggs. As an illustration of criteria i and ii, the evolution of mimetic eggs by the Cuckoo cuts the effectiveness of rejection on the basis of shell pattern to roughly $1/4^{\text{th}}$ of its initial effectiveness. This remaining effectiveness could be cut into even further if the Cuckoo evolves the tendency to depredate Reed Warbler nests to initiate a new cycle of egg laying. Because it is a response to physical realities of incubation time (instead of a countermeasure) it represents an instantiation of criterion iii. However, just as unparasitized species have no need to pay the cost of occasional mistakes to maintain rejection behavior, the Cuckoo gens that primarily parasitizes the non-discriminating Dunnock does not pay the cost of making their eggs less acceptable to secondary hosts (criteria iv). Finally, though the order is not clear this process repeats and yields an accumulation of discrimination criteria (timing, size, color) and corresponding mimicry which are just a few of the accumulated costly measures that this arms races has produced (criterion v).

2.3 A game theoretic model of interspecific asymmetric arms races

Given that we have a qualitative description of the features of asymmetric arms races, I now turn to examining the adequacy of formal models to capture these features. I will first argue that no current model effectively captures the essential features of asymmetric arms races. Next I will propose a novel model which does have all of these features, and finally I will use this model to formally cash out a definition of reliability and robustness.

⁴ The numbers used in this example are taken from those reported in Davies and Brooke (1988)

2.3.1 Previous Models

In summary, the five essential features discussed above are: (i) the reliability of any strategy (once it is employed) typically decreases over time; this is because both (ii) opponent responses often attenuate the efficacy of one's strategy; and (iii) opponents engage in a search process to identify and exploit weaknesses; however, (iv) because measures are costly it is often disadvantageous to adopt new strategies until they are necessitated by an opponent; and (v) the process results in the gradual accumulation of costly measures. In 2.3.1 I will argue that no past models capture all these essential features before turning to my own model in 2.3.2.

Most previous models are unsatisfactory for our purposes because they only consider the emergence of a single behavior. Whether these models adequately capture the particular aspect on which they focus is beyond the scope of this chapter. What is important is that because they only explore one aspect of an arms race, they cannot possibly shed light on the accumulation of many costly measures over time. This fails to capture the fifth feature of arms races.

One example of such an analysis is the model proposed by Servedio & Hauber (2006). In their game a host has three possible strategies, they can either eject an egg, abandon their nest, or do nothing. A host has some probability of being parasitized based on the frequency of parasites. A host surveys their clutch and if a sufficiently distinct egg is detected the host employs one of the three strategies. An egg ejector rids the nest of the aberrant egg, a deserter starts a new nest and lays a clutch at some fitness cost, an acceptor does nothing. Servedio and Hauber show that when the cost of being parasitized is high (e.g. the new-born cuckoo destroys all the host's eggs), then ejection is virtually always the preferred strategy. In contrast when the cost of being parasitized is low (e.g. the cowbird chick is raised alongside the host's nestlings), then the parameter values (parasitism rates, relative cost of re-nesting vs. raising a parasite, etc.) determine if egg ejection or re-nesting is the dominant strategy.

Because a host must choose between actions, the model is not geared to capturing the accumulation of costly measures that occur in arms races. Further, as the authors themselves note, “a limitation of this approach is that we could not evaluate the coexistence of alternative behavioural strategies (abandon vs. eject) within the same population, even though it occurs to different extent in several host species” (p. 1587). Other models that are limited for this reason include: Broom, Ruxton, & Kilner’s (2008) model of nest desertion (host) and egg destruction (parasite); and Takasu’s (1998) model of egg mimicry and egg rejection.

A second sort model that does not serve current purposes occur are those where multiple strategies are available, but only for one side of the arms race. These models present a fixed target which thus fails to capture features ii and iii. One such model is presented by Planque et. al. (2002). In his model a host can accept a clutch, reject eggs, reject chicks, or both. The model seeks to explain why chick rejection is infrequent in cuckoo bird hosts. Essentially, they argue that redundant defenses are unneeded when the parasite load is low and/or the effectiveness of one of the defenses is high. In the latter case the host pays the cost for both measures but derives little benefit from the second defense as the parasite load has already been reduced significantly by the first effective measure. Because the model only considers the strategy of one of the populations it fails to capture how the development of countermeasures alters payoffs.

A final model is proposed by Harrison and Broom (2009). Their model can be broken down into two independent sub games. In the adult game, a host first decides how many eggs to lay, next the nest is visited by a parasite with some probability, the parasite then chooses whether to destroy any of the hosts eggs as it lays, nature then destroys some eggs with a fixed probability, and finally, in stage four, the host observes the eggs and chooses whether to accept the clutch, reject an egg, or abandon the nest. In the second subgame, nature again destroys some eggs with a fixed probability, next, if there is a parasite in the nest, it hatches and the nestling chooses whether to destroy some number of eggs, and

finally, the host observes the number of nestlings that remain and decides whether to raise the brood or abandon the nest. This model captures the fact that measures interact in terms of their payoffs, but it gives no insight into the dynamics of population evolution, which as we will see in the next section has non-obvious consequences for what strategies are selected for.

2.3.2.1 *A formal model*

To set up arms race, the first condition is two separately evolving populations, say Cuckoos and Reed Warblers. Each naïve population possesses neither measures nor countermeasures. Suppose that initially, a Cuckoo egg is a different color and size from a Reed Warbler's and it is often laid slightly before a Reed Warbler begins laying its own clutch. Clearly, the Reed Warbler has no interest in raising a Cuckoo and thus evolving the ability to discriminate its own eggs from cuckoo eggs presents an obvious gain in fitness. Supposing for simplicity that the Reed Warbler either has or lacks the ability to discriminate eggs on the basis of size, color, and, time, we can represent a Reed Warbler's strategy as an ordered triple. For example, $R(0,0,0)$ is a naïve Reed Warbler employing no measures and $R(1,1,1)$ is a fully armed Reed Warbler that discriminates on all three distinctions. By similar reasoning a Cuckoo has no interest in a Reed Warbler pitching out its eggs, so if eggs laid early get destroyed, there will be evolutionary pressure to lay eggs later. Similar pressures exist to match size and color if these characteristics become targets of discrimination. Thus, we can label the strategy of a naïve Cuckoo as $C(0,0,0)$ and a fully armed Cuckoo that employs all three countermeasures as $C(1,1,1)$.

For a first pass, neglecting the dynamics of how populations evolve, suppose measures and countermeasures work as follows. When a naïve Reed Warbler $R(0,0,0)$ is parasitized by naïve Cuckoo $C(0,0,0)$ life is typically bad for the Reed Warbler. Unless the egg is accidentally damaged or fails to incubate, the baby Cuckoo will hatch, destroy the other eggs in its nest, and the Reed Warbler will spend the rest of the breeding season rearing an unrelated chick. For simplicity's sake let's say the payoff for either side of a successful breeding season is one. Thus with some small probability (P) the Reed

Warbler lucks out and raises its own young and with some large probability (1-P) the Cuckoo fools the naïve host.

Next suppose that discrimination measure work as follows. Each discrimination measure allows the Reed Warbler to identify and destroy some portion of Cuckoo eggs that would otherwise have gone unnoticed. Let D, E, and F, represent the probabilities that a Reed Warbler will reject the egg of a naïve Cuckoo discriminating on the basis of color, size, or timing respectively. Though such an assumption is not necessary, for the example I will assume that each measure functions independently. Accordingly, the probability of a Cuckoo egg evading a discrimination measure is just (1-D) or (1-E) or (1-F). Thus the payoff for a naïve Cuckoo encountering a fully armed Reed Warbler is given in equation 1:

$$(1) \quad (1 - P)(1 - D)(1 - E)(1 - F)$$

Correspondingly, the payoff for the fully armed Reed Warbler is the baseline number of chicks plus some percentage of chicks it gains from identifying the cuckoo egg with at least one of the measures, specifically:

$$(2') \quad P + (1 - P) * (1 - ((1 - D) * (1 - E) * (1 - F)))$$

Equation 2' gives the probability of the Reed Warbler raising its own young, but it fails to capture an important aspect of many measures in an arms race, namely that they are costly. Such an equation would only be warranted if the Reed Warbler never made mistakes and always avoided breaking its own eggs in the process of ejecting others. Given that we know that such an assumption is unwarranted, we can assign costs J, K, and L for discriminating on the basis of size, color, and, timing. We might reasonably think of multiple costs being sequentially applied, reducing the remaining payoff by some fraction. Thus the cost of the second measure applies only to the fitness remaining after the first cost has been exacted. In essence it supposes that there is no further penalty for breaking your

own egg twice. Again, assuming that these costs are independent, the final payoff for the fully armed Reed Warbler is 2' reduced by the fraction of its own eggs it breaks (i.e. the costs):⁵

$$(2) \quad (J)(K)(L)(P + (1 - P) * (1 - ((1 - D) * (1 - E) * (1 - F))))$$

In response to the measures taken by the Reed Warbler, the Cuckoos develop countermeasures to attenuate the effectiveness of such discrimination. So if discriminating on the basis of timing caught 90% of Cuckoo eggs and the countermeasure was so successful that it reduced timing discrimination to 10% of its former effectiveness, now only 9% of Cuckoo eggs are discriminated against when both the measure and the countermeasure are in play. Just as measures have costs, so do countermeasures such as increasing the amount of surveillance necessary to lay. Let G, H, and I, represent the fraction of the original measure that remains effective after the counter has been employed and let M, N, and O be the cost of employing those counters. Note that a countermeasure does no good in absence of the appearance of the measure but it still incurs a cost. If our poor naïve Cuckoo finally evolved the first countermeasure and laid a smaller egg, the fitness of the fully armed Reed Warbler (R(1,1,1)) is now given in equation 3 (the change from equation 2 is bolded for clarity) and the Cuckoo's (C(1,0,0)) fitness is expressed in equation 4 (the change from equation 1 is bolded for clarity) :

$$(3) \quad (J)(K)(L)(P + (1 - P)(1 - ((1 - (D)(\mathbf{G}))(1 - E)(1 - F))))$$

$$(4) \quad (\mathbf{M})(1 - P)(1 - (D)(\mathbf{G}))(1 - E)(1 - F)$$

The specification of baseline probability, effectiveness and cost of measures and countermeasures fully specifies the payoff matrix. The presence or absence of three measures yields eight possible types for both the Reed Warbler and the Cuckoo. The general 8x8x2 payoff matrix is given in appendix 1 and an example payoff matrix is given in figure 2.

⁵ Though I use the brood parasite dynamic for the purpose of exposition, obviously nothing hangs on particulars. The model is intended to be general. For example the extra fuel costs of an MRAP stop accruing if a vehicle has been disabled, etc. This example is merely intended to be a base case and the model can accommodate interacting variables, different cost structures, etc. as suggested by the empirical phenomenon.

2.3.2.2 Model dynamics

The model uses the standard infinite population replicator dynamics with mutation. The proportion of cuckoos employing a strategy at time $(t+1)$ is primarily determined by their proportion at time t and their relative fitness given the distribution of Reed Warbler strategies at time t . Specifically where $x_{(c,i)}$ is the proportion of cuckoos using strategy i , $F_{(c,i)}(t)$ is the average fitness of strategy i , and $F_{(c)}(t)$ is the average fitness of the whole population:

$$(5) \quad x_{(c,i)}(t + 1) = x_{(c,i)}(t)F_{(c,i)}(t)/F_{(c)}(t)$$

The proportion of Reed Warblers is primarily determined in the same way, *mutatis mutandis*.

The second contribution to the population of a strategy is the probability of mutation of one strategy into another. Instead of allowing for the allowing the probability of mutating from one strategy into any other to be equal, a distance metric is created by allowing each of the three registers to have a mutation frequency. Thus, let the probability that a Reed Warbler adopting the first measure in $(t+1)$ if it does not employ it at time t (or vice versa) be δ and the probability of remaining the same = $(1 - \delta)$. For the sake of simplicity, let us assume that each of the six registers has an equal probability of mutation. For example, the probability that $C(0,0,0)$ mutates into $C(0,0,1)$ is much more likely (assuming mutation rates are low) than $C(0,0,0)$ mutating into $C(1,1,1)$. In line with this commitment, for the dynamics presented here the probability of mutating one register is $(\delta)(1-\delta)(1-\delta)$, whereas the probability for mutating all three registers is $(\delta)^3$. In general, common strategies will lose some small percentage of its population to mutation and extremely rare strategies will experience a small influx from mutations.

2.3.3.1 Example

In this section I shall consider a specific instantiation of the arms race model. First I will present a graphic representation of the model and highlight some salient features of the evolution. As I do so I will argue that this model captures each of the essential features of an arms race. In 2.3.4 I will use the model to cash out a formal notion of reliability.

As a first pass at understanding the arms race we examine the payoff matrix in figure 2. The first thing to note is that if the game was played as a series of sequential best responses then the game would be similar to rock-paper-scissors. Cuckoos can move up and down in a given column and Warblers can move left and right in a given row. The best response for a Reed Warbler against C(0,0,0) is R(0,0,1). The ensuing series of best responses is as follows: C(0,0,1); R(0,1,0); C(0,1,0); R(0,0,1); and these four moves would then simply cycle. Indeed we can say something stronger. Any opening move in a sequential game other than a fully armed opening, ultimately ends in this 4 move cycle.

The second thing to note is that given a monomorphic Reed Warbler population the Cuckoo's best response is to employ the requisite countermeasures, but given a pure Cuckoo population a Reed Warbler is always better of dropping a defeated (and costly) measure and adopting a new measure that

| | R(0,0,0) | R(0,0,1) | R(0,1,0) | R(1,0,0) | R(0,1,1) | R(1,0,1) | R(1,1,0) | R(1,1,1) |
|----------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| C(0,0,0) | 0.1000 0.9000 | 0.6667 0.2000 | 0.5833 0.3000 | 0.3833 0.5400 | 0.6481 0.0667 | 0.6111 0.1200 | 0.5694 0.1800 | 0.5556 0.0400 |
| C(0,0,1) | 0.1000 0.7500 | 0.1708 0.6625 | 0.5833 0.2500 | 0.3833 0.4500 | 0.5104 0.2208 | 0.3632 0.3975 | 0.5694 0.1500 | 0.4867 0.1325 |
| C(0,1,0) | 0.1000 0.7500 | 0.6667 0.1667 | 0.1833 0.6500 | 0.3833 0.4500 | 0.5741 0.1444 | 0.6111 0.1000 | 0.3694 0.3900 | 0.5185 0.0867 |
| C(1,0,0) | 0.1000 0.7500 | 0.6667 0.1667 | 0.5833 0.2500 | 0.2033 0.6300 | 0.6481 0.0556 | 0.5778 0.1400 | 0.5194 0.2100 | 0.5463 0.0467 |
| C(0,1,1) | 0.1000 0.6250 | 0.1708 0.5521 | 0.1833 0.5417 | 0.3833 0.3750 | 0.2160 0.4785 | 0.3632 0.3312 | 0.3694 0.3250 | 0.3395 0.2871 |
| C(1,0,1) | 0.1000 0.6250 | 0.1708 0.5521 | 0.5833 0.2083 | 0.2033 0.5250 | 0.5104 0.1840 | 0.2307 0.4638 | 0.5194 0.1750 | 0.4499 0.1546 |
| C(1,1,0) | 0.1000 0.6250 | 0.6667 0.1389 | 0.1833 0.5417 | 0.2033 0.5250 | 0.5741 0.1204 | 0.5778 0.1167 | 0.2394 0.4550 | 0.4944 0.1011 |
| C(1,1,1) | 0.1000 0.5208 | 0.1708 0.4601 | 0.1833 0.4514 | 0.2033 0.4375 | 0.2160 0.3987 | 0.2307 0.3865 | 0.2394 0.3792 | 0.2438 0.3349 |

Baseline probability for Reed Warblers = (1/10) Mutation rate for a single register = (1/10,000)
 Reed Warbler measures = (2/5, 2/3, 7/9) Cuckoo countermeasure = (2/5, 1/5, 3/20)
 Cost of Reed Warbler measures = (5/6, 5/6, 5/6) Cost of Cuckoo's countermeasures = (5/6, 5/6, 5/6)

Figure 2: Above is the payoff matrix for the sample arms race. The column gives the Reed Warbler strategy and the row gives the strategy of the Cuckoo. In the cell the payoffs are given for both birds according to the color code.

is not yet countered. The exception is when there are no uncountered measures (i.e. a fully armed opponent) in which case the best response is to fully arm. Finally, both populations fully armed is the unique strict Nash equilibrium, though there are six combinations of strategies where both parties receive better payoffs (e.g. $R(1,1,0)/C(0,1,0)$). As can be seen from the graph in figure 4, when the simulation is run, the loop alluded to above is avoided and the population settles at the Nash equilibrium by roughly the 500th generation.

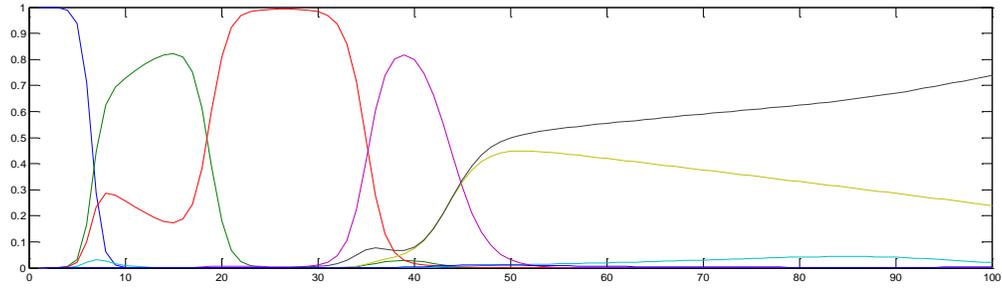
2.3.3.2 *Sample dynamics*

Figure 3 presents the dynamic evolution of the Reed Warbler and Cuckoo populations over the first 100 generations from two completely naïve populations. The first major event happens between generations 5 and 8 as both $R(0,0,1)$ and $R(0,1,0)$ begin to replace the naïve population in response to the pressure exerted from parasitism, then because $R(0,0,1)$ has a higher fitness than $R(0,1,0)$ the latter begins to be replaced by the former. Yet because $R(0,0,1)$ begins to dominate the population of Red Warblers, the Cuckoo countermeasure is now highly selected for and within 10 generations is sufficiently prevalent that $R(0,0,1)$ is selected against. This captures the first and second criteria for an arms race. As can be seen in figure 3, the effectiveness of any strategy that is employed typically decreases over time and this is because the opponent's response attenuates the efficacy of ones actions.⁶ This can be seen by referencing the bottom figure to the two above. For example the red line representing the fitness of $R(0,1,0)$ stays high as the strategy takes over the Reed Warbler population, but begins decreasing as Cuckoos evolve the countermeasure around generation 25.

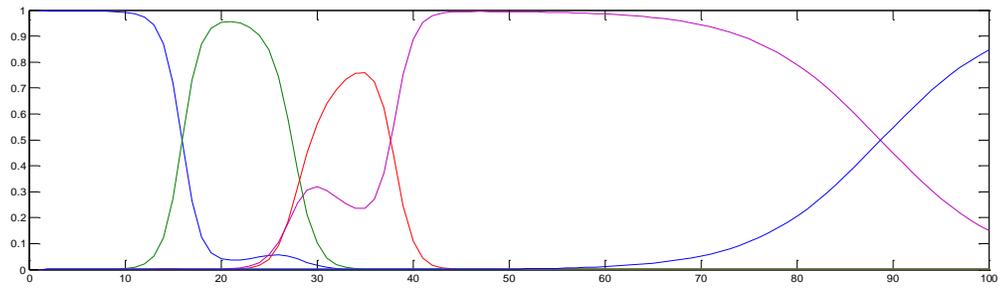
As such phenomena happen in actual arms races, it is worth observing the effectiveness for Cuckoos evolving the first countermeasure was attenuated by the presence of an effective Reed Warbler

⁶ The third criteria—opponents engage in a search process to identify and exploit weaknesses—is not applicable to infinite population models. After $t=2$, every strategy is present in the population in some small proportion. However, in a finite case it would certainly be possible for a population to evolve a new superior strategy before an opponent evolved a countermeasure to the initial strategy.

Frequency of Reed Warbler strategies (100 generations)



Frequency of Cuckoo strategies (100 generations)



Fitness of Reed Warbler strategies (100 generations)

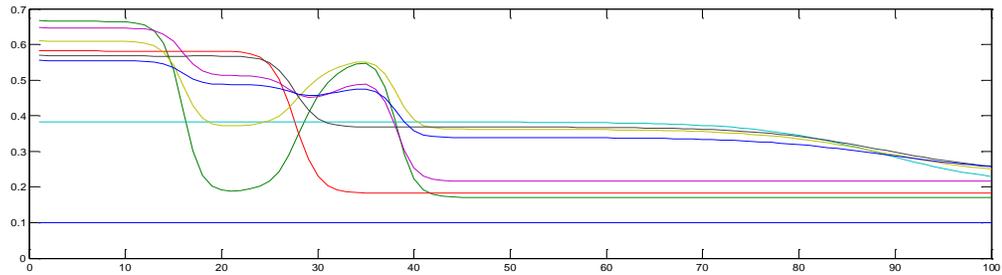
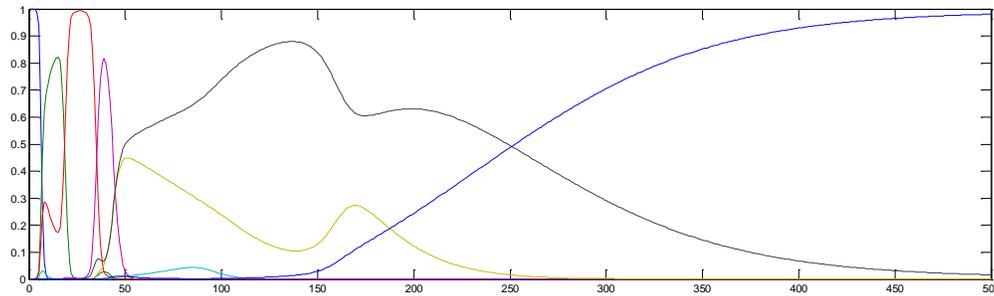


Figure 3: The dynamics of Reed Warblers (above) and Cuckoo (middle) populations for 100 generations. The bottom graph displays the fitness of the Reed Warbler strategies. In both cases the colors represent the following strategies: leftmost blue line (0,0,0); green (0,0,1); red (0,1,0); purple (0,1,1); dark green (1,1,0); olive (1,0,1); light blue (1,0,0); rightmost blue line (1,1,1).

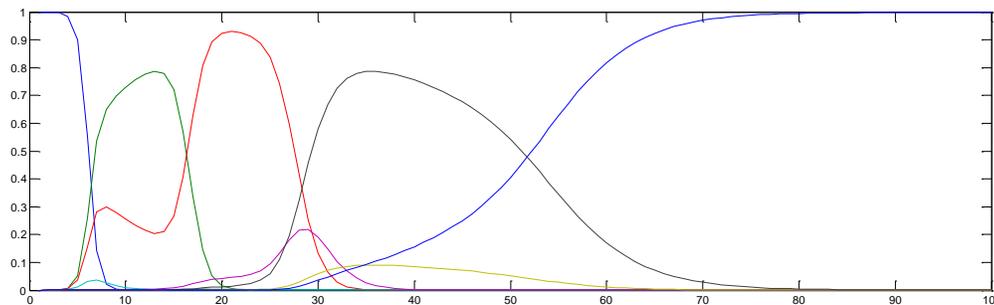
subpopulation R(0,1,0) which quickly took over as the first strategy R(0,0,1) was countered. The consequence of protecting against a prevalent and dangerous threat, when there is an existent alternative threat in the population is an almost immediate switch to the alternative strategy. The ascendance of R(0,1,1) has the same effect on the counterstrategy C(0,1,1) between generation 30 and 39. Note that here the Cuckoo population is only a generation or two behind.

Once $C(0,1,1)$ dominates the Cuckoo population (around the 40th generation) the Reed Warblers should drop the defeated measures and employ $R(1,0,0)$ as a best response, but two phenomena prevent this. First is the now familiar fact that there are other strategies in the population that

Frequency of Reed Warbler strategies with unequal mutation rates and costs (500 generations)



Frequency of Reed Warbler strategies with unequal mutation rates, but without costs (100 generations)



Frequency of Reed Warbler strategies without costs or unequal mutation rates

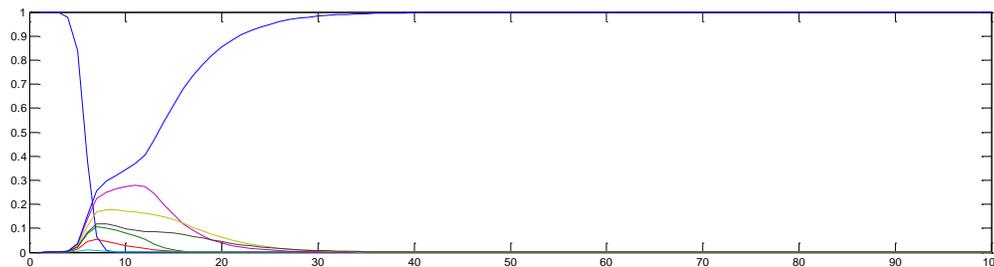


Figure 4: These graphs charts the evolution of the Reed Warbler populations if there is a cost for measures (top) and when measures are costless (middle). Note that the two graphs have different time scales. Whereas with costs fully armed Reed warblers do not achieve fixation until the 500th generation, fixation occurs by roughly the 75th generation when no cost is imposed. Indeed the only thing that holds back fully armed Reed Warblers $R(1,1,1)$ from taking over immediately is the evolutionary distance from the initial population of all naïve birds $R(0,0,0)$ as can be seen when all mutations are made equally likely (bottom).

outperform the population average. Second is the fact that even if the population starts from a pure state of $R(0,1,1)$ and $C(0,1,1)$, $R(1,0,0)$ will not emerge because the “evolutionary distance” is so great (three mutations are required), that the Cuckoo population will have changed significantly before $R(1,0,0)$ can get a foothold (see appendix 2 for the simulation). Instead, two “nearer” strategies $R(1,0,1)$ and $R(1,1,0)$ come to dominate and against the polymorphic population, Cuckoos are forced to adopt a fully armed strategy. This creates a situation where fully armed Reed Warblers are selected for (See figure 4 for the continuation of the Reed Warbler evolution).

There are many ways to see that costly actions are disadvantageous before they are necessitated by an opponent’s action (criteria four). One way is a simple inspection of the payoff matrix in figure 2. The only reason that adding measures does not necessarily lead to a fitness gain is because measures have attendant costs. Facing a naïve Cuckoo, the fitness of $R(0,0,1) > R(0,1,1) > R(1,1,1)$. Without costs, this order would be reversed. In terms of the dynamic evolution, this pushes the fixation of a fully armed reed Warbler from roughly the 70th generation to the 500th as seen in figure 4.

The final criteria, is the gradual accumulation of costly measures. Clearly since each population ends up fully armed and each measure has a cost this criterion is fulfilled. This is represented graphically in figure 5 which displays the average fitness of each population as well as the decreasing average sum

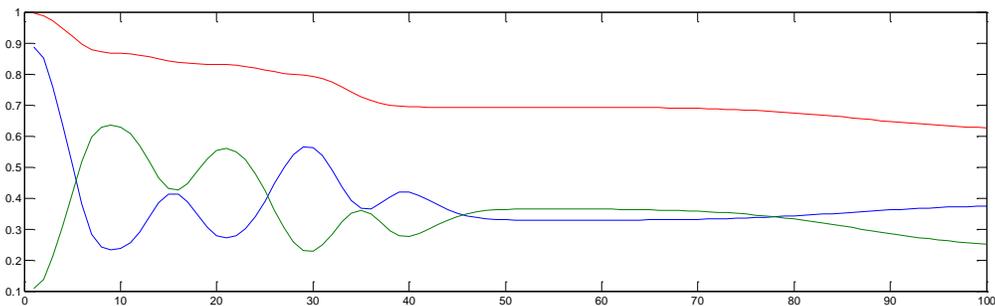


Figure 5: This graph charts the running average fitness (five generations) for the Cuckoo (blue) and Reed Warbler (green) populations as a whole (generations 5-104). The red line charts the declining sum of the fitnesses as fitness is diverted from reproduction to costly measures. By the 100th generation nearly 1/3 of the overall fitness has been so diverted.

of the combined fitnesses. As each population accumulates costly measures a greater portion of total fitness is diverted to the arms race to maintain relative fitness against other strategies within the population.

2.3.4 Dynamics, reliability and robustness.

Clearly the particulars of the population dynamics will depend on the specific values of the population parameters. This is as it should be. For example, when the cost of a measure outstrips its benefit, the measure will not emerge as part of any successful strategy. A real instantiation of this phenomenon is the lack of nestling discrimination by Reed Warblers. Though nestling discrimination has evolved in some parasitized species, the cost of employing the measure for Reed Warblers is too high (Davies, 2000). Similarly, some measures may be worth the cost only when a countermeasure is below some frequency. In such cases instead of a stable end state, there is no pure strategy Nash equilibrium and the result is oscillating strategy frequencies (see appendix 3). Given that this is what we would expect, such phenomena are a feature, not a limitation of the model.

Finally, we can turn to the motivating question of reliability. The most straightforward way of cashing out reliability is to assert that a strategy is reliable to the extent that employing it brings about the desired outcome. In the context of this example, it is clear that this question cannot be answered in terms of a single measure, but rather in terms of a strategy at a given time. As can be seen in the bottom graph in figure 3 the most reliable strategy for a Reed Warbler at time $t=50$ is $R(1,0,0)$; light blue). Though context is important, given a model that specifies the necessary parameters we can specify a precise notion of reliability in terms of the fitness of a strategy at a given time:

$$(6) \quad \text{reliability}_{(i,t)} = F_{(i)}(t)$$

This definition captures what is often desired when we evaluate how measures are working. For example, in considering possible options during the Operation Iraqi Freedom, the military assessed how reliably the M1114 and the MRAP were at protecting American soldiers against the threat they faced in

October 2005. This overall assessment took into account both effectiveness of withstanding IED attacks and the relative cost of the two vehicles.

Yet there is another question that is very often the question that should be asked when reliability is assessed. That question is how reliable would various strategies would be if they were employed on a mass scale. Just because a strategy is reliable in the current environment does not mean it will continue to be reliable if that strategy is implemented on a mass scale because in all likelihood this will change the evolutionary dynamics. Let us define the *robustness* of strategy i as the average reliability from time t to time $t+n'$ given that it is made the unique population strategy:⁷

$$(7) \text{ robustness}_{(i,t,t+n')} = (\text{reliability}_{(i,t)} + \text{reliability}_{(i,t+1')} + \dots + \text{reliability}_{(i,t+n')}) / (n + 1)$$

Given this notion of robustness we may state that a strategy is optimally robust to the extent that for any strategy j , $\text{reliability}_{(i,t)} > \text{reliability}_{(j,t)}$ and for the relevant period n , $\text{reliability}_{(i,t)} = \text{reliability}_{(i,t+n)}$. The later will be true when making strategy i the unique population strategy does not provoke a counterstrategy that substantially degrades the reliability of strategy i by time $t+n$. In some cases, the strategy that is the most reliable at t is not the most robust solution for t through $t+n$, and so no solution is optimally robust. Nevertheless, when considering an intervention, it is robustness not reliability that is the crucial desiderata. It may not be too much to say that had the military considered robustness instead of reliability, they would have fielded the MRAP instead of the M1114 in 2005 as insurgents quickly (and foreseeably) adapted to the defenses of the M1114, a facility they have not demonstrated with the MRAP.

⁷ Note that if we are looking retrospectively, the distribution of the other population at time $t+1$ will not be the same as in the original model because the evolutionary dynamics will change as a result of the intervention, a new simulation will need to be run with the population frequency in population A altered at time t . Further, we may just as easily ask about the robustness of a mixed strategy (i.e. 80% $i=2$ and 20% $i=7$).

Appendix 1: The generalized payoff matrix

| | |
|--|-------------|
| Baseline probability of Reed Warbler success | = P |
| Baseline probability of Cuckoo success | = C = (1-P) |
| Effectiveness of Reed Warbler measures | = (D, E, F) |
| Effectiveness of Cuckoo's countermeasures | = (G, H, I) |
| Cost of Reed Warbler measures | = (J, K, L) |
| Cost of Cuckoo's countermeasures | = (M, N, O) |

For the sake simplicity I will use the following additional notation

Effectiveness for a Cuckoo of failing to adopt a countermeasure = (Q, R, S) = (1-D, 1-E, 1-F)

Effectiveness for a Warbler when playing a countered measure = (X, Y, Z) = (DG, EH, FI)

Effectiveness for a Cuckoo of playing a countermeasure = (U, V, W) = (1-X, 1-Y, 1-Z)

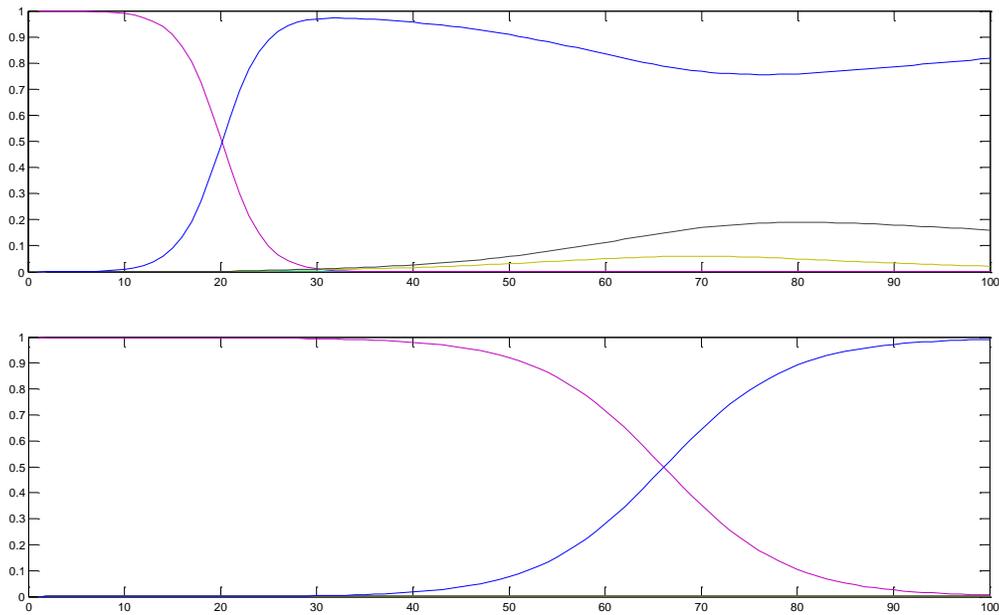
| | R(0,0,0) | R(0,0,1) | R(0,1,0) | R(1,0,0) | R(0,1,1) | R(1,0,1) | R(1,1,0) | R(1,1,1) |
|-----------------|-----------|------------------|------------------|------------------|-------------------------|-------------------------|-------------------------|----------------------------|
| C(0,0,0) | P C | (P+FC)L CS | (P+EC)K CR | (P+DC)J CQ | (P+C(1-RS))KL CRS | (P+C(1-QS))JL CQS | (P+C(1-QR))JK CQR | (P+C(1-QRS))JKL CQRS |
| C(0,0,1) | P CO | (P+ZC)L COW | (P+EC)K COR | (P+DC)J COQ | (P+C(1-RW))KL CORW | (P+C(1-QW))JL COQW | (P+C(1-QR))JK COQR | (P+C(1-QRW))JKL COQRW |
| C(0,1,0) | P CN | (P+FC)L CNS | (P+YC)K CNV | (P+DC)J CNQ | (P+C(1-VS))KL CNVS | (P+C(1-QS))JL CNQS | (P+C(1-QV))JK CNQV | (P+C(1-QVS))JKL CNQVS |
| C(1,0,0) | P CM | (P+FC)L CMS | (P+EC)K CMR | (P+XC)J CMU | (P+C(1-RS))KL CMRS | (P+C(1-US))JL CMUS | (P+C(1-UR))JK CMUR | (P+C(1-URS))JKL CMURS |
| C(0,1,1) | P CNO | (P+ZC)L CNOW | (P+YC)K CNOV | (P+DC)J CNOQ | (P+C(1-VW))KL CNOVW | (P+C(1-QW))JL CNOQW | (P+C(1-QV))JK CNOQV | (P+C(1-QVW))JKL CNOQVW |
| C(1,0,1) | P CMO | (P+ZC)L CMOW | (P+EC)K CMOR | (P+XC)J CMOU | (P+C(1-RW))KL CMORW | (P+C(1-UW))JL CMOUW | (P+C(1-UR))JK CMOUR | (P+C(1-URW))JKL CMOURW |
| C(1,1,0) | P CMN | (P+FC)L CMNS | (P+YC)K CMNV | (P+XC)J CMNU | (P+C(1-VS))KL CMNVS | (P+C(1-US))JL CMNUS | (P+C(1-UV))JK CMNUV | (P+C(1-UVS))JKL CMNUVS |
| C(1,1,1) | P CMNO | (P+ZC)L CMNOW | (P+YC)K CMNOV | (P+XC)J CMNOU | (P+C(1-VW))KL CMNOVW | (P+C(1-UW))JL CMNOUW | (P+C(1-UV))JK CMNOUV | (P+C(1-UVW))JKL CMNOUVW |

Appendix 2: Simulating the evolution of R(0,1,1) vs. C(0,1,1)

Given every Cuckoo plays C(0,1,1) the best responses are:

R(1,0,0; light blue) = .3833 > R(1,1,0; dark green) = .3694 > R(1,0,1; olive) = .3632 > R(1,1,1; blue) = .3395

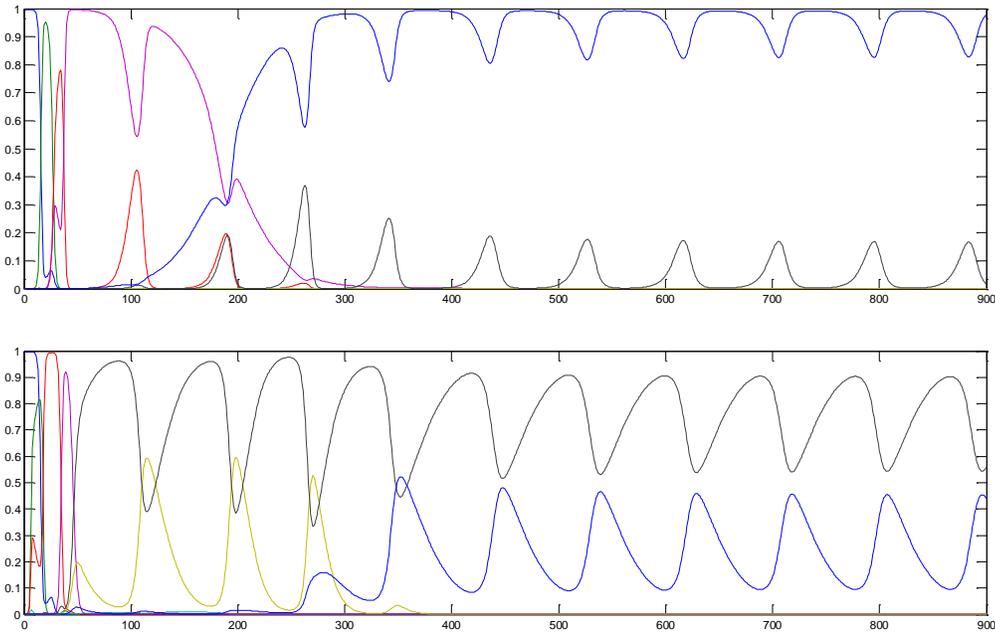
The least favorable alternative takes over because of the evolutionary distance between the currently played strategy R(0,1,1; purple) is nearest for a fully armed reed Warbler than other strategies. Indeed the best response is so far away evolutionarily it does not show up in a proportion large enough to register on the graph. The top graph charts 100 generations of Reed Warblers beginning from 100% R(0,1,1), the bottom charts the evolution of Cuckoos over the same time starting from 100% C(0,1,1).



Appendix 3: A simulation with no pure strategy Nash equilibrium

In the following case there is no pure strategy Nash equilibrium. The best response to a fully armed Cuckoo C(1,1,1) is to stop discriminating on the basis of time R(1,1,0). As R(1,1,0) takes over the Reed Warbler population, it no longer pays to maintain the counterstrategy and C(1,1,0) begins to be selected for. The begins to start selection pressure for a fully armed Reed Warbler R(1,1,1), which in turn restores the selection pressure for a fully armed Cuckoo C(1,1,1). The graph below displays 900 generations and contains numerous iterations of this cycle.

| | |
|---|--------------------|
| Baseline probability of Reed Warbler success) | = 9/10 |
| Baseline probability of Cuckoo success) | = 1/10 = (1-P) |
| Effectiveness of Reed Warbler measures | = (1/3, 2/3, 7/9) |
| Effectiveness of Cuckoo's countermeasures | = (1/2, 1/5, 1/10) |
| Cost of Reed Warbler measures | = (5/6, 5/6, 5/6) |
| Cost of Cuckoo's countermeasures | = (5/6, 5/6, 5/6) |



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