9 In the Light of Introduction: Importance of Introduced Populations for the Study of Brood Parasite–Host Coevolution

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Introduction

Avian brood parasitism represents an extreme and mindboggling reproductive strategy: parasites avoid various costs of parental care and delegate those to other birds, either conspecific or heterospecific. Causes and consequences of brood parasitism have attracted the attention of evolutionary biologists for decades: few natural antagonistic relationships in nature are so amenable to experimental manipulations and quantification of their pros and cons (Rothstein, 1990).

Although representing a mere single per cent of avian phylogenetic diversity, *c.* 100 species, avian obligate brood parasites receive disproportionately high attention from both amateur ornithologists and scientists in evolutionary ecology (Feeney *et al.*, 2014). Such 'full-time' parasites, like *Cuculus* cuckoos or *Molothrus* cowbirds, never build their own nests and consign their progeny to the care of heterospecific hosts. Naturally, this form of parasitism is always interspecific. The other major form of avian brood parasitism is conspecific parasitism, which has been found in *c.* 250 species. Such intraspecific parasites lay eggs into their own nests, but deposit additional eggs into the nests of conspecific neighbours. These parasites, prevalent in, for instance, waterfowl and colonially breeding birds, are always facultative. Rarely, some species, for example some ducks or *Coccyzus* cuckoos, show a mixed strategy of victimizing both conspecifics and heterospecifics apart from laying eggs into their own nests. In recent decades, such natural-born cheats, either conspecific or heterospecific, became popular models to study coevolution, because they allow the investigation of selective pressures on evolution of coevolved traits, the importance of genes, environment and learning, and the resulting trait expressions at various stages of the breeding cycle (Feeney *et al.*, 2014).

Here we highlight the heuristic value of shifting population ranges and introduced populations for studies on brood parasite–host coevolution. First, we outline basic coevolutionary assumptions in this field of study and point to a fundamental problem

of studies concerning evolution of coevolved adaptations: the length of parasite–host contact is, in almost all cases, unknown, being estimated only indirectly. Second, we consider advantages of studies related to expanding, declining and introduced host and parasite populations, and review the few existing studies of populations with known recent length of parasite–host contact. Finally, we discuss prospects for future studies and suggest suitable candidate model systems.

Brood Parasite–Host Studies: Opportunities, Limitations and Solutions

Opportunities

The basic assumption/scenario behind all coevolutionary models is intuitive and simple (Davies and Brooke, 1989). A naïve host, lacking any specific anti-parasite defences, starts to become victimized by a parasite. Parasitism is costly for hosts. Thus, host individuals showing any cognitive and behavioural traits that lower the impact of parasites (e.g. breeding in 'safe' sites, increased nest guarding and aggression, removal of odd eggs or chicks) enjoy higher fitness. Higher host fitness means lower parasite fitness and this selects for parasite counter-adaptations (e.g. furtive laying, mimetic eggs, competitive chicks). If there is enough genetic variation for both host and parasite 'battle' traits, each host adaptation and parasite counter-adaptation would improve (i.e. become more effective) over time. Additionally, new offensive and defensive traits could arise. These principles hold for all developmental stages of the parasite–host battle, i.e. front-line defences against parasite adults (i.e. before they deposit their eggs), then against their eggs, and chicks and finally fledglings (Feeney *et al.*, 2014).

The crucial parameters that affect all aspects of parasite–host coevolution are time (above) and space. Within a specific host, not all populations are necessarily parasitized at the same time (and at the same rate), creating mosaics of coevolutionary hot and cold spots (Thompson, 2005). Knowing when parasites and their hosts came into contact is critical to achieving a better understanding of the adaptations they both may express.

As parasite and host traits coevolve in time and space, the sophistication of host and parasite armoury may provide an indirect measure of the length (time) and intensity (parasitism costs) of coevolution. For example, unsuitable or novel 'hosts' should show no anti-parasite defences, recent hosts in evolutionary time should show poor defences, and hosts used for a long time should show fine-tuned defences (Davies and Brooke, 1989; Moksnes *et al.*, 1991). Such hosts may have even extirpated their parasites, as documented by the almost total rejection of simulated experimental parasitism, combined with historical but not current evidence of natural parasitism (Honza *et al.*, 2004). Importantly, the level of defence among species may very well vary with developmental stage, conditional cues, learning and individual personality, resulting in diverging evolutionary trajectories within and between host–parasite systems (Feeney *et al.*, 2014).

There are many examples of both spatial and temporal variation in adaptations within single host species depending on parasitism pressure, which are likely to reflect genetic differences, phenotypic plasticity or both (Briskie *et al.*, 1992; Nakamura *et al.*, 1998;

Soler *et al*., 1999; Moskát *et al*., 2002; Avilés and Møller, 2003; Stokke *et al*., 2008; Spottiswoode and Stevens, 2012; Kuehn *et al*., 2014). In turn, this variation may reflect evolutionary lag (Igic *et al*., 2012) or spatiotemporal changes in parasite adaptations (Thorogood and Davies, 2013). Several studies, however, suggest that egg rejection behaviour may be retained for long time periods even in the absence of parasitism by brown-headed cowbirds, *Molothrus ater* (Rothstein, 2001; Peer *et al*., 2011). Similarly, several potential hosts of common cuckoos, *Cuculus canorus*, show sophisticated anti-parasite adaptations, even though they are not currently regularly parasitized (Davies and Brooke, 1989; Moksnes *et al*., 1991; Martín-Vivaldi *et al*., 2013). These studies suggested that maintenance of egg rejection in these species is cost-free (but this remains to be tested in most species apparently retaining egg rejection).

However, this may represent only a misleading inference resulting from overlooking alternative selection agents unrelated to defences against brood parasites (Avilés and Parejo, 2011; Avilés *et al*., 2014). In traits with multiple functions, a previously secondary function may maintain a trait after the primary function is lost (Lahti *et al*., 2009). Trnka and Grim (2014) showed that in great reed warbler, *Acrocephalus arundinaceus*, females, aggression towards adult cuckoos strongly correlates with aggression against human observers ('self-defence') and nest guarding (but not with probability of and latency to egg rejection). If the warbler's anti-cuckoo aggression is an integrated part of a suite of correlated behavioural characters (behavioural syndrome), then selection on other components of behaviour may indirectly lead to the maintenance of high anti-cuckoo aggression even in the absence of cuckoos in a population that is no longer parasitized. By the same logic, egg discrimination may be theoretically maintained by other selection pressures unrelated to interspecific parasitism, e.g. conspecific parasitism (Samas *et al*., 2014a, b) or nest sanitation (Peer and Sealy, 2004). However, the latter might apply only to rejection of poorly mimetic interspecific eggs: rejection of mimetic eggs (especially conspecific eggs) requires extremely fine-tuned cognitive abilities that, in principle, cannot represent a by-product of very rough discrimination of objects needed in the context of nest cleaning (Samas *et al*., 2014a). Importantly, nest sanitation is present in virtually all passerines and therefore cannot explain taxonomic variation in egg rejection (Peer and Sealy, 2004). No matter the mechanism, maintenance of anti-parasite defences after relaxation from parasite pressure would make it difficult for brood parasites to re-invade such hosts (Rothstein, 2001).

Limitations

To disentangle the causes responsible for observed patterns of covariation between host adaptations and parasite presence/absence, we would ideally need to know historical patterns of parasite–host contact. However, we know little about the length of the host–parasite interactions. Naturally, the (non)existence of long-term parasite–host contact, i.e. the scale of thousands and millions of years, is unknown in all cases. A currently parasitized population may have become parasitized only recently, thus being effectively allopatric at relevant evolutionary time-scales. By the same logic, a population that is

currently not parasitized may have escaped from parasitism only recently, thus being effectively sympatric at evolutionary time-scales.

Most studies so far have concerned specific host and/or parasite populations at a specific time and place, representing 'snap-shots' of only a few breeding seasons. Such studies have resulted in important advances in our knowledge of coevolutionary interactions, and work adequately for addressing various questions related to brood parasitism, like variables affecting risks of parasitism, nest site selection, baseline levels of defences, egg mimicry, demography, and molecular analyses and dispersal patterns. However, it is impossible to track the temporal variation in coevolutionary interactions of specific populations based on just couple of years of study. Studies of long-term interactions are rare in general (Thompson, 2005), simply due to the work load required to undertake such investigations.

Assessing the length of the host–parasite interactions is further complicated considering that any host population we currently observe may have become locally extinct and recolonized its current geographical location multiple times. This effect is certain in northern areas: no current Scandinavian cuckoo or host population can be older than 10 000 years *in situ*. Pleistocene climate dynamics, with over 30 glaciation events during the last 2 million years, massively affected the ranges of all species globally, including tropics (e.g. Joseph *et al.*, 2002). Even today, 10 millennia after the end of the last glaciation, we witness range shifts that reflect Pleistocene climatic events (e.g. continuing westward range expansion of various East Asian species). With this large-scale persistent dynamic, it proves extremely difficult to assign a long-term sympatry/allopatry status to any host populations.

For example, Vikan *et al.* (2010) studied various native brambling, *Fringilla montifringilla*, populations and found the same level of host defences in both one parasitized and three currently non-parasitized populations. They explained this pattern by intense gene flow; under this scenario all studied populations would represent a single panmictic population. Indeed, gene flow might have been substantial historically: any of these populations could not have existed for longer than 10 000 years because of Pleistocene glaciations. The maintenance of strong anti-cuckoo defences in current allopatry thus may be explained by fixation of rejection alleles at the level of the whole species. Such species-fixed defences may be retained for longer than defences that are variable within species because selection has erased genetic variation in the defence traits (Foster and Endler, 1999). Alternatively, rejection alleles became fixed not in Scandinavia but during cuckoo–brambling coevolution in glacial refugia in more southern parts of Europe (or even earlier, in the Tertiary) and were retained in all populations that colonized Scandinavia after glaciers retreated 10 000 years ago. The same holds for hosts of brown-headed cowbirds in temperate America. Defences in allopatry may not necessarily reflect 'introgression of rejecter genes from sympatric populations' (Briskie *et al.*, 1992): after glacial retreat, host populations, e.g. American robins, *Turdus migratorius* (Figure 9.1), might have spread further north than cowbird populations and simply brought their defences from glacial refugia with no current gene flow needed.

The longest record of parasitism rates and host responses to standardized model eggs covers only 30 years. In reed warblers, *Acrocephalus scirpaceus*, decline in parasitism

Figure 9.1 Full diversity of types of hosts and parasites that should become the focus of future brood parasitism studies. Upper row shows examples of model introduced species: brood parasite (pin-tailed whydah), host (village weaver) and control non-host (goldfinch). Lower row shows examples of model species that expanded their ranges naturally: brood parasite (shiny cowbird), host (American robin) and control non-host (fieldfare). Note that these examples do not reflect parasite–host relationships between these particular species and come from geographically varied areas to exemplify research opportunities at global scales. See text for details on these and other potential model systems (photo credits: T. Grim).

rates caused by a population crash in cuckoos was accompanied by a parallel decline in host rejection rates (Thorogood and Davies, 2013). Imagine that we did not have the evidence accumulated over the three decades and were starting to study the population only now. We would observe low parasitism rates and low levels of host defences, inferring that parasitism is probably a recent phenomenon and hosts had not evolved strong defences yet. It is only due to the benefit of the existing evidence that we may firmly say that such a conclusion would be erroneous. Unfortunately, such historical evidence is lacking for almost all other sites where brood parasites and their hosts are studied (but see Igic *et al.*, 2012). Therefore, any studies about the evolution of parasite and host coevolutionary features that are not based on direct evidence of past parasitism might be inconclusive in principle.

Solutions

We envisage two possible research opportunities that may be particularly fruitful in overcoming these limitations. First, natural expansions or retractions of parasite or host

population ranges allow direct measurement of the length of sympatry and allopatry, at least at short time-scales (inferences at long time-scales are impossible in principle, see above). Second, host or parasite populations introduced from their native ranges into novel geographically and genetically isolated populations represent invaluable 'natural experiments' (*sensu* Diamond, 1986) to study how coevolved traits may be affected by changing selective pressures. Avian invaders are often and productively studied to address various aspects of avian biology (e.g. Blackburn *et al*., 2009), but their potential for understanding brood parasite–host coevolution has so far been poorly utilized. Such large-scale introduction experiments are ethically and legally unacceptable today. Fortunately, in a scientific sense, today's researchers can already harvest data from non-native populations that underwent decades or even centuries of evolution in isolation from their source populations.

Solution I: Range Shifts

Natural changes in host and parasite biogeography, including both expansions and retractions of their ranges, lead to novel host–parasite associations and new ecological and coevolutionary relationships (Morand and Krasnov, 2010). Therefore, natural range dynamics may help to elucidate parasite–host coevolution.

Expansions of novel parasites and hosts to areas both with and without native (indigenous) parasites may provide interesting study systems. If parasites invade locations where another parasite is already present (Cruz *et al*., 1998), hosts may be pre-adapted to cope with the novel parasite (e.g. previously evolved egg discrimination), decrease parasite success, and slow down or prevent the new parasite's range expansion (Dinets *et al*., 2015). Further, native and novel parasites might differ in their virulence. The presence of a new highly virulent parasite may increase overall parasite pressure, selecting for host defences which may, as a by-product, decrease fitness of a native less virulent parasite (cf. collateral damage hypothesis: Lyon and Eadie, 2004; Samas *et al*., 2014a). Also host range expansion may bring the host into contact with new parasites; if the new parasites are sufficiently virulent they could constrain the host's range spread and prevent further coevolution.

Natural parasite or host population declines, local extinctions and consequent range retractions also represent an opportunity to study evolutionary dynamics of host–parasite coevolution, especially relaxed selection (Lahti *et al*., 2009) when a parasite goes extinct and host switching (Morand and Krasnov, 2010) when a host goes extinct. The decline in the cuckoo population in the UK provided one such natural experiment showing that the resulting relaxed selection led to rapid decline of host defences, perhaps within the limits of phenotypic plasticity (Thorogood and Davies, 2013). In another study in the Czech Republic, a decline in the great reed warbler host population forced cuckoos to switch to an alternate host, the reed warbler, with a resulting evolutionary lag in adaptations of both cuckoos and the locally new host (Igic *et al*., 2012).

Cuckoo females are specialist parasites, but other parasites are generalists parasitizing many hosts (see below). These differences may have large effects on successful establishment of naturally invading or introduced parasites. An invasive East Asian freshwater mussel, for instance, has spread throughout Central Europe because its parasitic larvae are able to complete its development on novel fish species (Douda *et al*., 2012). Similarly, invading or introduced generalist brood parasites may have the best odds in novel host communities, simply because their more flexible host choice increases the chances of finding appropriate fosterers. Indeed, the most famous case of range expansion with effects on native host populations entails an extremely generalist parasite, the brown-headed cowbird (Smith *et al*., 2000; Baker *et al*., 2014). This cowbird was in historical times closely associated with distribution of bison, *Bison bison*, on the Great Plains of North America. After the arrival of European settlers the cowbirds experienced a significant range expansion due to clearing of forests and introduction of domestic livestock. This range expansion continued well into the twentieth century. Cowbird parasitism is often most pronounced in forest fragments and edge areas, and may severely reduce host population viability, often in tandem with habitat destruction. Many hosts used today lack defences against the parasite while experiencing high parasitism rates (Smith *et al*., 2000). Nevertheless, the strength of the 'expanding range effect' on hosts is debated because cowbirds might have older historical contacts with various hosts (Rothstein and Peer, 2005) and many cowbird hosts retain their defences long after parasitism declines (Peer *et al*., 2011). Extreme Pleistocene dynamics of animal ranges, and consequently parasite–host contacts, makes most of the inferences about historical cowbird–host coevolution largely uncertain. In contrast, currently witnessed range changes may at least provide some certainty, although only at short timescales, about parasite–host interactions and their consequences.

The shiny cowbird, *Molothrus bonariensis* (Figure 9.1), is another generalist brood parasite distributed throughout South America. From 1860 onwards, it colonized the islands of the West Indies, most probably with the aid of humans. In Puerto Rico, high rates of parasitism (~80%) led to a pronounced reduction in host reproductive output. Since novel hosts often show weak defences against brood parasitism coupled with the typical low population sizes in island endemics, concerns are raised about their ability to withstand the high costs of shiny cowbird parasitism (Woodworth, 1997). The shiny cowbird has continued its range expansion: the first individual was observed in the United States in 1985, and has since spread across the south-eastern part of the United States (Cruz *et al*., 1998). No direct evidence for parasitism has been documented in the country, but females in a state ready to lay eggs have been encountered (Post and Sykes, 2011). Shiny cowbirds have also expanded their range in South America due to human-induced habitat fragmentation, just as has happened in North America with brown-headed cowbirds (Cruz *et al*., 1998). The range expansion in parts of South America may have been boosted by introductions (Marín, 2000).

An additional level of complexity is seen in rare cases of multiple parasites colonizing the same geographic area. The south-eastern United States was recently invaded by three generalist parasites: shiny cowbirds (above), bronzed cowbirds, *Molothrus aeneus*, and

brown-headed cowbirds, providing a unique three-parasite invasion system in Florida (Cruz *et al.*, 1998). Future research should address how previously cowbird-free host populations respond to the novel parasite pressure. On the other hand, it is important to stress that previous absence of cowbirds does not imply that the population was 'naïve' before the cowbirds arrived – gene flow can lead to an influx of rejecter alleles into phenotypically allopatric populations making them effectively genetically sympatric (see also Moskát *et al.*, 2008). Therefore, studies of 'naïve' native host population would benefit from quantifying gene flow among host populations sympatric and allopatric with brood parasites (Soler *et al.*, 1999).

Overall, local adaptation – including decay of traits that are no longer adaptive – requires that the spatial scale of selection is larger than scale of gene flow (Foster and Endler, 1999). In other words, restricted gene flow speeds up evolutionary change. Therefore, any study reporting maintenance of defences in native allopatric host populations that does not assess genetic similarities with sympatric populations is inconclusive – gene flow among parasitized and non-parasitized populations may have retarded a decline of host defences in currently allopatric populations (Soler *et al.*, 1999; Moskát *et al.*, 2008; Vikan *et al.*, 2010). This does not apply to introduced populations where gene flow is excluded by distances between source and introduced populations being extremely large compared to host dispersal distances (Lahti, 2006; Samas *et al.*, 2014a; Yang *et al.*, 2014). Gene flow also represents a potential statistical problem for source populations: if such populations are connected by gene flow they may not represent independent units; statistical analyses ignoring this then would be biased with overestimated degrees of freedom.

However, even populations subject to intense gene flow may express fine-tuned adaptations against parasites through phenotypic plasticity. Comparatively, populations isolated from each other (i.e. low dispersal and gene flow) tend to evolve non-plastic genetically 'rigid' defences. This paradigm would predict that perfectly isolated populations (e.g. introduced to distant geographical areas) should lose plasticity and/or evolve non-plastic defences towards novel parasites encountered in novel ranges (Foster and Endler, 1999; Tojo and Nakamura, 2014).

Despite all of the mentioned range expansions above, to our knowledge, no study has yet tested the same host population before and after a brood parasite colonized that host population (i.e. temporal allopatry followed by sympatry). Expansions of the three cowbird species provide an opportunity to glimpse at coevolution in action. This could be done by studying currently allopatric host populations that are expected to come into contact with the parasite(s) soon. Such populations should be tested with non-mimetic and mimetic foreign eggs, including conspecific eggs (Briskie *et al.*, 1992; Samas *et al.*, 2014a). Additionally, researchers need to quantify egg phenotypes of both hosts and arriving parasites (including those currently allopatric from the point of view of the focal population), and the population would need to be characterized genetically to quantify gene flow from additional conspecific populations, both allopatric and sympatric with parasites. Such procedures would need to be repeated across years and, more likely, decades, to document predicted changes in host and parasite egg phenotypes,

host egg rejection rates, etc. Only such long-term studies will allow assessment of both phenotypic plasticity and genetic evolutionary change.

Range of Geographic Scales: Between Urbanization and Intercontinental Invasion

Most studies of native parasite and host populations performed so far have focused on an intermediate subcontinental scale where sympatric versus allopatric populations were distanced by dozens to hundreds of kilometres. We envisage that our understanding of enemy–victim coevolution will be greatly advanced if the research focus is extended from 'snap-shots' at intermediate scales to shifting ranges at both small and large scales.

Colonization of urban settlements by birds represents a special case of range shifts at the smallest geographic scale. Urban areas strikingly differ both abiotically and biotically from neighbouring rural landscapes. Yet some species, including various passerine hosts of brood parasites, termed 'urban exploiters', show strong preferences for such human-dominated environments, and other species, termed 'urban adapters' readily adapt to urban areas although they also commonly live in rural areas (Gil and Brumm, 2014). Similarly, some parasites, like brown-headed cowbirds, prefer disturbed urbanized areas (Barnagaud et al., 2015). Unlike these, most brood parasites are among the shyest birds and avoid human proximity (Erritzøe et al., 2012). Thus, host populations may become allopatric with parasites like common cuckoos through occupying urban areas (Grim et al., 2011) or even breeding indoors (Liang et al., 2013). The timing of the origin of urban populations (and, by implication, of allopatry) is often known (Evans et al., 2010), providing a crucial advantage over non-urban populations where the length of sympatry/allopatry is almost never known. Urban passerines represent largely ignored study systems where effects of sympatry versus micro-allopatry can be studied at finest distance scales (Samas et al., 2014a).

At the opposite spatial extreme, transoceanic expansions seem to be feasible in some brood parasites. Common cuckoos are increasingly often recorded in North America (including wintering and courting) and brown-headed cowbirds in Eurasia (Dinets et al., 2015). The first study that addressed the potential coevolution between native hosts and presumably invasive parasites (Dinets et al., 2015) suggested that interactions will be complex: specific outcomes of the first contact between new enemies and victims will depend on particular host species egg rejection reaction norms and, in the case of cuckoos, on particular invading gens (host-specific race) and its gens-specific egg phenotype. Future studies should test additional potential hosts and their populations located in the range extension zone of both brood parasites, both before and after the new contact.

A recent study showed that the successful establishment of a species in an exotic range is best predicted by its urbanization in the ancestral range (Møller et al., 2015). This provides an exciting opportunity to study the same species at all scales: in native range sympatric with parasites, native (urban) range allopatric with parasites, and exotic

range allopatric with original parasites. So far this opportunity has been employed in only two model species, in blackbirds, *Turdus merula*, and song thrush, *T. philomelos* (Samas *et al*., 2014a).

Solution II: Introductions

For any study of relaxed or novel selection, it is necessary to know the history of focal populations (Foster and Endler, 1999). Unfortunately, as we showed, historical sympatry/allopatry status of a host species/population is in most cases impossible to estimate. Therefore, the most reliable way to know the length of host–parasite contact is to manipulate it experimentally. This was essentially done by our ancestors who introduced many bird species, including hosts and even some parasites, outside their natural ranges (Blackburn *et al*., 2009), creating large-scale natural experiments with many replicates (Diamond, 1986; Table 9.1). The human-assisted 'Great Escape' of hosts to novel areas without their parasites and related selection pressures may teach us much about changes in expression and evolution of host defensive traits within the framework of enemy release (Morand and Krasnov, 2010) and relaxed selection hypotheses (Lahti *et al*., 2009).

Introduced populations show multiple advantages for studies on brood parasite–host coevolution which enable researchers to overcome some of the research and inferential constraints that are hard or impossible to overcome in native unmanipulated populations. Introduced host populations lack any recent experience with ancestral parasites. Thus, in the terms of geographic mosaic theory of coevolution, invasive populations effectively represent coevolutionary cold spots (Thompson, 2005). This is because their brood parasites were almost never co-introduced (but see Payne, 2010) and introduced hosts are only rarely parasitized by native parasites (Table 9.1; Tojo and Nakamura, 2014). Researchers also know accurately the length of allopatry (Hale and Briskie, 2007) which allows them to determine if time since isolation covaries with changes in host resistance traits across independent introduced populations (Lahti, 2006).

Introduced host populations have left behind not only their brood parasites but also a majority of their conspecifics. This is crucial, because in native populations, patterns of host defences incongruent with local parasitism pressure were often explained by possible (i.e. unknown) gene flow from other conspecific populations, but without actually quantifying it. Therefore, host populations introduced to remote oceanic islands (e.g. Hawaii) or old continental islands (e.g. New Zealand) provide fundamental advantages: chances of gene flow between source and recipient populations are typically zero. This is clear even without any molecular data: lifetime dispersal of hosts is often at the scale of kilometres, whereas distances between native and introduced populations including their migratory pathways are typically thousands of kilometres making any contact between the source and recipient populations effectively impossible.

Detectable evolutionary changes in traits related to parasite–host coevolution can be rapid, taking less than a century (egg colour: Lahti, 2005, 2008; Spottiswoode and Stevens, 2012; clutch size: Samas *et al*., 2013). This is no surprise: various bird

Table 9.1 Overview of introduced passerine populations with information on their status as hosts of brood parasites in native and introduced range

Host species	Origin	Parasitism in native range	Number of introduced populations	Introduced ranges	Parasitism in introduced range
Alaudidae					
Alauda arvensis	Eurasia	CuCa (o), HiHy (r)	4	Australia, North America, Pacific islands	Not reported
Cardinalidae					
Cardinalis cardinalis	North America	MoAe (u), MoAt (f)	2	Pacific islands, West Indies	Not reported
Corvidae					
Corvus splendens	Asia	EuSc (f)	16	Africa, Arabia, Australia, Europe, Indian ocean islands, Middle East	Israel: ClGl (u)
Gymnorhina tibicen	Australia	ScNo (f)	2	Pacific islands	Not reported
Emberizidae					
Paroaria coronata	South America	MoBo (u)	4	Indian ocean islands, North America, Pacific islands	Not reported
Sicalis flaveola	South America	MoBo (o)	3	Pacific islands, West Indies	Not reported
Estrilidae					
Amandava amandava	Asia	Not reported	13	Africa, Arabia, Europe, Indian ocean islands, Pacific islands, West Indies	Not reported
Estrilda astrild	Africa	ViFu (r), ViMa (f), ViWi (r)	14	Atlantic islands, Europe, Indian ocean islands, Pacific islands, South America	Not reported
Estrilda melpoda	Africa	ViMa (u)	6	Europe, North America, Pacific islands, West Indies	Puerto Rico: ViMa (u)
Estrilda troglodytes	Africa	ViMa (u)	6	Atlantic islands, Europe, Pacific islands, West Indies	Not reported
Lonchura castaneothorax	Malay, Australia	Not reported	2	Pacific islands	Not reported
Lonchura cucullata	Africa	ViCh (r), ViMa (r)	2	Indian ocean islands, West Indies	Puerto Rico: MoBo (u)
Lonchura malabarica	Asia	Not reported	3	Europe, Pacific islands, West Indies	Not reported
Lonchura malacca	Asia	Not reported	6	Pacific islands, West Indies	Not reported

(*cont.*)

Table 9.1 (*cont.*)

Host species	Origin	Parasitism in native range	Number of introduced populations	Introduced ranges	Parasitism in introduced range
Lonchura oryzivora	Asia	Not reported	11	Africa, Atlantic islands, Australia, Indian ocean islands, North America, Pacific islands, West Indies	Not reported
Lonchura punctulata	Asia	Not reported	9	Australia, Indian ocean islands, Pacific islands, West Indies	Puerto Rico: MoBo (r)
Fringillidae					
Carduelis carduelis	Eurasia	CuCa (r)	5	Atlantic islands, Australia, Pacific islands, South America, West Indies	Australia: CaFl (u), CaPa (o), ChBa (r), ChLu (r)
Carduelis chloris	Eurasia	CuCa (o)	4	Atlantic islands, Australia, Pacific islands, South America	Australia: CaPa (r), ChBa (r). New Zealand: UrTa (u)
Carduelis flammea	Circumpolar	CuCa (r), MoAt (r)	2	Australia, Pacific islands	Not reported
Fringilla coelebs	Eurasia	CuCa (o)	2	Africa, Pacific islands	New Zealand: ChLu (u)
Serinus mozambicus	Africa	ChKl (u)	3	Indian ocean islands, Pacific islands	Not reported
Passeridae					
Passer domesticus	Eurasia	CuCa (r)	30	Africa, Atlantic islands, Australia, Indian ocean islands, Malay, North America, Pacific islands, South America, West Indies	Africa: ChCa (u). Australia: CaFl (u), CaPa (r), ChBa (r), ChLu (r). Brazil and Chile: MoBo (r/o). New Zealand: ChLu (r), UrTa (o). South Africa: ChKl (p). USA: MoAt (r/o)

Passer montanus	Eurasia	CuCa (r)	4	Australia, North America, Pacific islands	Not reported
Ploceidae					
Euplectes afer	Africa	Not reported	4	Europe, Pacific islands, West Indies	Not reported
Euplectes orix/franciscanus	Africa	ChCa (f), ChCu (u), ChKl (u), ViPa (p)	2	North America, West Indies	Not reported
Foudia madagascariensis	Indian ocean islands	Not reported	2	Arabia, Atlantic islands	Not reported
Ploceus cucullatus	Africa	ChCa (f), ChCu (f), ChKl (f), CuSo (p), ViMa (p)	4	Europe, Indian ocean islands, West Indies	Puerto Rico: MoBo (u)
Ploceus intermedius	Africa	ChCa (f), ChKl (u)	2	Arabia, Pacific islands	Not reported
Pycnonotidae					
Pycnonotus cafer	Asia	CaPs (p), ClJa (u), CuCa (u), HiSp (p), SuDi (u), SuLu (u)	8	Arabia, Pacific islands	Not reported
Pycnonotus jocosus	Asia	CaSo (u)	6	Arabia, Australia, Indian ocean islands, North America, Pacific islands	Australia: CaPa (r)
Sturnidae					
Acridotheres cristatellus	Asia	Not reported	4	North America, South America, Pacific islands	Not reported
Acridotheres fuscus	Asia	Not reported	2	Pacific islands	Not reported
Acridotheres tristis	Asia	EuSc (f)	23	Africa, Arabia, Atlantic islands, Australia, Europe, Indian ocean islands, North America, Pacific islands	South Africa: ClGl (u)
Gracula religiosa	Asia	EuSc (u)	3	North America, Pacific islands, West Indies	Not reported

Table 9.1 (*cont.*)

Host species	Origin	Parasitism in native range	Number of introduced populations	Introduced ranges	Parasitism in introduced range
Sturnus vulgaris	Eurasia	CuCa (r)	7	Africa, Australia, North America, Pacific islands, West Indies	USA: MoAt (r)
Timaliidae					
Garrulax canorus	Asia	ClCo (u), HiSp (u)	2	Pacific islands	Not reported
Leiothrix lutea	Asia	CuCa (u)	4	Europe, Pacific islands	Not reported
Turdidae					
Turdus merula	Eurasia	CuCa (o), CuMi (u)	2	Australia, Pacific islands	Australia: CaPa (r). New Zealand: ChLu (r)
Turdus philomelos	Eurasia	CuCa (r)	2	Australia, Pacific islands	New Zealand: UrTa (u)

Only cases with successful establishment in two or more geographical entities were extracted from Sol *et al*. (2012). According to Sol *et al*. (2012), only two obligate brood parasites were successfully introduced outside their native range (*Vidua paradisaea, V. macroura*).

Pacific islands include New Zealand.

Data on parasite distribution and host use from Friedmann (1963, 1971), Friedmann *et al*. (1977), Friedmann and Kiff (1985), Moksnes and Røskaft (1995), Johnsgard (1997), Payne (2005), Yang *et al*. (2012) and Lowther (2014). Parasitism categorized into 'frequent' (f, commonly used host), 'occasional' (o, irregularly used host), 'rare' (r, only a few cases of parasitism), 'used' (u, no information on regularity of host use, but probably rare or occasional in most cases) and 'possible' (p, uncertain host status).

Brood parasite, abbreviations:

Cacomantis flabelliformis (CaFl); *Cacomantis pallidus* (CaPa); *Cacomantis passerines* (CaPs); *Cacomantis sonneratii* (CaSo); *Chrysococcyx basalis* (ChBa); *Chrysococcyx caprius* (ChCa); *Chrysococcyx cupreus* (ChCu); *Chrysococcyx klaas* (ChKl); *Chrysococcyx lucidus* (ChLu); *Clamator coromandus* (ClCo); *Clamator glandarius* (ClGl); *Clamator jacobinus* (ClJa); *Cuculus canorus* (CuCa); *Cuculus micropterus* (CuMi); *Cuculus solitarius* (CuSo); *Eudynamys scolopaceus* (EuSc); *Hierococcyx hyperythrus* (HiHy); *Hierococcyx sparverioides* (HiSp); *Molothrus aeneus* (MoAe); *Molothrus ater* (MoAt); *Molothrus bonariensis* (MoBo); *Scythrops novaehollandiae* (ScNo); *Surniculus dicruroides* (SuDi); *Surniculus lugubris* (SuLu); *Urodynamis taitensis* (UrTa); *Vidua chalybeata* (ViCh); *Vidua funerea* (ViFu); *Vidua macroura* (ViMa); *Vidua paradisaea* (ViPa); *Vidua wilsoni* (ViWi).

species, such as those that have colonized urban environments at time-scales equal to those of introduced populations (from decades up to two centuries), have shown micro-evolutionary changes (Miranda *et al*., 2013), genetic divergence (Evans *et al*., 2010) and even micro-geographical differentiation within urban populations (Björklund *et al*., 2010). Similarly, some introduced bird populations diverged from their ancestors, sometimes even to the magnitude of subspecific differences (Baker and Moeed, 1987). Within a century and half from being introduced, two *Turdus* thrushes naturalized in New Zealand converged to local species life histories (e.g. smaller clutch sizes and no seasonal clutch size trends) and, consequently, fit large-scale macro-ecological patterns (Samas *et al*., 2013). This indicates that one-and-a-half centuries was sufficient to allow for an apparent micro-evolutionary change in host phenotypes (actually the clutch size changes stabilized within the first century after introductions and did not change afterwards; Samas *et al*., 2013). This directly confirms that introduced populations had enough time to respond to relaxed/new selection and thus are useful for testing coevolutionary hypotheses (Thompson, 1998). However, these studies of changes in expression of traits should also be accompanied by molecular studies to disentangle effects of plasticity and genetic changes.

Importantly, even if there was not enough time for an evolutionary (i.e. genetic) change, the same direction of changes between native and introduced populations is predicted from phenotypic plasticity. Lowered realized or perceived parasitism risk should produce relaxed expression of anti-parasite adaptations. Thus, both genetic and developmental change in allopatry should lead to lowered levels of defence. Crucially, increased levels of defences in allopatry would be unambiguous evidence against a presumed function of host behaviour in the context of interspecific parasitism: decreased parasitism pressure cannot select for increased host defences in principle. Alternative explanations (e.g. conspecific parasitism, see below) then need to be addressed (Samas *et al*., 2014a, b).

Searching the literature, we found only a few publications investigating introduced populations in light of avian brood parasitism (see also Baker *et al*., 2014). In the following sections, we will discuss the model systems that have been studied so far and possibilities for future research on introduced populations.

Introduced Hosts: Current State of Knowledge

The village weaver, *Ploceus cucullatus* (Figure 9.1), is a species native to sub-Saharan Africa, but was introduced to Hispaniola, West Indies, in the eighteenth century (Cruz and Wiley, 1989). In Africa, it is known to be a host of the diederik cuckoo, *Chrysococcyx caprius*, which lays eggs mimicking at least some of the weaver egg types (Erritzøe *et al*., 2012). Weaver hosts have well-developed egg rejection skills, and show sophisticated defensive mechanisms like intricate egg signatures, extreme interclutch variation and remarkably low intraclutch variation in egg appearance (Cruz and Wiley, 1989; Lahti and Lahti, 2002). Weaver eggs may have a white, light green or dark blue-green ground colour, either with or without spots. A high interclutch variation

between different females makes it more difficult for the cuckoo to mimic any clutch, and a low intraclutch variation may make it easier for the host to recognize even a mimetic egg (Feeney *et al*., 2014). Intricate egg signatures enhance the effect of both these traits, making successful parasitism even more difficult for the parasite. Village weavers base their rejection decisions on differences in colour and spots between own and foreign eggs (Lahti and Lahti, 2002). These mechanisms work well against cuckoo parasitism, but also against parasitism by conspecifics, which is an additional selective pressure for the evolution of egg rejection, especially in colonially nesting birds like weavers. However, Lahti (2006) did not find any evidence for conspecific parasitism in both native and introduced study populations (see also Cruz *et al*., 2008).

On arrival in Hispaniola, the weavers faced no brood parasite. If interspecific parasites are responsible for evolution of host defences, defensive mechanisms should deteriorate with time, especially if there are costs related to rejection behaviour. Indeed, rejection of foreign eggs has been found to be lower in Hispaniola than in Africa (Cruz and Wiley, 1989). Furthermore, intraclutch variation has increased and interclutch variation has decreased in the population compared to the native one, just as in another introduced population in a parasite-free environment in Mauritius (Lahti, 2005). An interesting twist to this story is the arrival of brood parasitic shiny cowbirds to Hispaniola in the 1970s, about 200 years after the introduction of village weavers on the island. Unlike diederik cuckoos, this parasite is a generalist using many hosts and laying eggs that resemble weaver eggs in size but not in colour. Cowbird parasitism on village weavers increased from about 1% in the 1970s to about 16% in 1982, and costs of parasitism to weavers were high (Cruz and Wiley, 1989). Due to this new selective pressure, Hispaniolan weavers were therefore likely to evolve better defences in the future. A study in 1998 confirmed this expectation, as high weaver rejection rates of experimental eggs were reported. The authors suggested that the rapid change in egg rejection rates may be due to both genetic processes and learning (Robert and Sorci, 1999). Lahti (2006), however, came to a different conclusion. He suggested that egg rejection abilities had not deteriorated, but were hampered due to changes in egg phenotypes. Yet, Cruz *et al*. (2008) found that rejection of experimental eggs were highest in areas where shiny cowbirds were present, suggesting phenotypic plasticity in the egg rejection behaviour due to costs of rejection.

Interestingly, a recent comparison of red-billed leiothrix, *Leiothrix lutea*, defences in a native and introduced population showed similar patterns as in the weaver case above (Yang *et al*., 2014). Leiothrixes are parasitized by common cuckoos in Asia, but an introduced population in Hawaii has been living in a parasite-free environment for 100 years. Introduced leiothrixes have retained their egg rejection ability. Intraclutch variation was lower and interclutch variation was higher in the source than in the introduced population.

Chaffinches, *Fringilla coelebs*, introduced to New Zealand from Europe have kept their advanced egg rejection abilities even after separation from their European counterparts for more than 100 years (Hale and Briskie, 2007). Song thrush and blackbirds even rejected eggs at higher rates than in Europe (Hale and Briskie, 2007); however, model types used in native and introduced populations differed and therefore are not quantitatively comparable. Samas *et al*. (2011, 2012, 2013, 2014a) studied both

above-mentioned thrushes and greenfinches, *Carduelis chloris,* in New Zealand. Using identical model types across both species of thrushes and all populations, they found that thrush responses to non-mimetic eggs did not decline in New Zealand under the presumed relaxed selection from cuckoos. Also individual egg rejection repeatability remained virtually identical between native (Grim *et al.*, 2014) and introduced populations (Samas *et al.*, 2011). In contrast, responses to natural conspecific eggs even increased in New Zealand compared to native populations, leading to one of the highest conspecific egg rejection rates revealed in passerines (~60%). Thrushes are only accidentally prone to interspecific parasitism at present, both in source and New Zealand populations. Maintenance of defences in both native and introduced populations cannot be explained by selective neutrality: both thrushes suffered substantial rejection costs and errors in all populations (Hale and Briskie, 2007; Samas *et al.*, 2014a). Thus, even though we cannot rule out other possibilities (just like in any study that infers historical causes of current host anti-parasite adaptations; Samas *et al.*, 2014b), the most likely explanation is that thrush egg discrimination evolved and was maintained due to conspecific parasitism; this is in line with current unsuitability of thrushes as cuckoo hosts (Grim *et al.*, 2011).

Phenotypic plasticity predicts immediate changes in host responses to changed parasitism pressure: some cuckoo hosts adjust their responses across years, and even during a single breeding season (Thorogood and Davies, 2013). Therefore, virtually identical responses to foreign eggs between Europe and New Zealand after dozens of generations clearly reject the phenotypic plasticity hypothesis in the context of cuckoo parasitism. Still, it remains to be shown whether the elevated rejection of conspecific eggs in New Zealand reflects micro-evolutionary change or phenotypic plasticity, both due to elevated breeding densities in New Zealand which increase risks of conspecific parasitism (Samas *et al.*, 2013).

In Africa, 20 species of the Viduidae family (whydahs and indigobirds) are obligate brood parasites (Payne, 2010). The pin-tailed whydah, *Vidua macroura* (Figure 9.1), for example, exploits several species of waxbills *Estrilda* spp., where the parasitic chick is reared together with host young. The *Vidua* species and their hosts show similar egg appearance (due to shared phylogeny; Payne, 2010) and similar gape patterns (due to convergence; Payne, 2010). Because of their colourful breeding plumages and voice, the whydahs and indigobirds have been popular in aviculture as cagebirds for centuries, similarly to many of their host species. One host of the pin-tailed whydah, the orange-cheeked waxbill, *Estrilda melpoda*, has been introduced to Puerto Rico several times, most recently in the 1950s. Here it established a free-ranging population. Similarly, pin-tailed whydahs were also introduced here about 10 years later and started to use the waxbills as hosts. As far as we know, both species are still present there representing an exciting yet unused research opportunity.

Introduced Hosts: Limitations

Although introduced host and parasite populations provide important heuristic advantages compared to native, expanding (including urbanized) or retreating populations

(see above), they also show some limitations. Out of the total diversity of hosts and parasites, only a small subset has been introduced (Table 9.1). We note, however, that even among native hosts and parasites only a minor proportion of them is studied anyway. At a finer scale, only a subset of individuals (and hence genetic variation and adaptations) have been introduced. Thus, genetic constitution of introduced populations may not be representative of native ones leading to founder effects. However, many introduced host populations resulted from massive propagule pressure that prevented non-adaptive confounding effects (Briskie and Mackintosh, 2004). Variation in the propagule pressure provides opportunities to test how founder effects or genetic drift affect altered coevolutionary relationships.

There is also a possibility that only generalist parasites will choose exotic hosts, which would reduce the opportunity for coevolution. However, this will not necessarily be so because parasites can change their host specificity in invaded ranges (Douda et al., 2012). Rather than as a limitation, we see this as an opportunity to test what particular general life history and specific parasitism-related traits affect host selection and coevolution (see Grim et al., 2011).

Virtually all introductions that are of interest to students of brood parasitism were done within several last centuries. This may raise concerns whether this time frame is sufficient to detect noticeable evolutionary responses and whether studies of such populations would not be limited in their focus on early stages of evolution of the coevolutionary system. Ample evidence suggests that animal behaviour may evolve remarkably fast (Thompson, 1998; Miranda et al., 2013) while other case studies suggest limited evolutionary change even in the long term (Lahti et al., 2009; Peer et al., 2011). Whether anti-parasite defence declines after pressure from interspecific parasitism relaxes depends on multiple factors, including standing genetic variation (Vikan et al., 2010), gene flow (Soler et al., 1999), trait covariation (Avilés and Parejo, 2011), secondary trait function (Lahti et al., 2009), alternative selection pressures (Lyon and Eadie, 2004), or costs and errors associated with the behaviour (Samas et al., 2014a). These and additional parameters are typically idiosyncratic, preventing unambiguous general conclusions on how the length of human-assisted allopatry of host and parasite populations limits detection of coevolutionary changes. Anyway, the few pioneering studies of such populations (above) persuade us to be optimistic.

A problem common to both expansions and introductions is that the newly colonized host ranges differ from ancestral ranges in multiple factors, not only presence/absence of parasites. For example, adaptations involved in coevolutionary interactions may also be under selection from abiotic factors. Village weavers freed from diederik cuckoo parasitism on Hispaniola and Mauritius have, in general, more blue-green eggshell pigments (biliverdin) resulting in lower interclutch variation, which may be an adaptation to protect embryos against solar radiation (Lahti, 2008). Parasitized populations in Africa have moved away from this optimum due to selection on high interclutch variation among females as a defence against egg mimicry by diederik cuckoos. However, even between the source populations, the one experiencing more exposure to sun had more intense blue-green colours than the one experiencing less sun exposure (Lahti, 2008). Hence, care should be taken in concluding that specific traits have evolved solely as a response to coevolution without considering alternative explanations.

The same cautionary note applies to biotic factors: also these vary between native versus exotic ranges. There are new predators, competitors or non-brood parasites. These lead to changes in selective pressures on traits, including those related to parasitism. Without appropriate controls (see next section), resulting changes might be incorrectly interpreted as if they were causally related to changed parasite pressure. Further, new adaptations to these novel selection pressures may, via trade-offs (Ricklefs and Wikelski, 2002) or trait covariances (Trnka and Grim, 2014), also affect focal anti-brood parasite adaptations. However, such confounding effects are measurable and thus can be taken into account in carefully planned studies. In our view, these complexities therefore do not detract from the huge research potential of introduced host and parasite populations.

Conclusions and Future Avenues

As we have seen, studies of introduced populations offer a unique opportunity to study how expression of traits varies according to specific selective pressures, and also how parasites may affect host populations. To avoid comparing only one population to another (i.e. pseudoreplication: Hurlbert, 1984), future studies should ideally focus on hosts introduced to several isolated locations (Table 9.1). We acknowledge that such multiple-population studies are logistically demanding, but we stress that they are doable (Lahti, 2006; Samas *et al*., 2014a). Ideally, researchers should compare parasitized and unparasitized introduced populations. For example, the orange-cheeked waxbill was introduced to several parasite-free islands (Hawaii and Oahu in the Hawaiian Islands, Bermuda, and Saipan in the Northern Mariana Islands). Its parasite, the pin-tailed whydah was co-introduced with waxbills but only to several places (Puerto Rico, Guadeloupe, Martinique; Payne, 2010). Thus, this unique model system provides multiple replicates of both parasitized and non-parasitized populations (see also red-billed leiothrix; Tojo and Nakamura, 2014; Yang *et al*., 2014). Whydah and allies are famous for the intricate similarity of their gape patterns to those of the host young, although it is unclear who mimics whom (Hauber and Kilner, 2007). Comparison of introduced parasitized and non-parasitized waxbill populations may help resolve this enigma.

Studies on species *not* parasitized in either native, shifted or introduced ranges are also important (Table 9.1). This is because potential interpopulation differences in adaptations would reflect variation in selective pressures unrelated to parasitism (Lahti, 2008). Such species can therefore serve as controls (if the same direction and magnitude of genetic and phenotypic changes in novel ranges is recorded in both former host and control species, then such changes in hosts cannot be interpreted as a response to relaxed selection from parasite). The controls should be those species that are primarily unsuitable (*sensu* Grim *et al*., 2011) as hosts of interspecific parasites and, thus, the microevolution of their traits would not be confounded by parasite–host coevolution. Such control species should include both those that expanded their ranges naturally (e.g. fieldfares, *Turdus pilaris*, that recently colonized Iceland and Greenland from Europe; Figure 9.1), and those that were made allopatric from potential native parasites by human transport (e.g. goldfinches, *Carduelis carduelis*, introduced from Europe to New Zealand; Figure 9.1). Just like in the case of focal host species, the best control species allopatric

populations are those that became established via long-distance dispersal or introduction to distant and well-isolated places (i.e. no additional gene flow from native populations). In the ideal case, conditions in introduced ranges should differ from those in native ranges as little as possible in traits other than the presence of brood parasite(s), to avoid confounding effects of multiple changed selection pressures.

Most studies of brood parasitism have concerned a specific host and/or parasite population at a specific time and place. Work based on more representative sampling across time (longitudinal studies) or space (multiple populations) is rare, simply due to the workload required to undertake such investigations. However, because a traditional single host population approach cannot answer some relevant questions in principle, we argue for a change in the focus from such studies (even though they might cover more host species) to larger-scale studies (even though they are demanding and fewer species can be addressed).

Such a metareplication approach (Kelly, 2006) is not only relevant for the study of introduced populations, it is fundamental for the study of native populations too (Soler *et al*., 1999; Vikan *et al*., 2010; Grim *et al*., 2011). For example, if sympatry/allopatry affects host responses and mostly parasitized populations are studied, then this biased sampling may affect interspecific trends. Further, intraspecific variation can be extreme (rejection rates varying from 5 to 69% in a single species: Stokke *et al*., 2008), highlighting that no single population can be representative of a 'species-typical' behaviour (Foster and Endler, 1999). Instead, we suggest that species may show species-specific reaction norms (e.g. species-specific patterns of covariation between parasitism and egg rejection rates), which can be revealed only by sampling across multiple populations subject to varying parasitism risks. This highlights the crucial importance of metareplication for any studies in ecology (Kelly, 2006).

In science, results are always determined by methods. For example, even seemingly subtle differences in model eggs design can have profound consequences for host responses. Any comparison in science needs to be based on experimental design that is consistent across all units (individuals, populations, species) that are being compared. This methodological aspect is crucial in studies of introduced or expanding populations because data are often collected by different researchers in different locations. Therefore, we strongly recommend that methods are not similar but *identical* across all spatial replicates.

Any defence in the absence of a threat is a wasteful investment. All previous work (but see Samas *et al*., 2014a) made a simplistic assumption that only rejection costs and errors at non-parasitized nests select against retention of anti-parasitic adaptations after parasites no longer use a particular host. For an adaptation to decay, rejection costs and errors are not necessary because multiple other mechanisms erase the adaptation (mutation pressure, genetic drift, costs of maintenance of neural networks, trade-offs with currently useful adaptations). This also highlights a necessity to consider alternative hypotheses, namely conspecific brood parasitism as a viable alternative to the interspecific parasitism hypothesis (Lyon and Eadie, 2004). We note that in contrast to interspecific parasitism, in the case of conspecific parasitism rejection costs and errors at all nests (i.e. not only non-parasitized ones) select against host defences, because

conspecific parasites do not evict host progeny and are raised jointly (Samas *et al.*, 2014a).

Generally in biology, the most rapid micro-evolutionary changes, i.e. those happening at the scale of decades or centuries (Thompson, 1998), are typically found in populations introduced to novel environments (Blackburn *et al.*, 2009) and in urbanized populations (Gil and Brumm, 2014). Therefore students of brood parasite–host interactions should capitalize on many such systems that are currently available, yet remain unexamined. The major advantage of such an approach, especially in the case of introduced populations, is that it is best suited to answer some big unanswered questions in the study of brood parasitism. For example (Rothstein, 2001), does host–parasite coevolution follow a coevolutionary cycles scenario (host adaptations decline after parasitism pressure ceases, allowing parasites to re-invade) or a single-trajectory model (host adaptations are retained after parasitism pressure ceases, preventing parasites from re-invading)?

This central question is hardly possible to answer through the study of native populations because of confounding effects of gene flow and always unknown long-term length (time) and extent (ancient parasitism rates and costs) of parasite–host contact. Introduced populations are free from these two fundamental problems. Indeed, a few pioneering studies have already employed the framework that we detailed in this chapter, addressed the central question and changed our long-held views of parasite–host coevolution. We believe that future studies following the above listed conceptual and methodological framework, especially (a) metareplication across phylogeny, space and time, (b) standardized methods, (c) inclusion of control species, (d) attention to alternative hypotheses, and (e) realistic consideration and quantification of all costs and benefits, will bring novel, robust, and exciting evidence that will fundamentally deepen our understanding of enemy–victim coevolution.

Acknowledgements

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