Strikingly, *Wolbachia* also induce a form of male sterility, a phenomenon called cytoplasmic incompatibility (CI), which is widespread in arthropods. CI results in embryonic mortality when males infected by *Wolbachia* mate with uninfected females. However, fertility is restored if the female is also infected. Although the underlying mechanism is presently unknown, it is clear that, in infected females, the bacterium provides the eggs with an antidote, protecting them from the action of a poison produced in germline of the males. This idea was explicitly formulated by Werren[6] as the *mod*/*resc* model: *mod* (modification) is the poison and *resc* (rescue) is the antidote. Four theoretical kinds of *Wolbachia* can be envisaged: *mod*+/*resc*+ (sterilizer/rescuer), *mod*–/*resc*– (harmless/non-rescuer), *mod*–/*resc*+ (harmless/rescuer) and *mod*+/*resc*– (sterilizer/non-rescuer). To date, the first three have been discovered[7–9]. If one envisages mitochondria-induced sterility within the general framework of this model, the two following propositions emerge.

First, the existence of sterilizing mitochondria exemplifies that the '*Wolbachia* of the fourth kind' (*mod*+/*resc*–) might exist in natural populations. Indeed, nothing opposes the maintenance of such a variant in host populations infected by *mod*–/*resc*– bacteria. One possible way to explain why such 'suicidal' *Wolbachia* have not yet been discovered is that laboratory host lines are often founded from single mothers (this is true at least for *Drosophila*). If the founder female is infected by a *mod*+/*resc*– bacterium, her daughters and sons will be self-incompatible, resulting in sterile sib-mating in the first generation.

Second, if *Wolbachia* have the ability to rescue their own sterilizing effect, one might speculate that mitochondria possess the same function. Some cases of sterility (more precisely, cases where sterility is the result of early embryonic mortality) could then be owing to a confrontation between incompatible mitochondrial variants, just like different *mod*+/*resc*+ *Wolbachia* strains can be incompatible with each other[10]. Such a pattern could reflect an ancestral situation, when mitochondria were able to establish themselves in a host cell via CI, opening the way to a successful association. Alternatively, CI might have evolved seondarily, when the association was already stable: CI would be advantageous for any maternally inherited symbiant, including mutualistic ones[11].

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Lice as probes

Clayton and Johnson's[1] recent *Research News* in *TREE* provides a service in publicizing our results on 'Using lice to identify cowbird hosts'[2] to a wider audience interested in general concepts of host specificity and parasite community structure (http://www.pwrc.usgs.gov/research/products/hahn/aukreprint1). Because Brown-headed Cowbird *Molothrus ater* fledglings function as natural ecological probes of louse communities on songbirds, they can be used to study evolutionary questions as well as to serve as the conservation tool that we tested[1].

Clayton and Johnson questioned whether size of foster hosts biased the survival of lice from foster parents on cowbird fledglings. Our data[2] (extracted in Table 1) show that host body size did not constrain the survival of passerine lice as it did the lice on cave swiftlets (Apodidae)[4]. Four louse species infested two very different-sized passerine species – birds more different in size from each other than one or both are from the cowbird. Swiftlets are infested only with lice from the family Menoponidae (genera *Dennyus* and *Eureum*), which could differ significantly in behavior from lice of the family Philopteridae (e.g. *Philopterus*, *Brueelia* and *Sturnidoecus*).

Clayton and Johnson suggested that our 18% infestation level on cowbird fledglings was low because we only used a fumigation technique to collect the lice. We did also use the dust ruffling technique[5] they suggested on all 463 fledgling and adult cowbirds, and although it yielded additional lice, it did not yield additional louse species, the relevant data to our study.

They also suggested that our 18% infestation level of live cowbird fledglings was low in comparison to a 46% infestation reported for adult cowbird museum skins[6]. However, the relevant comparison is between cowbird fledglings and host fledglings, and Ash[7] showed that the level of louse infestation in young songbirds is lower than that in adults – 22.4% of juveniles (similar to our findings) and 1.7% of broods.

Finally, Clayton and Johnson questioned whether all 11 louse species found on cowbird fledglings were acquired from their foster parents, suggesting 'It is possible that some of the eight species of lice recovered only from cowbirds are host-specific parasites of cowbirds…' Nothing in our louse data suggests there are lice specific only to Brown-headed Cowbirds. Cowbird-specific lice would have been collected repeatedly in our large sample of 463 cowbirds and would not have been found on any host birds. Only five cowbird louse species were not assigned to any host (*Menacanthus quiscali* and *M. chrysophaeus* have been previously found on grackles and sparrows respectively[8]), and they most probably originated on other local songbird hosts, because we trapped only 30 out of 37 of the common local host species that cowbirds parasitize.

Table 1. Louse species tolerate differences in bird body size[a]

Louse species	Bird host	Bird weight (g)[b]
Myrsidea fuscomarginata[c]	Common Grackle *Quiscalus quiscula*	113.5
	Red-winged Blackbird *Agelaius phoeniceus*	52.5
Philopterus agelaii[c]	Red-winged Blackbird	52.5
	Red-eyed Vireo *Vireo olivaceus*	16.7
Myrsidea sp. # 2[d]	Wood Thrush *Hylocichla mustelina*	47.7
	Common Yellowthroat *Geothlypis trichas*	10.1
Brueelia sp. # 3	Veery *Catharus fuscescens*	41.2
	Common Yellowthroat	10.1

[a]Data taken from Table 1, Ref. 2.
[b]From Ref. 3.
[c]Also found on Brown-headed Cowbird *Molothrus ater* adults (43.8 g: Ref. 3) and fledglings.
[d]Also found on Brown-headed Cowbird fledglings.

It is treacherous to address the question of host-specific lice in brood parasites by investigating the Brown-headed Cowbird, because it is an extreme host generalist that parasitizes at least 132 songbird species[9]. We believe that the remarkable 14 species and seven genera of lice that we collected from cowbird fledglings and adults most probably resulted from transference of lice to nestling cowbirds from a variety of host species and that the total number of lice potentially found on Brown-headed Cowbirds is much larger than we have shown. Future work will have to resolve this issue, and Clayton and Johnson's questions aptly demonstrate how Hutchinson's principle of growth by intussusception[10] applies to the study of dual coevolutionary systems.

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Lice as probes

Response from Clayton and Johnson

Hahn and Price[1] use a subset of the data from Hahn *et al.*[2] to '…show that host body size does not constrain the survival of passerine lice as it did lice on cave swiftlets'[3]. Their table contains records of four species of lice (out of 22 species collected) that were found on host species that differ in body size. Contrary to Hahn and Price's implication[1], the cave-swiftlet study[3] also documented lice on hosts that differ in body size. Indeed, this was central to the study, which used experimental transfers to show that lice do not survive for more than a week on some hosts, in spite of the fact that they might occasionally disperse to those hosts and survive for brief periods[3]. Testing the relationship of host body size to parasite survival (and reproduction) requires an experimental approach, or a properly controlled comparative analysis[4].

Hahn and Price chose not to comment on the other role of host body size addressed in our article[5]. It is well established that large-bodied species have more individual lice than do small-bodied species[6,7]. A probable consequence of this is that cowbirds reared by large-bodied hosts are more likely to acquire foster lice in the first place, which would have biased Hahn *et al.*'s method toward the detection of large-bodied foster species. Host body size is relevant to the interpretation of Hahn *et al.*'s data[2] because of its impact both on the population ecology of lice, as well as on the host associations of lice.

The quality of data on parasite populations depends on the method used to collect them[8]. Hahn *et al.*'s fumigation technique[2] recovered lice from only 20% of adult cowbirds, compared with 46% of adult cowbirds in Geist's study of freshly collected birds[9] (not museum skins, as Hahn claims). In another study, Starks recovered lice from 41% of freshly collected cowbirds (K.J. Starks, MSc Thesis, University of Oklahoma, 1951). We maintain that Hahn *et al.*'s lower returns are a consequence of their suboptimal methodology.

We reiterate that some of the lice found only on cowbirds might, in fact, be host-specific parasites of cowbirds, similar to the host-specific lice found on other species of brood parasites[10,11]. The best candidates for this distinction are one or more of the *Brueelia* spp. of lice collected from cowbirds by Hahn *et al.*[2]. Other species of *Brueelia* are host-specific parasites found on other species of cowbirds[12]. Why should Brown-headed cowbirds be the exception?

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