

Coevolution, communication, and host-chick mimicry in parasitic finches: who mimics whom?

Mark E. Hauber · Rebecca M. Kilner

Received: 2 June 2006 / Revised: 13 October 2006 / Accepted: 13 October 2006 / Published online: 21 November 2006
© Springer-Verlag 2006

Abstract Why do brood parasitic *Vidua* nestlings mimic the intricate gape patterns of their hosts' young so precisely? The classic explanation is that mimicry is the outcome of a coevolutionary arms race, driven by host rejection of odd-looking offspring. Selection favors parasitic nestlings that converge on the host young's mouth markings, and simultaneously benefits hosts whose mouth markings diverge from those of the parasite. The outcome is highly elaborate mouth markings in host young that are accurately mimicked by parasite nestlings. Our review of recent work provides mixed support for this traditional view and, instead suggest that complex mouth markings function to stimulate adequate provisioning, rather than to signal species identity. Thus, similarly elaborate gape morphologies in hosts and parasites could have evolved through nestling competition for parental care. According to this view, and in contrast with existing hypotheses, it is host young that mimic parasitic offspring, in order to compete effectively for food.

Keywords Coevolution · Indigobirds · Parent–offspring conflict · Sibling rivalry

Introduction

Estrildid finches in Africa are exploited by 19 species of *Vidua* finch, obligate brood parasites, which typically victimize a single host species (Payne 1997). The elaborate and complex gape patterns displayed by host offspring are precisely matched by the parasite (Fig. 1), sometimes to the extent that the two species cannot easily be distinguished when they share the same nest (Sorenson et al. 2003). It calls to mind the accurate mimicry of host egg color and patterning shown by some host races of common cuckoos *Cuculus canorus* (Brooke and Davies 1988; Davies and Brooke 1989; Moksnes and Roskaft 1995), known to be the result of a coevolutionary arms race played out between parasite and host (Rothstein and Robinson 1998). Hosts defend themselves against exploitation by the cuckoo by removing odd-looking eggs from their nests, thus selecting female parasites whose eggs survive because they look like part of the host's own clutch (Davies 2000; Payne 2005b). The traditional view maintains that a similar signature forgery arms race is responsible for the evolution of the perfectly matching and elaborate gape morphologies in the parasitic *Vidua* finches and their hosts (Neunzig 1929; Nicolai 1964).

In this review, we suggest an alternative to this classic (Lack 1968), textbook (Gill 2003) interpretation of mimicry evolution in *Vidua* finches. Recent observations in the laboratory and the field reveal that host estrildid finches

Communicated by A. Cockburn

M. E. Hauber (✉)
School of Biological Sciences, University of Auckland,
PB 92019, Auckland, New Zealand
e-mail: m.hauber@auckland.ac.nz

R. M. Kilner
Department of Zoology, University of Cambridge,
Downing Street,
Cambridge CB2 3EJ, UK



Fig. 1 A snapshot of the nestling begging display of the brood parasitic pin-tailed whydah (*left*) and common waxbills (*right*) from the same brood. All photo credits: Justin G. Schuetz

appear not have special behavioral adaptations to reject parasite nestlings from their broods (Payne et al. 2001; Schuetz 2005a). Furthermore, experimental data imply that elaborate gape morphologies function to attract care rather than to signal species identity (Payne et al. 2001; Schuetz 2005b). Finally, comparative analyses suggest that *Vidua* parasitism might have corrupted some aspects of the usual channel of communication between host young and their parents (Payne 2005a). As a result, host young might be under selection to mimic the appearance of their more competitive parasitic nestmates to beg effectively for food. We suggest, therefore, that the often perfect match between nestling *Vidua* parasites and those of their host is caused by selection on host young to mimic their parasites rather than by selection on parasitic young to mimic their hosts.

Why are host estrildid mouth markings so complex?

Complex nestling mouth markings and ornamentation are not confined to hosts of *Vidua* finches, but are a distinctive feature of all the 130 or so estrildid finch species, including Australian grassfinches that presumably have never been exposed to brood parasitism by African *Vidua* species (Payne 2005a) (Fig. 2). It is possible that the elaborate and interspecifically diverse mouth markings in the Australian grassfinches are an evolutionary product of coevolutionary arms races between extant estrildids and their extinct brood parasites, and are a kind of “ghost of adaptation past,” analogous to the antiparasite adaptations retained by cuckoo and cowbird hosts long after the threat of parasitism has passed (Lindholm 1999; Rothstein 2001; Lahti and Lahti 2002). A more parsimonious alternative is that elaborate gape structures were an ancestral character for

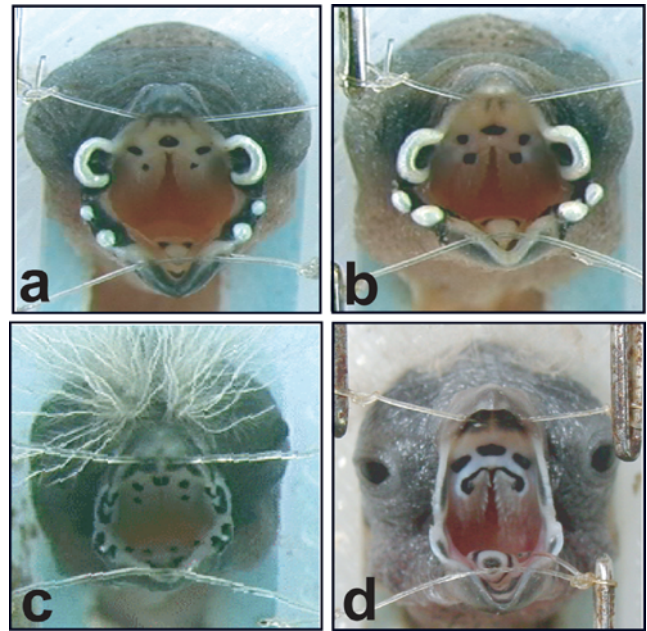


Fig. 2 Diversity of chick gape markings of *Vidua* (a) and nonparasitic estrildid (b–d) finches markings. Host young (b) are raised alongside parasitic young (a). a *Vidua macroura*, b *Estrilda astrild*, c *Amandara subflava*, all from Africa; and d *Stizoptera bichenovii*, from Australia

the entire family of estrildid finches, predating any association with brood parasites or even the ancient split of estrildid and *Vidua* lineages (Sorenson and Payne 2001; Alcock 2005).

Several explanations have been advanced to account for the evolution of complex mouth markings in estrildid finches (Davies 2000), none of which are mutually exclusive.

- (1) One possibility is that complex mouth markings arose simply by historical accident, and are selectively neutral today. In the most comprehensive comparative survey to date, Payne (2005a) reports that much of the variation within the estrildids in the particular color and form of the gape decorations can be explained by shared ancestry, implying a role for phylogenetic inertia (Blomberg and Garland 2002).
- (2) A second possibility is that complex gape morphologies were selected by the avian visual system to be detectable in the typically dimly lit estrildid nest (Endler and Mielke 2005). For example, gape papillae glow in the near dark in several African, South Asian, and Australian species, although they are not luminescent. Furthermore, gape flanges are brighter or thicker in some estrildid species nesting in darker, more forested habitats (Payne 2005a) and in species whose young are raised in darker nests (Schuetz 2004).
- (3) Third, it is possible that the particular colors of the globes set in the gape flanges of finch chicks (Fig. 2) may have been selected to indicate nestling hunger or perhaps health status (Davies 2000) because they fade

quickly after death (Payne 1997). In addition, it is possible that these elaborate signals serve to compensate any size-related disadvantages that young experience as a consequence of hatching asynchrony (Davies 2000), although this idea has yet to be tested.

While these hypotheses may explain some of the detail in gape morphology, they are not sufficient alone to fully account for the evolution of superbly complex estrildid mouth markings. Each hypothesis has also been advanced to account for the diversity of palate markings, gape flanges, and mouth coloration displayed by other young birds from different passerine and cuckoo lineages (Kilner and Davies 1999; Payne 2005a,b; Kilner 2006), none of which come close to matching estrildid finches in visual or structural complexity.

Among the birds, nestling estrildid finches are rivaled perhaps only by young rails in the extent of their ornamentation as offspring (Boyd and Alley 1948; Lyon et al. 1994; Krebs and Putland 2004). Davies (2000) suggests that a comparison of the two families can offer a more general explanation for the evolution of elaborate offspring ornamentation. In both families of birds, chick mortality is high and, unusually, can be the result of infanticide rather than siblicide (Horsfall 1984; Burley 1986; Leonard et al. 1988; Lyon et al. 1994; Payne et al. 2001; Schuetz 2005a). Parents thus maintain significant control over their progeny's fate and appear to be fully in charge of the provisioning decisions for different offspring. This means that dependent young can compete for food only by attracting parental attention. Furthermore, with a high incidence of nestling mortality, even in the absence of nutritional or energetic constraints on parents (Payne et al. 2001; Schuetz 2005b), the penalties are severe for offspring that fail to stimulate provisioning by parents. Perhaps, then, complex mouth ornamentation in the estrildid hosts has evolved under parental choice (West-Eberhard 1983) initiated by an arbitrary sensory bias (Alcock 2005; Grim 2005), which has become elaborate to reach extreme ornamentation (Rice and Holland 1997) in a process that is analogous to Fisherian sexual selection (Fisher 1958; Lyon et al. 1994).

The evolution of host-*Vidua* similarity: mechanisms and consequences of host discrimination

Theoretically, host-parasite similarity can evolve for several distinct reasons, both in the presence and absence of host discrimination against brood parasitic young (Grim 2005). The hypotheses listed below are not necessarily mutually exclusive because different aspects of complex displays may evolve under different selection pressures (as discussed by Davies 2000; Payne 2005a; see "Host-parasite

coevolution driven by parasite mimicry of host signals" section below).

Similarity without coevolution with the host: the absence of host discrimination between parasitic and own young

Recent shared ancestry with the host

If hosts and parasites are closely related, or are sister taxa [Emery's rule (Emery 1909)], then their similarity might be due to a lack of divergence in species-specific phenotypes. For example, similarly white egg colors of estrildid and viduid finches may be explained by phylogenetic inertia in these related lineages (Sorenson and Payne 2001).

Yet, in the parasitic viduids (Sorenson and Payne 2001), closely related species have divergent mouth markings (Schuetz 2004; Payne 2005a). Moreover, among the specialist parasites, mouth markings are more similar to distantly related estrildid finch hosts than they are to closely related parasitic viduid species. Thus, neither line of evidence for the evolution of variable viduid and estrildid gape markings is consistent with the shared ancestry hypothesis. Therefore, similarity to the host progeny by the parasite must have a selective advantage and is not simply a consequence of recent shared ancestry with the host (Blomberg and Garland 2002).

Parasite mimics host: parasites converge on host mouth markings

A second possibility is that parasites converge on host mouth markings to extract adequate levels of care from their hosts (Payne 2005a; Schuetz 2005a,b). According to this hypothesis, the host adults' provisioning rules are unchanged by parasitism, as are the gape morphologies of their offspring. The nestling *Vidua* is a rare parasite (Grim 2006a) that taps into a preexisting channel of parent-offspring communication in its host. Perhaps it mimics those aspects of the host begging display that will most effectively attract provisioning without inducing coevolution with its host, much like the common cuckoo chick in the nest of a reed warbler *Acrocephalus scirpaceus* (Kilner and Davies 1999; Kilner et al. 1999; Madden and Davies 2006).

Experimental work certainly supports the suggestion that the estrildid finches' intricate mouth markings are instrumental in eliciting adequate care. In the laboratory, nestling zebra finches *Taeniopygia guttata* of the white morph, which lack the mouth markings displayed by their wild-type counterparts, were correspondingly less successful at obtaining provisioning, especially when food abundance was restricted (Skagen 1988; Reed and Freeman 1991). Similarly, in field experiments, when the glowing white

flanges displayed by common waxbill *Estrilda astrild* offspring were covered with black marker pen, these young grew more slowly than either sham-manipulated controls, dyed with solvent, or untreated nestlings (Schuetz 2005b).

Mimicry as a consequence of coevolution with the host: behavioral discrimination between parasite and own young by host

Host–parasite coevolution driven by parasite mimicry of host signals

The traditional explanation for the evolution of *Vidua* nestling mimicry is that it results from selection by hosts, defending themselves against parasitism by removing or otherwise discriminating against, odd-looking chicks in the nest (Neunzig 1929; Nicolai 1964). While this selection favors parasites that converge on host mouth markings, the argument goes, it simultaneously favors hosts whose mouth markings diverge from those of the parasite (Neunzig 1929). Thus, complex host gape patterns ease the host parents' task of discriminating and identifying alien young, with the implicit assumption that host parents recognize mutant host chicks either through learning of the phenotype of their own young (Lotem 1993) or through a genetic correlation between alleles associated with both chick phenotypic markers and parental sensory preferences. Species or lineages with a protracted history of exploitation by brood parasites should therefore have nestlings with more varied and elaborate mouth markings than those unscathed by parasitism (Payne 2005a).

The evidence in support of this hypothesis is rather mixed, however. On the one hand, recent comparative work suggests that coevolution between parasites and hosts has indeed taken place (Payne 2005a). Many of the African waxbills are routinely targeted for exploitation by the *Vidua* finches, and their nestlings' gapes have more colors, as judged by human eyes, than those seen in nonparasitized estrildid lineages (p. 34, gape index c in Payne 2005a). The flanges of waxbills in Africa are also more colorful than the flanges of ecologically similar grassfinches in Australia (p. 34, gape index b in Payne 2005a), with displays of more red, orange, and blue colors and shades from black to gray to white. In an additional analysis, Payne compared the mouth markings of hosts of generalist parasites, with those that were exploited by a single, highly mimetic parasite and again found the same pattern of greater complexity and more color in species with specialist parasites (p. 34, gape index b in Payne 2005a).

Field observations also lend some support to the suggestion that coevolution between parasites and hosts has elaborated host nestling mouth markings. Payne et al. 2002 reported a recent switch to a novel host by the village

indigobird *Vidua chalybeata*. Nestlings of the old host, the red-billed firefinch *Lagonosticta senegala* and the parasite look very similar, each displaying yellow palates decorated with three black spots and white gape papillae bordered with blue. The new host, the congeneric brown firefinch *Lagonosticta nitidula*, has offspring that look quite different. Their mouths are pinkish white, rather like those of the nonparasitized Australian finches and, perhaps, of the nonparasitized ancestral estrildids, and marked with only three black spots, and their simple white gape papillae lack the blue borders seen in the old hosts (Payne et al. 2002).

On the other hand, there is neither comparative nor behavioral evidence to suggest that the intricate black palate spots of estrildid finches have evolved in response to brood parasitism by *Vidua* species. While there is a close-to-perfect match of these palate marks between hosts and their specialist parasites (Figs. 1 and 2), the number, size, and complexity of these palate markings were similar between parasitized and nonparasitized waxbill taxa (index d in Payne 2005a). The cause and maintenance of variation in these visual traits of estrildid begging displays remain to be revealed through detailed studies of Australian and Asian estrildid taxa that have not experienced brood parasitism by *Vidua* (Davies 2000).

In short, there is at least some evidence demonstrating that *Vidua* parasitism has changed some aspects of both parasite and host gape morphology through evolutionary time. But is there any the evidence showing that this coevolution is driven by hosts' rejection of odd-looking nestlings?

Schuetz's (2005a) careful field observations document that *Vidua* parasites survived worse than host common waxbills' chicks, which appears consistent with the suggestion of chick discrimination but does not demonstrate that *Vidua*-specific gape markings caused the higher mortality of the parasitic chicks. Schuetz found that host young also suffered high rates of mortality, both in parasitized and nonparasitized broods (Schuetz 2005a). Indeed, brood reduction appears to be a common feature of estrildid breeding biology, occurring naturally at a similar rate in infrequently parasitized orange-breasted waxbills *Amandava subflava*, in the nonparasitized Australian zebra finch (Schuetz 2005a), and in the nests of these and other species of estrildids in captivity (Payne et al. 2001). There is no indication, therefore, that brood reduction is a specific response that was selected by *Vidua* parasitism. The deaths of *Vidua* young observed by Schuetz did not appear to result from targeted discrimination of foreign young by hosts through a specific antiparasite behavior (Schuetz 2005a), but seemed to be part of the collateral damage resulting from brood reduction, usual when estrildids reproduce (Kilner 1998; Payne et al. 2001; Schuetz 2005a).

Studies within different cuckoo populations show that individuals reduce the incidence of egg rejection when there is a low risk that their clutch is parasitized (Moksnes et al. 1991; Davies et al. 1996; Brooke et al. 1998; Lindholm and Thomas 2000; Moskat et al. 2002). However, there is no equivalent evidence for *Vidua* chick rejection; Schuetz instead found that the incidence of *Vidua* mortality was similar across years and two different study sites, independent of the rate of local parasitism (Schuetz 2005a).

Set against these field observations are the experiments on captive birds carried out by Payne et al. 2001, which report high rates of mortality for odd-looking nonparasitic estrildid finch nestlings, experimentally cross-fostered into the nests of the red-billed firefinch. But do these results constitute evidence of parental discrimination against odd-looking gapes or were these odd-looking chicks doomed for other reasons? Schuetz (2005b) points out that a drawback of the cross-fostering paradigm is that hosts may have discriminated against other aspects of the begging display, which differ between fostered and fosterer species, such as calling (Payne and Payne 2002) and posturing (Mines 2004). In addition, foster parents may have been less stimulated to provision by foreign chicks' displays or the experimental offspring may have simply thrived less well in an alien environment due to thermal or nutritional constraints (Schuetz 2005b) that can critically differ between related host taxa and their potential parasites (Grim 2006b). Therefore, we suggest that it is too soon to conclude that *Vidua* hosts recognize and reject odd-looking offspring as a strategy for defense against brood parasitism.

Host parasite coevolution driven by host mimicry of parasite signals

The final hypothesis for the evolution of *Vidua* nestling mimicry considers the dynamics of nestling competition for parental attention in parasitized nests (Kilner 2006). The starting point is identical to the situation described above (in the “Parasite mimics host: parasites converge on host mouth markings” section), with *Vidua* chicks tapping into the preexisting channel of communication between host offspring and parents by mimicking those aspects of the host young's begging displays that are most likely to attract care. What happens next? The *Vidua* has no genetic stake in the fitness of host offspring with whom it shares the nest and so is under selection to behave more selfishly than host young (Hamilton 1964; Briskie et al. 1994). It may hit on a novel visual trick or manage to exaggerate a specific aspect of the gape structure that more effectively exploits host parents, and thus gain an edge in the battle for parental attention. *Vidua* that are about to exploit a new host species might by chance already possess aspects of the visual, behavioral, and acoustic trickery that will give them a

competitive advantage as they begin to exploit the new host, especially if the new host is a close relative of the old host, sharing both ecology and habitat (Blomberg and Garland 2002) and the associated sensory systems (Hauber and Sherman 2001).

Once some parental resources are lost to the unrelated parasite, the host young are under selection to be more competitive themselves. This may cause their gape morphologies to converge on the parasite's, thereby reducing the competitive prowess of the foreign chick until it again comes up with another visual trick for attracting additional food. The parents, meanwhile, may also change their provisioning rules in response to exploitation by the parasite because it has effectively reduced their average relatedness to their brood. Consequently, they may require a greater level of visual stimulation to determine their provisioning rate at the nest (Godfray 1995). A prolonged and specific history of interaction between parasite and host could thus result in the evolution of increasingly elaborate mouth markings in both species, as parasitic young attempt to outpace host young in the evolutionary battle to capture parental attention (Kilner 2006). The arms race might eventually come to a stable conclusion with parasitic and host young using similar begging displays, but only if hosts start to discriminate against odd-looking parasitic nestlings, or if sibling parasites are commonly reared in the same nest, thereby reducing the relatedness asymmetry between parasitic and host young.

The key feature of this coevolutionary scenario is that host young are constantly catching up with parasites to receive sufficient care from their own genetic parents (Kilner 2006). By contrast, in the classical view of estrildid and *Vidua* coevolution, host young are constantly escaping the increasingly accurate mimicry by the parasite so that the species-specific signature remains uncorrupted.

The experimental and comparative evidence described above is consistent with the hypothesis of parasite-driven elaboration of host gapes because it predicts that intricate mouth structures serve to attract provisioning (West-Eberhard 1983; Rice and Holland 1997), rather than to signal species identity (Schuetz 2005a,b), and it also anticipates some of the coevolved changes in parasite and host offspring gape markings, as reported by Payne's (2005a) comparative work. However, no line of evidence uniquely supports this new idea and further work is now required to test whether it is a valid explanation for the high degree of resemblance between host and parasitic young.

Coevolution without rejection?

The interactions between brood parasites and their hosts have long been regarded as model systems for the study of

coevolution (Payne 1977; Davies and Brooke 1988; Rothstein 1990). Until now, however, the principal driving force for coevolution, identified by experimental work, was the rejection or desertion of parasitic offspring by discriminating hosts (Davies 2000; Langmore et al. 2003; Moskat 2005). Our review of recent work on the *Vidua* brood parasites suggests a new engine for coevolution, which can also cause precise parasite mimicry of host offspring. Competition among unrelated broodmates for parental resources, carefully doled out by hosts in response to complex offspring cues and signals, might have propelled the elaboration of gape ornamentation in host and parasitic young alike. With the interactions of more than a dozen *Vidua* species and their hosts still remaining to be described, there is plenty of scope for testing the general validity of our conclusions in future work.

Acknowledgments We thank M. Anderson, N. Davies, B. Gill, T. Grim, N. Langmore, N. Leuschner, C. Millar, J. Schuetz, M. Sorenson, R. Payne, and other anonymous referees for comments and discussion; V. Ward for help with the illustrations; and the New Zealand Marsden Fund, the National Geographic Society, and the University of Auckland Research Council for funding. R.M.K. was supported by a Royal Society University Research Fellowship and a Leverhulme Trust Research Grant.

References

- Alcock J (2005) Animal behavior. Sinauer, Sunderland, MA
- Blomberg SP, Garland TJ (2002) Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J Evol Biol* 15:899–910
- Boyd HJ, Alley R (1948) The function of head-coloration of the nestling coot and other nestling Rallidae. *Ibis* 90:582–593
- Briskie JV, Naugler CT, Leech SM (1994) Begging intensity of nestling birds varies with sibling relatedness. *Proc R Soc Lond B* 258:73–78
- Brooke M de L, Davies NB (1988) Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* 335:630–632
- Brooke M de L, Davies NB, Noble DG (1998) Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. *Proc R Soc Lond B* 265:1277–1282
- Burley N (1986) Sex-ratio manipulation in color-banded populations of zebra finches. *Evolution* 40:1191–1206
- Davies NB (2000) Cuckoos, cowbirds and other cheats. T & A D Poyser, London
- Davies NB, Brooke M de L (1988) Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim Behav* 36:262–284
- Davies NB, Brooke M de L (1989) An experimental study of coevolution between the cuckoo, *Cuculus canorus*, and its hosts. 1. Host egg discrimination. *J Anim Ecol* 58:207–224
- Davies NB, Brooke M de L, Kacelnik A (1996) Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc R Soc Lond B* 263:925–931
- Emery C (1909) Über den Ursprung der dulotischen, parasitischen und myrmekophilen Ameisen. *Biol ZentBl* 29:352–362
- Endler JA, Mielke PW (2005) Comparing colour patterns as birds see them. *Biol J Linn Soc* 86:405–431
- Fisher RA (1958) The genetical theory of natural selection, revised 2nd edn. Dover, New York
- Gill FB (2003) Ornithology. Freeman, New York
- Godfray HCJ (1995) Signaling of need between parents and young: parent–offspring conflict and sibling rivalry. *Am Nat* 146:1–24
- Grim T (2005) Mimicry vs. similarity: which resemblances between brood parasites and their hosts are mimetic and which are not? *Biol J Linn Soc* 84:69–78
- Grim T (2006a) The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evol Ecol Res* 8:785–802
- Grim T (2006b) Cuckoo growth performance in parasitized and unused hosts: not only host size matters. *Behav Ecol Sociobiol* 60:716–723
- Hamilton WD (1964) The genetical theory of social behaviour, I, II. *J Theor Biol* 7:1–52
- Hauber ME, Sherman PW (2001) Self-referent phenotype matching: theoretical possibilities and empirical tests. *Trends Neurosci* 10:609–616
- Horsfall JA (1984) Brood reduction and brood division in coots. *Anim Behav* 32:216–225
- Kilner RM (1998) Primary and secondary sex ratio manipulation by zebra finches. *Anim Behav* 56:155–164
- Kilner RM (2006) Function and evolution of color in young birds. In: Hill GE, McGraw KJ (eds) Bird coloration: function and evolution, vol 2. Harvard University Press, Cambridge, MA, pp 201–232
- Kilner RM, Davies NB (1999) How selfish is a cuckoo chick? *Anim Behav* 58:797–808
- Kilner RM, Noble DG, Davies NB (1999) Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature* 397:667–672
- Krebs EA, Putland DA (2004) Chic chicks: the evolution of chick ornamentation in rails. *Behav Ecol* 15:946–951
- Lack D (1968) Ecological adaptations for breeding in birds. Chapman & Hall, London
- Lahti D, Lahti A (2002) How precise is egg discrimination in weaverbirds? *Anim Behav* 63:1135–1142
- Langmore NE, Hunt S, Kilner RM (2003) Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* 422:157–160
- Leonard ML, Horn AG, Eden SF (1988) Parent–offspring aggression in moorhens. *Behav Ecol Sociobiol* 23:265–270
- Lindholm AK (1999) Brood parasitism by the cuckoo on patchy reed warbler populations in Britain. *J Anim Ecol* 68:293–309
- Lindholm AK, Thomas RJ (2000) Differences between populations of reed warblers in defenses against brood parasitism. *Behaviour* 137:25–42
- Lotem A (1993) Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature* 362:743–745
- Lyon BE, Eadie JM, Hamilton LD (1994) Parental choice selects for ornamental plumage in American coot chicks. *Nature* 371:240–243
- Madden JR, Davies NB (2006) A host–race difference in begging calls of nestling cuckoos *Cuculus canorus* develops through experience and increases host provisioning. *Proc R Soc Lond B* 273:2235–2343
- Mines B (2004) Brood parasitism in South African whydahs. Ph.D. dissertation, University of Cambridge, Cambridge
- Moksnes A, Roskaft E (1995) Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *J Zool* 236:625–648
- Moksnes A, Roskaft E, Braa AT, Korsnes L, Lampe HM, Pedersen HC (1991) Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* 116:64–89

- Moskat C (2005) Common Cuckoo parasitism in Europe: behavioural adaptations, arms race and the role of metapopulations. *Ornithological Science* 4:3–15
- Moskat C, Szentpeteri J, Barta Z (2002) Adaptations by great reed warblers to brood parasitism: a comparison of populations in sympatry and allopatry with the common cuckoo. *Behaviour* 139:1313–1329
- Neunzig R (1929) Zum Brutparasitismus der Viduinen. *J Ornithol* 77:1–21
- Nicolai J (1964) Der Brutparasitismus der Viduinae als ethologisches problem. *Z Tierpsychol* 21:129–204
- Payne RB (1977) The ecology of brood parasitism in birds. *Ann Rev Ecol Syst* 8:1–28
- Payne RB (1997) Avian brood parasitism. In: Moore J (ed) *Host–parasite evolution: general principles and avian models*. Oxford University Press, Oxford, pp 338–369
- Payne RB (2005a) Nestling mouth markings and colors of Old World finches Estrildidae: mimicry and coevolution of nesting finches and their *Vidua* brood parasites. *Miscellaneous Publications, Museum of Zoology, University of Michigan*, no. 194, Ann Arbor
- Payne RB (2005b) *The cuckoos*. Oxford University Press, Oxford
- Payne RB, Payne LL (2002) Begging for parental care from another species: behavioural specialization and generalization in brood-parasitic finches. In: Wright J, Leonard ML (eds) *The evolution of begging: competition, cooperation and communication*. Kluwer, The Netherlands, pp 429–450
- Payne RB, Woods JL, Payne LL (2001) Parental care in estrildid finches: experimental tests of a model of *Vidua* brood parasitism. *Anim Behav* 62:473–483
- Payne RB, Hustler K, Stjernstedt R, Sefc KM, Sorenson MD (2002) Behavioural and genetic evidence of a recent population switch to a novel host species in brood-parasitic indigobirds *Vidua chalybeata*. *Ibis* 144:373–383
- Reed HJ, Freeman NH (1991) Does an absence of gape markings affect the survival of leucistic young in the zebra finch? *Bird Behavior* 9:58–63
- Rice WR, Holland B (1997) The enemies within: intergenomic conflict, interlocus context evolution (ICE), and the intraspecific Red Queen. *Behav Ecol Sociobiol* 41:1–10
- Rothstein SI (1990) A model system for co-evolution: avian brood parasitism. *Ann Rev Ecol Syst* 21:481–508
- Rothstein SI (2001) Relic behaviours, coevolution and the retention versus loss of host defences after episodes of avian brood parasitism. *Anim Behav* 61:95–107
- Rothstein SI, Robinson SK (1998) *Parasitic birds and their hosts: studies in coevolution*. Oxford University Press, Oxford
- Schuetz JG (2004) Brood parasitism in African finches and its consequences for the evolution of host parenting behavior and nestling morphology. Ph.D. dissertation, Cornell University, Ithaca
- Schuetz JG (2005a) Low survival of parasite chicks may result from their imperfect adaptation to hosts rather than expression of coevolved host defenses. *Evolution* 59:2017–2024
- Schuetz JG (2005b) Reduced growth but not survival of chicks with altered gape patterns: implications for the evolution of nestling similarity in a parasitic finch. *Anim Behav* 70:839–848
- Skagen SK (1988) Asynchronous hatching and food limitation: a test of Lack's hypothesis. *Auk* 105:78–88
- Sorenson MD, Payne RB (2001) A single ancient origin of brood parasitism in African finches: implications for host–parasite coevolution. *Evolution* 55:2550–2567
- Sorenson MD, Sefc KM, Payne RB (2003) Speciation by host switch in brood parasitic indigobirds. *Nature* 424:928–931
- West-Eberhard MJ (1983) Sexual selection, social competition, and speciation. *Q Rev Biol* 58:155–183