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REVIEW

Wing-shaking and wing-patch as nestling begging strategies: their importance and evolutionary origins

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Abstract Avian chicks use different begging strategies when soliciting parental care. A novel begging strategy was recently observed in Horsfield's hawk-cuckoo *Hierococcyx hyperythrus* (=*Cuculus fugax*). Chicks of this brood-parasitic species raise and shake their wings and display to fosterers a gape-coloured patch on the undersides of their wings. Although the gape-coloured wing-patch may be a unique trait of Horsfield's hawk-cuckoo, wing-shaking in the context of begging is virtually universal in both brood parasites and their hosts. A simple qualitative comparison across different avian taxa suggests that wing-shake begging is most probably an ancestral feature of cuckoos and perhaps all altricial birds. The wing-shaking may be an honest signal of chick quality. It could also reduce the risk of predation if wing-shaking was coupled with reduced loudness of begging. Horsfield's hawk-cuckoo chicks could have exploited the universal pre-existing host responsiveness to wing-shake begging. Evolution could have then further proceeded by making the wing-shaking more conspicuous by addition of another stimulus—the unique colourful wing-patch. I also hypothesize that wing-shake begging may have evolved from pre-fledging restlessness and is used secondarily in courtship displays, threatening postures, and distraction displays by adults. Further discussions and tests of these hypotheses may facilitate research into the so far unstudied phylogenetic history of avian chick-begging strategies.

Keywords Begging · Brood parasitism · Phylogeny · Pre-existing preferences · Signalling

The most conspicuous behaviour of avian nestlings is probably begging. Chicks call, gape, shake, jostle, stretch, and quiver their wings to obtain sufficient food from parents (Kilner and Johnstone 1997). There is high interspecific variance of both chick begging strategies and parental responsiveness to different aspects of begging signals (reviewed by Wright and Leonard 2002).

Although most begging strategies described are based on calling and gaping (Kilner and Johnstone 1997), a ''distinct form of signalling used by Horsfield's hawk-cuckoo [*Hierococcyx hyperythrus* = *Cuculus fugax*] nestlings to obtain sufficient food'' was recently reported (Tanaka and Ueda 2005; Tanaka et al. 2005). Whereas other brood parasites, e.g. the common cuckoo *Cuculus canorus*, are fed according to the same rules as the host, e.g. the reed warbler *Acrocephalus scirpaceus*, nestlings (Kilner et al. 1999), this is not so for Horsfield's hawk-cuckoo. Perhaps because of the high risk of predation, Horsfield's hawk-cuckoo chicks ''rarely beg loudly'' (Tanaka and Ueda 2005; Tanaka et al. 2005). Instead, when begging the Horsfield's hawk-cuckoo chick ''raises and *shakes* the wing when host parents deliver food to the nest'' and displays a gape-coloured skin patch on the underside of its shaking wing (Tanaka

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et al. 2005; italics added). Tanaka et al. (2005) supported the hypothesis that these wing-patches simulate extra gapes with three lines of evidence: the frequency of the wing-patch display increased with increasing intervals between feedings (i.e. a surrogate measure of nestling hunger); experimentally reducing the conspicuousness of the patch by dyeing reduced feeding rates from hosts; and the parents sometimes mistakenly ‘‘fed’’ the wing-patch itself. Thus both observational and experimental evidence indicate that Horsfield’s hawk-cuckoos evolved gape-coloured wing-patches to solicit extra food from their hosts.

For wing-patch begging to be effective several components must function simultaneously: (1) wing raising, (2) wing-patch, and (3) parental attentiveness not only to chick’s gape but also to the wing that bears the patch (an additional condition is that the wing-patch signal should not be too strong otherwise it would stimulate the fosterers to feed the patch constantly instead of the gape). Because fosterers only very rarely misfeed the patch instead of the gape (Tanaka et al. 2005) this host mistaken behaviour cannot explain why the patch arose in the first place. Therefore, parental attentiveness to the wing (and the patch) is non-trivial and requires an explanation per se. Obviously, the patch must have evolved from the state of no patch and could have evolved through parental preferences for cuckoo chicks with more conspicuous patches. Under this scenario, parental attentiveness to wing movement must have preceded the evolutionary origin of the patch. Unsurprisingly, there is strong evidence that the behavioural component of wing-patch begging display (wing-raising and shaking) is not a unique trait of the Horsfield’s hawk-cuckoos and that parents of other species of birds pay attention to wing movements when feeding chicks (see below). Some of the results of Tanaka et al. are, furthermore, open to alternative interpretations. I will, therefore, separately discuss both behavioural (wing-raising and shaking) and morphological (wing-patch) components of this begging signal. Hereafter, *wing-shake begging* is defined as begging when the nestling raises one or both of its wings at an angle up to a maximum of ~90° above the horizontal and slightly shakes or quivers its wing(s) in that raised position (for two examples see a video supplementary to this paper, and Tanaka and Ueda 2005). The objectives of this review are to treat the following issues related to wing-shake begging in general and to exploitation of host parental care by parasite chicks in particular:

1. Wing-shaking during begging is virtually universal in the cuckoo family and seems to be an ancient trait in all passerines and other altricial birds.
2. The wing-shaking could serve as an honest signal of chick quality. It may also reduce the risk of predation if wing-shaking leads to a reduced loudness of begging.
3. I discuss the possible functions of the conspicuous underwing-patch of the common cuckoo, a species whose nestlings seem to elicit higher provisioning by fosterers by wing-shake begging (own unpublished data), and present two alternative hypotheses that may explain wing-patch evolution in the Horsfield’s hawk-cuckoo.
4. I suggest that pre-fledging restlessness might be an evolutionary precursor to wing-shaking behaviour.
5. Horsfield’s hawk-cuckoos may have exploited hosts’ responsiveness to this common feature of avian begging and have enhanced this behavioural stimulus with a morphological trait, the colourful patch, as an additional stimulus to obtain higher feeding rates.

Behavioural component: wing-shaking and begging in other bird taxa

Horsfield’s hawk-cuckoos are not the only species that use wing-shake begging. A good example is the common cuckoo—chicks of this parasite raise and shake *one* of their wings every time they are fed when older than 15–16 days (Glutz von Blotzheim and Bauer 1980: p. 210; Wyllie 1981: p. 157; Cramp 1985: p. 411; Malchevsky 1987: p. 113; Johnsgard 1997: p. 189; Davies 2000: the book cover illustration; own observations). In contrast, non-parasitic cuckoo chicks raise and shake their wings shortly after hatching, probably because they have to compete with their nest-mates from the start (see Payne 2005).

There is correlative evidence that wing-shaking by common cuckoo chicks is a begging strategy (own unpublished data). Younger cuckoo chicks beg normally by gaping and calling (Kilner et al. 1999). Both visual (i.e. gape area) and vocal (i.e. call rates) signals level off 4–7 days before fledging (Kilner et al. 1999: Figs. 4b, 6), whereas feeding frequencies and body mass increase up to fledging in common cuckoos raised by reed warblers (Grim and Honza 2001; Grim 2006b; own unpublished data). Gaping and calling are therefore insufficient to explain observed trends of growth and provisioning in old cuckoo chicks (>15 days of age). Wing-shaking seems to explain this discrepancy because:

1. it is performed solely in the presence of fosterers;
2. it is always directed toward the foster parent approaching the nest with food;

3. the wing-shaking display starts to be used after both gape area and call rates level off (i.e. when chicks reach the age of 15–16 days); and
4. there is a positive correlation between the proportion of parental feeding visits when a cuckoo chick raises and shakes its wing and the chicks' age (own unpublished data).

Although this hypothesis should be tested experimentally, even these non-random patterns of prevalence, timing, and laterality of wing shaking provide strong evidence in its favour. Importantly, alternative hypotheses to explain the wing-shaking can be rejected. Wing-shaking is unlikely to be related to balance, because chicks raise and shake their wing even when deeply seated in the nest without any risk of falling out (Fig. 1). The fact that common cuckoo chicks raise one wing solely in the presence of fosterers and only during begging rejects the hypothesis that the behaviour is just a by-product of pre-fledging restlessness (own observations). Raised wings may increase the apparent size of the chick but fosterers do not increase their feeding rates in response to large body size alone (Davies et al. 1998). Moving of wings both within and outside the nest may make the particular chick more conspicuous within a brood; under this chick-competition scenario the wing-shaking is a possible way of increasing the chance that the particular chick, instead of its nestmates, will be targeted with food. This hypothesis cannot be valid for cuckoo chicks that evict their nestmates soon after hatching, however. Some estrildid finches (Estrildidae) beg with one wing up (the wing on the far side of the begging bird) to conceal the more distant nestling or fledgling from the vision and parental feeding of the adult (Goodwin 1982: p. 27). This hypothesis cannot apply to the common cuckoo in principle, because the chick is always raised alone (Davies 2000). Finally, the behavioural component of the signal in the common cuckoo is identical with that of Horsfield's hawk-cuckoo chicks, as is clearly apparent from the on-line video material supplementary to this note (compare with Tanaka and Ueda 2005 supplementary on-line video material; compare also Fig. 1 in this paper and Fig. 1 in Tanaka and Ueda 2005).

Fig. 1 Common cuckoo *Cuculus canorus* chick wing-shake begging in the nest of a rare host—the song thrush *Turdus philomelos*. The chick is 17 days old

In general, wing-shaking (or ''flapping'' or ''quivering'') is regarded as one of the mechanisms of begging and sibling competition in general (Wright and Leonard 2002, Mock 2004). Shaking of both wings is commonly used as a stimulus to induce parental feeding by begging nestlings of a variety of passerines from several phylogenetically unrelated families, e.g. Eastern kingbirds *Tyrannus tyrannus* (Morehouse and Brewer 1968), magpies *Pica pica* (Redondo and Castro 1992), canaries *Serinus canaria* (Kilner 1995), tree swallows *Tachycineta bicolor* (Leonard and Horn 1998), southern grey shrikes *Lanius meridionalis* (Budden and Wright 2001), and rufous-bellied thrushes *Turdus rufiventris* (Lichtenstein 2001). It is, in fact, more noteworthy when the young of some species *do not* show this typical passerine behaviour than when they do (O'Brien and Dow 1979; Goodwin 1982: p. 26). Also non-passerine chicks raise and/or shake their wings when begging, e.g. downy woodpeckers *Dendrocopos pubescens* (Kilham 1962), Australian pelicans *Pelecanus conspicillatus* (Vestjens 1977), great egrets *Egretta alba* (Mock 2004), common terns *Sterna hirundo* (Smith et al. 2005), and black storks *Ciconia nigra* (R. Hampl, personal communication). Wing-shake begging is, as a standard, interpreted as signalling the highest nutritional need of the chick (see all the references above).

Brood parasites are no exception to wing-shake begging, because brown-headed cowbirds *Molothrus ater* (Dearborn and Lichtenstein 2002; Hauber and Ramsey 2003), shiny cowbirds *M. bonariensis* (Lichtenstein 2001), great-spotted cuckoos *Clamator glandarius* (Cramp 1985; Soler et al. 1999), and common cuckoos (see above) also shake their wings when begging. The claim that ''nestling brood–parasitic *Cuculus*... do not flutter their wings [when begging], and do so only inconspicuously after they fledge'' (Payne 2005, p. 92) is therefore incorrect. In the family Cuculidae many examples of ''flapping'', ''fluttering'', and ''quivering'', usually with ''stretched'' wings, have been observed during begging in both parasitic and non-parasitic chicks. This behaviour was described for at least 23 species in the genera *Guira*, *Crotophaga*, *Geococyx*, *Centropus*, *Coua*, *Phaenicophaeus*, *Clamator*, *Coccycua*, *Coccyzus*, *Eudynamys*, *Scythrops*, *Chrysococcyx*, *Cacomantis*, *Hierococcyx*, and *Cuculus* (Armstrong 1965; Wyllie 1981; Payne 2005). Wing-shake begging is, therefore, known from all the main cuckoo clades (Crotophaginae, Neomorphinae, Centropodinae, Couinae, and both Phaenicophaeni and Cuculini within Cuculinae). This phylogenetic distribution (Harvey and Pagel 1991) of wing-shake begging clearly shows the trait is ancestral to the cuckoo clade. The presence of wing-shake begging in other clades of birds, e.g. Passeriformes, Pelecaniformes, Ciconiiformes, Charadriiformes, and Piciformes (see above), suggests this begging strategy is ancestral to all birds. Unfortunately, the anecdotal nature of descriptions of the wing-shaking behaviour in the literature does not currently enable robust phylogenetic analysis.

The widespread taxonomic distribution of wing-shake begging in birds is crucial, because it may explain why the hosts of Horsfield's hawk-cuckoos are responsive at all to this display, shown by the parasite chicks. Similarly, wing-shake begging in magpie chicks explains why magpie fosterers are responsive to the same behaviour in the great spotted cuckoo (Soler et al. 1999) and wing-shake begging by reed warbler nestlings (own observations) seems to explain why reed warbler fosterers increase their provisioning in response to the common cuckoo chick's wing-raising and shaking and why they do not ignore the signal. Tanaka and Ueda (2005) did not describe begging behaviour of their host species; on the basis of the arguments given above I predict the host nestlings beg with raised wings.

In summary, if there was no universal parental responsiveness to nestlings' wing-shaking in passerines, the Horsfield's hawk-cuckoo's and other parasites' chicks could hardly be successful in eliciting any parental care by use of wing-related traits (both behavioural and morphological), because their fosterers would simply not recognize those as signals of need. Parental attentiveness to wing-raising and shaking is a necessary prerequisite for subsequent evolution of wing-patches. An alternative scenario in which hosts do not show any pre-existing parental preference (Götmark and Ahlström 1997; Grim 2005) for wing related traits and where the preference evolves only in response to the cuckoo behaviour is meaningless, because a host mutant paying any attention to this behaviour in parasitic chicks would be less fit than a host without that preference.

Nestlings of some species raise and shake both wings when begging (Redondo and Castro 1992) whereas other species, e.g. Horsfield's hawk-cuckoos (Tanaka and Ueda 2005), common cuckoos (Wyllie 1981), or Alpine accentors *Prunella collaris* (Armstrong 1965), raise only one wing at a time. This interspecific variability in the form of wing-shaking has no bearing on the conclusion that wing-shaking is an ancestral trait, at least for cuckoos and passerines, because in all instances the behaviour is used solely during begging (references above). Because nestling behaviour for most cuckoo species is virtually unknown (Payne 2005), there are obvious opportunities for fruitful research in the future.

What is the adaptive value of wing-shaking?

All the above-mentioned authors regarded the wing-shaking display as a signal of chick hunger. In addition, or as an alternative, I suggest wing-shaking may be a honest signal of chick phenotypic quality and health—a chick able to make many wing movements is more likely to fledge and will possibly fly better than a chick with a poor wing-shake performance. It may, therefore, pay parents to scrutinize their chicks' wing-raising and shaking performance and adjust their investment accordingly. This is not (only) because chicks would be signalling their hunger but because their vigour would signal higher chances of survival in the post-fledging period, irrespective of current nutritional needs. The wing-shaking signal would be honest, because of its energy costs and because any infections and diseases usually reduce the performance of animals.

Wing-shake begging could also reduce the risk of predation if wing-shaking was coupled with reduced loudness of begging (Tanaka and Ueda 2005).

Morphological component: is there any role for underwing "patch" in the common cuckoo?

Horsfield's hawk-cuckoo chicks do more than just raise and shake their wings—they stimulate their hosts with the naked gape-coloured underwing-patch (Tanaka and Ueda 2005). The common cuckoo chick has no gape-coloured patch but the underside of its wing has visible naked skin in the distal ulnar and proximal carpometacarpal region (i.e. in the same part of the wing as the Horsfield's hawk-cuckoo chick, cf. Fig. 1 in Tanaka and Ueda 2005). In younger common cuckoos the naked skin cannot be observed by hosts, because young chicks do not raise their wings (<15 days) but during later development (approximately at the age of 17 days) this skin area becomes covered with white lesser underwing coverts which are quite conspicuous during wing-shaking even for a human observer distant from the nest (Wyllie 1981; own observations). Common cuckoo chicks might use this patch to attract fosterers both at the nest and during the long post-fledging period (Wyllie 1981; Davies 2000: see cover illustration of the book). The underwing of the common cuckoo chick is:

1. visible, because of wing-raising and shaking;
2. has conspicuous colour; and
3. the foster parents will see it most frequently when feeding older cuckoo chicks which have the highest feeding demands (see above).

This suggests some signalling of hunger and it would therefore be worthwhile to test the function of the patch with a dyeing experiment similar to that conducted by Tanaka and Ueda (2005).

It would, furthermore, be interesting to examine whether the colour of the patch of Horsfield's hawk-cuckoo chicks is important in itself. The results of the dyeing experiment, in which dyeing with black colour reduced feeding rates (Tanaka and Ueda 2005), may be interpreted in two different ways:

1. Under the ''conspicuous wing-patch'' hypothesis any conspicuous patch is good enough to elicit host feeding. This is essentially equal to the question ''does a yellow patch work with a same efficiency as an orange or red one?''
2. Under ''gape-mimicking patch'' hypothesis the particular colour is crucial to successful exploitation of hosts.

Although the colour similarity of patch to gape in Horsfield's hawk-cuckoo chicks strongly suggests the colour of the patch matters (supporting the latter hypothesis), the issue cannot be resolved without experimental changes in patch colour. Theoretically, parasitic chicks could also evolve a ''supernormal'' (Alvarez 2004) patch whose colour would be even more attractive to fosterers than the chick gape colour. Such a trait would be evolutionarily unstable, however: a ''supernormal'' colour patch would be *too effective* at attracting the fosterer because they would prefer to feed the patch instead of the gape of the same chick and the super-colour patch would be selected against.

Although the wing-patch in Horsfield's hawk-cuckoo chicks seems to be a unique trait so far, it is feasible that similar traits might have evolved in other species, because:

1. the behavioural component of this begging strategy is virtually universal (see above);
2. this behavioural component is a necessary prerequisite for subsequent evolution of the wing-patch; and
3. ''the whole of the [wing] skin is not fully covered with feathers... in many altricial species'' (Tanaka et al. 2005: p. 462).

There are, therefore, both behavioural and morphological traits that could serve as pre-adaptations for evolution of colourful wing-patches in a variety of taxa.

Evolutionary origins: is pre-fledging restlessness an evolutionary precursor of wing-shake begging?

If wing-shake begging is to function in Horsfield's hawk-cuckoo, all its components, including the conspicuous wing-patch, wing-raising (and perhaps shaking), and parental responsiveness to it, must be present at once. In other words, the wing-patch could not evolve without wing-raising and specific parental responsiveness to wing-raising (see above). It is, of course, highly unlikely that all components of such a complex system would suddenly all appear in one individual—this argument is valid for any complex trait (Dawkins 1989). We should therefore look for evolutionary precursors that enabled the existence of wing-patch begging in Horsfield's hawk-cuckoo and wing-shake begging in many other birds.

Wing-shaking during begging is common in a variety of altricial nestlings after fledging (Wright and Leonard 2002; own personal observations in several species of Callaeidae, Eopsaltriidae, Fringillidae, Muscicapidae, Pachycephalidae, Paridae, Sylviidae, Turdidae and Zosteropidae), including brood parasitic birds (e.g. Icteridae; Hauber and Ramsey 2003). Furthermore, some passerines, e.g. reed warblers, frequently stretch and/or shake their wings shortly before fledging when parents are not present at the nest and this is accompanied by stretching of legs and feather preening (Gill 1990; own observations). This behaviour in the absence of parents is very similar to wing-shaking during feeding by parents and suggests that wing-shaking and stretching could be related to pre-fledging restlessness (i.e. a suite of behaviour performed before fledging, including leg and wing stretching, preening etc.; Gill 1990: p. 385). Behavioural patterns of pre-fledging restlessness could—because of their conspicuous nature and perhaps an ability to signal chick quality and health (see above)—serve as evolutionary precursors for evolution of wing (patch) begging.

To summarise, wing-shaking in the presence of parents may serve to solicit feeding (Wright and Leonard 2002) whereas wing-shaking by older nestlings in the absence of parents is most probably a manifestation of pre-fledging restlessness. Wing-shake begging may, moreover, be secondarily used in social interactions among adult conspecifics including courtship feeding (e.g. Armstrong 1965; own observations), male sexual displays (e.g. Frith 1982), threatening postures (e.g. Goodwin 1982: p. 27) or appeasement displays (McLean 1988; Lott 1991). Some cuckoos use wing raising and shaking in threat postures (Johnsgard 1997) and it has been hypothesized that wing-shake begging is an evolutionary precursor of distraction displays that include ‘‘injury-feigning of the wing quivering type’’ which, unsurprisingly, occur solely in species with *altricial* nestlings (Armstrong 1965: p. 97). Interestingly, asymmetrical wing-shaking (raising and shaking of only one wing at a time) has been found in a wide variety of taxa, ranging from the ostrich *Struthio camelus*, through many shorebirds and crakes, to passerines, e.g. reed buntings *Emberiza schoeniclus* and Alpine accentors (Armstrong 1965). Symmetrical wing-shaking (with both wings raised and/or shaken at a time) seems to be much more prevalent, however (see above).

Obviously, even movement alone can attract the attention of hosts and increase feeding rates (Redondo and Castro 1992; Kilner 1995; Smith et al. 2005). This modified hypothesis needs further testing in Horsfield's hawk-cuckoo chicks, because Tanaka and Ueda (2005) and Tanaka et al. (2005) did not experimentally test for the possible effect of movement itself (e.g. by observing feeding rates to cuckoo chicks experimentally restrained from wing-shaking). Further, Tanaka et al. did not test for a possible effect of chick age on the frequency of wing-raising and shaking. Data from the common cuckoo show that only older chicks of this species use wing-shake begging (Wyllie 1981; own observations). Certainly, Horsfield's hawk-cuckoo chicks cannot use the wing-raising begging strategy immediately after hatching—all altricial hatchlings are helpless, wings are too small to bear any reasonably big colourful patch and thus any wing-shake begging is phenotypically constrained shortly after hatching. The ontogeny of wing-patch (morphological development) and wing-raising and shaking (behavioural development) also deserves more attention, therefore, in the same way as chick vocal begging ontogeny (Kilner et al. 1999; Leonard and Horn 2006). Finally, the effects of the amplitude and frequency of wing-shaking are unclear, because Tanaka and Ueda (2005) studied only the presence or absence of wing-raising and shaking during particular feedings of nestlings.

I stress that there are obvious differences between the wing-shake begging of the common cuckoo and Horsfield's hawk-cuckoo. On the one hand, both species raise only one wing at a time, keep it high above the horizontal (at an angle of ~90°) and slightly shake it in that position. On the other hand, the common cuckoo chick lacks the gape-coloured wing-patch typical of Horsfield's hawk-cuckoo. Taking ‘‘wing-patch begging’’ by the latter species as a *unique* trait inevitably means that we cannot understand its evolutionary origin. It is, therefore, crucial to study *similar* (and perhaps not identical) behaviour and morphological structures in (un)related taxa as exemplified above. Only by use of phylogenetic comparative methods may we achieve more profound insight into how the wing-patch begging strategy originated. This is, of course, a standard approach used in all areas of evolutionary biology (Harvey and Pagel 1991).

Future directions

On the basis of the evidence discussed above I hypothesize that wing-shake begging is an ancestral trait in altricial birds (or at least in passerines and cuckoos) which may have been derived from the pre-fledging restlessness. Wing-shaking could also be positively selected for because it may augment the visual effects of gaping, i.e. wing-shaking is similar to head and gape shaking during begging, at least in terms of frequency. Although the similarity is crude it is not surprising that it successfully elicits higher feeding rates (references above), because most birds readily feed alien chicks with totally dissimilar begging calls, gape morphology, and begging postures (Sealy and Lorenzana 1997; Grim 2005). An ability to shake wings may honestly signal good health and/or phenotypic quality of the nestling. In some species selection could further increase the conspicuousness of the signal by converging wing-patch colour to gape colour (Tanaka and Ueda 2005; Tanaka et al. 2005), to which parents are already responsive (Alvarez 2004), or to any conspicuous colouration (Götmark and Ahlström 1997). This hypothetical scenario provides a framework for future research on the understudied chick stage of brood parasites (Grim 2005, 2006a, 2007) and virtually unexplored phylogenetic history of chick begging strategies in all birds.

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