

Signal exploitation by parasitic young in birds: a new categorization of manipulative signals

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ORNITHOLOGICAL SCIENCE

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Abstract Many studies revealed that parasitic young mostly emit signals that are used in parent-offspring communication of hosts, but sometimes not. The terms used to explain host manipulation signals are not unified, then presenting confusion. Here we propose a new categorization of signals used for parasitic manipulation. Host manipulative signals could roughly be divided into two patterns according whether a parasite exploits signals actually used in parent-offspring communication of hosts (signal exploitation) or not (sensory exploitation), in relation to particular selective pressures that parasites face, such as nestling discrimination by hosts or deficient stimulation by parasites to obtain sufficient food.

Key words Brood parasitism, Mimicry, Sensory exploitation, Signal exploitation, Supernormal stimulus

It has long been one of the most fascinating issues for behavioural and evolutionary biologists why host parents always feed a huge cuckoo chick of odd looking, resulting in much damage not only on their current reproduction but also ones in the future (Darwin 1859; Dawkins & Krebs 1979; Wylie 1981; Davies 2000). Although the reason was once regarded that a cuckoo chick sheds a “drug” like allurements that fosterers could not resist (Dawkins & Krebs 1979), many studies have revealed that parasites emit signals that are used in parent-offspring communication of hosts in quantitatively equivalent ways (Brooke & Davies 1989; Davies et al. 1998; Kilner et al. 1999; Grim & Honza 2001), or that parasites exploit parental rules for resource allocation (Redondo 1993; Soler et al. 1995; Lichtenstein & Sealy 1998).

Nevertheless, the terms used to represent host manipulation signals are not unified, then presenting confusion (e.g. Dawkins & Krebs 1979; Soler et al. 1995; Davies et al. 1998; Kilner et al. 1999; see Tinbergen 1989). We now focus on the perceptive mechanisms by which parasitic young elicit appropriate nutrition and care from their host parents, and recon-

struct the perspective of such manipulative signals for better understanding, by applying concepts developed in the other contexts of evolutionary and behavioural ecology (see Ryan 1990; Heeb et al. 2003; Shaefer et al. 2004).

Here we propose a new categorization of signals used for parasitic manipulation: the signal exploitation and the sensory exploitation. We define signal exploitation as the exploitation by parasites of an established communication signal of their hosts, such as mimicry or a supernormal stimulus. They deceive their hosts by emitting signals that their own chicks signal demands in nutrition and care, status (Redondo & Castro 1992; Kilner et al. 1999), and also, relatedness (Kilner 1999; Payne et al. 2001). Mimicry and supernormal stimulus are just different from each other in terms of the selective pressures to form the exploitation: for mimicry, resemblance (similarity as a whole; see Payne et al. 2001); for supernormal stimulus, signal efficacy (strength of a signal; see Kilner et al. 1999), so leading to different consequences (see below).

On the contrary, when parasites gain resources with stimuli not being used in the parent-offspring communication of hosts, we assign it to sensory exploitation. The concept of sensory exploitation has been developed in the context of sexual selection and

(Received 13 February 2004; Accepted 17 January 2005)

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conflict between the sexes at the beginning (Ryan 1990), however, recently is expanded to the other communication systems due to its plausibility (Heeb et al. 2003; Shaefer et al. 2004). The sensory exploitation hypothesis assumes that signals composed of stimuli that could most effectively stimulate the sensory system of a receiver not only by exploiting a preexisting cognitive bias but also by just stimulating nervous systems strongly have been favoured in the evolution (Basolo 1990; Ryan 1990; Ryan et al. 1990). The former is to exploit receivers' established reactivity that has been evolved to deal with a different matter (e.g. anti-predatory mechanisms). The latter is to exploit physical specificities of receivers' sense organs or nervous systems with a strong stimulation: e.g., conspicuousness or contrast between components or against backgrounds. This argument could be applicable for host manipulative traits of brood parasites because many young parasites, especially ones much larger than their hosts, need to stimulate host parents more strongly with additional stimulations to succeed to survive (Kilner et al. 1999; Kilner et al. 2004; Tanaka & Ueda 2005).

SIGNAL EXPLOITATION—FROM NORMAL TO SUPERNORMAL—

Because of the homogeneity of signals between hosts and parasites, we assign both mimicry and a super-

normal stimulus into the same category (Fig. 1a, b). That is, the focal signal contains the same information both in ones of host nestlings (model) and of parasites (mimic). However, they differ in terms of the constraints that a deceiver faces. The aim of a mimic is to deceive specific receivers by disguising itself as something else, without any necessity of amplification of stimulation, that is, a normal signal exploitation. In the case of brood parasites, the mimetic manipulation is required when the hosts have an ability to discriminate the parasitism (Lotem 1993; Fraga 1998; Payne et al. 2001; Langmore et al. 2003), while the supernormal manipulation takes an advantage when the nutritional demand of parasites is higher (Kilner et al. 1999; Tanaka & Ueda 2005).

Fist example for the mimetic manipulation is about the nestlings of *Vidua* finches, obligate parasitic passerines in Africa, which display a gape with the same pattern as ones of their host chicks (Wickler 1968; Payne 1973). Each viduine species has a specific host, and the gape pattern of host nestlings varies with species. Parents of these hosts use such patterns as a cue for care and food allocation and species recognition (Payne et al. 2001). Thus a parasite nestling hatched in an inappropriate host nest is unfed and starved to death. Although its evolutionary and genetic mechanisms have not been clarified (Sorenson et al. 2003), this mimicry has a function in the host manipulation by *Vidua* finches (Payne et al.

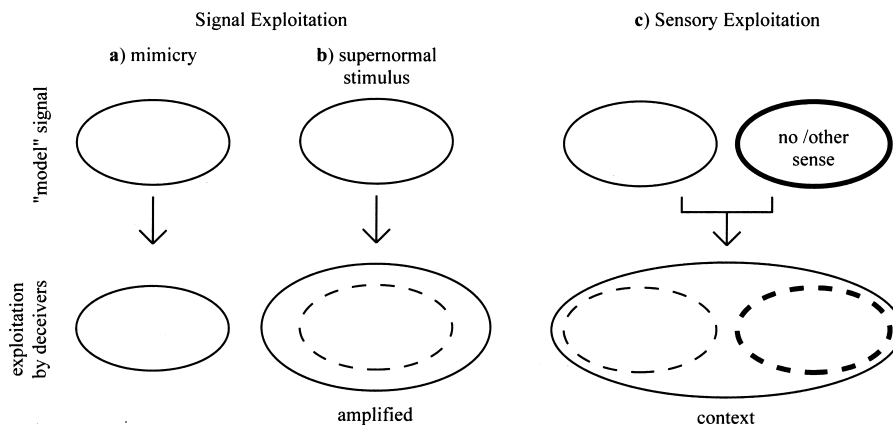


Fig. 1. A new categorization of signals used for host manipulation. Supernormal stimulus (b) differs from mimicry (a) just in the amplification of a component stimulus, both of which are defined as signal exploitation. Sensory exploitation (c), once confused with a supernormal stimulus, is distinguished from signal exploitation due to the sense of a part of the component stimuli before introduced by deceivers into the same context. Each solid circle presents a component of the focal signal and broken lines show the original intensity or sense to clarify the differences against ones altered by deceivers. In the sensory exploitation, the left circles in both upper and lower line represent a normal begging stimulus (e.g. the gape colour of both Magpie and Great Spotted Cuckoo chicks). The thick gray line (both solid and broken) shows a signal component without any sense in the context of parental care (e.g. white palatal papillae of the Great Spotted Cuckoo chick).

2001).

The next one is about the Screaming and Shiny Cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the Bay-winged Cowbird (*M. badius*; Fraga 1998; Lichtenstein 2001). This system is much complicated because all attendants, including the host, belong to the same genera. Furthermore confusing, only Screaming Cowbird nestlings out of two parasites perfectly mimic the appearance of host nestlings. Because the inside of Bay-winged Cowbirds' nests is dark, nestlings of Shiny Cowbirds are able to obtain food from host parents. However, after fledging, non-mimetic parasites sometimes fail to survive unlike the mimetic Screaming Cowbirds (Fraga 1998). The mimicry by the Screaming Cowbird nestlings would not be due to shared ancestral traits, but would have evolved for avoiding discrimination by Bay-winged hosts, supported by a phylogenetic study (see Lanyon 1992).

In the case of parasitic Horsfield's Bronze-cuckoos (*Chrysococcyx basalis*) and Shining Bronze-cuckoos (*C. lucidus*), the Superb Fairy-wren (*Malurus cyaneus*) hosts discriminate and abandon parasitic nestlings in spite of the incomparability with their own chicks due to the eviction by these parasites (Langmore et al. 2003; see Lotem 1993). The Superb Fairy-wren is also multiply parasitized by these two bronze-cuckoo species. They are suggested to detect the number of nestlings in the nest, then desert it when it contains a single chick (Langmore et al. 2003). The key stimulus the hosts use to detect the number of the nestlings is their begging calls. Fairy-wren hosts abandon nests in a similar rate when it contains a single fairy-wren chick or a single Horsfield's Bronze-cuckoo chick, which mimics the begging call of host nestlings. On the contrary, host parents dump all the Shining Bronze-cuckoo chicks, which call for begging much differently.

For supernormal manipulation, in turn, the best example is a chick of the Common Cuckoo (*Cuculus canorus*), which spreads widely in Eurasian continent and is studied precisely (Wylie 1981; Higuchi 1998; Davies 2000). Kilner et al. (1999) shows a huge common cuckoo chick, compared with a whole brood of host, displays a smaller gape area in begging, which could not stimulate host parents sufficiently to provide an appropriate amount of food. The way that a cuckoo chick compensates for the deficient visual stimuli is to amplify its vocal stimulus extremely, that is, the intense begging call (Kilner et al. 1999). Precise analyses reveal that cuckoo chicks integrate

vocal and visual signals in a quantitatively equivalent way that a brood of Reed Warbler (*Acrocephalus scirpaceus*) nestlings signal their need to the parents.

A nestling of the Horsfield's Hawk Cuckoo (*Cuculus fugax*), displays a gape-coloured patch on the underside of each wing to the host parents that deliver food to the nest (Fig. 2; Yamaguchi 1994; Tanaka et al. in press). By the conformity of the colour to a gape, a hawk cuckoo chick would exploit some kinds of visual signals of hosts to obtain sufficient food. Some host parents actually tried to place food mistakenly into the wing-patch instead of an actual gape (Tanaka et al. in press). Tanaka & Ueda (2005) demonstrates that the yellow wing-patch induces parental feeding by hosts. Although preliminarily, these results suggest that the wing-patch would stimulate host parents to deliver sufficient food by inducing overestimation of brood size. Although whether the hosts actually misperceive the patch as a gape is obscure without physical evidences, a hawk cuckoo chick is likely to simulate multiple gapes with the wing-patch to exploit parental rules for food allocation (Trivers 1972; see Brooke & Davies 1989; Davies et al. 1998).

To sum up, although both mimetic and supernormal manipulations rely on the same signals as used in the social communication systems of hosts, the mimetic manipulation would be selected by discrimination and the response induced may have thresholds toward both directions in terms of stimulus quantities (neither too little nor too much stimuli would be selected; i.e. stabilizing selection; Hansen 1997; but see Johnstone 2002). On the other hand, in the supernormal manipulation, a signal is preferred when it emits stronger stimulation (i.e. chase-away antagonism; see Holland & Rice 1998; Mead & Arnold 2004). A receiver consequently "extrapolates" its response to an abnormally intensified stimulus (see Tinbergen 1989).

SENSORY EXPLOITATION

A Great Spotted Cuckoo (*Clamator glandarius*) nestling gains sufficient food from the Magpie (*Pica pica*) hosts by displaying a pair of conspicuous white papillae on the palate (Soler et al. 1995). Soler et al. (1995) regarded it as a supernormal stimulus, however, it is more suitable to define it as a sensory exploitation (Heeb et al. 2003). Since a magpie nestling completely lacks such a papilla on the palate, a Great Spotted Cuckoo does not exploit, or amplify any



Fig. 2. A fledgling of the Horsfield's Hawk Cuckoo displays a yellow skin patch on the wing for food solicitation to the host parent that delivers food.

communication signal of hosts. What a Great Spotted Cuckoo chick does would be to use a strong and effective stimulus that has no sense in the context of parental care of Magpies. These papillae would have evolved because they could stimulate host parents more effectively combined with other begging stimuli, such as the coloration or shape of a begging gape (see Fig. 1c). The consequence may depend on the context, such that host parents have no choice but to feed young in the presence.

In dimly lit magpie nests, conspicuousness of flickering dots in the mouth of a Great Spotted Cuckoo chick could induce host parents to prefer the parasite for feeding to their own young, so enabling it to defeat nestmates and survive. However, when the host has an opportunity to learn the appearance of parasites in the nest (Lotem 1993; Langmore 2003), this sensory exploitative tactic becomes disadvantageous because hosts could easily discriminate and reject parasites by comparison. Since the evolution of discrimination depends on the intensity of parasitism on the population of hosts (Soler & Møller 1990; Lotem 1993; Holen 2001; Langmore 2003), the interaction between the signal heterogeneity and the parasitism intensity should be evaluated precisely especially when parasites are reared together with host young, including the host-parasite system of the Great Spot-

ted Cuckoo.

In addition, although there are many evidences that parents prefer to feed a chick with a brighter gape (Kilner 1997; Götmark & Ahlström 1998; but see Noble et al. 1999), bright mouth colour of parasite chicks may also be a consequence of the sensory exploitation since their gape colour is not always the same as the ones of host nestlings (see Kilner & Davies 1998). It may be an exploitation of the parental bias just as reactivity to conspicuousness or at least the precursor of a preference for carotenoid-base pigments (see Shaefer et al. 2004). But there still remains a great necessity for a further accumulation of evidences and criticism in detail.

CONCLUSION

We suggest that host manipulative signals can be categorized into two patterns according whether a parasite exploits signals actually used in parent-offspring communication of hosts (signal exploitation) or not (sensory exploitation). In the signal exploitation, host discrimination favours mimicry while the supernormal manipulation is selected for an enormous food acquisition. Manipulative signals as sensory exploitation are combined with normal begging stimuli (Fig. 1c), because of the necessity for the ad-

ditional effects (compensation for a deficient stimulus due to excessive demands/competition with nest-mates), and because of the particular aim (eliciting care).

To identify which kind of exploitation a parasite adopts, it is essential to disintegrate the begging display into components, and to analyze precisely both qualitatively and quantitatively (see Kilner et al. 1999). Especially for sensory exploitation, it would be useful to add conspicuous stimuli to the display of host nestlings, which could also provide, more generally, a prospect to evolutionary pathways of complicated begging displays in the context of parent-offspring conflict (Trivers 1972; Kilner 1999).

ACKNOWLEDGMENTS

We thank Fugo Takasu and Hiroshi Nakamura for editorial conducts and Noriyuki Yamaguchi for comments.

REFERENCES

- Basolo AL (1990) Female preference predates the evolution of the sword in swordtail fish. *Science* 250: 808–810
- Brooke M de L & Davies NB (1989) Provisioning of nestling cuckoos *Cuculus canorus* by reed warbler *Acrocephalus scirpaceus* hosts. *Ibis* 131: 250–256
- Darwin CMA (1859) *The Origin of Species: By Means of Natural Selection*. John Murray, London
- Davies NB (2000) *Cuckoos, Cowbirds and other Cheats*. Poyser, London
- Davies NB, Noble DG & Kilner RM (1998) Nestling cuckoos, *Cuculus canorus*, exploit hosts with begging calls that mimic a brood. *Proc R Soc Lond B* 265: 673–678
- Dawkins R & Krebs JR (1979) Arms race between and within species. *Proc R Soc Lond B* 205: 489–511
- Fraga RM (1998) Interactions of the parasitic screaming and shiny cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the bay-winged cowbird (*M. badius*). In: Rothstein SI & Robinson SK (eds) *Parasitic Birds and Their Hosts: Studies in coevolution*. pp 173–193. Oxford Univ Press, New York.
- Götmark F & Ahlström M (1997) Parental preference for red mouth of chicks in a songbird. *Proc R Soc Lond B* 264: 959–962
- Grim T & Honza M (2001) Does supernormal stimulus influence parental behaviour of the cuckoo's host? *Behav Ecol Sociobiol* 49: 322–329
- Heeb P, Schwander T & Faoro S (2003) Nestling detectability affects parental feeding preferences in a cavity-nesting bird. *Anim Behav* 66: 637–642
- Higuchi H (1998) Host use and egg color of Japanese cuckoos. In: Rothstein SI & Robinson SK (ed) *Parasitic Birds and Their Hosts: Studies in Coevolution*. pp 80–93. Oxford Univ Press, New York.
- Holen ØH, Sætre G-P, Slagsvold T & Stenseth NC (2001) Parasites and supernormal manipulation. *Proc R Soc Lond B* 268: 2551–2558
- Holland B & Rice WR (1998) Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* 52: 1–7
- Johnstone RA (2002) The evolution of imperfect mimics. *Nature* 418: 524–526
- Kilner RM (1997) Mouth colour is a reliable signal of need in begging canary nestlings. *Proc R Soc Lond B* 264: 963–968
- Kilner RM (1999) Family conflict and the evolution of nestling mouth colour. *Behaviour* 136: 779–804
- Kilner RM & Davies NB (1998) Nestling mouth colour: ecological correlates of a begging signal. *Anim Behav* 56: 705–712
- Kilner RM, Madden JR & Hauber ME (2004) Brood parasitic cowbird nestlings use host young to procure resources. *Science* 305: 877–879
- 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
- Lagmore NE, Hunt S & Kilner RM (2003) Escalation of coevolutionary arms race through host rejection of brood parasitic young. *Nature* 422: 157–159
- Lanyon SM (1992) Interspecific brood parasitism in blackbirds (Icterinae): a phylogenetic perspective. *Science* 255: 77–79
- Lichtenstein G (2001) Selfish begging by screaming cowbirds, a mimetic brood parasite of the bay-winged cowbird. *Anim Behav* 61: 1151–1158
- Lichtenstein G & Sealy SG (1998) Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. *Proc R Soc Lond B* 265: 249–254
- Lotem A (1993) Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature* 362: 743–745
- Hansen TF (1997) Stabilizing selection and the comparative analysis of adaptation. *Evolution* 51: 1341–1351
- Mead LS & Arnold SJ (2004) Quantitative genetic models of sexual selection. *Trends Ecol Evol* 19: 264–271.
- Noble DG, Davies NB, Hartley IR & MacRae SB (1999) The red gape of nestling cuckoos (*Cuculus canorus*) is not a supernormal stimulus for three com-

- mon hosts. *Behaviour* 136: 759–777
- Payne RB (1973) *Behavior, Mimetic Songs and Song Dialects, and Relationships of the Parasitic Indigobirds (Vidua) of Africa*. Ornithological Monographs No. 11. The American Ornithologist Union, Washington DC.
- 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
- Redondo T (1993) Exploitation of host mechanisms for parental care by avian brood parasites. *Etología* 3: 235–297
- Redondo T & Castro F (1992) Signalling of nutritional need by magpie nestlings. *Ethology* 92: 193–204
- Ryan MJ (1990) Sexual selection, sensory systems and sensory exploitation. *Oxford Surv Evol Biol* 7: 156–195
- Ryan MJ, Fox JH, Wilcynski W & Rand AS (1990) Sexual selection for sensory exploitation in the frog *Physalaemus postulosus*. *Nature* 343: 66–67
- Schaefer HM, Schaefer V & Levey DJ (2004) How plant-animal interactions signal new insights in communication. *Trends Ecol Evol* 19: 577–584
- Soler M, Martinez JG, Soler JJ & Møller AP (1995) Preferential allocation of food by magpies *Pica pica* to great spotted cuckoo *Clamator glandarius* nestlings. *Behav Ecol Sociobiol* 37: 7–13
- Soler M & Møller AP (1990) Duration of sympatry and coevolution between the great spotted cuckoo and its magpie host. *Nature* 343: 748–750
- Sorenson MD, Sefc KM & Payne RB (2003) Speciation by host switch in brood parasitic indigobirds. *Nature* 424: 928–931
- Tanaka KD, Morimoto G & Ueda K (in press) Yellow wing-patch of a nestling Horsfield's hawk cuckoo *Cuculus fugax* induces miscognition by hosts: mimicking a gape? *J Avian Biol.*
- Tanaka KD & Ueda K (2005) Horsfield's hawk-cuckoo nestlings simulate multiple gapes for begging. *Science* 308: 653.
- Tinbergen N (1989) *The Study of Instinct*. Oxford Univ Press, New York
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual Selection and the Descent of Man, 1871–1971*. pp 136–179. Aldine, Chicago.
- Wickler W (1968) *Mimicry in Plants and Animals*. World University Library, New York
- Wylie I (1981) *The Cuckoo*. Universe Books, New York
- Yamaguchi Y (1994) Tanzawa-sanchi ni okeru chourui no kishou na hanshoku rei ni tsuite (Rare breeding records of some birds in Tanzawa mountains, Kanagawa prefecture). *Nat Hist Kanagawa* 15: 49–51 (in Japanese).