

# Ecological approaches to species recognition in birds through studies of model and non-model species

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All birds propagate sexually and reproduction critically depends on individuals' abilities to secure matings within their own species. Discrimination of conspecifics from heterospecifics may also improve fitness in many additional social contexts, including foraging, roosting, migrating, and antipredator behaviour, that are separate from mating. Understanding the developmental basis of any universal behavioural trait, including avian species recognition, may benefit from the development and use of model systems where genetic, ontogenetic, and environmental variables can be identified and controlled. Indeed, extensive initial progress in the study of social affiliation and preference in birds was made based on laboratory studies of a handful of precocial and altricial species, especially in the context of filial and sexual imprinting. This research helped to establish ontogenetic paradigms and generated testable hypotheses for further laboratory and field studies of both avian and non-avian taxa regarding the importance of imprinting and early experience in the development of social choice. Here, we review and interpret the findings of species recognition studies in the context of ecological variation in avian taxa across gradients of parental care strategies, including "non-parental" megapodes and brood parasites. We highlight the benefits of a recent paradigm shift to describe the importance of non-imprinting based recognition mechanisms in the study of avian recognition systems and argue to include the full range of life history variation that birds exhibit in order to confirm or reject long-standing hypotheses regarding the constraints and flexibilities of avian cognitive architecture and their contributions to species recognition systems.

## Introduction

Birds are popular model systems in the study of evolutionary biology, in areas such as sexual selection (Andersson 1994) and speciation (Mayr 1963). Species recognition is an essential

component of these evolutionary processes. For young birds, correct species recognition is crucial in social interactions, and forms the basis of premating isolation between species (Price 1998, Irwin & Price 1999). For adults, correct species recognition is essential for mate choice and

reproduction, as hybrids from matings with heterospecifics generally have lower survival rates or are infertile (Fisher 1958).

Correct discrimination of conspecifics from heterospecifics can also be adaptive in social contexts other than mating, such as foraging, roosting, migrating, and antipredator behaviour. For instance, young male brown-headed cowbirds *Molothrus ater* preferentially associate with older males in foraging flocks during their first winter and learn population-specific sexual displays; here, it is difficult to separate foraging and eventual mating benefits of such socialisation (White *et al.* 2002a). However, species recognition for mate choice is ubiquitous in birds since all reproduce sexually. Hence, species recognition and mate choice are often dealt with together, such as in the study of speciation and sexual selection (Immelmann 1972, Ryan & Rand 1993, Laland 1994, Price 1998, Irwin & Price 1999), and in models of evolutionary processes (ten Cate 2000). In our overview we concentrate on findings that deal with the species recognition process *per se*, while purposely sidestepping the issue that many of these results can also explain aspects of mate choice and sexual selection. Instead, we focus on proximate bases of species recognition (i.e. ontogeny of the perception process, cues and referents used for recognition templates; Sherman *et al.* 1997, Mateo 2004) and on the process by which birds recognise conspecifics.

The review does not cover contexts in which recognition of heterospecifics plays a role, such as in predator recognition (e.g. Griffin *et al.* 2001, Sowards & Sowards 2002), prey recognition (e.g. Speed 2000), or the recognition contexts between brood parasites and their hosts (Payne *et al.* 2000, Slagsvold & Hansen 2001, Langmore *et al.* 2003). It only marginally covers the interaction between species recognition and song learning (e.g. Marler 1970, Shettleworth 1994a, Soha & Marler 2000); this would require a review on its own (Zeigler & Marler 2004). Finally, the neurobiological correlates of imprinting and other perceptual and cognitive aspects of species recognition are also beyond the scope of this review, although much progress has been made in identifying the brain regions, and the physiological and molecular mechanisms, that

underlie early social learning in precocial birds (Horn 1998) and songbirds (Zeigler & Marler 2004).

To discover the proximate processes of species recognition, we need to consider the diversity of birds, in particular the variation of developmental maturity and behavioural repertoire of avian young at the time of hatching, including the continuum from altricial to precocial modes of development, and those taxa that are raised by foster parents or grow up with no parents at all (Table 1). These differences in maturity at hatching affect the degree of dependence between young and their parents, which, in turn, affects the opportunities for learning the traits of conspecifics soon after hatching (Shapiro 1980).

The first aim of this paper is to summarise findings on a few model systems representing precocial and altricial birds that are raised by their parents. We acknowledge the fact that our list is far from exhaustive, and that developmental stages can be assigned to more than just these two categories (Nice 1962). This review demonstrates, though, that the study of altricial and precocial model systems has resulted in well-established theories on species recognition in birds, many of which accommodate a process called imprinting as a core aspect of the development of species recognition (Hess 1964, ten Cate & Vos 1999).

To fully understand the diversity of animal behaviour, theories must be able to accommodate the unusual, the different, the atypical (West *et al.* 2003). Reviews of imprinting and species recognition have long stressed the importance of studying two groups of birds in which opportunities for imprinting do not occur: interspecific brood parasites and megapodes (Shapiro 1980, Suboski 1989). Here, we also summarise some recent findings on these non-model systems, in which hatchlings are not raised by their parents. We review studies on some obligate brood-parasites, in particular the brown-headed cowbird, and on the megapode Australian brush-turkey *Alectura lathami*. These non-model systems can provide us with insights into how species recognition can develop in birds that are not raised by their own parents and are thus not exposed to any socially available phenotypic cues that are crucial to species recognition in other species.

## Model systems

### Precocial birds

#### Model systems in the study of filial imprinting

Precocial birds follow an ontogenetic trajectory where young are highly mobile and capable of self-maintenance (e.g., feeding, thermoregulation), soon after hatching. Parental care in these species is typically limited to directing young to profitable foraging grounds and protecting them from social and physical harm. Because social affiliations between family groups form rapidly in precocial species, historically the first model systems in the study of the formation of social attachments in birds were precocial taxa including ducklings (e.g. mallard *Anas platyrhynchos*), goslings (e.g. greylag goose *Anser anser*) and chicks (e.g. domestic chicken *Gallus gallus domesticus* or Burmese red junglefowl *Gallus g. spadiceus*). These studies concentrated on filial imprinting, a process first discussed by Spalding (1873) and then elaborated upon by Lorenz (1935, 1937). Lorenz described filial imprinting as the process by which young birds form an attachment to, and a preference for, the parent, parent-surrogate or siblings. Young ducklings, chicks or goslings approach and follow a

conspicuous object they are exposed to during a particular 'sensitive period'. In nature, that object is usually a parent, but under experimental conditions, they also form attachments to people or inanimate objects, such as boxes or cylinders.

Since Lorenz's work, numerous studies have looked at detailed aspects of filial imprinting in chickens, geese, ducks and also Japanese quail *Coturnix coturnix* (reviews in Salzen & Cornell 1969, Gottlieb 1971, Shapiro 1980, Horn 1985, Suboski 1989, ten Cate 1989, 1994, Johnson & Bolhuis 1991, Lickliter *et al.* 1993). As a result, filial imprinting today is commonly defined as a process through which social behaviour of the young animal becomes limited to a particular object or class of objects, as a result of exposure to an object (Horn 1985, Bateson 1990, Bolhuis 1991). The underlying process can involve both learning through exposure to an object, but also visual and auditory predispositions, as described in the following.

#### Imprinting, species recognition, and the role of predispositions

Lorenz (1935) suggested that imprinting was important in species recognition. However, most authors today agree with Bolhuis (1996: p. 163)

**Table 1.** Degrees of development in bird hatchlings, and study systems for each developmental stage covered in this review.

	Developmental mode	
	Precocial	Altricial
<b>Raised by conspecific parents</b>		
Description	Hatchlings leave the nest and can thermoregulate, find their own food or parents help locate it	Hatchlings naked, cannot thermoregulate efficiently, do not locomote, must be fed by parents
Study species	Chicken <i>Gallus gallus</i> Mallard <i>Anas platyrhynchos</i> Greylag goose <i>Anser anser</i> Quail <i>Coturnix coturnix</i> Bobwhite quail <i>Colinus virginianus</i>	Estrildine finches, e.g.: Zebra finch <i>Taeniopygia guttata</i> Bengalese finch <i>Lonchura striata</i>
<b>Not raised by conspecific parents</b>		
Description	Megapodes: use of external heat sources for incubation, no parental care after hatching	Obligate brood-parasites: eggs laid in nest of other species, young raised by foster parents
Study species	Australian brush-turkey <i>Alectura lathami</i>	Brown-headed cowbird <i>Molothrus ater</i> Common cuckoo <i>Cuculus canorus</i> Indigobirds and whydahs <i>Vidua</i> spp. Great spotted cuckoo <i>Clamator glandarius</i>

that imprinting is “not necessary to achieve a filial preference for the animal’s own species”. Filial imprinting can describe processes such as that chicks acquire preferences for individual stuffed fowl (Johnson & Horn 1987), or that ducklings and chicks can learn to prefer maternal calls from particular individuals (review in Bolhuis & Van Kampen 1992). Imprinting thus mediates the development of preferences for individuals (Bateson 1990), or for artificial objects (Horn 1985).

Also Lorenz (1937) noted that while goslings of the greylag goose followed their human keeper and showed all the usual signs of filial imprinting, newly hatched chicks of the curlew (*Numenius arquata*) could not be made to follow a human. He argued that the curlew has an ‘innate perceptory pattern’ of the appropriate ‘companion’ (‘Kumpan’), while in the goose, the perceptory pattern is formed by experience with a particular object (Lorenz 1937: p. 247). The latter describes imprinting, the former is approximately equivalent to what is described as predisposition today (Gottlieb 1971, Horn 1985, Johnson & Bolhuis 1991, Lickliter 1993, ten Cate 1994).

The interplay between learning and predispositions in the formation of social attachments has received much discussion over the last decades (reviews in Gottlieb 1971, Bateson 1979, Horn 1985, Johnson & Bolhuis 1991, Lickliter 1993, Shettleworth 1994b, ten Cate 1994). In general, predispositions are regarded as perceptual preferences that develop in young animals without experience with the particular stimulus involved (Bolhuis 1996). Predispositions, however, do not imply that preferences develop in an external or internal vacuum. Instead, common environmental influences, such as natural sounds, or also self-cues, such as, colours, vocalizations, or odours, might contribute to the development of perceptual filters that influence subsequent preference for certain, unfamiliar social partners (Hauber *et al.* 2000, Mateo & Johnston 2000, Hauber & Sherman 2001). It remains to be elucidated, for each taxa, whether such perceptual filters are encoded as neural networks in the central nervous system or are actual filtering mechanisms imposed by the anatomy and physiology of sensory organs.

A series of behavioural experiments has confirmed that when young chicks form social attachments, both imprinting and predispositions interact with each other (e.g. Bolhuis & Trooster 1988, Bolhuis *et al.* 1989, Johnson *et al.* 1992). They revealed that under certain rearing conditions, chicks preferred a stuffed adult hen over a box, regardless of the stimulus with which they had been trained, and that such preference also develops if chicks had been raised in the dark before testing. Furthermore, the activation of predispositions is also influenced by rearing conditions, such as the period of time chicks are raised in darkness. However, once activated, predispositions may ensure that the young animal directs its attention to a particular class of objects (i.e. stimuli with a head and neck — Johnson & Horn 1988) or to conspecifics (Gottlieb 1971, Lickliter 1993, Bolhuis & Hampton 1994).

### The role of pre-hatching experience

Studies on bobwhite quail *Colinus virginianus* and ducklings have shown that the expression of species-specific visual preferences after hatching is also affected by stimulation given before hatching, both visual stimulation (Banker & Lickliter 1993, Lickliter 1993), and auditory stimulation (Gottlieb 1971, 1976, 1988, Lickliter & Stoumbos 1991). Bobwhite quail, for example, failed to develop a visual predisposition for their own species when visually deprived before and after hatching but raised in groups during the short period before testing (Banker & Lickliter 1993). This supports the idea that studies on the formation of social attachments should consider the complex visual and auditory experience that young birds receive both before and after hatching (Rogers 1995).

### Altricial birds

#### Model systems in the study of visual and acoustic imprinting

Altricial birds follow a developmental trajectory in which hatchlings obligately require parental assistance in feeding, thermoregulation, and

other aspects of self-maintenance. All songbirds and other avian taxa that learn to sing from social partners are altricial. These birds are thus not only model systems for visual, but also for acoustic imprinting. As a result, studies of the role of early social experience in species recognition and song learning in altricial birds have become intertwined. Estrildine finches, such as the zebra finch *Taeniopygia guttata* and Bengalese finch *Lonchura striata*, are one of the most studied groups of altricial birds in regards to both visual and acoustic imprinting.

### Visual imprinting in estrildine finches

Recognition studies in estrildine finches concentrated more on sexual imprinting than filial imprinting (Immelmann 1969, 1972, ten Cate 1984, ten Cate *et al.* 1984, Clayton 1988). Sexual imprinting is defined as a learning process in young animals that determines what their preferences will be in pair formation (Immelmann 1972). In estrildine finches, filial and sexual imprinting are two closely associated processes, as sexual imprinting occurs very early in life, close to filial imprinting. The reason for this may be found in these birds' life history. Zebra finches are nomadic, frequently breed in colonies containing several species, and form life-long pairbonds rapidly at a young age. The young birds undergo sexual imprinting before they are active enough to move about and meet birds of other estrildine species nesting nearby, and their early and rapid sexual imprinting may be an adaptation to this situation (Chalmers 1983).

In zebra finches, females have bills that are orange and males have bills that are more red. Vos (1994, 1995a, 1995b) raised male zebra finches in captivity with mothers whose bills had been painted red or orange. He found that male chicks learn their mother's plumage and bill colour and later recognise and court females based on these characteristics. No such mechanisms existed in young female zebra finches, for which the bill colour of the stimulus birds did not determine preference. The apparent sex bias in the ability to imprint seems to result from sex-specific differences in when and how the birds learn (summary in ten Cate & Vos 1999).

Sex differences in visual learning and imprinting have also been confirmed in recent studies that tested how young estrildine finches imprint sexually on species atypical, novel visual traits in parents (e.g. crests: Burley & Symanski 1998, Witte *et al.* 2000). These experiments showed that young male finches had to experience a mother with an artificial crest — compared with non-crested, wild-type females — in order to prefer such a novel, species-atypical trait in subsequent mate choice trials. Females, however, showed a consistent preference for crests, regardless of early social experience. An exciting avenue for future research is to determine the ontogeny and organization of the sensory filters and the underlying anatomical and neurophysiological mechanisms that encode for social experience-dependent and -independent preferences within and between sexes (Whaling *et al.* 1997).

### Acoustic imprinting in estrildine finches

Similarly to visual imprinting, auditory production learning, or learning to sing, is a sexually dimorphic trait in zebra finches, with both the vocal activity and the underlying neuroanatomical architecture possessing one of the most extensive sexual dimorphism among songbirds (Theunissen *et al.* 2004). In contrast, both sexes seem to follow a similar developmental pathway in auditory perception learning, that is in memorizing male song and other auditory species-specific cues (Riebel 2003). Such perception learning follows a similar time course and has similar strength and consistency of preference for familiar vocalizations of male tutors in both female and male zebra finches (Riebel *et al.* 2002). These results confirm prior findings for a preference for familiar songs by female zebra finches (Miller 1979).

Experimental perturbation of the early acoustic social environment of zebra finch young results in predictable errors in species-specific behaviours. For instance, when zebra finches were raised by Bengalese finches in the lab (cross-fostering), males sang the song of the heterospecific tutor species. Hence, production learning was shaped by early experience (Clayton 1989). Females showed a sexual preference

for unfamiliar exemplars of the heterospecific tutor song over conspecific song, implying that perception learning too was shaped by early experience (Clayton 1988).

Experience also shapes the stability and quality of the preference for conspecific song in female zebra finches. When raised in acoustic isolation from conspecifics that sang their species-specific song, individuals still preferred unfamiliar conspecific over heterospecific song (Braaten & Reynolds 1999, Lauay *et al.* 2004). However, preference for specific songs was not stable in males that were prevented from singing their own songs (Pytte & Suthers 1999). Also, females raised in isolation from males were more likely to switch their preference between two particular conspecific songs than females raised with foster fathers (Riebel 2000). When females were raised in the absence of singing males, they did not behaviourally discriminate between social *vs.* isolate songs of conspecific males, in contrast to female zebra finches that had been raised by their own fathers (Lauay *et al.* 2004). Hence, experience and familiarity with conspecific songs appears to finetune females' tendency to display preferences between specific classes of conspecific songs. Whether there is a parallel development of females' abilities to discriminate and to form a preference between song classes is unknown and will require detailed analyses of the neural circuitry and hormonal mechanisms underlying female auditory perception (Theunissen *et al.* 2004).

In summary, these results indicate that both male and female zebra finches imprint on certain visual and auditory characteristics of their parents after hatching. Nonetheless, some studies have shown that young zebra finches can also respond to conspecifics even if they have no social experience with other zebra finches (Immelmann 1969, Braaten & Reynolds 1999). This supports the idea that imprinting does not have to play an essential role in species recognition, as suggested by studies on ducks and chickens (*see above*).

### Summary: model species

Appendix 1 lists the many possible questions that can be asked when taking an ontogenetic, mech-

anistic, functional, and evolutionary approach to avian species recognition. What becomes obvious from the work summarised so far is that our current understanding of species recognition is based upon a relatively small number of model systems, representing taxa in which imprinting has been observed. It is problematic to generalise these results to many bird species that differ in their degree of social interactions among conspecifics, and in the developmental stage at which these interactions typically take place. Imprinting tends to occur in species in which attachment to parents or to the family group is an important aspect of the social experience and interactions (McFarland 1993). Imprinting is not essential for species recognition (Bolhuis 1996) and it may be more important for kin recognition (Bateson 1979). These ideas are supported by the data that the sensitive period for imprinting usually ends before the juvenile bird is likely to mix with birds other than its immediate kin (McFarland 1993).

The summary on model systems further reveals that the cues used for species recognition in birds include both visual and acoustical stimuli. Regarding olfactory cues, recent studies have shown that crested auklets *Aethia cristatella* use odour cues to discriminate between conspecifics and heterospecifics while breeding (Hagelin *et al.* 2003). It remains to be asked whether such signals also serve as species recognition cues for young, and what role experience with parents and other conspecifics *vs.* self plays in the development of olfactory preference in these — and perhaps other — avian species.

This brief overview also shows that a large proportion of studies on species recognition took place from the 1950s to the 1990s. In part, this can be explained by the rising popularity of fields such as behavioural ecology and sociobiology. Researchers increasingly recognise the ecological and evolutionary significance of mate recognition, such as the effects of these processes on inbreeding avoidance, sexual selection, and speciation (Lewis *et al.* 2004). As a result, most studies on recognition systems in animals overwhelmingly focused on mate choice (Fig. 1). Species recognition was often treated only as it pertains to mate recognition and has received little attention *per se* (Fig. 1). Studies on parent–

offspring recognition, for example, placed more emphasis on the mechanisms that mediate kin and mate recognition during this process rather than species recognition (Beecher 1988, Holmes 1990, Halpin 1991).

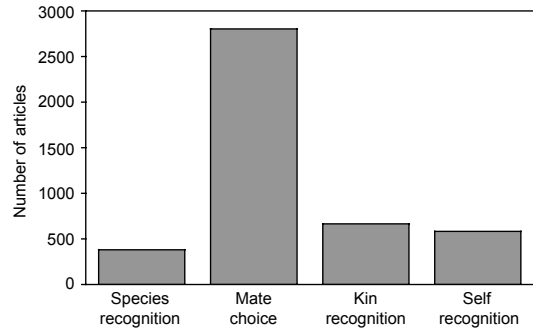
## Non model systems

The model systems described so far all have one fact in common: the young birds reliably encounter at least one conspecific individual (e.g. one of their parents) after hatching and have the opportunity to learn about traits that reliably identify conspecifics. In addition, young birds often encounter conspecific full- or half-siblings, and learning aspects of their phenotypes yields predictable templates for species recognition (Sherman *et al.* 1997). Sometimes, young may not encounter their biological parents, because of intraspecific brood parasitism that is frequent in many precocial and some altricial species (Yom-Tov 2001), including captive zebra finches (Burley & Symanski 1998). But even in these instances, foster parents and siblings will belong to the same species as the young and conspecific recognition mechanisms are not expected to differ between species with and without intraspecific parasitism.

However, two groups of birds, the megapodes and interspecific brood-parasites, reveal that other developmental pathways can evolve: chicks are not raised by their parents or other conspecifics after hatching and thus have no or few direct opportunities to learn to recognise conspecific traits from early social partners (Hauber *et al.* 2000, Göth & Evans 2004). These non-traditional systems provide us with the unusual evolutionary and ecological context in which the boundaries of species recognition systems can be challenged and examined. In the following, we summarise some recent studies that represent new attempts to reveal the alternative solutions that these birds have developed to confront the challenge of species recognition.

### Altricial: interspecific brood parasites

All interspecific brood parasites depend on some form of direct parental care, including incuba-



**Fig. 1.** A comparison of the number of publications focusing on avian recognition systems from the social and functional contexts of affiliative behaviours. The number of articles represents the total number of publications between 1964 and 2003 that were found by the Web of Science™, using the key word searches of *birds* and *species recognition*, *mate choice*, *kin recognition*, or *self recognition*, respectively.

tion, and they typically also receive brooding, protection, and food from foster parents. The ontogeny of species recognition in brood parasitic birds must clearly be different from that of non-parasitic species (Hauber & Sherman 2001). In these taxa imprinting is overwhelmingly implicated by experimental studies that used cross-fostering to create individuals with misleading recognition templates in the laboratory (e.g. zebra finches: Clayton 1988, 1989) and in the field (e.g. blue tits *Parulus caeruleus*: Slagsvold & Hansen 2001).

Many interspecific brood parasites, especially precocial taxa, follow facultative tactics: they lay some of their eggs into nests of other species while others are incubated in nests of their own species (intraspecific brood parasitism) or by themselves ('typical' avian parental care) (Davies 2000). To date, the species recognition processes of facultative brood parasitic birds have not been described in detail, whether in precocial (redhead *Aythya americana*, Sorenson 1991) or altricial (yellow-billed cuckoo *Coccyzus americanus*, Fleischer *et al.* 1985) taxa. Nevertheless, the study of life histories of altricial and precocial facultative brood parasites has benefited from recent new methodological tools, both theoretical constructs (e.g. evolutionary models regarding clutch size evolution: Lyon 1998, Ruxton & Broom 2002) and practical procedures (e.g. molecular analyses to detect parasitism: McRae & Burke 1996). These tools provide appealing

quantitative bases for investigations into the evolution of reproduction and development in parasitic vs. non-parasitic species (Yom-Tov 2001).

The single known precocial species among the obligate interspecific brood parasites is the black-headed duck (*Heteronetta atricapilla*) of South America, whose ducklings leave nests of host coots and gulls shortly after hatching (Rees & Hillgarth 1984). All other species of obligate parasitic birds are altricial, including common cuckoos (*Cuculus canorus*), great spotted cuckoos (*Clamator glandariensis*), *Vidua* indigobirds and whydahs, and *Molothrus* cowbirds. Their young require parental care in the form of both incubation and posthatching care, such as brooding and feeding by host parents. Interspecific brood parasites have developed a diverse array of behavioural strategies that allow them to choose host species whose nests and parental care strategies (e.g., clutch size, incubation patterns, feeding regimes, postfledging care) are compatible with the development of the parasitic young (Ortega 1998, Sealy *et al.* 2002). Host recognition strategies by obligate parasites are critically relevant to discussions of the evolution of species recognition systems, and these topics have already been discussed and reviewed extensively in the recent literature (Rothstein & Robinson 1998, Davies 2000, Hauber *et al.* 2001, Vogl *et al.* 2002).

A notable pattern of sociality in obligate brood parasitic birds is that many brood parasitic young join conspecifics soon after fledging and well before the onset of sexual maturity (Hahn & Fleischer 1995, Soler *et al.* 1995). For instance, great spotted cuckoo nestlings are sometimes visited by adults, and fledglings may aggregate with each other prior to nutritional independence from host black-billed magpies *Pica pica* (Soler & Soler 1999). Fledgling brown-headed cowbirds are also visited by adult female cowbirds (Hauber 2002) and start foraging in the presence of other conspecifics within weeks of becoming independent from foster parents (Hahn & Fleischer 1995). At the functional level, the benefit of early socialization with other parasites could be related to safer and more efficient foraging, roosting, migration, and communication, and distinguishing between these alternatives should be a fruitful avenue for future research (Appendix 2). Whether these benefits arise

from group augmentation (i.e. are simply due to increased numbers of conspecifics occurring and interacting with each other), or are effected by culturally transmitted behavioural traits that are learned from (O’Loughlen & Rothstein 2002a, White *et al.* 2002a, Freeberg 2004) and taught by more mature individuals (West & King 1988), also remains to be evaluated in future research on these and many other brood parasitic taxa.

Regardless of the function, socialising with conspecifics for sex and, to some degree, for food shelter, and safety, requires conspecific recognition. The several ontogenetic pathways that lead to the recognition of conspecifics can be sorted into several non-exclusive categories. Indirect recognition (Waldman *et al.* 1988) implies discrimination based on non-phenotypic cues (e.g., preferences for time or location), that would lead to preferential association with conspecifics. For instance, juvenile brown-headed cowbirds and great spotted cuckoos are often seen feeding and roosting in the company of conspecifics (Hahn & Fleischer 1995, Soler & Soler 1999, Hauber 2002). Young cowbirds’ preferences for foraging in open areas and near large mammals, including livestock (Ortega 1998), may explain such apparent spatial and, consequently, social proximity to conspecifics, but experimental support for such a mechanism is currently lacking. In turn, direct recognition implies memorizing traits of referent individuals that are conspecifics and later preferentially associating (or avoiding) individuals whose traits match these recognition templates. Direct recognition includes learning via (A) self-referencing, (B) social learning, or (C) social mediation. Experimental evidence suggests a role for all three direct recognition paths in brood parasitic birds.

(A) *Self-referencing*: In the absence of predictable exposure to conspecifics, individuals may learn about phenotypic attributes that predict species identity. Hence, to form their recognition templates individuals may inspect their own traits (Dawkins 1982). Whether self-referencing is used for species recognition, sex recognition in dimorphic species, or kin recognition in the context of inbreeding avoidance or nepotistic foraging and alarm calling, depends on the social ecology of each species (Holmes & Sherman 1982, Sherman 1991). Because self-phenotype



is the result of the interactions of genetic and environmental factors during development, self-traits are the best predictors of the phenotypic attributes of other, genetically related individuals that developed in a similar environment.

To detect self-referencing observationally, a researcher has to be able to discount the opportunity for all other known mechanisms of social recognition, including social learning and social mediation (*see below*, also Hauber & Sherman 2003, Mateo & Holmes 2004). For instance, Graham and Middleton (1989) conducted an intensive study of species recognition mechanisms in juvenile brown-headed cowbirds by hand-raising parasitic young in social isolation from other avian stimuli and testing their preference for conspecifics using inanimate stuffed models. Young cowbirds at 35 but not at 25 days of age preferentially associated with conspecific models *vs.* heterospecific models of other icterine species, perhaps using body shape and size as the self-referenced traits (Graham & Middleton 1989).

In turn, to detect self-referencing experimentally, a researcher has to eliminate the opportunity for social learning and mediation by cross-fostering and randomly mixing individuals of different genetic backgrounds. In addition, to unambiguously identify the recognition cues used in self-referencing, the researcher has to be able to manipulate that self-cue that is available to an individual and cause predictable recognition errors in the future interactions of this individual (Hauber & Sherman 2003). Such a study was conducted with individually hand-raised parasitic brown-headed cowbird chicks whose feathers were painted black or sham-manipulated from the time they broke sheath (Hauber *et al.* 2000). Two months later juvenile black-painted individuals showed a greater spatial preference than did sham-manipulated juveniles for conspecific adult females that were also painted blacks *vs.* sham-manipulated females. This study satisfied the requirement of both eliminating external, social cues for species recognition and manipulating the potential recognition cue to predictably alter social preference in experimental young (Hauber & Sherman 2003).

It remains to be seen, however, whether self-referencing in juvenile cowbirds is used in

contexts other than species recognition. Accordingly, during their first winter juvenile male and female cowbirds preferentially associate spatially with older same-sex individuals (Freeberg 1999, White *et al.* 2002b). Sexual segregation may be based on self-referencing because of the sexual dimorphism of plumage patterns, size, and vocalizations of young cowbirds (O'Loughlen & Rothstein 2002b, Hauber & Ramsey 2003). Furthermore, it also remains to be determined experimentally how important self-referent phenotype matching is in the development of species recognition in other parasitic birds. For instance, in screaming cowbirds (*Molothrus rufoaxillaris*), juvenile parasites are visual mimics of host bay-winged fledglings (*Agelaioides badius*, formerly bay-winged cowbird *M. badius*) (Ortega 1998), and so even self-referencing could be a misleading source of parasite-typical species recognition cues. Finally, the relevance of self-referencing to acoustic recognition cues remains to be investigated experimentally. For example, naïve juvenile (~2 month old) and mature (~1 year old) cowbirds already preferentially respond to conspecific vocalizations, such as chatter call (Hauber *et al.* 2001) and perched song (King & West 1977) (but *see* Graham & Middleton 1989), and this is the case even in the absence of prior exposure to other conspecifics and their sounds. Do cowbirds prefer their own species' calls because these resemble more closely their own vocalizations during development (*see also* Payne *et al.* 2000 for such a case in *Vidua* spp.)? To test the role of self-referencing in acoustic species recognition would require the alteration of the self-perceived vocalizations by developing parasitic young, perhaps through the use of altering the frequency range of self calls in a lower density heliox atmosphere (Nowicki 1987, Brittan-Powell *et al.* 1997). From an evolutionary perspective (Appendix 2) it will be particularly relevant to compare the acoustic species recognition mechanisms of brood parasitic songbirds and non-oscine passerines where hearing conspecific songs is also not critical in the development of species-specific vocalizations (Kroodsma *et al.* 2001).

(B) *Social learning*: Brood parasitic young have the opportunity to interact with conspecifics despite the parasitic parental care strategy

at several stages of their development. Parasitic embryos, chicks, or fledglings are sometimes exposed to conspecific adults that visit and perhaps vocalise at parasitised nests, such as in brown-headed cowbirds (Hahn & Fleischer 1995, Hauber 2002) or great spotted cuckoos (Soler & Soler 1999). The outcome of adult visits to parasitised nests, however, is not always compatible with species affiliation, because adult parasites can also be predators of host nests (Arcese *et al.* 1996, Elliot 1999). Alternatively, parasitic embryos or nestlings could interact with each other in nests that had received multiple parasitic eggs. Multiple parasitism is not uncommon in parasitised host nests in several host–parasite systems, such as in some populations of great spotted cuckoos and magpie hosts (Martinez *et al.* 1998), shiny cowbirds *M. bonariensis* and house wren *Troglodytes aedon* hosts (Lea & Kattan 1998), common cuckoos and great reed warbler *Acrocephalus arundinaceus* hosts (Moskát & Honza 2002), and brown-headed cowbirds and wood thrush (*Hylocichla mustelina*) hosts (Trine 2000).

However, most host nests receive only a single parasitic egg (Hauber 2001, McLaren *et al.* 2003), rendering species recognition based on cues learned from conspecific nestmates a typically unpredictable source of recognition templates. Nonetheless, in some brood parasitic young social exposure to conspecifics has been found to mediate or, at least, to enhance subsequent social choice. In the great spotted cuckoo of the western Mediterranean, individual chicks raised singly in host nests that were in allopatry from adult cuckoos were less likely to join other young cuckoos upon fledgling than cuckoo chicks raised in host nests with another parasitic chick (Soler & Soler 1999). In contrast juvenile (< 3 month old) brown-headed cowbirds early exposure to conspecifics did not increase subsequent preference for conspecifics over heterospecifics (Graham & Middleton 1989, Hauber 2002).

Additional evidence for the role of social experience in parasitic species recognition comes from investigations of the acoustic signals that are critically important in the species recognition mechanisms of several brood parasitic species. On the one hand, *Vidua* indigobirds learn to memorise and mimic host parents' songs and a female

preferentially mates with males that incorporate mimicking elements of her own foster species (Payne & Payne 2002). Juvenile brown-headed cowbirds also show plasticity in their acquisition of species-specific song templates in that song production learning in pre-reproductive males is influenced by exposure to conspecific adults (West & King 1988, O'Loughlen & Rothstein 2002a, 2002b). The preference for and the production of some species-specific signals can be altered experimentally by limiting juvenile male cowbirds' exposure to heterospecifics instead of conspecifics; this results in species atypical songs and courtship patterns directed at heterospecifics by experimental young males (Freeberg *et al.* 1995). What the potential roles of experience-dependent learning of acoustic signals may be in the species recognition systems of other brood parasitic taxa, including the duck, old- and new-world cuckoos, and honeyguides, are still unclear. This requires much empirical research into the natural and life history of previously unstudied parasitic taxa.

(C) *Social mediation*: Young brood parasites in some species show a remarkable pattern of affiliative behaviours towards heterospecifics. For instance, juvenile brown-headed cowbirds often beg from heterospecifics, whether or not individuals are of the same species as their foster parents (Ortega 1998, Hauber 2003). A cognitive architecture that allows brood parasites to solicit parental care and assistance from individuals irrespective of species identity should be highly advantageous especially in generalist brood parasites such as brown-headed cowbirds (Davies 2000, Hauber 2003). In contrast, non-discrimination would hinder affiliation with conspecifics unless heterospecifics responded differently to the approaches by juvenile parasites. For instance, juvenile cowbirds look much like adult female cowbirds that are in turn typically attacked physically by many host species during the breeding season (Strausberger & Horning 1998). Yet, if young parasites continued to associate with only individuals that are not aggressive and/or socially responsive to their approaches, social mediation of interactions would lead to the inclusion of juvenile parasites into conspecific flocks. Such a scenario is a likely mechanism for conspecific aggregation in some cuckoos and

cowbirds, where adult parasites seek the company of conspecific juveniles preferentially over heterospecifics (Soler & Soler 1999, Hauber 2002, *see above*).

The hypothesis of early social association between adult and juvenile parasites was tested experimentally in the laboratory; adult brown-headed cowbirds of both sexes approached conspecific young above random levels in simultaneous choice trials over heterospecific young (Hauber 2002). In turn, isolation-raised juvenile cowbirds affiliated more with conspecific adult females and spatial and behavioural preference for conspecifics was associated with lower aggressive displays (pecks) delivered at young parasites by the female cowbird stimuli than host adults (Hauber 2002).

Whether social mediation can be a general mechanism for conspecific recognition in cowbirds and other parasites is unclear especially given the presumably asocial ontogeny of some populations of cowbirds (Rothstein & Fleischer 1987, O'Loughlen & Rothstein 1993) and many other species of parasitic birds (Davies 2000). Nonetheless, to test conclusively these ideas in a specific experiment would require the construction of robot stimuli of different species that can deliver varying amounts of aggressive displays at naïve juvenile parasites (following Patricelli *et al.* 2002, Göth & Evans 2004).

Finally, evidence for social mediation does not negate the possibility of self-referencing, social learning, or other ontogenies to combine in the recognition systems of parasitic and other birds. Multiple pathways that function as failsafe methods to achieve the same recognition goal are expected in taxa with such unpredictable socio-ecological milieu during early development (Hauber & Sherman 2001, 2003) as is seen, for example, in brown-headed cowbirds that successfully parasitise over 100 host species (Ortega 1998).

Alternatively, different ontogenies may function at different times during the social development of parasitic young. For example, brown-headed cowbird chicks respond preferentially to conspecific chatter calls as early as 6 days of age and also at 2 months of age even when raised in isolation from adult conspecifics (Hauber *et al.* 2001). In turn, young parasites may use conspe-

cific contact calls (e.g. chatters) as a password (Soha & Marler 2000, Hauber *et al.* 2001): they recognise and approach flocks of birds that produce chatters. Once in the company of such a flock, which will inevitably contain conspecifics, social mediation may ensure affiliation of the young cowbird with adult cowbirds (King & West 1977, Hauber 2002). Self-referencing using body shape and colour (Graham & Middleton 1989, Hauber *et al.* 2000) may then mediate the fine-scale structure of such affiliation (e.g. spatial proximity of juvenile and adult males, Freeberg 1999). Social learning of additional species-specific traits (e.g. acoustic and visual courtship signals: Freeberg *et al.* 1995, O'Loughlen & Rothstein 1995), would further ensure the association of the young cowbird with conspecifics, and increase successful reproduction with compatible mates (O'Loughlen & Rothstein 2002a, White *et al.* 2002a).

### **Precocial: megapodes**

Megapodes (Galliformes: Megapodiidae) form no bonds with any model that can provide the early experience that is crucial to species recognition in most other birds. All 22 species use external heat sources for incubation, and do not look after their young (Jones *et al.* 1995). Some megapodes lay their eggs in geothermally heated burrows, others build large mounds of organic material, in which the eggs are incubated by the heat from microbial decomposition, and some additionally use solar heat to incubate their eggs (Booth & Jones 2002). Megapode chicks are highly precocial. They hatch in the soil, in depths of up to 170 cm, and their first challenge in life is to dig themselves out of their underground nest, unaided by their parents. In Australian brush-turkeys, this process takes, on average, 40 hours (Göth 2002).

After reaching the surface, chicks may sometimes encounter their parents, but they never cohabit with them (Pycraft 1907, Heinrich 1932, Frith 1956, Clark 1964, Göth & Vogel 2002b, Göth & Jones 2003). They meet other chicks rarely and at an unpredictable age, for several reasons. First, chicks hatch at different times and also emerge asynchronously from incubation

sites, which are typically widely distributed, and they then quickly disperse into dense vegetation away from these sites (Jones 1987, Benshemesh 1992, Göth & Vogel 2002a, 2002b, 2003). Second, young megapodes are well camouflaged, with a brown plumage, and they lack any loud contact calls (Baltin 1969, Göth *et al.* 1999). Additionally, these omnivorous birds are capable of finding adequate food alone (Göth & Proctor 2002) and of detecting predators innately (Göth 2001a), and these features enable them to survive without assistance from others.

In summary, megapode chicks grow up under conditions that do not seem to favor predictable encounters with conspecifics from which chicks could learn about species-specific cues. So far, all detailed studies on megapode ontogeny have been conducted on the Australian brush-turkey, a common species that occurs on the East coast of Australia and close to research facilities. Most other megapodes are highly endangered and/or occur on remote islands between the Nicobar group near India and the Tonga islands in the South Pacific.

Wong (1999) demonstrated that brush-turkey hatchlings do not imprint on conspecifics, under conditions that favour imprinting in chickens. She repeated the classic experiments designed to test visual imprinting in other birds (Hess 1958), and found that, in a circular runway, young domestic chickens followed a ball that was moved away from them, and thereby imprinted on it, but hatchlings of the brush-turkey showed no such response.

However, despite the lack of visual imprinting, young brush-turkey chicks do occasionally form groups with other similar-aged chicks in the wild. In a radio-tracking study, they were detected with another chick in 6% of all encounters ( $n = 166$  encounters with a total of 31 chicks aged 2 days to 4 weeks; chicks observed for periods of 1–30 min; Göth 2001b), but never with any heterospecific species, such as sympatric ground-living quail (e.g. Black-breasted button quail, *Turnix melanogaster*), or with adult brush-turkeys. Juveniles, from the age of approximately 100 days, are frequently seen moving in conspecific groups (Jones 1988). Such aggregations seem to particularly occur in areas of rich food supply, such as under trees that provide

seeds or fruit (Göth & Vogel 2002b). Food, and to some extent shelter from predators, are thus the main factors that favor aggregation in brush-turkey chicks.

Also in captivity, brush-turkey chicks aggregate in groups from an early age: when encounters were induced between 2-day-old socially naïve hatchlings and up to 49-day-old brush-turkey chicks in a large outdoor aviary, social responses to similar-aged conspecifics were apparent from as early as two days (Göth & Jones 2003). All of the behaviour patterns found in older chicks were present in hatchlings, and these did not change appreciably with age (Göth & Jones 2003). In addition, hatchlings stayed close together (median distance 0.1 m while feeding and 0.34 m while resting), despite the large size (76 m<sup>2</sup>) of the aviary (Göth & Jones 2003).

Socially-naïve brush-turkey chicks thus have competent social behaviour when they first encounter a conspecific. This fact, together with the observations of chicks moving in conspecific groups in the wild, strongly suggest that brush-turkeys are capable of recognizing conspecifics at a young age. To prove this assumption, one could give chicks a choice between a live conspecific and similar-sized heterospecific in an experimental setup. However, results obtained by taking such an approach could be difficult to interpret. First, because the behaviour of the two stimulus birds — conspecific and heterospecific — could affect the brush-turkey chick's choice, and may differ considerably between trials. Heterospecific species could not only differ in their visual, but also in their acoustic behaviour — chicks of the domestic chicken, for example, would utter frequent calls, while brush-turkey chicks rarely call. The use of one-way mirrors or acoustic barriers to address these problems would change the light conditions under which the stimulus birds are viewed, and this makes it difficult to consider the role of body colour as species recognition cue.

To address these problems, Göth and Evans (2004) used robot brush-turkey chick models, which allowed for better control of the behaviour and body colour of stimulus birds. Robots have the advantage that they standardise behaviour and remove social interactions between stimulus

and focal animal that might otherwise complicate interpretation of the results. Göth and Evans focused on likely visual cues in species recognition that included pecking movements and body colour. Pecking movements were chosen because earlier work showed that chicks often approached a pecking companion and then fixated upon the food it was feeding on (Göth & Jones 2003). Also, galliform chicks generally are highly responsive to pecking movements of conspecifics, including maternal pecking (Turner 1965). Body colour was included because it plays an important role in evoking social aggregation in cowbird fledglings, which face a similar developmental challenge to megapodes (*see above, Hauber et al.* 2000). Calls, on the other hand, were not included in these first experiments, because brush-turkey hatchlings rarely call.

Choice experiments with robotic chicks as stimuli were conducted under naturalistic conditions in a large outdoor aviary. Two types of robots were built, using the skins of chicks that had died naturally plus servo engines for remote-controlled cars (pictures in Göth & Evans 2004). One pecked at the ground, indicating feeding movements, the other moved from side to side, indicating scanning movements. Simultaneous choice tests revealed that brush-turkey chicks preferred the pecking robot over the scanning robot or a static model. The pecking robot successfully evoked a range of social responses resembling those to a live companion.

Subsequent tests aimed at revealing the importance of body colour as recognition cue (Göth & Evans 2004). Chicks were presented with a choice of a pecking robot with manipulated body colour and a normal-looking pecking robot. Colour manipulations were achieved by using four types of colour filters mounted above the robots (*see Göth & Evans 2004 for a discussion on the use of colour filters versus body dye*). These filters removed either UV, short-wave, medium-wave, or long-wave radiance from the body of the robot, and thus altered the spectral shape of the ambient light under which the robot was presented. When UV or short-wave radiance were removed from the robot, chicks spent significantly more time near the second, normal-looking robot. By contrast, removal of

medium-wave and long-wave radiance did not have such a detrimental effect on the attractiveness of the robot — chicks did not avoid it significantly more often. Chicks were thus sensitive to changes in appearance, but only to those that affected radiance at short wavelengths (fig. 5 in Göth & Evans 2004).

In summary, these experiments suggest that responsiveness to conspecifics depends upon body colours in the UV and short-wave range, and on particular movement patterns. Pecking movements may be particularly suitable for evoking approach behaviour, as they indicate a potential food source. Future tests still need to test whether such perceptual preferences are sufficiently specific to function as species recognition mechanisms, by giving chicks the choice between a con- and heterospecific. The results described above show that, when designing such choice tests, we need to use a heterospecific species that has a similar body colour to brush-turkey chicks and shows a similar behaviour, in particular pecking behaviour. Such a comparison makes most sense in an ecological meaningful context, that is by presenting chicks with a choice they would experience in nature. In northern Queensland (Australia), brush-turkeys occur sympatrically with the orange-footed megapode *Megapodius reinwardt*. The chicks of both closely related species look similar to the human eye, behave similarly and live in the same habitat. Chicks of the orange-footed megapode thus seem the ideal heterospecific stimulus for future tests on the brush-turkeys' species recognition abilities.

Future studies also need to investigate recognition cues other than morphology and motor patterns, particularly acoustic signals. Brush-turkey hatchlings rarely call; while they utter none to very few of their soft, one-syllable calls during the first two weeks, the frequency of calling increases significantly thereafter (Göth & Jones 2003). Chicks of other megapode species also call rarely and at unpredictable times (Göth *et al.* 1999). However, young brush-turkey chicks kept in outdoor aviaries do occasionally respond to each others' calls, resulting in minute-long counter-call series (Göth & Jones 2003). Future choice tests should include acoustic stimuli such as the calls of other chicks and adults to reveal

the role of acoustic cues in the species recognition process. Acoustic signals could potentially also act as recognition cues for megapode embryos in the egg, as is the case in other birds (Gottlieb 1976). However, eggs are buried in the soil, in depths anywhere between 40 cm and 170 cm, and soil is a rather effective sound-attenuating material. Future studies should nevertheless test whether chicks utter any calls in the egg, before hatching, and whether exposure to calls of conspecifics as embryos affects their behaviour after hatching.

The studies described above only provide some first insights into species recognition in megapodes, and much remains to be learned (*see* Appendix 3). For example, one question to be asked is on the role of learning in megapode species recognition. The perceptual bias observed in the study so far seems to be largely experience independent, as chicks had absolutely no social contact prior to the choice tests in which visual stimuli were presented. This result can be the basis for exploration of the role of experience in the development of species recognition in megapodes. Learning processes, such as self-referent phenotype matching (Hauber & Sherman 2001), may occur and could be triggered by specific cues that are inherently salient. If this is the case, then megapodes have properties convergent with those of cowbirds, in which such processes play an important role (*see* above, Hauber *et al.* 2000, 2001). If not, then megapodes may have developed a unique solution to the challenge of species recognition; a solution, which involves a high proportion of experience independent recognition templates.

## Concluding remarks

Avian species with unusual life history strategies offer powerful empirical comparisons for knowledge gained about species recognition mechanisms in model systems. We have seen that “non-parental” species, such as interspecific brood parasites and megapodes, provide evidence for the role of ontogenetic pathways and recognition cues that are different or not yet fully demonstrated in model species. This

is perhaps not surprising since avian models for recognition studies typically include species with biparental care (e.g. zebra finches, greylag geese) or female-only parental care (e.g. domestic fowl, mallards). We predict that the exploration of species recognition mechanisms within the full spectrum of variation in parental care strategies among birds, including facultatively mono-parental (e.g., painted quail *Excalfactoria chinensis*) and sex-role reversed species (e.g., wattled jacanas *Jacana jacana*: Emlen & Wrege 2004), will provide further insights and discoveries into the diversity of avian species recognition systems.

Our overview of the proximate bases of avian species recognition reveals that diverse ecological and life history attributes can critically shape both the ontogeny and the mechanisms, including the cues and the timing, of how individual birds acquire and utilise conspecific recognition templates. The above account of model and non-model species also reveals that when discussing the relative contribution of learning and predispositions in the formation of social attachments, we need to treat each species differently and in the context of its ecology and life history strategies. Shapiro (1980) suggests that the predisposition to respond in a particular way to conspecifics is intimately involved with the opportunities the newly hatched chick has to interact with its environment: are both parents present (or even several group members), one parent, or none? As Shapiro (1980: p. 77) states “Given the various patterns of incubating and rearing, and the diverse ecological systems supportive of avian existence, each of which interacts uniquely with the morphological characteristics of each species, it is not likely that researchers are going to be able to gain a complete understanding of the process of forming an attachment to one’s species in each species of bird in the near future”. In other words, today, 70 years after Lorenz’s studies on filial imprinting, the field of avian species recognition continues to offer research questions that span multi-levels of analysis and are truly integrative as this field remains rich in theoretical, empirical, and practical challenges for biologists across many subdisciplines.

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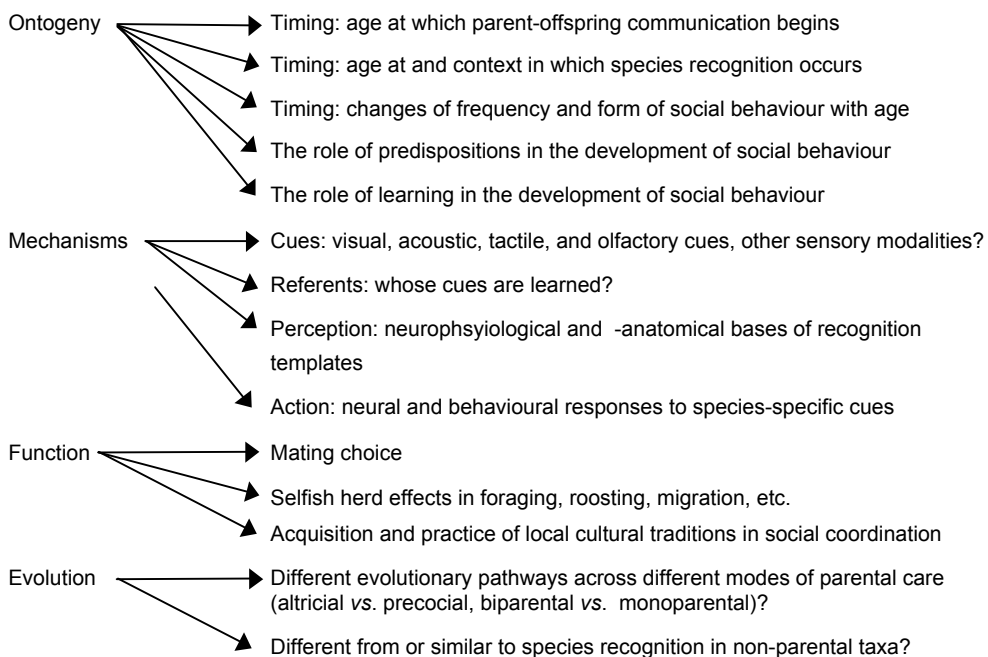


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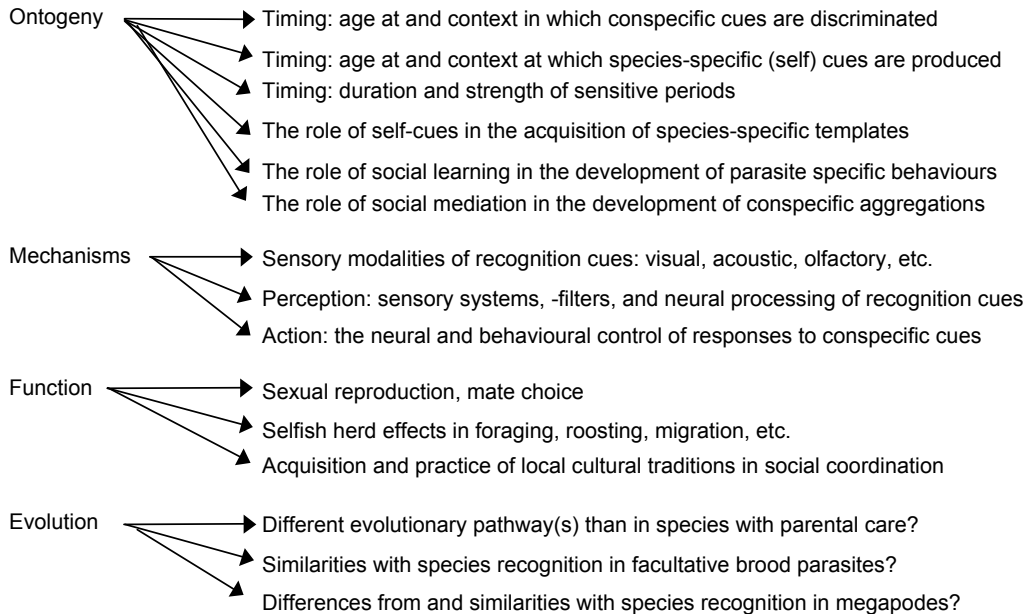
#### Appendix 1. Species recognition and social behaviour in parental species: research directions.



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**Appendix 2.** Species recognition in obligate brood parasites: research directions.
 

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**Appendix 3.** Species recognition and social behaviour in megapodes: research directions.
 

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