

‘O sibling, where art thou?’ – a review of avian sibling recognition with respect to the mammalian literature

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ABSTRACT

Avian literature on sibling recognition is rare compared to that developed by mammalian researchers. We compare avian and mammalian research on sibling recognition to identify why avian work is rare, how approaches differ and what avian and mammalian researchers can learn from each other. Three factors: (1) biological differences between birds and mammals, (2) conceptual biases and (3) practical constraints, appear to influence our current understanding. Avian research focuses on colonial species because sibling recognition is considered adaptive where ‘mixing potential’ of dependent young is high; research on a wider range of species, breeding systems and ecological conditions is now needed. Studies of acoustic recognition cues dominate avian literature; other types of cues (e.g. visual, olfactory) deserve further attention. The effect of gender on avian sibling recognition has yet to be investigated; mammalian work shows that gender can have important influences. Most importantly, many researchers assume that birds recognise siblings through ‘direct familiarisation’ (commonly known as associative learning or familiarity); future experiments should also incorporate tests for ‘indirect familiarisation’ (commonly known as phenotype matching). If direct familiarisation proves crucial, avian research should investigate how periods of separation influence sibling discrimination. Mammalian researchers typically interpret sibling recognition in broad functional terms (nepotism, optimal outbreeding); some avian researchers more successfully identify specific and testable adaptive explanations, with greater relevance to natural contexts. We end by reporting exciting discoveries from recent studies of avian sibling recognition that inspire further interest in this topic.

Key words: sibling recognition, birds, mammals, kin recognition, kin discrimination, individual recognition, direct familiarisation, indirect familiarisation.

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I. INTRODUCTION

Social recognition is one of the most important abilities for establishing and maintaining relationships in many societies (Wilson, 1975; Colgan, 1983). Within a given social system, animals may benefit from recognising mates, parents, offspring, siblings, group members, neighbours and/or other types of acquaintances.

One subclass of social recognition, kin recognition, has attracted considerable attention (Holmes & Sherman, 1983; Fletcher & Michener, 1987; Hepper, 1991*a*; Pfennig & Sherman, 1995) since the introduction of kin selection theory (Hamilton, 1963, 1964*a, b*; Maynard Smith, 1964; but, for recent debate over kin selection, see Clutton-Brock, 2002; Griffin & West, 2002; West, Pen & Griffin, 2002). Kin recognition and discrimination (Table 1) facilitate the evolution of altruistic behaviour through inclusive fitness (Hamilton, 1964*b*; note that kin selection can occur in the absence of kin recognition and discrimination; Maynard Smith, 1976; Dawkins, 1979). Within the inclusive fitness framework, three types of kin recognition are paramount: parent, offspring and sibling recognition (in each case, assuming ‘full’ siblings, the coefficient of relatedness would be 0.50; Hamilton, 1964*a*). Of these, we consider sibling recognition the most complex because: (1) recognition is often required during early ontogeny when animals may lack experience and a fully developed sensory system (also true for parent recognition), (2) target animals (i.e. siblings) may just be developing distinctive features or cues (also true for offspring recognition), (3) siblings can vary in relatedness (e.g. full *versus* half genetic siblings), and (4) animals may encounter unfamiliar siblings (i.e. siblings not reared together) from different broods of the same mother and/or father.

Despite the potential importance of sibling recognition, studies of kin recognition in birds have focused largely on parent and offspring recognition (Beecher, 1988; Halpin, 1991; Komdeur & Hatchwell, 1999). Sibling recognition studies in birds are rare, and have been conducted primarily on larids (i.e. gulls and terns; e.g. Noseworthy & Lien, 1976; Burger, Gochfeld & Boarman, 1988; Pierotti, Brunton & Murphy, 1988). Although avian sibling recognition has gained more attention in recent years (Wanker *et al.*, 1998; Palestis & Burger, 1999, 2001*a, b*; Nakagawa, Waas & Miyazaki, 2001), information on a wider range of species from different ecological circumstances is now urgently required. For example, many studies exist for cooperatively breeding birds (Brown, 1987; Stacey & Koenig, 1990).

Although they could benefit from sibling recognition, only one study (on long-tailed tits, *Aegithalos caudatus*, Hatchwell *et al.*, 2001*b*) has examined sibling recognition, experimentally, in cooperatively breeding birds.

The paucity of sibling recognition studies for birds is in stark contrast to the availability of such studies in the mammalian literature, especially for rodents (Blaustein, Bekoff & Daniels, 1987; Blaustein *et al.*, 1991; Halpin, 1991). For example, many empirical studies providing evidence for sibling discrimination exist for house mice (*Mus domesticus*, see Barnard, Hurst & Aldhous, 1991). The emphasis on mice is partly the result of interests in associations between kin recognition, mate preference and the major histocompatibility complex (MHC – a cluster of genes primarily involved in immune response regulation that also play a role in the production of individual odours; Zavazava & Eggert, 1997; Eggert, Müller-Ruchholtz & Ferstl, 1999); these associations are particularly well studied for mice (reviewed in Barnard & Aldhous, 1991; Brown & Eklund, 1994; Lenington, Cooper & Williams, 1992; Penn & Potts, 1999; see also Hurst *et al.*, 2001 for recently discovered connections between individual recognition and major urinary proteins in house mice). However, the main reason for the numerous studies of mice probably relates to their availability as laboratory subjects and the fact that it is easy to obtain individuals with different levels of relatedness.

In an early landmark study of kin recognition, Wu *et al.* (1980) reported that pigtail macaque (*Macaca nemestrina*) infants discriminated unfamiliar siblings from unfamiliar non-siblings. Their results provided the first solid evidence of ‘true’ kin recognition in a mammalian species (Table 1; note, however, that the result has been difficult to replicate; Fredrickson & Sackett, 1984; Sackett & Fredrickson, 1986). Following this pioneering study, many researchers tested other mammals, often using cross-fostering designs, giving subjects four choices: familiar siblings/non-siblings and unfamiliar siblings/non-siblings. Some studies obtained evidence for true kin recognition (e.g. house mice, Kareem & Barnard, 1982, 1986; white-footed deermice, *Peromyscus leucopus*, Grau, 1982; Arctic and Belding’s ground squirrels, *Spermophilus parryi* and *S. beldingi*, Holmes & Sherman, 1982; golden-mantled ground squirrels, *S. lateralis*, Holmes, 1995; golden hamsters, *Mesocricetus auratus*, Heth, Todrank & Johnston, 1998; Mateo & Johnston, 2000), while others did not (e.g. thirteen-lined ground squirrel, *S. tridecemlineatus*, Holmes, 1984; prairie voles, *Microtus ochrogaster*, Gavish, Hofmann & Getz, 1984; Paz-y-Miño C. & Tang-Martínez, 1999*c*; deer mice, *Peromyscus maniculatus*, Dewsbury, 1982;

Table 1. Definitions for four important terms

Term	Definition
Individual discrimination	A process occurring when an organism responds differentially (behaviourally or physiologically) towards specific conspecifics on the basis of features or cues that make them distinctive (individually distinctive cues)
Kin discrimination	A process occurring when an organism responds differentially (behaviourally or physiologically) towards conspecifics on the basis of features or cues that correlate with genetic relatedness. When the cues used to identify individuals are shared exclusively by members of family (kin-specific cues), ‘true’ kin discrimination occurs
Individual recognition	An ability possessed by organisms that allows them to create a cognitive distinction among specific conspecifics by using features or cues that make them distinctive (individually distinctive cues). In order to display individual discriminations, an organism must be capable of individual recognition. However, individual recognition could still occur in the absence of obvious individual discrimination
Kin recognition	An ability possessed by organisms that allows them to create a cognitive distinction among conspecifics on the basis of features or cues that correlate with genetic relatedness. When the cues are shared exclusively by members of family (kin-specific cues), ‘true’ kin recognition occurs. In order to display kin discriminations, an organism must be capable of kin recognition. However, kin recognition could still occur in the absence of obvious kin discrimination

Note that these definitions were developed for clarifying our position with respect to these key terms. Alternative definitions and extended discussions of kin recognition and kin discrimination can be found elsewhere (e.g. Byers & Bekoff, 1986; Waldman, Frumhoff & Sherman, 1988; Grafen, 1990; Barnard, Hurst & Aldhous, 1991; Hepper, 1991*b*; Bekoff, 1992; Tang-Martinez, 2001; see also Stoddard, 1996 for definitions and discussion of discrimination and recognition). Discrimination is experimentally measurable while recognition is not. If organisms discriminate or recognise kin using individually distinctive cues (which may encompass kin-specific cues), kin discrimination/recognition may simply be the result of individual discrimination/recognition (but see Barnard, 1991; Barnard *et al.*, 1991; Hepper, 1991*b*). ‘True’ kin recognition, however, must involve the ability to recognise kin even in the absence of previous encounters with the target animals. Thus, individual recognition and true kin recognition are under the control of different mechanisms (see Table 2).

Colombian ground squirrels, *S. columbianus*, Hare & Murie, 1996; mandarin voles, *M. mandarinus*, Fadao, Tingzheng & Yajun, 2000).

Another landmark study, by Bateson (1982), showed that Japanese quail (*Coturnix coturnix*) could discriminate between familiar siblings, unfamiliar siblings, unfamiliar cousins and unfamiliar unrelated individuals, providing the first evidence for true kin recognition in birds. However, in contrast to the mammalian literature, researchers did not look for similar evidence in other avian species (with a few exceptions, e.g. zebra finches, *Taeniopygia guttata*, Burley, Minor & Strachan, 1990; peafowl, *Pavo cristatus*, Petrie, Krupa & Burke, 1999). An examination of the existing sibling recognition literature in birds showed that cross-fostering experiments like those used in mammalian studies were rarely employed; instead, researchers tend to compare responses to familiar siblings with those to unfamiliar (or less familiar) non-siblings (e.g. Beecher & Beecher, 1983; Nakagawa *et al.*, 2001).

Significant differences in research effort devoted to assessing sibling recognition and in the approach used to examine sibling discrimination across birds and mammals may result from three factors. The first relates to important differences in the biology of birds and mammals, especially in their recognition systems (e.g. types of recognition cues). The second relates to conceptual differences and biases developed by bird and mammal researchers investigating sibling recognition (we refer to these as ‘avian researchers’ and ‘mammalian researchers’ from now on – the two groups rarely overlap). The third relates to practical opportunities and constraints associated with sibling discrimination tests (e.g. availability of subjects).

In the first part of our review, to characterise avian sibling recognition studies, we identify major differences between the avian and mammalian literature by contrasting characteristics of subject species and experimental methodologies. We provide examples of how the three factors mentioned above (and their interactions) contribute to the differences. In the next part of our review, we consider the adaptive significance of sibling recognition, looking first at how the two groups of researchers approach recognition functions, and then at exciting new data presented by researchers investigating three different avian breeding systems in relation to recognition function. We also offer suggestions for future research on avian sibling recognition, based on important benchmarks established by mammalian researchers; further, we suggest that mammalian researchers can, in turn, benefit from studying the avian literature.

II. COMPARING AVIAN SIBLING RECOGNITION STUDIES WITH MAMMALIAN COUNTERPARTS

We conducted an extensive search for publications that included experimental discrimination tests to assess sibling recognition in birds (presenting more than two choice stimuli including siblings to a subject). Studies were organised chronologically and headings were used to identify primary characteristics of subject species and methodological details of each study (Tables 2 and 3). We also compiled a summary of selected mammalian sibling recognition studies (Table 4). Because of the many studies investigating mammalian

Table 2. Explanations of terms used in Tables 3 and 4 to categorise sibling recognition studies

Heading	Explanation
Breeding environment	Two broad types of breeding environments were recognised: mixing and non-mixing. In ‘mixing’ environments, the inter-mingling of dependent young (fed and/or protected by parents) from different broods can occur, whereas in ‘non-mixing’ environments inter-mingling does not normally occur
Status	Subjects were grouped into three categories: dependent young, juveniles, and adults (sexually capable). When the distinction between ‘juveniles’ and ‘adults’ was not made clear in the original source, the term ‘juveniles/adults’ was used. If a single sex was subjected to experimentation, gender is given in parentheses
Measure	Variables recorded in discrimination tests, described in simple terms
Choice and response relations	Choice stimuli presented in discrimination tests are listed along with the direction of recorded responses (<, >, = and ≠; ≠ means that responses were different but bi-directional depending on responses considered). The terms familiar, less familiar and unfamiliar were used to describe stimulus individuals. By ‘familiar’ we mean subjects and stimulus individuals had substantial social contact (in most cases they were reared together). By ‘less familiar’ we mean subjects and stimulus individuals were not reared together and had less social contact compared to familiar stimulus animals. We used ‘less familiar 1’ and ‘less familiar 2’ when experiments included different levels of familiarity in the ‘less familiar’ category (relative amounts of social contact: 1 > 2). By ‘unfamiliar’ we mean subjects and stimulus animals had no or very little social contact. The word ‘sibs’ indicates that stimulus individuals were genetically related to subjects, and ‘non-sibs’ indicates that stimulus individuals were not related to subjects
Test	We distinguished between experiments that assessed an animal’s ability to detect familiarity and (genetic) relatedness. To examine discrimination on the basis of familiarity, choice stimuli with different degrees of familiarity but with the same degree of relatedness should be presented. To demonstrate an ability to discriminate relatedness, choice stimuli with different degrees of relatedness but with the same degree of familiarity should be presented. The test for relatedness is the only acceptable test for ‘true’ kin discrimination (Table 1). If choice stimuli assessing familiarity and relatedness were confounded in the experiment, ‘neither’ was used to indicate that the factors could not be disentangled. Thus, four types of tests were identified: (1) familiarity (i.e. only familiarity was tested), (2) relatedness, (3) both, and (4) neither
Mechanism	Recognition mechanisms were identified for subject species, as inferred from experiments in the study. We used a classification scheme developed by Porter (1988), and recently reviewed by Tang-Martínez (2001). Only one general recognition mechanism is proposed (i.e. recognition by association or familiarity), but two classes are identified: ‘recognition by direct familiarisation’ (i.e. a previous association between the subject and stimulus individual(s) is necessary for later recognition) and ‘recognition by indirect familiarisation’ (i.e. an association between the subject and stimulus individual(s) is not necessary but association with other kin or ‘self’ is necessary). The former class is more widely known as recognition by association, and the latter as phenotype matching. The latter is synonymous with ‘true’ kin recognition (Table 1). To demonstrate the former class, familiarity tests are necessary, while to demonstrate the latter relatedness tests are necessary. Only by conducting both tests, can one determine whether subject species rely on direct, indirect, or both forms of familiarisation. Six categories were distinguished: (1) direct, (2) indirect, (3) both (direct and indirect familiarisation), (4) direct + (at least direct familiarisation was demonstrated but indirect familiarisation could not be excluded), (5) indirect + (at least indirect familiarisation was demonstrated but direct familiarisation could not be excluded) and (6)? (unidentified as no specific tests were conducted)

sibling recognition, we limited numbers for comparison to avian studies using the following technique. We searched for all papers between 1974 and 2001 with the key words ‘sibling recognition’ using ISI Web of Science[®]. Among the resulting papers ($N=86$), we chose only experimental studies with the phrase ‘sibling recognition’ in their titles and/or abstracts (note that many sibling recognition studies in the mammalian literature use the phrase ‘kin recognition’ instead, to refer to sibling recognition; see below for the explanation of why this is the case). We used the same approach to create a sub-sample of avian research. Comparisons between avian and mammalian studies were only made among papers meeting these criteria (‘comparison studies’). This way, we objectively obtained a sample of papers whose focus was ‘sibling recognition’ for comparison. Because we wanted to present a complete list of avian sibling recognition studies, Table 3 includes two sections: ‘comparison studies’ and ‘other available studies’. The list of

‘other available studies’ excluded papers that did not use biological siblings or appropriate choice stimuli (Gottlieb, 1968, 1971; Zajonc, Wilson & Rajecki, 1975; Bateson, 1980; Schimmel & Wasserman, 1991). In addition to the headings described in Table 2, three questions were addressed and organised in Table 5 to characterise further avian and mammalian studies of sibling recognition.

Because we restricted our mammalian sample by using the search term ‘sibling recognition’ (see above), the sample may have been biased in terms of the specific characteristics of subject species and methodological approaches used in the represented studies. To confirm that our sample provided an accurate representation of mammalian sibling recognition studies, we compared our sample to those generated by Blaustein *et al.* (1987, 1991) (they listed commonly cited mammalian sibling recognition studies, excluding primate studies). The trends we identified, with respect to mammalian literature, mirror those identified in these

independent reviews. Furthermore, although our mammalian sub-sample (Table 4) did not include articles which investigated sibling recognition without using the term in the title or abstract, we consider many of the most relevant ‘excluded’ research articles within the actual text of our review.

(1) Characteristics of subject species

Eleven comparison studies investigating eight bird species were identified (Table 3). With one exception, all were colonial where mixing of dependent young is common (7/8; 87.5%). Authors studying sibling recognition in colonial birds predict that dependent young will benefit from sibling recognition (Evans, 1970; Noseworthy & Lien, 1976; Beecher & Beecher, 1983; Palestis & Burger, 1999, 2001 *a, b*; Nakagawa *et al.*, 2001); for example, sibling recognition could facilitate a chick’s ability to locate its nest easily in dense colonies or to detect feeding opportunities. It appears that a large proportion of avian researchers have focused on colonial birds because they provide opportunities to test the prediction that sibling recognition evolves in crowded environments where mixing potential is high (Beecher & Beecher, 1983; Palestis & Burger, 1999, 2001 *b*; Nakagawa *et al.*, 2001).

Our sampling criteria also identified 18 comparison studies for mammals, investigating 12 species (Table 4). Almost half of these species (5/12; 41.7%) also breed where mixing occurs, but this trait may not have directed species selection. All but one of the species are rodents. Most evidence for litter mixing in rodents (e.g. communal nesting where nests may contain litters of several mothers; see Hayes, 2000) is recent (e.g. Norway rats, Mennella *et al.*, 1990; white-footed mice, Jacquot & Vessey, 1994) so it is unlikely that earlier authors used this criterion to select species. It appears mammalian researchers have paid little attention to the mixing issue in the context of sibling recognition (only one comparison study even mentions the issue; Ferkin & Rutka, 1990).

Moreover, many mammals used in sibling recognition studies are laboratory or domesticated animals. There are relatively few mammalian sibling recognition studies on non-rodents (humans, *Homo sapiens*, Porter & Moore, 1981; sheep, *Ovis aries*, Shillito Walsler, Hague & Yeomans, 1983; Nowak, 1990; Porter *et al.*, 1997; swine, *Sus domesticus*, Stookey & Gonyou, 1998; pigtailed macaques, Fredrickson & Sackett, 1984; Sackett & Fredrickson, 1986; rhesus monkeys, *Macaca mulatta*, Rendall, Rodman & Emond, 1996). It seems that the species selections of mammalian researchers have been directed by practical opportunities and constraints (e.g. availability and size of subjects). Practical considerations may also have directed avian studies (e.g. sibling discrimination studies on colonial seabirds may be easier to conduct than those on cooperative breeders), but presumably to a lesser extent.

(2) Subject status and the ontogeny of recognition

Nine of 11 comparison studies in birds (81.8%) employed dependent young as subjects, whereas only four of 18

mammalian studies did so (22.2%; Tables 3 and 4). The frequent use of dependent young in bird research may be due to at least two factors. First, the benefits of sibling recognition hypothesised by avian researchers are typically associated with the period of dependency (e.g. the ability to relocate nest sites); as a natural result, avian researchers selected dependent young rather than older birds to test their predictions. Second, flight makes it difficult to study sibling recognition in juvenile and adult birds. Only two of the avian comparison studies (18.2%) have determined if sibling discrimination extends beyond infancy (Røskaft & Espmark, 1984; Wanker *et al.*, 1998). For mammalian researchers, neither of these factors is likely to have directed the selection of subjects to the same extent.

Almost half of the comparison studies for birds (5/11; 45.5%; Table 5) examined age effects (i.e. how responses of subjects at different ages differ towards choice stimuli) on sibling discrimination. These studies focused on the timing of discrimination because avian researchers predicted that sibling discrimination should be in place before the mixing of broods. A similar proportion of mammalian comparison studies (6/18; 33.3%) also examined age effects (Table 5; for further examples, see Holmes & Sherman, 1982; Shillito Walsler *et al.*, 1983; Kareem & Barnard, 1986; Nowak, 1990; Holmes, 1997). However, half of these mammalian studies did not focus on identifying the onset of sibling discrimination; instead, they studied how subjects, who already displayed discrimination abilities, changed responses towards choice stimuli over time (Hepper, 1983, 1986 *c*; Watanabe, Inada & Borlongan, 1995). For example, at 12 days of age, house mouse pups prefer siblings to non-siblings but, at 20 days of age, pups prefer non-siblings to siblings, independent of familiarity (Hepper, 1983).

(3) Recognition measures and cues

Five bird (45.5%) and five mammal (28.7%) comparison studies pinpoint sensory cues used for discrimination (Table 5). All five avian examples involved playback of recorded calls of different individuals, showing discriminations could be made using acoustic cues alone. The remaining avian comparison studies presented subjects with live individuals so it was not possible to identify the specific cues subjects used (some authors speculated that subjects used vocal and/or visual cues; Radesäter, 1976; Palestis & Burger, 1999). Of the five mammalian studies where sensory cues were known, three presented isolated odours of different individuals (Ferkin & Rutka, 1990; Sun & Müller-Schwarze, 1997; Paz-y-Miño C. & Tang-Martinez, 1999 *a*; for examples of other mammalian studies presenting isolated odours, see Block, Volpe & Hayes, 1981; Heth *et al.*, 1998; Mateo & Johnston, 2000); the other two showed that subjects became unable to discriminate siblings from non-siblings after zinc-sulphate induced anosmia (Porter, Wyrick & Pankey, 1978; Holmes, 1984). The rats tested by Hepper (1983; Table 4) probably used olfactory cues as well (his experimental device prevented physical and visual contact, and white noise was used to dampen auditory cues).

Halpin (1991) reviewed studies of kin recognition that specified the sensory modality of recognition. The studies in

Table 3. Avian sibling recognition studies and their main characteristics (see Table 2 for definitions of terms)

Study ^a	Species	Breeding environment ^b	Experiment				
			Status	Measure	Choice and response relations	Test	Mechanism
Comparison studies							
B1 – Radesäter (1976) ^c	Canada geese, <i>Branta canadensis</i>	Non-mixing ¹	Dependent young	Proximity to individual	Familiar sibs > unfamiliar non-sibs	Neither	?
B2 – Beecher & Beecher (1983)	Bank swallows, <i>Riparia riparia</i>	Mixing ²	1 Dependent young	Response to playback	Familiar sibs > unfamiliar non-sibs	Neither	Direct +
B3 – Røskaft & Espmark (1984)	Rooks, <i>Corvus frugilegus</i>	Mixing	1 Juveniles	Response to playback	Familiar non-sibs > non-sibs Familiar nestmates (sibs/non-sibs) ^c > less familiar non-sibs	Familiarity Neither	?
			2 Adults	Affinity and aggression to individual	Familiar nestmates (sibs/non-sibs) ^c ≠ less familiar non-sibs	Neither	
B4 – Burger <i>et al.</i> (1988)	Common terns, <i>Sterna hirundo</i>	Mixing	Dependent young	Proximity to individual, response to playback	Familiar nestmates (non-sibs) ^f > less familiar non-sibs	Familiarity	Direct +
B5 – Pierotti <i>et al.</i> (1988) ^c	Western gulls, <i>Larus occidentalis</i>	Mixing ³	Dependent young	Proximity to individual	Familiar sibs/non-sibs > unfamiliar sibs/non-sibs	Both	Direct
B6 – Burger (1998) ^c	Herring gulls, <i>Larus argentatus</i>	Mixing	Dependent young	Proximity to individual	Familiar nestmates (non-sibs) ^f > less familiar non-sibs	Familiarity	Direct +
B7 – Wanker <i>et al.</i> (1998)	Spectacled parrotlets, <i>Forpus conspicillatus</i>	Mixing ⁴	1 Juveniles	Response to playback	Familiar sibs > less familiar non-sibs	Neither	?
			2 Adults	Response to playback	Mate > familiar sibs > less familiar non-sibs	Neither	
B8 – Palestis & Burger (1999) ^c	Common terns, <i>Sterna hirundo</i>	Mixing	Dependent young	Proximity to individual with/without visual cues	Familiar nestmates (non-sibs) ^f > less familiar non-sibs	Familiarity	Direct +
B9 – Nakagawa <i>et al.</i> (2001)	Little blue penguins, <i>Eudyptula minor</i>	Mixing	Dependent young	Response to playback	Familiar sibs > less familiar non-sibs > unfamiliar non-sibs	Familiarity	Direct +
B10 – Palestis & Burger (2001 <i>a</i>)	Common terns, <i>Sterna hirundo</i>	Mixing	Dependent young	Proximity to individual	Familiar nestmates (sibs/non-sibs) ^c > less familiar neighbours (sibs/non-sibs) ^c	Neither	?
B11 – Palestis & Burger (2001 <i>b</i>)	Common terns, <i>Sterna hirundo</i>	Mixing	Dependent young	Proximity to own nest with different stimuli	Familiar sibs > empty nest = less familiar non-sibs	Neither	?
Other available studies							
Evans (1970) ^c	Ring-billed gulls, <i>Larus dellawarensis</i>	Mixing	1 Dependent young	Proximity to individual	Familiar sibs > unfamiliar non-sibs	Neither	Direct +
			2 Dependent young	Proximity to individual	Familiar non-sibs > unfamiliar non-sibs	Familiarity	

Noseworthy & Lien (1976) ^c	Herring gulls, <i>Larus argentatus</i>	Mixing	1 Dependent young 2 Dependent young	Proximity to individual Proximity to own nest with different stimuli	Familiar sibs > unfamiliar non-sibs Familiar sibs > empty nest > unfamiliar non-sibs	Neither Neither	?
Slater & Clements (1981) ^c	Zebra finches, <i>Taeniopygia guttata</i>	Mixing ⁶	Adults	Frequency of pairing with opposite sex	Familiar sibs > unfamiliar non-sibs	Neither	?
Bateson (1982)	Japanese quail, <i>Coturnix coturnix</i>	Non-mixing ⁵	Adults	Proximity to individual	Unfamiliar 1st cousins > unfamiliar 3rd cousins > unfamiliar sibs > familiar sibs, unfamiliar non-sibs	Both	Both
Schubert, Ratchiff & Boag (1989)	Zebra finches, <i>Taeniopygia guttata</i>	Mixing ⁶	Adults	Frequency of pairing with opposite sex	Familiar sibs = unfamiliar non-sibs = cousins	Neither	N.A. ^g
Waldman & Bateson (1989)	Japanese quail, <i>Coturnix coturnix</i>	Non-mixing ⁵	Dependent young	Proximity to individual	Familiar sibs > familiar non-sibs	Relatedness	Indirect +
Burley <i>et al.</i> (1990) ^c	Zebra finches, <i>Taeniopygia guttata</i>	Mixing ⁶	1 Adults (male) 2 Adults (female)	Proximity to individual of same sex Proximity to individual of opposite sex	Familiar/unfamiliar sibs > familiar/unfamiliar non-sibs Familiar/unfamiliar cousins > familiar/unfamiliar non-sibs (familiar sibs < unfamiliar non-sibs)	Both Both	Indirect
Fetherston & Burley (1990)	Zebra finches, <i>Taeniopygia guttata</i>	Mixing ⁶	Adults	Frequency of pairing with opposite sex	Familiar sibs = unfamiliar non-sibs	Neither	N.A. ^g
Petrie <i>et al.</i> (1999)	Peafowl, <i>Pavo cristatus</i>	Non-mixing ⁷	Adults (male)	Proximity to individual of same sex	Familiar/unfamiliar sibs > familiar/unfamiliar non-sibs	Both	Indirect
Hatchwell <i>et al.</i> (2001 <i>b</i>)	Long-tailed tits ^d , <i>Aegithalos caudatus</i>	Non-mixing	1 Adults (males) 2 Adults	Response to playback ‘Helping’ breeding individuals	Familiar sibs ≠ unfamiliar non-sibs Familiar sibs/non-sibs > unfamiliar sibs/non-sibs	Neither Both	Direct

^a Studies with B(number) were selected for comparison and are listed in chronological order.

^b Extra sources were consulted where necessary: ¹Cramp (1977); ²Beecher, Beecher & Lumpkin (1981); ³Pierroti (1981); ⁴Wanker, Bernate & Franck (1996); ⁵Cramp (1980); ⁶Zann (1996); ⁷Johnsgard (1999).

^c Only the most relevant experiments are shown from these sources (studies included more experiments than presented).

^d Cooperative breeding is reported (see Hatchwell *et al.*, 2001 *a*).

^e Nestmates (and neighbours) consisted of related sibs and unrelated non-sibs, but no distinction was made between them in the data analysis.

^f Nestmates consisted of unrelated non-siblings so that no biological siblings were used in the experiment.

^g N.A. = not applicable because no discrimination occurred between choice stimuli.

Table 4. Mammalian sibling recognition studies and their main characteristics (see Table 2 for definitions of terms)

Study ^a	Species	Breeding environment ^b	Experiment				
			Status	Measure	Choice and response relations	Test	Mechanism
M1 – Porter <i>et al.</i> (1978) ^c	Spiny mice ^d , <i>Acomys cahirinus</i>	Mixing ¹	Juveniles	Frequency of pairing	Familiar sibs > unfamiliar non-sibs	Neither	?
M2 – Porter & Wyrick (1979) ^{c, e}	Spiny mice ^d , <i>Acomys cahirinus</i>	Mixing ¹	Dependent young	Frequency of pairing	Familiar sibs > unfamiliar non-sibs	Neither	?
M3 – Porter <i>et al.</i> (1981)	Spiny mice ^d , <i>Acomys cahirinus</i>	Mixing ¹	Juveniles	Frequency of pairing	Familiar non-sibs > unfamiliar sibs/non-sibs	Both	Direct
M4 – Davis (1982)	Richardson's ground squirrel, <i>Spermophilus richardsonii</i>	Non-mixing ²	Juveniles	Frequency of social interactions	Familiar sibs ≠ unfamiliar non-sibs, unfamiliar sibs ≠ unfamiliar non-sibs, familiar sibs ≠ unfamiliar sibs, familiar non-sibs ≠ unfamiliar non-sibs, familiar sibs ≠ familiar non-sibs	Both	Both
M5 – Hepper (1983) ^c	Norway rats ^d , <i>Rattus norvegicus</i>	Mixing ³	Dependent young	Proximity to individual	Familiar non-sibs ≠ unfamiliar non-sibs, familiar sibs ≠ unfamiliar sibs, unfamiliar sibs ≠ unfamiliar non-sibs	Both	Both
M6 – Holmes (1984)	Thirteen-lined ground squirrel, <i>Spermophilus tridecemlineatus</i>	Non-mixing ²	Juveniles	Frequency of social interactions	Familiar sibs/non-sibs < unfamiliar sibs/non-sibs	Both	Direct
M7 – Gavish <i>et al.</i> (1984) ^c	Prairie voles ^d , <i>Microtus ochrogaster</i>	Non-mixing ⁴	1 Juveniles/adults	Frequency of successful mating	Familiar sibs/non-sibs < unfamiliar sibs/non-sibs	Both	Direct
			2 Juveniles/adults	Frequency of successful mating	Familiar sibs < less familiar 1 sibs < less familiar 2 sibs	Familiarity	
M8 – Hepper (1986 <i>b</i>)	Domestic dogs, <i>Canis familiaris</i>	Non-mixing ⁵	Dependent young	Proximity to individual	Familiar sibs < unfamiliar non-sibs	Neither	?
M9 – Hepper (1986 <i>c</i>)	Norway rats ^d , <i>Rattus norvegicus</i>	Mixing ³	1 Dependent young	Proximity to individual	Unfamiliar sibs ≠ unfamiliar non-sibs	Relatedness	Indirect +
			2 Juveniles	Proximity to individual	Unfamiliar sibs < unfamiliar non-sibs	Relatedness	
M10 – Halpin & Hoffman (1987) ^c	White-footed mice ^d , <i>Peromyscus leucopus</i>	Mixing ⁶	Adults	Proximity to individual	Familiar sibs > unfamiliar sibs, familiar sibs = familiar non-sibs, unfamiliar sibs = unfamiliar non-sibs, unfamiliar sibs < familiar non-sibs	Both	Direct
M11 – Fuller & Blaustein (1990)	Townsend's chipmunk, <i>Tamias townsendii</i>	Non-mixing	Juveniles	Frequency of social interactions	Familiar sibs ≠ familiar non-sibs ≠ unfamiliar sibs ≠ unfamiliar non-sibs	Both	Both
M12 – Ferkin & Rutka (1990) ^c	Meadow voles ^d , <i>Microtus pennsylvanicus</i>	Mixing ⁷	Adults	Proximity to individual odour	Familiar sibs > unfamiliar sibs, familiar sibs = familiar non-sibs, unfamiliar sibs = unfamiliar non-sibs, unfamiliar sibs < familiar non-sibs	Both	Direct
					Familiar sibs > unfamiliar non-sibs, unfamiliar sibs < familiar non-sibs	Both	
M13 – D'Amato (1994)	House mice ^d , <i>Mus domesticus</i>	Mixing ⁵	Adults (male)	Decrease in pain sensitivity	Familiar/unfamiliar sibs > familiar/unfamiliar non-sibs	Both	Indirect
M14 – Watanabe <i>et al.</i> (1995) ^c	Golden hamsters, <i>Mesocricetus auratus</i>	Non-mixing	Juveniles (male)	Proximity to individual	Familiar sibs < less familiar 1 non-sibs < less familiar 2 sibs < unfamiliar non-sibs	Familiarity	Direct +

Study	Species	Non-mixing	Adults	Frequency of agonism to individual odour	Unfamiliar sibs < unfamiliar non-sibs, unfamiliar sibs of mate < unfamiliar non-relatives	Relatedness	Indirect +
M15 – Sun & Müller-Schwarze (1997)	Beavers ^d , <i>Castor canadensis</i>	Non-mixing	Adults	Frequency of individual odour	Unfamiliar sibs < unfamiliar non-sibs, unfamiliar sibs of mate < unfamiliar non-relatives	Relatedness	Indirect +
M16 – Paz-y-Miño C. & Tang-Martinez (1999a) ^c	Prairie voles ^d , <i>Microtus ochrogaster</i>	Non-mixing ^d	Juveniles/adults	Frequency of social interactions with individual or odour	Familiar sibs ≠ less familiar sibs = unfamiliar non-sibs	Familiarity	Direct +
M17 – Paz-y-Miño C. & Tang-Martinez (1999b) ^c	Prairie voles ^d , <i>Microtus ochrogaster</i>	Non-mixing ^d	1 Juveniles/adults 2 Juveniles/adults	Frequency of social interactions	Familiar sibs = less familiar 1 sibs ≠ less familiar 2 sibs Familiar sibs ≠ unfamiliar non-sibs, less familiar sibs = unfamiliar non-sibs	Familiarity Neither	Direct +
M18 – Paz-y-Miño C. & Tang-Martinez (1999c)	Prairie voles ^d , <i>Microtus ochrogaster</i>	Non-mixing ^d	Juveniles/adults	Frequency of social interactions	Familiar sibs/non-sibs ≠ unfamiliar sibs/non-sibs	Both	Direct

^a Studies with M(number) were selected for comparison and are listed in chronological order.

^b Extra sources were consulted where necessary: ¹Porter & Doane (1978); ²Murie & Michener (1984); ³Mennella *et al.* (1990); ⁴Getz, Gutermauth & Benson (1992); ⁵Nowak (1999); ⁶Jacquot & Vessey (1994); ⁷McShea & Madison (1984).

^c Only most relevant experiments are shown from these sources (studies included more experiments than presented).

^d Cooperative breeding is possible (see Hayes, 2000).

^e These studies also or mainly investigated the effect of isolation of subjects from stimulus individuals.

her review showed that birds tended to use vocal cues for kin discrimination while mammals used olfactory cues. However, animals may often use a combination of sensory cues for recognition (Halpin, 1991). Among three major types of recognition cues (visual, auditory and olfactory), visual cues are the most difficult to manipulate experimentally, primarily because human display devices (e.g. projectors, video monitors) rarely present realistic images to other animals (with the possible exception of animals, like primates, that have human-like visual apparatus; Fleishman *et al.*, 1998; D’Eath, 1998; Oliveira *et al.*, 2000). It is, therefore, not surprising that visual cues have not been investigated as often as other cues – however, this does not mean they are less important.

Several studies suggest that visual cues may be more important than vocal cues for at least some birds (e.g. Evans, 1970; Miller & Emlen, 1975; Bateson, 1982; Burley *et al.*, 1990; Palestis & Burger, 1999; Petrie *et al.*, 1999). For example, surgically muted ring-billed gull chicks were immediately accepted by their parents but those with an altered appearance were not (Miller & Emlen, 1975). For the three bird species (i.e. Japanese quails, zebra finches, peafowl) where ‘true’ kin discrimination has been demonstrated (Table 3), visual cues may be used to identify phenotypically similar individuals as kin (Bateson, 1982, 1983; Burley & Bartels, 1990; Burley *et al.*, 1990; Sherman, 1999). Burley & Bartels (1990) demonstrated that morphological similarities and genetic relatedness correlated in male zebra finches. A few studies also suggest that birds recognise individuals by plumage (e.g. white-throated sparrows, *Zonotrichia albicollis*, Watt, 1986; turnstones, *Arenaria interpres*, Whitfield, 1986).

Although avian researchers have barely begun to investigate the role visual cues play in the recognition process, they often conclude that birds mainly use vocal cues for kin recognition. This conceptual bias has had a great impact on the course of sibling recognition studies in birds (see below).

(4) Recognition mechanisms

Four potential kin recognition mechanisms dominate the existing literature: (1) spatially based recognition, (2) recognition by association or familiarity, (3) phenotype matching, and (4) recognition alleles (Holmes & Sherman, 1983; Sherman & Holmes, 1985; Hepper, 1986a; Waldman, 1987). Because of major conceptual problems with spatially based recognition and recognition alleles (see Blaustein, 1983; Waldman, 1987; Halpin, 1991; Tang-Martinez, 2001), researchers have favoured and focused on the other two mechanisms. Since the early 1980s, many researchers have employed cross-fostering designs to investigate whether animals use association, phenotype matching or both to discriminate kin (Blaustein *et al.*, 1987; Tang-Martinez, 2001). We believe that this popular dichotomisation of recognition mechanisms and the use of the terms ‘recognition by association’ and ‘phenotype matching’ are misleading because both mechanisms involve associative learning and matching of learned phenotypes (Waldman, 1987; Porter,

Table 5. Three questions used to characterise further the comparison studies

Question	Avian studies (yes) ^a	Yes/all (%)	Mammalian studies (yes) ^b	Yes/all (%)
Was an age (or ontogeny) effect on sibling discrimination investigated?	B1, B2, B4, B6, B10	5/11 (45.5)	M2, M3, M5, M7, M9, M14	6/18 (33.3)
Were specific recognition cues used by subjects identifiable?	B2, B3, B4, B7, B9	5/11 (45.5)	M1, M6, M12, M15, M16	5/18 (27.8)
Were sex effects controlled for in experiments?	No	0/11 (0)	M1, M2, M3, M4, M6, M7, M10, M11, M12, M13, M14, M15, M16, M17, M18	15/18 (83.3)

^a See Table 3 for references.

^b See Table 4 for references.

1988; Tang-Martinez, 2001). Therefore, we adopt Porter's (1988) scheme, where the only recognition mechanism is by association (familiarisation) with two classes: 'recognition by direct familiarisation' and 'recognition by indirect familiarisation' (see Table 2 for definitions; see also Tang-Martinez, 2001).

(a) Discrimination tests and mechanism classes

Among 11 avian comparison studies, only one examined both familiarity and relatedness (9.1%), while five examined only familiarity (45.5%) and five tested neither independently (45.5%; Tables 2 and 3). Among 18 mammalian studies, 10 studies examine both familiarity and relatedness (55.6%), three only familiarity (11.1%), two only relatedness (11.1%), and three examined neither independently (16.7%; Table 4; it is notable that two of the three studies which only examined familiarity investigated prairie voles that had already been known to rely only on direct familiarisation from other studies; see Gavish *et al.*, 1984; Paz-y-Miño C. & Tang Martinez, 1999*a-c*). None of the avian comparison studies identified recognition by indirect familiarisation (however, only one investigated the possibility), while six mammalian studies (33.3%; investigating five species) provide evidence for indirect familiarisation (Tables 3 and 4). The lack of studies examining recognition by indirect familiarisation in birds does not necessarily mean researchers were uninterested in mechanisms of sibling discrimination. The rare use of both tests in avian comparison studies probably results from a conceptual bias – birds are widely assumed to recognise kin by direct familiarisation alone. The role relatedness plays in avian sibling recognition is rarely contemplated. This is reflected by the fact that three of the avian comparison studies used a collection of non-siblings as a 'sibling group' (Burger *et al.*, 1988; Burger, 1998; Palestis & Burger, 1999), while two (Røskaft & Espmark, 1984; Palestis & Burger, 2001*a*) used a mixture of related and unrelated individuals, without properly analysing the effect of relatedness [although Røskaft & Espmark (1984) mention no differences in amicable or aggressive behaviour occurring between related and unrelated nest-mates]. However, avian researchers have often had good reasons for designing their studies this way (see Beecher, 1988; Pierotti *et al.*, 1988; Palestis & Burger, 1999). The

avian perspective may also be associated with the belief that kin discrimination is usually accomplished with learned vocal cues.

Vocal cues may not be valuable for recognition by indirect familiarisation because learned features may not correlate with relatedness. McGregor (1989) argued that kin recognition by song in songbirds would be rare because males usually learn song from neighbours and females do not sing (see Payne, Payne & Doehlert, 1987 for evidence supporting McGregor's logic; but see McGregor & Krebs, 1982 for an example where female great tits, *Parus major*, use song to predict the relatedness of their mates).

In songbirds, patterns of acquisition for 'calls' are less investigated than those for song (Kroodsma & Miller, 1982; Catchpole & Slater, 1995); calls may prove useful in predicting kinship (P. J. B. Slater cited in McGregor, 1989). Price (1998, 1999) showed that cooperatively breeding striped-backed wrens (*Campylorhynchus nuchalis*) have kin-specific calls [the WAY call ('Where Are You?')], which are fundamentally different from the group-specific vocalisations reported in other species (Mundinger, 1970; Mammen & Nowicki, 1981; Trainer, 1989; Farabaugh & Dooling, 1996). A given wren could discriminate WAY calls of unfamiliar relatives (which share similar WAY calls; Price, 1998) from those of unfamiliar unrelated individuals (although wrens could not use WAY calls to identify specific individuals; Price, 1999). Price (1998) also showed WAY calls were learned, not inherited. Thus, certain learned vocal cues like kin-specific WAY calls may help predict relatedness in stable avian societies where intra- and inter-species brood parasites are rare. However, Price provides the only evidence that kin-specific calls can be used to discriminate kin by indirect familiarisation.

A very strong heritable component can be found in vocalisations like begging calls in species where brood mixing occurs; for example, sibling sets of colonial cliff swallows (*Hirundo pyrrhonota*) have very similar begging calls but the calls of non-siblings, experimentally reared together, remain distinct (Medvin, Stoddard & Beecher, 1992). However, even heritable kin-specific vocalisations may be confounded by subsequent modification through learning, especially in comparison to the heritable family-specific olfactory cues often found in mammals (see Boyse *et al.*, 1991; Brown & Eklund, 1994).

(b) Isolation tests

Four of 18 mammalian comparison studies investigated the effects of isolation on sibling recognition (22.2%; Table 4). Sibling recognition may be weakened and eventually lost after long separations in species relying on direct familiarisation (Holmes, 1988; Ims, 1989; Kawata, 1990; Paz-y-Miño C. & Tang-Martinez, 1999*a, b*). Paz-y-Miño C. & Tang-Martinez (1999*a–c*), who demonstrated that direct familiarisation was necessary for sibling discrimination in prairie voles, manipulated periods of isolation from siblings and the frequencies of exposures to siblings, to investigate how social memories of siblings were maintained (see also Paz-y-Miño C. *et al.*, 2002). They found that, after 20 days of isolation, sibling discrimination broke down (Paz-y-Miño C. & Tang-Martinez, 1999*b*), but that regular exposure to sibling odour alone could maintain discriminations (Paz-y-Miño C. & Tang-Martinez, 1999*a*). Although many avian researchers have assumed familiarity is more important than relatedness for sibling recognition, no one has investigated the effects of isolation on sibling discrimination. By using isolation tests, some mammalian researchers have advanced well beyond avian researchers in understanding the maintenance of sibling recognition when animals rely on direct familiarisation.

(5) Sex effects

None of the 11 avian comparison studies considered the sex of subjects when designing experiments (Table 5), while most mammalian counterparts did so (15/18, 83.3%; Table 5). This striking difference may be due to the presence or absence of obvious variation in morphological features between the sexes (e.g. the obvious variation in sexual organs of mammals but not of birds). Avian researchers may find it harder to identify the gender of birds they study, especially young.

Mammalian literature suggests sex differences may be very important for sibling recognition. Sister discriminations in Belding’s ground squirrels (*S. beldingi*) are a case in point. Unfamiliar female–female pairs of biological siblings were less aggressive towards one another than non-biological siblings; this was not the case for male–male or male–female pairs (Holmes & Sherman, 1982; but see Mateo, 2002). In *Spermophilus*, males disperse while females are philopatric; therefore, nepotism occurs primarily among females (for *S. beldingi*: Sherman, 1977, 1981 and Holekamp, 1984; for other *Spermophilus* species: Murie & Michener, 1984 and references therein; but also see Davis, 1984 for *S. richardsonii*). Where such sex-biased patterns of dispersal and nepotism occur, selection pressure for female/female discrimination may be greater than that for male/male or male/female discrimination.

For chimpanzees, Parr & de Waal (1999) suggest that sex-biased dispersal patterns affect phenotypic similarities between relatives. Chimpanzees perceive similarities in the faces of unfamiliar mothers and sons but not mothers and daughters; facial similarities in sons, or males, may be more noticeable. Selection associated with male philopatry may promote facial similarities between males (and their mothers;

Parr & de Waal, 1999). As in chimpanzees, male birds are generally the philopatric sex (Greenwood, 1980; Greenwood & Harvey, 1982). We predict greater phenotypic divergence in recognition cues between males in comparison to females, and also that sibling recognition abilities of philopatric males will be more advanced than that of dispersing females.

As discussed earlier, many avian researchers investigating sibling recognition have concentrated on the period of dependency. Chicks may be able to discriminate the sex of siblings and may act differently towards each sex depending on ecological circumstances. Siblicide has been reported in many species of birds (reviewed in Mock, Drummond & Stinson, 1990; Drummond, 2001). The sex composition of avian broods may influence levels of agonism within them, although there are no reported cases of variation in siblicide associated with the sex of chicks (Drummond, 2001). In spotted hyenas, *Crocuta crocuta*, siblicidal attacks occur primarily when siblings are of the same sex (Frank, Glickman & Licht, 1991; Frank, 1997). This suggests that infants may discriminate the sex of siblings and act accordingly. Investigations on discrimination of siblings’ sex at early stages of life may prove interesting both in mammals and birds.

Controlling sex effects in avian recognition work may be valuable but has been difficult in practical terms. The recent development of simple DNA-based methods for sexing in birds (Ellegren, 1996; Ellegren & Sheldon, 1997; see also Dawson *et al.*, 2001) will overcome many difficulties. Sex differences in life history and phenotypic traits must have had significant effects on kin recognition abilities and cues, not just in some mammals, but also in birds.

(6) Other available avian studies

The ‘non-comparison’ studies of birds (Table 3) appear to show profiles different from the 11 comparison studies. This is mainly due to our criterion for selecting comparison studies: the title and/or abstract had to include the phrase ‘sibling recognition’. This criterion excluded studies whose focus was not on ‘recognition’ of ‘siblings’, although the studies included discrimination tests that assessed sibling recognition. Five of the 10 studies investigated kin preferences of potential mates (employing adults as subjects; Table 3). Two recent studies (Petrie *et al.*, 1999; Hatchwell *et al.*, 2001*b*), employing cross-fostering designs, preferred the word ‘kin’ to ‘sibling’, which is typical of mammalian studies (see references in Blaustein *et al.*, 1987; for recent examples, Heth *et al.*, 1998; Todrank, Heth & Johnston, 1998; Mateo & Johnston, 2000). The preferred use of ‘kin’ to ‘sibling’ in mammalian literature probably occurs because kin recognition studies concentrate on the ability of siblings to recognise one another (see Hepper, 1999). The main difference between avian comparison and non-comparison studies is that half of the non-comparison studies (5/10) included relatedness tests (four also tested for familiarity; Table 3), while only one (1/11) comparison study did so. Nevertheless, when all the avian sibling recognition studies are combined (Table 3), only six (6/21; 28.6%) tested relatedness, while 13 mammalian comparison studies did so (13/18; 72.2%; Table 4). There are, of course, more

mammalian studies examining relatedness outside the 18 comparison studies (see Table 3 in Blaustein *et al.*, 1987; for recent examples, Holmes, 1995, 1997; Hare & Murie, 1996; Heth *et al.*, 1998; Todrank *et al.*, 1998; Mateo & Johnston, 2000). Two-thirds of avian sibling recognition studies investigated sibling recognition in the context of individual recognition (Table 1), probably assuming that sibling discrimination occurred as a result of direct familiarisation; by contrast, many mammalian studies investigated sibling recognition from the perspective of kin recognition (Table 1), testing relatedness (and often familiarity as well) to look for evidence of true kin recognition (see Beecher, 1988; Halpin, 1991; Tables 3 and 4). The scarcity of sibling recognition studies in birds may be due to a lack of attention to the possibility of indirect familiarisation.

III. FUNCTIONAL SIGNIFICANCE OF SIBLING RECOGNITION

The two major adaptive explanations for sibling recognition are essentially the same as those proposed for kin recognition: (1) facilitating nepotism towards related animals (Hamilton, 1964*b*, 1987), and (2) avoiding extreme inbreeding or outbreeding [creating opportunities for 'optimal inbreeding' (Shields, 1982, 1983) or 'optimal outbreeding' (Bateson, 1980, 1983); see also Blouin & Blouin (1988); Pusey & Wolf (1996)]. Both functions enhance the inclusive fitness (directly and/or indirectly) of those capable of discriminations (Fletcher, 1987; Wilson, 1987; Barnard, 1989). The mechanism (direct, indirect or both forms of familiarisation; see Table 2) by which individuals benefit from recognition will be highly dependent on life history (e.g. sociality, patterns of dispersal and philopatry). Many mammalian researchers and a few avian researchers have used activities which can be interpreted as expressions of assumed benefits, to identify recognition mechanisms (Tables 3 and 4; also see Blaustein *et al.*, 1987). For example, researchers commonly measure rates of aggressive and/or amicable behaviour, when nepotism is viewed as driving the evolution of sibling recognition (e.g. Holmes & Sherman, 1982; Davis, 1982; Fuller & Blaustein, 1990; Heth *et al.*, 1998). Similarly, time spent with or, in proximity to, particular individuals has been interpreted as an expression of inbreeding avoidance (e.g. Bateson, 1982; Barnard & Fitzsimons, 1988; Burley *et al.*, 1990; Fadao *et al.*, 2000). Researchers using this approach have been very successful at identifying recognition mechanism(s) used by particular species. Most, however, have not measured the assumed benefits of sibling discrimination, especially in the wild. This may reflect a lack of information on the natural history of studied species because researchers rely heavily on laboratory experiments that remove animals from natural contexts (see Blaustein *et al.*, 1991; Gamboa, Reeve & Holmes, 1991; Sherman, Reeve & Pfennig, 1997). For example, two recent studies of sibling discrimination in golden hamsters (Heth *et al.*, 1998; Mateo & Johnston, 2000) discuss results in the context of nepotism and optimal outbreeding. However, little is known

about the social organisation of golden hamsters in the wild (but see Murphy, 1977; Huck, Quinn & Lisk, 1985; Huck *et al.*, 1986), so functional interpretations are speculative, as Heth *et al.* (1998) admit (see also Hauber & Sherman, 2000).

(1) Different approaches by avian and mammalian researchers

Despite numerous mammalian studies examining sibling recognition, few investigate or identify the value of observed discrimination abilities in the wild (see Table I in Blaustein *et al.*, 1991; see also Hare, 1992, 1994, 1998), although as we indicate above, mammalian researchers often interpret their results in the broad framework of nepotism and/or optimal outbreeding. A number of colonial bird researchers exploring sibling discrimination in dependent young have attempted to pose more specific adaptive explanations with potentially measurable benefits (Evans, 1970; Noseworthy & Lien, 1976; Beecher & Beecher, 1983; Palestis & Burger, 1999, 2001*a, b*; Nakagawa *et al.*, 2001).

For example, Nakagawa *et al.* (2001) list four possible functions of sibling recognition for chicks of colonial birds: (1) facilitating a chick's ability to locate its nest in dense colonies where locational cues cannot be relied upon, (2) detecting feeding opportunities even when wandering from the nest (e.g. by recognising begging calls siblings produce on the return of parents), (3) avoiding nest sites of unrelated adults or non-siblings and thus the possibility of aggressive reactions, and (4) preventing unrelated siblings from entering the nest and competing for food. Noseworthy & Lien (1976) and Palestis & Burger (2001*b*) provided clear experimental support for the first adaptive explanation by placing different target animals (e.g. siblings and non-siblings) at subject chicks' nests (see Table 3).

Overall, our review reveals that mammalian researchers have tended to foster a focused mechanistic approach, examining recognition within the very broad functional context of nepotism and optimal breeding (*cf.* Schwagmeyer, 1980; Holmes & Sherman, 1982; Hare, 1992, 1994, 1998). On the other hand, avian researchers (like those mentioned above) have focused less on mechanisms and more on the development of specific and testable hypotheses to explain the occurrence of sibling recognition in nature (although, overall, studies investigating the adaptive value of sibling recognition are still rare; Palestis & Burger, 2001*b*).

(2) Recognition functions in different breeding systems

Only an extensive knowledge of behavioural ecology will enable identification of specific functions of sibling discrimination associated with different stages of life history. Several ecological situations where kin recognition is expected to evolve (or has evolved) have been discussed elsewhere (e.g. Sherman & Holmes, 1985; Waldman, 1988; Porter & Blaustein, 1989; Hauber & Sherman, 2000; Perrin & Lehmann, 2001). Here, to highlight a few exciting recent discoveries, we focus attention on three breeding systems in birds and examine possible functions of sibling recognition in each context.

(a) *Colonial breeding birds*

Colonial breeders (especially seabirds) have been a main target of avian sibling recognition studies, with researchers concentrating on the period of dependency. However, no one has investigated whether seabirds could recognise siblings or other relatives as adults. Bukaciński, Bukacińska & Lubjuhn (2000) suggest that some adult colonial seabirds may be able to discriminate close relatives. They used DNA fingerprinting to detect close kin clusters of neighbours (particularly males) in common gulls, *Larus canus* (see also Brown, 1998). Kin groups may simply occur through strong natal philopatry and/or nest site tenacity, but it is possible that aggregations form through recognition of close kin. They also found adult common gulls were more likely to adopt closely related chicks than less-related chicks. The adoption of closely related chicks, which may enhance indirect fitness, could be an important function of kin recognition for common gulls whose adoption rates are high (Bukaciński *et al.*, 2000). However, it is unclear whether adoption of related chicks occurs as the result of kin recognition, a simple consequence of breeding near relatives (which may, in effect, be adaptive; see Queller, 1992, 1994) or by other means. Kin aggregation and kin adoption in common gulls may well involve sibling recognition, which may therefore extend into adulthood for this species.

(b) *Lekking birds*

Leks (aggregations of displaying males that females visit primarily to be fertilised; Höglund & Alatalo, 1995) are not uncommon in birds (Johnsgard, 1994; Höglund & Alatalo, 1995). The multiple matings associated with leks generate many unfamiliar relatives that will not be reared together. Petrie *et al.* (1999) suggest lekking individuals may recognise close kin without prior encounters. They showed that peacocks, *Pavo cristatus*, discriminate related (full- or half-) siblings from non-siblings by indirect familiarisation. In lek breeding systems, only a few preferred males may gain most copulations (Höglund & Alatalo, 1995). However, Petrie *et al.* (1999) show siblings may actively gather to create leks of related individuals and, thus, even non-preferred members can increase their fitness indirectly (see Kokko & Lindström, 1996; but, for alternative interpretations of kin structuring in leks, see Sæther, 2002). Mating opportunities are greater in large leks (Alatalo *et al.*, 1992; Höglund & Alatalo, 1995; Widemo & Owens, 1995). Therefore, cooperating with close kin to increase lek size may represent an important function of sibling recognition in birds like peafowl. Other bird species have also been reported to form leks with close relatives (black grouse, *Tetrao tetrix*, Höglund *et al.*, 1999; white-bearded manakins, *Manacus manacus*, Shorey *et al.*, 2000; see also Sherman, 1999).

(c) *Cooperatively breeding birds*

The social structure and behaviour of many cooperatively breeding birds have been extensively investigated (Brown, 1987; Stacey & Koenig, 1990) and the function of kin recognition seems straightforward – helping relatives allows

individuals to increase their inclusive fitness (*cf.* Clutton-Brock, 2002; Griffin & West, 2002; West *et al.*, 2002). However, as a recent review by Komdeur & Hatchwell (1999) highlighted, few experimental studies of kin recognition exist for cooperatively breeding birds (for recent exceptions see Hatchwell *et al.*, 2001*b*; Russell & Hatchwell, 2001). There are two major types of helping behaviour: (1) helping parents rear siblings, and (2) helping siblings rear nieces and nephews (for both, helping effort should vary according to relatedness). Seychelles warblers (*Acrocephalus sechellensis*) help parents rear siblings and, as Komdeur (1994) observed, are more likely to feed full-siblings (produced by their parents) than half-siblings (produced by a parent and an unrelated step-parent); similar observations have been reported for white-fronted bee-eaters (*Merops bullockoides*; Emlen & Wrege, 1988) and Florida scrub jays (*Aphelocoma coerulescens*; Mumme, 1992). These discriminations probably occur through parent recognition (i.e. helpers vary feeding rates on the basis of whether a step-parent is involved). For species like long-tailed tits, where helpers usually assist siblings to rear nieces and nephews (Hatchwell *et al.*, 2001*a*), the identification of siblings may be the primary functional explanation for the recognition system. Hatchwell *et al.* (2001*b*) recently investigated the mechanism of sibling recognition in long-tailed tits, using a cross-fostering design. Helping behaviour was directed more to nestmates (reared together) regardless of relatedness; therefore, direct familiarisation at the nest is probably necessary for sibling discrimination (Hatchwell *et al.*, 2001*b*). Komdeur & Hatchwell (1999) have suggested that direct familiarisation is the most likely mechanism of kin recognition, enabling helpers to discriminate kin from non-kin (but see Price, 1999). Empirical studies of a greater range of cooperatively breeding birds are now required to test their predictions.

IV. FUTURE DIRECTIONS

What can avian researchers learn from the mammalian literature (and also, what can mammalian researchers learn from the avian literature)? Avian researchers need to invest more time investigating sibling recognition in a range of species with different life-history strategies. They should also focus more attention on the mechanisms of sibling discrimination examining both familiarity and relatedness independently as mammalian researchers have done. However, some avian researchers have made important contributions to the development of specific and testable functional explanations for sibling recognition in natural contexts, something mammalian researchers have not always accomplished and something they should aim to accomplish in the future. Two recent avian papers (Petrie *et al.*, 1999; Hatchwell *et al.*, 2001*b*) provide superb examples of studies integrating the identification of recognition mechanisms with clear functional interpretations in the context of natural settings. Avian work should look beyond auditory cues to investigate fully mechanisms of recognition; similarly, mammalian researchers should look beyond olfactory cues. Our review of the mammalian literature has identified several avenues of research that need attention from avian

researchers. For example, given how important memories of familiar individuals are for direct familiarisation (especially for species relying solely on familiarity to recognise siblings), avian researchers should examine how memories are maintained over time, as mammalian researchers have done. Sex differences in discrimination ability should also be considered in future avian recognition studies, especially where significant behavioural and ecological differences in sex roles are evident. We emphasise that avian and mammalian researchers can learn a great deal from one another, particularly when cross-fertilisation leads them to go beyond their 'traditional' approaches. It has been a long time since Beecher & Beecher (1983) suggested that avian researchers devote more attention to sibling recognition and other possible types of individual and kin recognition – we hope our review will encourage colleagues to focus more attention on this neglected but exciting area of research.

V. CONCLUSIONS

(1) Three factors (biological differences between birds and mammals, researchers' biases, and practical constraints) appear to influence the current state of knowledge of avian sibling recognition. The scarcity of avian sibling recognition studies may be largely due to a lack of studies investigating recognition mechanisms (i.e. direct and/or indirect familiarisation). Because birds are thought mainly to use vocal cues for recognition, the possibility that birds can use indirect familiarisation for kin recognition has rarely been considered or tested.

(2) Sibling recognition studies in birds tend to take a functional approach, investigating adaptive value in natural contexts, and putting less emphasis on identification of recognition mechanisms. By contrast, mammalian counterparts tend to take a mechanistic approach by using cross-fostering designs in laboratory settings, interpreting findings in terms of broad functional contexts such as nepotism and optimal breeding.

(3) Avian researchers can learn a great deal from the approaches taken by mammalian researchers to investigate sibling recognition, but the opposite is also true. Future work in avian sibling recognition should investigate species from a wider variety of behavioural and ecological circumstances; researchers should also investigate recognition mechanisms more thoroughly, and consider a variety of recognition cues as well as sex differences in recognition abilities.

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