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Sexual Imprinting and Evolutionary Processes in Birds: A Reassessment

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Both in the past and up to the present, birds have figured prominently as models in several areas of evolutionary biology, such as those of speciation (e.g., Mayr, 1963) and sexual selection (e.g., Andersson, 1994; Møller, 1994). Mate choice mediates these evolutionary processes and, although the actual choices and their functional and evolutionary significance have been studied intensively, noticeably less research has addressed the development of mate preferences. It has long been known that certain birds acquire their mate preferences through the developmental process known as "sexual imprinting," in which sexual preferences are acquired through learning the characteristics of the parents. It has been acknowledged that sexual imprinting might play a role in evolutionary processes like speciation (e.g., Seiger, 1967; Gill and Murray, 1972; Grant and Grant, 1996, 1997), the evolution of interspecific brood parasitism (Nicolai, 1964; Payne, 1973; Payne and Payne, 1998), and sexual selection (e.g., Gould and Gould, 1989; Christidis and Schodde, 1993; Andersson, 1994, pp. 438–439) and that the implications of this must be elucidated. Nevertheless, the mechanism does not figure in most theoretical models of evolutionary processes. For instance, while many models of sexual selection have been explicitly inspired by research on birds (e.g., O'Donald, 1980; Lande, 1981; Andersson, 1986), a common assumption in these models is that variation in mate preference is due to genetic variation and that preferences are inherited by genetic transfer from one generation to the next. Only very recently have some

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models of sexual selection incorporated the acquisition of mate preferences by imprinting (Laland, 1994) or other types of learning (Kirkpatrick and Dugatkin, 1994). In the past the evidence seemed to justify a marginal position for the phenomenon of sexual imprinting in relation to evolutionary processes. The aim of this review is to make it clear that this situation has changed considerably in recent years and to indicate areas where this may affect current views about evolution.

Below, we first provide a short summary of the traditional view of sexual imprinting and concentrate on three issues which seemed to justify the small amount of attention given to it in theories concerning evolution. We then review several new findings relevant to these issues and next discuss their potential implications for the processes of speciation, hybridization, interspecific brood parasitism, and sexual selection. In doing so, we indicate areas where theoretical and empirical studies on sexual imprinting are needed to clarify its role.

I. Sexual Imprinting: The Traditional View

A. Imprinting and Evolution

It was Konrad Lorenz who made the phenomenon of imprinting familiar to the scientific community with his famous "Kumpan" paper (1935). He described how the young of various precocial bird species followed the first moving object they encountered after hatching and formed a social attachment to it; a phenomenon now known as "filial imprinting." Lorenz also noticed that, later in life, birds reared by foster parents of another species often attempt to mate with members of the foster species rather than with their own. These preferences had been acquired early in life and showed remarkable stability. This is the process of "sexual imprinting." Later on, other researchers carried out more systematic studies of sexual imprinting. Among the first studies were those by Schutz (1965), who demonstrated that male mallards (*Anas platyrhynchos*) prefer females of the species by which they had been fostered over their own species, and Immelmann (1969), who showed the same for zebra finch (*Taeniopygia guttata*) males. Other studies demonstrated sexual imprinting in pigeons (*Columba livia* (*dom.*)) (Warriner, Lemmon, and Ray, 1963) and in gulls (*Larus argentatus, Larus fuscus*) (Harris, 1970). Researchers were quick to realize that imprinting might have evolutionary consequences. One suggestion was that imprinting might play a role in the evolution of interspecific brood parasitism in birds through linking parasite species to their hosts (Nicolai, 1964; Payne, 1973). Another suggestion, tested in several simulation models, was that imprinting might help maintain a balanced polymorphism in a natural population, as occurs in the snow goose (*Anser caerulescens*) (Cooch and Beardmore, 1959; Cooke, Mirsky, and Seiger, 1972), or might lead to sympatric speciation (O'Donald, 1960; Mainardi, Scudo, and Barbieri, 1965; Kalmus and Maynard Smith, 1966; Seiger, 1967; Seiger and Dixon, 1970; Scudo, 1976). These models did indeed indicate that imprinting might result in such effects. By present-day standards, however, these models were primitive. They were single-locus models and assumed, for instance, that mating preferences were absolute and did not depend on the proportion of the preferred mates in the population. Also, the models considered the presence of two phenotypes only and thus could not track progressive changes in appearance (cf. Laland, 1994, for a recent evaluation of these models). Therefore, these results provide no more than an indication of what might happen. More importantly, and more relevant to our review, is the empirical evidence that guided both this modeling and the subsequent discussions of the evolutionary aspects of sexual imprinting (e.g., Brown, 1975; cf. Laland, 1994). We briefly summarize this evidence, concentrating on three issues: the taxonomic distribution of sexual imprinting, the existence of a sex difference in imprintability, and the preferences resulting from the imprinting process. We indicate how the neglect of sexual imprinting in current evolutionary theory arose. Thereafter we reassess the evidence.

B. Imprinting: A Special Case?

Some 25 years ago, available evidence suggested that imprinting (as indicated by a preference for birds of a foster species or for humans in hand-raised birds) was more abundant in some groups, most noticeably in ducks and geese, galliformes, doves, pigeons, and estrildid finches (Immelmann, 1975a), than in others. This led to the impression that imprinting had a relationship with "rapidly evolving group(s) of animals" and with "closely related and often, very similar species occurring in the same area" (Immelmann, 1975a). Under these circumstances imprinting would, it was thought, make it possible that changes in appearance were rapidly followed by matching changes in preferences, as the latter would be based on the new appearance. In this view, sexual imprinting was seen as an adaptation to a situation in which rapid evolution occurred (Immelmann, 1975a,b; Bateson, 1978a). If sexual imprinting was such an adaptation, it would be a rare process limited to a special situation and hence it need not concern theorists interested in developing general models for evolutionary processes in birds.

A second factor limiting the impact of sexual imprinting concerns the idea that imprinting is usually present in one sex only. The studies by

Schutz (1965, 1971), for instance, suggested that males learned to recognize conspecifics, but that females did so without experience. Schutz concluded, as did others after him, that females relied on a more crude, "innate," preference for conspecifics; that is, a preference for species-specific characteristics for the development of which no experience with these characteristics was required (Schutz, 1965, 1971). Here again, imprinting was seen as an adaptation to special circumstances. In this case the hypothesis was that it had evolved in males to enable them to discriminate female conspecifics from similar-looking females of related species.

Finally, imprinting was explicitly seen as a mechanism involved in species recognition. At the time, in contrast to more recent views (e.g., Dabelsteen and Pedersen, 1985; Nelson, 1989; Ryan and Rand, 1993), species recognition was seen as a preference for invariant, average traits. This was considered incompatible with sexual preferences for dynamic and exaggerated traits, such as those generated by sexual selection. The reason for considering sexual imprinting as a mechanism for species recognition only was that imprinting studies showed that the most preferred mates usually belonged to the species or color morph of the (foster) parents. This preference for the familiar stimulus was generalized to the notion that imprinting resulted in a mate preference for "those objects bearing the closest similarity to the original stimulus" (Immelmann, 1975b). Sexual imprinting was hence assumed to provide stability and consistency in mate preference from one generation to the next. Seiger (1967), for instance, mentions that "imprinting would tend to limit the number and types of forms in a dimorphic population to those which already exist" and "if a new color mutant occurred, or if an individual of a new color migrated into the population, individuals bearing the new color would be rejected by the rest of the population." The consequence of a choice for similarity was assumed to be that "no 'supernormal' stimuli can be created and no exaggerated, 'luxuriant' characters are required for species recognition" (Immelmann, 1975b). Both the consistency in mate preference over generations and the seeming incompatibility of learned preferences with preferences for exaggerated traits were thus seen as being at odds with the process of sexual selection. It is hence no wonder that, with only a few exceptions (ten Cate and Bateson, 1988; Gould and Gould, 1989; ten Cate, 1991; Weary, Guilford, and Weisman, 1993; Laland, 1994; Andersson, 1994), imprinting has not been seen as a mechanism relevant in the context of sexual selection.

The views outlined above, all based upon the evidence available some 20 years ago, identified sexual imprinting as having limited distribution and therefore being of limited significance to evolutionary processes. However plausible these views were at the time, new findings and reinterpretations of earlier studies force us now to reconsider this evolutionary significance.

II. Reassessing the Evidence

A. The Taxonomic Distribution of Sexual Imprinting

A first survey was made by Klinghammer (1967), and this indicated the presence of sexual imprinting in some 23 species or genera of birds belonging to 6 different orders (taxonomic classifications in this paper follow Howard and Moore, 1991). Immelmann (1972) summarized the available evidence and concluded that sexual imprinting was present in approximately 40 species belonging to 11 different orders. Immelmann's survey covered both experimental and anecdotal evidence for sexual imprinting. Of all the species he listed, the majority belonged to the groups mentioned earlier: ducks and geese, galliformes, columbiformes, and estrildid finches. In spite of his conclusion that "imprinting occurs in groups of different systematic position and with very different ecological requirements" (Immelmann, 1972), later publications, including his own (Immelmann, 1975a), emphasized the relationship with rapid evolution. The suggestion of Hess (1973), that imprinting might be a widespread and phylogenetically old type of learning mechanism, does not seem to have caught on. This may have been because his conclusion was mainly based on examining the occurrence of filial, rather than sexual, imprinting.

Immelmann's survey seems, as far as we know, to have been the last one to summarize the taxonomic distribution of sexual imprinting. We have attempted to update his list with recent studies on imprinting, as well as with anecdotal evidence (including some passed on to us as personal communications). We define sexual imprinting in a loose sense as an effect of early experience on later mate preference, without the implication that it has to be the only factor or that it is irreversible. This criterion seems similar to that used by Immelmann. Table I and Appendix A show a total

TABLE I
Occurrence of Sexual Imprinting among Birds

	Extant[a]	Showing imprinting	Percentage
No. of species	>9200	≥101	1
No. of families	173	33	19
No. of orders	27	15	56

[a] According to Howard and Moore (1991).

of over 100 species for which there is evidence for sexual imprinting (the Appendix is an update of earlier, less detailed, lists in ten Cate, Vos, and Mann, 1993; and ten Cate, 1995). We are not aware of studies which show convincingly that imprinting is absent in a particular species. Our tentative conclusion is that sexual imprinting is present wherever it has been looked for. Although the number of species in which it has been found is just over 1% of all bird species existing today, it has been shown in species belonging to over half of all orders. This includes representatives of orders with a limited number of species, like Casuariiformes and Sphenisciformes (penguins). Even if anecdotal evidence is excluded and only more systematic studies are counted (see Appendix), 36 species belonging to 8 orders (30% of the total) show sexual imprinting. The presence of imprinting among birds may initially have been underestimated as researchers have only more recently become aware of experiential influences which counteract the effect of the foster parents in imprinting experiments, such as partial imprinting on conspecific broodmates (e.g., Kruijt, ten Cate, and Meeuwissen, 1983), an effect of the social circumstances during rearing (ten Cate, 1982, 1984, 1989, 1994), or the plasticity which enables adult birds to modify preferences acquired earlier (Immelmann, Lassek, Pröve, and Bischof, 1991; Kruijt and Meeuwissen, 1991, 1993; Bischof, 1994). The relationship between imprinting and rapidly evolving groups thus disappears in the light of the present evidence. In addition, some of the species are brood parasites, like the cowbirds (*Molothrus ater*) (Freeberg, King, and West, 1995) and the redhead duck (*Aythya americana*) (Sorensen, 1994). In these species, the development of own-species recognition by means of learning might be a disadvantage and special adaptations may be required in order to prevent imprinting on the host rather than on conspecifics. For another group of brood parasites, the whydahs (Nicolai, 1964) and indigobirds (Payne, 1973) (*Viduinae*), imprinting on the host plays a role in maintaining the linkage between the hosts and their parasites (see Section III,B for a discussion concerning the role of sexual imprinting in the evolution of avian interspecific brood parasitism). The presence of sexual imprinting in such parasitic species is at odds with the view that it has evolved under specific ecological circumstances. Rather, it supports the notion that the phenomenon is widespread, even though its role may vary between species. Although more systematic studies on the presence and specific variations of imprinting are necessary, the tentative conclusion from the present survey is that learning processes may contribute to the development of mate preferences in many birds, as anticipated by Hess (1973). Imprinting seems the rule rather than the exception.

As for a relationship with rapidly evolving groups, and its possible advantage to them, sexual imprinting still might, as indicated by Laland (1994;

see Section III,A), promote or maintain polymorphism or even lead to speciation. However, it seems unlikely that it evolved as an adaptation to this situation.

B. IMPRINTING AND SEX DIFFERENCES

1. Reconsidering Functional Explanations

The suggestion that there were sex differences in imprintability gained considerable plausibility because of the intuitively appealing functional explanations for it based on studies of the mallard. The first explanation was that, in sexually dimorphic species with uniparental care, offspring of one sex are not exposed to parents with the plumage of the opposite sex and hence cannot learn the proper model to court later on (Schutz, 1965; Bateson, 1966). The second explanation rested on the assumption that acquisition of an image of the proper species through imprinting would allow a better, more detailed, discrimination between the bird's own species and other ones than discrimination based on a mechanism not involving learning (Schutz, 1965, 1971). According to this explanation, sexual imprinting would thus benefit that sex in a dimorphic species which has to discriminate between potential mates and other, sympatric and similar-looking, species. Male mallards face this difficulty, as females of many other duck species are similar in appearance. For the mallard, both functional explanations make sense intuitively and this will have contributed to their reiteration in the literature right up to the present day (e.g., McFarland, 1993). As with its taxonomic distribution, imprinting is thus seen as an adaptation to specific circumstances and hence as a consequence of, rather than a cause for, plumage evolution. However, the widespread occurrence of imprinting renders this sequence less likely. It is therefore not surprising that there are quite a few species for which the proposed explanations are not valid. While Schutz (1965) supported his views by the finding that both sexes are imprintable in the monomorphic Chilean teal (*Anas flavirostris*), Manning (1967) noted that Schutz's own data contain evidence for a sex difference in another monomorphic duck species, the shelduck (*Tadorna tadorna*). In this species both sexes are strikingly colored and the females do not resemble other sympatric species, which makes it less plausible that males need more accurate species discrimination than females. Although it can be argued that phylogenetic history might be the reason why the shelduck shows a sex difference, the example raises doubts about the validity of the reasoning. The same applies to the sexually dimorphic zebra finch, in which both sexes are imprintable (e.g., Immelmann 1969; Sonnemann and Sjolander 1977; Kruijt *et al.*, 1983; ten Cate and Mug 1984; Vos, Prijs, and ten Cate, 1993). Again, neither sex obviously resembles another species. Also, several sexually monomorphic species with biparental care like gulls (Harris, 1970) and pigeons (Warriner *et al.*, 1963) show sex differences in mate choice similar to the mallard. These findings weaken the linkage between sexual dimorphism and imprintability. Hence, the proposed functional explanations for the presumed sex difference in imprintability do not stand up to close examination.

2. *Is There a Sex Difference?*

Rather than formulating a new functional explanation for the presence or absence of sex differences, we will reassess the data concerning the presence of sex differences in imprinting. We do not deny that sex differences in mate preferences and in the effects of early experience may exist. The occurrence of sexually dimorphic species with uniparental care makes the existence of such differences quite plausible. However, the question is whether the evidence really shows that only one sex shows imprinting, while the other relies on a preference for conspecifics irrespective of rearing conditions.

What is the evidence for a distinction between an "imprintable" and a "nonimprintable" sex? The strongest claims come from studies where the occurrence of imprinting was deduced from the way in which cross-fostered individuals ended up being paired; that is, were based on the final outcome of the pair formation process (more extensive accounts of the results of these studies and of the arguments developed below can be found in ten Cate, 1985, 1988; see also Bateson, 1978a). In this way sex differences were found in mallards (Schutz, 1965) and pigeons (Warriner *et al.*, 1963) with males more likely to end up being paired with mates of the foster species or color morph than females. In lesser black-backed and herring gulls, Harris (1970) found that cross-fostered males were less likely than females to become mated to the foster species. However, being paired is the endpoint of a complex process which involves interactions between individuals of both sexes. Such interactions may be initiated more by one sex than by the other. As a result, the initial preference of one sex may be more dominant in the outcome of the process than that of the other. Hence, the preferences of one of the sexes might become obscured during the mate choice process. Both Warriner *et al.* (1963) and Harris (1970) emphasized this possibility to account for their results. If this is correct, an assessment of sexual preferences under controlled conditions, in which both sexes may express their initial preference for individuals of a certain appearance, should show an effect of early experience in both sexes. This seems to be true for a number of species, among them doves, mallards, and zebra finches.

Brosset (1971) and ten Cate, Hilbers, and Hall (1992) analyzed the preferences of both sexes of different dove species in a test situation and obtained no evidence for a sex difference in these species at the premating stage. Bossema and Kruijt (1982) and Cheng (1979) and Cheng, Schoffner, Phillips, and Lee (1978) examined the initial preferences of female mallards under controlled conditions, using preference tests. These studies showed them to have a clear preference for those males which were most active. Under the experimental conditions used by Schutz, these would have been normally reared males and hence this might have been the reason that his females ended up being paired to these males. However, when males are equally active, Kruijt, Bossema, and Lammers (1982) showed that female mallards do have a preference for males of the morph they had been fostered by, thus showing an effect of imprinting on plumage preferences in females. No indication was found that females were responding to the normal, wild-type plumage independent of experience with it.

A similar picture applies to the zebra finch. In the first studies females were not found to imprint (e.g., Immelmann, 1972; Walter, 1973), but in later studies under more controlled circumstances (Sonnemann and Sjolander, 1977; ten Cate and Mug, 1984) females showed a clear effect of rearing experience on the later preference. Table II compares the mate preferences of normal reared and cross-fostered zebra finch males and females found by Kruijt *et al.* (1983) and ten Cate and Mug (1984). Cross-fostered females showed fewer sexual displays (tail quivering) to the foster

TABLE II

EFFECT OF CROSS-FOSTERING ON MATE PREFERENCES OF MALE AND FEMALE ZEBRA FINCHES AS MEASURED IN TWO WAYS

		Most sexual displays for[a]		Most time spent near[b]	
		Zebra finch	Bengalese finch	Zebra finch	Bengalese finch
Raised with	♂♂	34	0	31	3
Zebra finch	♀♀	23	0	25	2
Raised with	♂♂	0	33	1	32
Bengalese finch	♀♀	16	8	4	28

[a] The number of normally raised and cross-fostered zebra finches which show a preference, as measured by *sexual displays* (song in males; tail-quivering in females), for birds of the own or the foster species. The data are based on choice tests with the stimulus birds behind wire mesh on both sides of a central cage. Further details about rearing and testing conditions are given in Kruijt *et al.* (1983) for males and in ten Cate and Mug (1984) for females.

[b] Same birds as above, but in this case the preference is measured as *time spent* near the stimulus birds (the number of females is higher in this category because not all females showed tail-quivering).

species (Bengalese finch, *Lonchura striata*) than did cross-fostered males (Table II). This suggests a more limited impact of early experience on females. However, as shown in Table II, the sex difference is not present if the preference is measured by time spent near the different males. This indicates that males and females are equally likely to seek the proximity of the foster species, but that the likelihood of showing sexual behavior when near this species is reduced in females, seemingly confirming the own-species bias in females. However, a further analysis of what was actually going on during the preference tests showed that the sexual display of the females occurred almost exclusively in response to male courtship (ten Cate and Mug, 1984). Under the usual testing conditions, zebra finch males courted the females more intensively than Bengalese finch males. This suggested that, although the attraction to the appearance of the male Bengalese finches was quite strong as evidenced by the time spent near them, the low courtship activity of these males compared with that of conspecific males prevented this attraction from expressing itself in many sexual displays toward them. If this explanation is correct, one would expect that, if the song output of the males was equal or reversed, females would express more sexual interest in Bengalese finch males. This was tested in an experiment in which nonsinging conspecific males were used in the choice tests. This again resulted in a clear bias in sexual behavior, but in this case for the foster species (ten Cate and Mug, 1984).

These results, and those mentioned above, refute the conclusion that one sex shows imprinting and the other relies on an "innate" preference for conspecifics. In fact, in all species for which such a sex difference has been suggested, female imprinting seems to be present. The sex differences observed in several earlier imprinting studies should thus be reinterpreted as a consequence of using less-sensitive or less-direct ways of testing for preferences in combination with the fact that the two sexes give different weight to the various stimuli which play a role during the process of pair formation (ten Cate, 1985, 1988; Vos, 1995b). Another source of confusion about the extent to which imprinting may affect mate preferences is that males and females reared in the same situation may differ in what they learn; that is, a sex difference in mate preference may also arise out of a sex difference in the learning process itself (Vos *et al.*, 1993; Vos, 1995a,b).

To conclude this section: Recent studies on sex differences in imprinting suggest that presumed differences in imprintability result from other factors interfering with, or obscuring, the expression of learned preferences for parental appearance or from differences in what the two sexes learn early in life. As with the taxonomic distribution of sexual imprinting, its occurrence in both instead of in one of the sexes has been underestimated.

C. IMPRINTING AND PREFERENCES FOR CONSPICUOUS FEATURES

1. *Perceptual Biases: Are They Present?*

That imprinting leads to a match between the stimulus to which the exposure occurred and the stimulus to be preferred later on seems a logical conclusion from many experiments. Birds exposed to a foster species or to a different color morph have been found generally to prefer these over other species or morphs, while no experimental evidence goes against this. However, as noticed by Bateson (1982), this view of the outcome of the imprinting process is axiomatic. This conclusion is inferred from experiments in which the imprinted bird had the choice between familiar stimuli and stimuli very different from them, either belonging to a different species or to a strikingly different color morph. Experiments thus focused on preferences at the (sub)species level, but the conclusions were, more or less implicity, extended to within-species variation. These conclusions were linked to the assumptions of such experiments that (1) imprinting served as a species recognition mechanism and (2) this was incompatible with a bias toward conspicuous features in the preference. Both assumptions have been challenged. With respect to the first one, it has been demonstrated that imprinting may also be a mechanism enabling kin recognition (Bateson, 1978a, 1980, 1982, 1983, 1988) and sex recognition (Immelmann, 1985; Vos, 1994). But, even if the evolutionary origin of sexual imprinting concerned species recognition, this need not imply a preference for the "average" individual. Various authors have emphasized that correct identification of an animal's own species may involve biased preferences which may help to prevent hybridization (e.g., Ryan and Rand, 1993; Andersson 1994). Such biases may form a starting point for sexual selection (Andersson 1994). The evidence for biases in mate preferences based on plumage characteristics or other features of the appearance of birds is rapidly accumulating (Andersson, 1994). It includes some species which are known to show sexual imprinting. In the zebra finch, for instance, Burley, Kranzberg and Radman (1982) demonstrated a preference for conspecifics with leg bands of certain colors. In particular, those colors seemed to be preferred which increased the contrast with the related and sympatric double bar finch (*Poephila bichenovii*) (Burley, 1986). As mentioned above, the presence of sexual imprinting in the zebra finch is well documented. A combination of imprinting and a perceptual bias is also present in the kestrel (*Falco tinnunculus*). Palokangas, Korpimäki, Hakkarainen, Huhta, Tolonen, and Alatalo (1992) showed that female kestrels prefer brightly colored males, whereas Bird and Goldblatt (1981) and Bird, Burnham, and Fyfe (1985) provide evidence for sexual imprinting in both males and females. Imprinting and biased mate preferences are also present in collared doves (*Strepto-*

pelia decaocto). Both normally reared collared doves and those reared by white ring doves (*Streptopelia risoria*) showed a preference for a stuffed white ring dove over a stuffed collared dove in choice tests. In addition, their preference in tests with living stimulus birds appeared to be biased toward the white ring doves (ten Cate *et al.*, 1992), while also showing a clear effect of early experience on the mate preference.

2. *Perceptual Biases: How Can They Arise?*

The above data suggest that biased mate preferences and the imprinting process may be compatible. But what might be the linkage between the two in terms of underlying mechanisms? One hypothesis for the origin of a bias is that imprinting sets the standard for prospective mates but that perceptual biases interfere to create an asymmetrical bias in the generalization around the standard. Biases in preferences are a familiar phenomenon from studies of filial imprinting. Extensive experiments by Kovach (1983a,b,c), for instance, have shown not only that Japanese quail chicks (*Coturnix japonica*) respond strongly to test stimuli with the same overall features as the imprinting stimulus, but also that test stimuli could be made more attractive than the imprinting stimulus by adding features that it lacked. Thus, quail chicks exposed to red or blue lights prefer the color to which they have been exposed (Kovach, 1983a). However, if vertical stripes are added to the test stimulus, it becomes more attractive (Kovach, 1983b). This preference for vertical stripes is also present in untrained, visually naive chicks and thus develops independent of the imprinting process (Kovach, 1983a; see ten Cate, 1994, for a more extensive discussion on the interactions between perceptual biases and filial imprinting). So, it is the combination of imprinting and perceptual bias which may determine the final preference.

The possible relationship between sexual imprinting and biases in mate preferences has, so far, been examined for two species, zebra finch and Japanese quail. For the latter species ten Cate and Bateson (1989, see also ten Cate, 1991) carried out an experiment in which quail chicks were exposed to one of three different types of imprinting stimulus. The stimuli were adult white quail with no, three, or six black dots dyed on their breast feathers. When adult, preference tests were conducted in which the birds were shown three stimulus birds simultaneously. Males exposed to a stimulus with no dots preferred stimuli with two dots over no or one dot. Males exposed to stimuli with three or six dots were given the choice between one individual with the familiar number of dots, one with fewer dots, and one with more dots. Stimulus birds which had a higher number of dots than the imprinting stimulus were preferred over those that had a lower number of dots (ten Cate and Bateson, 1989). In the "classic" imprinting test between the familiar stimulus and a wild-type bird the familiar stimulus was preferred, indicating that the preference for a dotted bird was not due to a preference for wild-type plumage. This experiment thus demonstrated that sexual imprinting affected the preference in combination with a bias for dots.

The experiment did not demonstrate whether the preference for more dots is open ended nor whether it depends upon the number of dots on the familiar bird. Therefore, the experiment allows no conclusion about the mechanism(s) giving rise to the bias. The developmental origin of a bias may be independent of the imprinting process, like the biases shown by Kovach (1983a,b) for young quail in the context of filial imprinting. However, recently Weary *et al.* (1993) raised the possibility that biases arise directly from the learning process itself. They suggested that in sexually dimorphic species preferences for exaggerated versions of the parental appearance could result from a well-known consequence of discrimination learning, called "peak-shift" (e.g., Purtle, 1973). During discrimination learning individuals can be exposed to a positive stimulus, predicting a reward (for instance food), and a negative stimulus, differing in one dimension, without a reinforcement (or predicting an aversive event, for instance a shock). In a later test between these stimuli and deviant ones, animals respond most to more extreme versions of the stimuli. Weary *et al.* (1993) suggested that the same phenomenon might result from sexual imprinting with the parents acting as "positive" and "negative" stimuli. This may only occur if parents differ in appearance as well as in their behavior toward the young birds. A first attempt to test the "peak shift" hypothesis has recently been undertaken for the zebra finch (Vos, 1995; see also Weisman *et al.*, 1994). The starting point was some studies which showed that zebra finch males discriminate between the physical appearance of males and females as a result of their early experience (Immelmann, 1985; Vos *et al.*, 1993; Vos 1994). Males develop a strong preference for females of their mother's morph. In addition, females of their father's morph are avoided (Vos *et al.*, 1993). Thus the conditions necessary for the occurrence of peak shift as a result of discrimination learning are present in this species. In a second experiment, males were reared by two parents of a white color morph. The only sex difference in the appearance of white parents was a difference in bill color, those of males being bright red and those of females orange-red. These bills were painted with nail polish. For half of the parental pairs the male's bill was painted red and the female's bill orange, for the other half the sex difference was reversed. Males raised under these conditions also exhibited a preference for females with the mother's bill color over females with the father's color (Table III; Vos, 1994). The males were next tested with a range of females with bill colors either in between

TABLE III
MATE PREFERENCES OF ZEBRA FINCH MALES RAISED BY WHITE CONSPECIFIC PARENTS SHOWING SEXUAL DIMORPHISM IN BILL COLOR[a]

	Preference for females with	
Parental bill color	Red bill	Orange bill
Father red Mother orange	1	13
Father orange Mother red	14	1

[a] Based on Vos (1994).

or more extreme than the parental ones (Vos, 1995). Although the results are not conclusive for various reasons, they suggested that males which had experience with the natural difference in bill color between the parents showed no peak shift. In contrast, males raised with parents with their bill colors reversed showed a preference for females with a redder bill than their mother over females with a less-red bill. So, the preference exhibited by the males in the latter group was biased toward versions which were less like the father's bill color and appears to have been induced by previous experience with the parental colors. This is what the peak shift hypothesis predicts, demonstrating the potential of the mechanism leading to evolutionary changes.

It must be emphasized that both the quail and the zebra finch experiments have so far only demonstrated the effects for males, and none could be shown for females (ten Cate, 1991; Vos, 1995a,b). Also, the imprinting stimuli and conditions of exposure were designed to maximize the chances of demonstrating the phenomena under laboratory conditions. Hence, the extrapolation of the findings to consider their implications for mate choice under natural conditions awaits more extensive study, as does the existence of peak shift in sexual imprinting. Nevertheless, the conclusion of this section must be that sexual imprinting is not only compatible with, but may potentially even induce a preference for exaggerated traits in mates.

III. SEXUAL IMPRINTING AND EVOLUTION: A REASSESSMENT

The previous sections have made it clear that mate preferences in many species and in both sexes are affected by early experience. This leads to a switch in perspective: if sexual imprinting is a phylogenetically ancient and general feature, as suggested by its widespread occurrence, its presence in a specific group is no more in need of a functional explanation than the presence of wings or feathers. Rather, functional studies should focus on the precise characteristics of the process in a particular species: the timing of its sensitive phase, the nature of experiences affecting it, the features which are learned, the presence of perceptual biases, the sex differences in the learning process, and so on. Also, the presumably ancient roots of imprinting raise the question of whether its presence may itself affect evolutionary processes. We suggest it does. Below we discuss three areas where this may be the case: (1) that of speciation and hybridization, (2) that of interspecific brood parasitism, and (3) that of sexual selection. While discussing the possible implications of imprinting for these processes, we will also identify open questions, indicating issues for future research.

A. IMPRINTING, SPECIATION, AND HYBRIDIZATION

A first attempt to introduce some of the recent findings on imprinting into mathematical models of evolutionary processes like speciation was carried out by Laland (1994). He considered the acquisition of mate preferences by imprinting as a learning mechanism based on cultural inheritance with vertical transmission. He used models of gene culture coevolutionary theory (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985) to study the evolutionary dynamics of the imprinting process. His models support some of the earlier claims of less-sophisticated models (e.g., O'Donald, 1960; Seiger, 1967) about the evolutionary consequences of imprinting. One of these is that imprinting may act as a barrier to gene flow, minimizing the impact of migration on genetic differences between populations. This suggests that imprinting may lead to sympatric speciation, albeit with the aid of additional factors (Laland, 1994). However, as already noticed by Seiger (1967), a paradoxical situation may arise. On the one hand imprinting may lead to assortative mating, making it possible for an existing trait to get firmly established and maintained in a population. On the other, if parents have a strong impact on the later preference, how can a new trait (e.g., a new color mutant) invade a population? Indeed, Laland's models indicate that sexual imprinting without a bias reduces the likelihood of novel traits spreading through a population, in line with Seiger's (1967) suggestion. However, a solution to the paradox arises when the model incorporates an asymmetry in mating preferences acquired by imprinting (ten Cate, 1991; Laland, 1994). The presence of a bias generates rapid selection for the favored trait, even if this impairs survival. The spread of the new trait is several magnitudes faster than it would have been in the absence of imprinting (Laland, 1994).

There may also be another solution to the paradox. Both Seiger's (1967) and Laland's (1994) models assume that the preferences are based on *parental* appearance. However, as is clear from studies on several species (e.g., mallard, Klint, 1978; snow goose, Cooke, 1978; quail, Bateson, 1980; zebra finch, Kruijt *et al.,* 1983), siblings may provide an important or additional model. Therefore, a new trait may spread when siblings develop a preference for an appearance resembling that of their mutant brother or sister. However, further modeling is required to assess the potential of this possibility. Empirical studies are also needed to examine the plausibility of this suggestion. This might be in the form of aviary experiments in which, for instance, a brood of a different color morph is raised in a colony of wild-type zebra finches. This may indicate the impact of mutant siblings on mate preferences in a seminatural situation.

As Laland's study indicates, the step from polymorphism in a population to sympatric speciation may be a big one. Even a limited degree of hybridization between different morphs may counteract the speciation process. As with speciation, the likelihood of the occurrence of both intra- and interspecific hybridization may itself be affected by imprinting. Interspecific hybridization has often been seen as an accidental responsiveness of allopatric individuals to heterospecific stimuli (e.g., Gill and Murray, 1972; Alatalo *et al.,* 1990). Nevertheless, hybridization is also considered an adaptive evolutionary strategy under particular circumstances; for instance, if choosing a heterospecific mate provides adaptive benefits in circumstances where there are no fitness costs to hybridization or if hybrids are superior competitors (Pierotti and Annett, 1993). Although hybridization can prevent speciation, this need not always be the case. In contrast, there is a growing recognition that hybridization and introgression may give rise to new animal species (e.g., Dowling and Secor, 1997). For birds such a scenario has been suggested to be a factor in the evolution of Darwin's finches (*Geospizinae*) (Grant and Grant, 1997), while the gull *Larus taimyrensis* may have evolved from hybrids between two other species (Pierotti and Annett, 1993). Most research on hybridization concentrates on the fitness consequences of the responsiveness to heterospecific stimuli (e.g., Gill and Murray, 1972; Moore, 1987; Pierotti, 1987; Alatalo *et al.,* 1990) rather than on the proximate mechanisms underlying it (but see Grant and Grant, 1997). Although increased receptiveness to such heterospecific stimuli in normal birds may lead to accepting mates from other species, the existence of imprinting suggests another scenario which may be at the root of hybridization. In recent years, it has become increasingly clear that intraspecific brood parasitism is present in many bird species (Rowher and Freeman, 1989). Such brood parasitism may also, if only by accident, result in laying eggs in the nest of another species, resulting in a mixed brood. Through sexual imprinting such birds may acquire a sexual preference for the foster species. If such birds are successful in acquiring a heterospecific mate, this results in hybridization. An experiment in which eggs were exchanged between herring gulls and lesser black-backed gulls demonstrated that this sequence may occur in the field (Harris, 1970; Harris, Morley, and Green, 1978). As the offspring of mixed pairs will be exposed to both species, they will also have an increased tendency to hybridize. If siblings are a model for the later mate preference, then hybridization might be further enhanced by the development of preferences for hybrid individuals. Such a scenario could result in the evolutionary origin of a hybrid species. In songbirds the scenario may be reinforced by the fact that songs and song preferences may also be affected by cross-fostering, as these are also acquired through early experience. However, experimental work mimicking these starting conditions, as well as theoretical modeling, is required to test the plausibility of the above scenarios.

B. IMPRINTING AND INTERSPECIFIC BROOD PARASITISM

Nicolai (1964) and Payne (1973) have suggested that imprinting has provided the basis for the evolution of interspecific brood parasitism in, respectively, whydahs and indigobirds. These are songbirds (family *Ploceidae*) which parasitise estrildid finches. Most of the parasite species are linked to a particular host species and their young often show a remarkable mimicry of the foster species in mouth markings and plumage, suggestive of an coevolutionary arms race. Nicolai (1964) suggested that the start of this parasitism occurred when an ancestral parasite female laid her eggs in the nest of an estrildid finch when her own nest had been damaged. In view of the above-mentioned evidence for intraspecific brood parasitism, a more likely scenario might have been that the ancestor of the parasites was a species showing a high degree of intraspecific parasitism. As in the hybridization scenario, laying eggs in the nest of another species may have resulted in young being sexually imprinted onto the foster species (Nicolai, 1964). As these birds are songbirds which acquire their songs through imitation, the cross-fostering has an additional effect: the young males copy the foster father's song and the females develop a preference for this song (Nicolai, 1964; Payne and Payne, 1998). What might have happened next is that cross-fostered young, once adult, may have attempted to mate with the foster species. If individuals of the foster species were resistant to these attempts, the cross-fostered birds may have settled for the "next best" option: mating with birds which also associated with the foster species and either sang their song or had a preference for it; that is other cross-fostered birds. As cross-fostered females presumably originate from a mother with parasitic tendencies and are more interested in the foster species than their own species, this may bias them to lay their own eggs in the nest of the foster species. This may start an intimate association between parasite and host species, leading to coevolution. Payne and Payne (1994, 1995, 1998) have argued that once the interspecific parasitism has started, involving imprinting on the host species, rapid evolutionary divergence may occur in the parasite species. A parasite female laying her eggs in the nest of a species other than the usual host will produce parasitic young which are attracted to the new foster species, again with the young themselves singing the foster species' song or having a preference for this song. Experimental tests in which the foster species was manipulated artificially showed that young indigo birds cross-fostered to Bengalese finches based their song on the new foster species, ignoring their traditional host (Payne and Payne, 1998). It must be noted that in this scenario the role of imprinting seems to have shifted over evolutionary times from a mechanism involved in species recognition to one involved in host recognition. But how do parasitic species develop a mating preference for conspecifics rather than for their hosts? One factor might be that the preference is less tightly linked to visual traits, but instead is based on other features, which are not learned; for instance, certain calls. Another option might be that while the learning mechanism has shifted to the context of host recognition, unlearned perceptual biases for visual features have become more oriented toward a preference for conspecific traits. Such a scenario might also be applicable to the European cuckoo (*Cuculus canorus*).

For some brood parasites there is evidence that early experience is still important for a bird to become sexually interested in conspecifics. Brown-headed cowbirds, for instance, express a sexual interest in birds of the species with which they have been kept in the period after independence of the foster parents, a period during which they normally flock with conspecifics (Freeberg, King, and West, 1995). The same is the case for redhead ducks (Sorenson, 1994). Whether imprinting plays a role in host recognition in these species is still unknown. These data suggest that among interspecific brood parasites, two variants might be present; one in which the imprinting process becomes adapted to serve primarily as a mechanism through which a specific parasite species becomes linked to a specific host and one in which imprinting may still be involved in recognizing the bird's own species. The latter may occur through a shift in the timing of the learning process to a phase in which the young are no longer dependent on the host species. In this case some crude biases guiding postfledging associations may be necessary to put the young in a context in which they are exposed to conspecifics.

Finally, what the previous section (IIIA) and this one suggest is that the phenomena of hybridization and brood parasitism may be different evolutionary outcomes with the same starting point: laying eggs in the nest of another species in combination with imprinting. At the moment, the various scenarios we have discussed are hypothetical. Modeling studies may indicate whether and under what conditions they may be valid and what factors may drive evolution in one or the other direction. Empirical studies are necessary to examine the nature of, and the relation between, the processes involved in host recognition and those involved in mate recognition in various groups of parasites.

C. IMPRINTING AND SEXUAL SELECTION

As shown above (Sections II,C,1, and II,C,2), the occurrence of imprinting is compatible with, or may even induce, preferences for exaggerated traits. By adding a consistent bias to an imprinted preference, the preferred mates become those deviating in a specific direction from the birds which served as models earlier on. The next generation may inherit the bias. As their preference is again affected by their parents' appearance, this will result in a preference which is slightly beyond that of their parents. Laland's model (1994) has shown that this may result in rapid evolution. This outcome indicates that sexual imprinting may play a role in sexual selection, as suggested by ten Cate and Bateson (1988) and ten Cate (1991). The value of the approach by Laland is that it indicates how more-traditional models of sexual selection (e.g., Kirkpatrick, 1982) can be modified to take imprinting into account and how this affects the evolutionary dynamics. However, this modeling must only be seen as a first step.

For instance, one aspect of sexual selection concerns the evolution of sexual dimorphism. On the one hand, the finding that male zebra finches use their mother as a model for their sexual preference (Vos *et al.*, 1993), and that male and female zebra finches learn different things (Vos, 1995a,b), may be factors which might lead to, or enhance, the evolution of sexual dimorphism. However, at the moment it is unclear whether these features are causes for such dimorphism or consequences in the form of special adaptations of the imprinting process to the dimorphism. Another area for further modeling concerns the finding that females may use different traits from males in their mate choice and/or might be affected differently by their early experience. In addition, if further experiments confirm the occurrence of peak shifts in the zebra finch and other species, this also needs to be taken into account in modeling studies. Finally, models for sexual selection concentrate on evolution by *female* preference. The finding that the clearest evidence for biases in sexual preferences in relation to imprinting is in males and that, for the zebra finch, male bill color seems a trait involved in intra- rather than in intersexual selection (Collins and ten Cate, 1996) indicates that more attention should be given to modeling evolutionary change through male–male interactions.

There is also a need for further empirical work on features of the imprinting process that are critical to further modeling. Several of the findings discussed above have, so far, only been studied in one or two species (e.g., the interaction of imprinting and perceptual biases, the peak shift phenomenon, learning differences between males and females) and there is a need to extend these studies to other species to assess how general the findings are. Comparative studies are needed to examine whether and how sex differences in imprinting are related to the presence of sexual dimorphism; for example, by examining closely related species with and without such dimorphism. Similarly, the occurrence and dynamics of sexual imprinting in species with uniparental care is far from clear. Here also, carefully controlled comparative studies are needed to indicate to what extent certain characteristics of the imprinting process can be adapted to such a situation and how mate preferences develop when the conditions for proper learning are limited. Finally, one can think of aviary studies aimed at mimicking the process of evolutionary change through biased preferences by introducing novel mates with preferred traits and by examination of subsequent preferences and biases in the offspring.

IV. Conclusion

We hope to have demonstrated that traditional views on sexual imprinting require updating. Our review has focused on a subset of features of the imprinting process, namely those likely to have evolutionary consequences. It will be clear that the present state of knowledge does not yet allow any definite conclusions about how imprinting may affect evolution. However, we have shown how several evolutionary and functional hypotheses about sexual imprinting that have been put forward in the past are no longer valid. We suggest that imprinting is a very basic and widespread mechanism for acquiring mate preferences. This view changes the questions to be examined and the phenomena to be explained. We advocate the view that imprinting brings about evolutionary changes through cultural inheritance, as has also been suggested for another developmental learning process, namely song-learning in songbirds (Grant and Grant, 1996, 1997). As a consequence, imprinting might enable or cause particular evolutionary scenarios rather than arising out of them. In addition, several empirical studies have raised questions, but not yet provided answers, about the characteristics of sexual imprinting, requiring further experimental work. Nevertheless we hope this paper will fulfill its aim: to identify a profitable area for further theoretical and empirical research on the interface between mechanisms and evolutionary processes.

V. SUMMARY

Theoretical models for evolutionary processes like speciation, hybridization, the evolution of brood parasitism, and sexual selection have generally ignored the fact that mate preferences in many birds are acquired by learning parental features through "sexual imprinting." The reason for this lack of attention is probably that sexual imprinting was considered to be a rare process limited (1) to special situations, like rapidly evolving groups, and (2) to one sex only. In addition it was (3) considered to be incompatible with preferences for conspicuous features like those involved in sexual selection. If this were true, the evolutionary significance of a learning mechanism underlying mate preferences would be limited. We review recent studies on several aspects of sexual imprinting and show that it occurs (1) in the majority of bird orders, and (2) in both sexes. Also, it may (3) be combined with, or even induce, a preference for conspicuous features. Sexual imprinting seems to be a very widespread and general feature of birds. Taking it into account as a mechanism for transfer of mate preferences from one generation to the next may alter the view of the dynamics of the evolutionary processes mentioned above and may lead to new empirical and theoretical issues for further research.

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APPENDIX

TAXONOMIC DISTRIBUTION OF SEXUAL IMPRINTING

Casuariiformes
  Dromaiidae
    Dromaius novaehollandiae, emu (Hediger, 1950, in Sluckin, 1964)

(*continues*)

TAXONOMIC DISTRIBUTION OF SEXUAL IMPRINTING (*continued*)

- Tinamiformes
  - Tinamidae
    - *Eudromia elegans*, elegant crested tinamou (pers. comm., Baptista)
- Sphenisciformes
  - Spheniscidae
    - *Aptenodytes patagonicus*, king penguin (Fisher, 1966)
    - *Spheniscus humboldti*, Humboldt penguin (Todd, 1981)
    - *Spheniscus demersus*, jackass penguin (pers. comm., Baptista)
- Ciconiiformes
  - Ardeidae
    - *Ardea purpurea*, purple heron (von Frisch, 1957, in Immelmann, 1972).
    - *Botaurus stellaris*, eurasian bittern (Portielje, 1926, in Immelmann, 1972)
  - Ciconiidae
    - *Ciconia ciconia*, white stork (Löhrl, 1961, in Immelmann, 1972)
- Anseriformes
  - Anatidae
    - *Anser fabalis*, bean goose (Fabricius, 1991)
    - *Anser albifrons*, white-fronted goose (Schutz, 1971)[a]
    - *Anser erythropus*, lesser white-fronted goose (Stevens, 1955; Fabricius, 1991)
    - *Anser anser*, greylag goose (Schutz, 1971; Fabricius, 1991)[a]
    - *Anser caerulescens*, snow goose (Cooke and McNally, 1975; Cooke, Mirsky, and Seiger, 1972)[a]
    - *Cereopsis novaehollandiae*, Cereopsis goose (Kear, 1960)
    - *Tadorna tadorna*, common shelduck (Schutz, 1965)[a]
    - *Cairina moschata*, muscovy duck (Schutz 1965)[a]
    - *Aix sponsa*, wood duck (Schutz, 1965)[a]
    - *Anas flavirostris*, Chilean teal (Schutz, 1965)[a]
    - *Anas platyrhynchos*, mallard (Schutz, 1965; Kruijt, Bossema, and Lammers, 1982)[a]
    - *Netta rufina*, red-crested pochard (Schutz, 1965)[a]
    - *Aythya americana*, redhead (Sorenson, 1994)[a]
    - *Aythya valisineria*, canvasback (Sorenson 1994)[a]
- Falconiformes
  - Cathartidae
    - *Gymnogyps californianus*, Californian condor (pers. comm., Baptista)
  - Accipitridae
    - *Accipiter nisus*, northern sparrow hawk (Mohr, 1960)
    - *Buteo platypterus*, broad-winged hawk (Mueller, 1970, in Immelmann, 1972)
    - *Aquila chrysaetos*, golden eagle (Hamerstrom, 1970, in Immelmann, 1972, Burder, 1972, in Grier, 1984)
  - Falconidae
    - *Falco sparverius*, American kestrel (Bird and Goldblatt, 1981, Bird, Burnham, and Fyfe, 1985)[a]
    - *Falco tinnunculus*, common kestrel (Bird and Goldblatt, 1981; Bird, Burnham and Fyfe, 1985)[a]
    - *Falco peregrinus*, perigrine falcon (Waller, 1942, in Immelmann, 1972)
- Galliformes
  - Gracidae
    - *Ortalis vetula*, plain chachalaca (pers. comm., Baptista)

TAXONOMIC DISTRIBUTION OF SEXUAL IMPRINTING (*continued*)

- Phasianidae
  - *Meleagris gallopavo,* common turkey (Räber 1948, Schein 1963, - in Immelmann 1972)
  - *Bonasa umbellus,* ruffed grouse (Hassler, 1968)
  - *Perdix perdix,* grey partridge (Heinroth and Heinroth, 1924–1933, in Hess, 1973)
  - *Coturnix japonica,* Japanese quail (Gallagher, 1976; Bateson, 1978)^{a}
  - *Gallus gallus,* red jungle fowl (Hess, 1959, in Immelmann, 1972; Schutz 1965)^{a}; domestic fowl (Fisher and Hale, 1959; Schein and Hale, 1959; Guiton, 1962, in Immelmann, 1972)
  - *Phasianus colchicus,* common pheasant (Heinroth and Heinroth, 1924–1933)
  - *Argusianus argus,* great argus pheasant (Bierens de Haan, 1926, in Hess, 1973)
  - *Pavo cristatus,* common peafowl (Heinroth and Heinroth, 1959, in Sluckin, 1964)
- Gruiformes
  - Gruidae
    - *Cranes sp.* (Archibald, 1974)
    - *Grus americana,* whooping crane (Gill, 1985)
  - Psophiidae
    - *Psophia crepitans,* common trumpeter (Horning, Hutchins, and English, 1988; pers. comm., Baptista)
    - *Psophia viridis,* green-winged trumpeter (pers. comm., Baptista)
  - Rallidae
    - *Crex crex,* corn crake (Heinroth, 1924–1933, in Immelmann, 1972)
    - *Fulica atra,* black coot (Schutz, 1965)^{a}
  - Eurypygidae
    - *Eurypyga helias,* sun-bittern (pers. comm., Baptista)
- Charadriiformes
  - Charadriidae
    - *Charadrius dubius,* little-ringed plover (Heinroth and Heinroth, 1924–1933)
  - Laridae
    - *Larus argentatus,* herring gull (Harris, 1970)^{a}
    - *Larus fuscus,* lesser black-backed gull (Harris, 1970)^{a}
    - *Sterna hirundo,* common tern (Busse and Franck, 1988)^{a}
    - *Sterna paradiseae,* Arctic tern (Busse and Franck, 1988)^{a}
- Columbiformes
  - Columbidae
    - *Columba livia (dom.),* feral rock pigeon (Warriner, Lemmon, and Ray, 1963)^{a}
    - *Columba palumbus,* wood pigeon (Goodwin, 1948)
    - *Streptopelia turtur,* turtle dove (Heinroth and Heinroth, 1924–1933; Goodwin, 1948)
    - *Streptopelia decaocto,* collared dove (ten Cate, Hilbers, and Hall 1992)^{a}
    - *Streptopelia roseogrisea,* African collared dove (Brosset 1971; Klinghammer and Hess, 1964)^{a}
    - *Streptopelia senegalensis,* laughing dove (Brosset, 1971)^{a}
    - *Zenaida macroura,* mourning dove (Klinghammer, 1967)^{a}
    - *Zenaida galapagoensis,* Galapagos dove (Brosset, 1971)^{a}
    - *Ptilinopus porphyrea,* pink-necked fruit dove (pers. comm., Baptista)
- Psittaciformes
  - Cacatuidae
    - *Eolophus roseicapillus,* Galah (Rowley and Chapman, 1986)^{a}
    - *Cacatua moluccensis,* salmon-crested cockatoo (Baptista *et al.,* 1993)
    - *Nymphicus hollandicus,* cockatiel (Meyers *et al.,* 1988)^{a}

(*continues*)

TAXONOMIC DISTRIBUTION OF SEXUAL IMPRINTING (*continued*)

- Psittacidae
  - *Eclectus roratus,* Eclectus parrot (Lantermann, 1994)
  - *Melopsittacus undulatus,* budgerigar (Stamm and Blum, 1971)
  - *Poicephalus senegalus,* Senegal parrot (Klinghammer, 1967)
  - *Agapornis roseicollis,* peach-faced lovebird (Preiss and Franck, 1974; Lassek, 1988)[a]
  - *Amazona finschi,* lilac-crowned Amazon (Lantermann, 1993; Baptista, 1993)
  - *Amazona aestiva,* blue-fronted Amazon (Lantermann, 1993; Baptista, 1993)
  - *Amazona autumnalis,* red-lored Amazon (Lantermann, 1993)
  - *Amazona ochrocephala,* Yellow-crowned Amazon (Lantermann, 1993)

Cuculiformes

- Musophagidae
  - *Tauraco hartlaubi,* Hartlaub's Turaco (pers. comm., Baptista)

Strigiformes

- Tytonidae
  - *Tyto alba,* barn owl (Smith and Olson, 1976)
- Strigidae
  - *Bubo bubo,* Northern eagle owl (Heinroth and Heinroth, 1924–1933)

Coraciiformes

- Coraciidae
  - *Coracias garrulus,* European roller (von Frisch, 1966, in Immelmann, 1972)
- Bucerotidae
  - *Ceratogymna brevis,* silvery-cheeked hornbill (pers. comm., Baptista)

Passeriformes

- Timaliidae
  - *Minla cyanouroptera,* blue-winged minla (Thielcke, 1966, in Immelmann, 1972)
- Muscicapidae
  - *Ficedula hypoleuca,* pied flycatcher (Löhrl, 1955)
  - *Fidecula albicollis,* collared flycatcher (Löhrl, 1955)
- Emberizidae
  - *Cardinalis cardinalis,* common cardinal (pers. comm., Yamaguchi)
- Icteridae
  - *Sturnella magna,* eastern meadowlark (Nice, 1965, in Immelmann, 1972)
  - *Molothrus ater,* brown-headed cowbird (Freeberg, King, and West, 1995)[a]
- Fringillidae
  - *Pyrrhula pyrrhula,* northern bullfinch (Nicolai, 1956, 1959)[a]
  - *Coccothraustes coccothraustes,* hawfinch (Kear, 1960)
- Estrildidae
  - *Pytilia afra,* orange-winged pytilia (Nicolai, 1964)
  - *Uraeginthus cyanocephala,* blue-capped cordon-blue (Goodwin, 1971)
  - *Amandava amandava,* red munia (Nicolai, 1964)
  - *Poephila guttata,* zebra finch (Immelmann, 1969; Kruijt, ten Cate, and Meeuwissen, 1983; Sonnemann and Sjölander, 1977; ten Cate and Mug, 1984)[a]
  - *Poephila cincta,* black-throated finch (Nicolai, 1964)
  - *Amadina fasciata,* cut-throat weaver (pers. comm., Baptista)
  - *Erythrura trichroa,* blue-faced parrot finch (Nicolai, 1964)
  - *Chloebia gouldiae,* Gouldian finch (Nicolai, 1964)
  - *Lonchura cantans,* African silverbill (Immelmann, 1969)[a]
  - *Lonchura striata,* white-backed munia (Bengalese finch) (Immelmann, 1969)[a]
  - *Padda oryzivora,* Java sparrow (pers. comm., Yamaguchi)

TAXONOMIC DISTRIBUTION OF SEXUAL IMPRINTING (*continued*)

- Ploceidae
  - *Viduinae (vidua sp.)* (Nicolai, 1964[a]; Payne, 1973)
  - *Passer domesticus,* house sparrow (Cheke, 1969)[a]
  - *Passer montanus,* Eurasian tree sparrow (Cheke, 1969)[a]
- Corvidae
  - *Pica pica,* black-billed magpie (Goodwin, 1948)
  - *Corvus monedula,* jackdaw (Lorenz, 1935)
  - *Corvus brachyrhynchos,* American crow (Klinghammer, 1967)
  - *Corvus corax,* common raven (Gwinner, 1964)

[a] Experimental studies or very well documented case studies with several individuals.

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