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# Delayed maturation in birds in relation to social foraging and breeding competition

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## ABSTRACT

Delay in the achievement of adult appearance is common in many species of birds, but the adaptive significance of delayed maturation is unclear. Most adaptive hypotheses focus on benefits of honestly advertising youth and inexperience during the breeding or non-breeding season. Generally, delayed maturation in traits such as plumage is expected to be more prevalent in species that experience more competition for resources. I examined the association between delayed maturation and extent of competition in a large number of pairs consisting of closely related species with contrasting modes of maturation. The occurrence of delayed maturation increased in species that foraged in flocks rather than solitarily, supporting the hypothesis that competition for food during the non-breeding season is associated with the evolution of delayed maturation. Delayed maturation was more likely in dichromatic species, which are thought to experience more intense sexual selection, suggesting an association between delayed maturation and breeding competition. Delayed maturation was also more prevalent in cooperative breeders, but more often involved non-plumage traits, such as iris coloration, suggesting a cost to the use of plumage signals. As dichromatic species and cooperative breeders often flocked in the non-breeding season, the relative contribution of factors acting in each season remains to be established. However, the results suggest that the scope for factors acting alone in the breeding season is limited.

*Keywords*: birds, breeding competition, cooperative breeding, delayed maturation, flocking, pairwise comparative method, plumage dichromatism.

## INTRODUCTION

In birds, individuals usually achieve full adult coloration at the end of the post-juvenile moult. In many species, however, full adult coloration is only achieved after a delay lasting from one season to several years (Lawton and Lawton, 1986; Chu, 1994). In delayed species, non-adult coloration can persist well into the first breeding episodes, although many species show no overlap between delayed maturation and the onset of breeding activity (Rohwer and Butcher, 1988). Adaptive hypotheses for delayed maturation, especially with respect to

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plumage, have focused on benefits of advertising youth and inexperience either during the breeding or non-breeding season.

During the breeding season, young birds may benefit from non-adult coloration in two contexts. First, the transitional coloration of young males has often been noted to be female-like in species with dichromatic plumage. Such female mimicry would allow young males to bypass more easily the territorial defences of older males and gain access deceptively to territories and females (Rohwer *et al.*, 1980). Second, the appearance of young birds could act as a signal of low status to reduce aggression from older males when competing for limited breeding resources (Lyon and Montgomerie, 1986).

From the perspective of breeding, delayed maturation may be expected to occur more often in species that are subjected to higher levels of competition for mates or territories. This should be the case in mating systems such as polygyny or lekking where males compete intensely for access to females (Lyon and Montgomerie, 1986; McDonald, 1989). Generally, competition may be more intense in species experiencing more sexual selection, as evidenced by greater size dimorphism or plumage dichromatism (Dunn *et al.*, 2001). Delayed maturation may also be more prevalent in colonial breeders, where opportunities for extra-pair copulations are thought to be more frequent (Møller and Birkhead, 1993; Westneat and Sherman, 1997).

In the non-breeding season, non-adult coloration may signal subordinate status in a dominance hierarchy where young birds are at a disadvantage when competing for food with older individuals (Rohwer, 1975; Rohwer and Butcher, 1988). The chances of survival for these young birds may be increased by avoiding costly fights. Competition may be expected to be more intense in species that forage in groups, where opportunities to interact with more dominant companions should be more frequent (Hardy, 1961; Rohwer, 1975; Lawton and Lawton, 1986). Groups may be composed of mostly unrelated individuals but may also comprise family parties in cooperative breeders where young birds delay dispersal and remain in the family territory outside the breeding season.

Although empirical studies in many species of birds have documented the consequences of delayed maturation in terms of acquisition of food or breeding resources (e.g. Hill, 1996; Muehter *et al.*, 1997; Senar *et al.*, 1998; Conover *et al.*, 2000), it remains unclear why the extent of delayed maturation varies across species. Previous comparative analyses have only been partially successful in identifying the ecological traits associated with the occurrence of delayed maturation. Analyses to date have usually considered variation across species using individual species as units of analysis (Rohwer *et al.*, 1980; Studd and Robertson, 1985; Lawton and Lawton, 1986; Lyon and Montgomerie, 1986; Montgomerie and Lyon, 1986; Rohwer and Butcher, 1988), ignoring the fact that closely related species often show similar morphological and ecological traits as a result of common ancestry rather than independent evolution (Harvey and Pagel, 1991). Previous analyses have also focused on very specific clades of birds such as North American dichromatic passerines (Rohwer and Butcher, 1988), corvids (Lawton and Lawton, 1986) or fringillids (Bjorklund, 1991). It remains to be shown whether patterns uncovered in these clades show any generality across a wider set of species.

Much of the emphasis on delayed maturation also centres on plumage, while other traits that often show delayed maturation, such as iris, beak or leg coloration (Miskelly, 1981; Lawton and Lawton, 1986; Craig, 1988), have received less attention. In contests for limited resources, these traits could also convey information about status, especially when their use is less costly than plumage signals (Grant, 1990; Johnson, 1999). Other traits, such as body size or ornament size, could also conceivably provide information about age, especially in large species with slow development. However, differences in size are mostly unavoidable consequences of growth patterns. Size-related features thus lack the flexibility in maturation rate often associated with trait coloration.

I examined the association between delayed maturation and extent of competition during the breeding and non-breeding season in a large set of species drawn after an examination of all extant bird families. The data set consisted of pairs of closely related species with contrasting modes of maturation. Since closely related species are quite similar morphologically and ecologically, consistent variation in ecological traits across pairs is likely to be associated with delayed maturation.

## METHODS

### Data collection

I collected data on morphological and ecological traits from books on avian ecology and behaviour and ornithological journals. Morphological traits included plumage, iris, beak and leg coloration, male and female body mass, sexual size dimorphism and plumage dichromatism. Ecological traits included breeding density, mating system, flocking during the non-breeding season and migration behaviour. Social mating system was not documented systematically in the data set. As plumage dichromatism and sexual size dimorphism are closely associated with social mating system (Dunn *et al.*, 2001), I used these two variables as proxy for social mating system. The criterion for data selection was a detailed knowledge of maturation rate and social tendencies during the breeding and non-breeding season.

I characterized each species with respect to maturation rate. Non-delayed species acquired their full adult coloration at the end of the post-juvenile moult. In delayed species, full adult coloration for at least one trait was not achieved at the end of the post-juvenile moult and, in some cases, was only achieved several years later. In delayed species, traits differed in terms of overall coloration or pattern.

A delay in plumage maturation may arise because birds moult new feathers, which are not coloured as in adults, or retain differently coloured or patterned juvenile feathers (Chu, 1994). In non-delayed species, retention of some juvenile feathers can occur and could thus provide a clue to ageing. In addition, feather abrasion during the first plumage season is often more pronounced for these retained feathers. However, ageing in these species, based on these criteria, is usually only possible to determine in the hand (Prater *et al.*, 1977; Jenni and Winkler, 1994). Here, I only classified species as delayed when differences in coloration or pattern could be distinguished easily from a picture or drawing. I assumed that birds could also use the same information to assess age.

Other morphological and ecological traits were treated as continuous or categorical data. Body mass was recorded, if available, in the non-breeding season to provide a more uniform assessment of body mass across species. Since male body mass was available more often, I used these values for further analysis. I determined sexual size dimorphism by dividing male body mass by female body mass. I coded each species for the presence or absence of plumage dichromatism based on a description of plumage differences between the sexes during the non-breeding period.

I classified species into one of three categories of flocking behaviour based on accounts of aggregations during the non-breeding season: (1) strictly solitary, birds forage singly;

(2) occasionally social, aggregations of more than two birds occur under peculiar circumstances but are not common and involve few individuals; and (3) strictly social, individuals search for food and feed in groups. Family parties that remained together after the breeding season were also considered flocks.

I coded species as migratory when short- or long-distance movements occurred commonly after breeding. Clearly nomadic species were also considered migratory for the purpose of the study. Otherwise, I considered species as sedentary. Moulting strategies are often timed in relation to migration activity and could thus vary as a function of the extent of movements after breeding (Voelker and Museum, 1996).

I classified species as colonial breeders when birds occasionally or always bred in groups or solitary otherwise. I classified species as cooperative breeders when more than the two putative parents participated in parental duties or non-cooperative breeders otherwise. Species were classified as lekking when males aggregated at communal display sites before the breeding season.

Delayed maturation can overlap with breeding activity when birds mate while still not fully developed in terms of coloration. Birds, on the other hand, can complete maturation before the first breeding episode. The amount of overlap can only be determined in species where the age at sexual maturity is known. Note that this may not always correspond to the age at first breeding, since sexually mature birds may be prevented from breeding in their early years.

### Phylogenetic analysis

I used the pairwise comparative method to control for possible similarities among closely related species due to common ancestry (Møller and Birkhead, 1992). I used recent phylogenetic information, based on molecular or morphological traits other than those considered here, to form closely related pairs of species with contrasting modes of maturation. Lack of information on morphological or ecological traits, together with insufficient knowledge of phylogenetic relationships, narrowed the number of species pairs that could be used for comparisons. One phylogenetic tree could yield several pairs as long as pairs failed to share common branches (Maddison, 2000). When phylogenetic information was not available at the species level, I formed pairs by selecting two species from the same genus with a preference for species that occurred in the same geographical area. I examined species from all extant bird families to increase the sample size and also to avoid sampling repeatedly in the same clades.

I used the sign test to examine the hypothesis of consistent changes across the set of species pairs in the states of morphological and ecological traits associated with the two modes of maturation. For the analysis of each independent variable, I only included pairs where the two species exhibited different values (Read and Nee, 1995). To control for repeated testing within the same data set, I used the sequential Bonferroni test procedure to determine statistical significance (Rice, 1989). I used chi-square tests to examine associations between categorical variables.

## RESULTS

I uncovered 159 pairs of species with contrasting modes of maturation among 74 families (for details, contact the author or see the online version of the paper at www.evolutionary-ecology.com).

Delayed maturation was significantly associated with flocking, plumage dichromatism and cooperative breeding. In the 69 pairs with contrasting values for the flocking state, the delayed species flocked to a greater extent than the non-delayed species in 54 pairs (78.3%, $P < 0.0001$). In the 39 pairs with contrasting values for plumage dichromatism, the delayed species was more dichromatic than the non-delayed species in 32 pairs (82.1%, $P < 0.0001$). The delayed species was more likely than the non-delayed species to be a cooperative breeder in 15 of the 18 pairs with contrasting values for cooperative breeding status (83.3%, $P = 0.008$). The lekking species showed delayed maturation in all five pairs with contrasting values for the trait; however, this finding was non-significant ($P = 0.063$). No other traits were significantly associated with delayed maturation after the Bonferroni adjustment (male body mass: 83 delayed species larger, $n = 137$, $P = 0.016$; breeding density: 19 delayed species with higher breeding density, $n = 27$, $P = 0.052$; migration: 25 delayed species more migratory, $n = 40$, $P = 0.15$; sexual size dimorphism: 38 delayed species more dimorphic, $n = 76$, $P = 1.0$).

Among the delayed species, flocking was not associated with the occurrence of plumage dichromatism ($\chi^2 = 0.13$, $P = 0.72$). Flocking occurred in all but one of the six lekking species, in all but four of the 36 colonial breeding species and in all but three of the 24 cooperative breeders. Plumage dichromatism was less frequent among the cooperative breeders (7 dichromatic species, $n = 14$) than among the non-cooperative breeders (77 dichromatic species, $n = 132$) ($\chi^2 = 6.9$, $P = 0.008$).

In species where age at sexual maturity could be determined, overlap between delayed maturation and the onset of breeding activity occurred in 58 pairs, while no overlap took place in 48 pairs. When an overlap took place, 39 species (67.2%) exhibited plumage dichromatism, 29 of which (74.4%) flocked during the non-breeding season. When no overlap occurred, the delayed species flocked to a greater extent than the non-delayed species in 22 of the 26 pairs with contrasting values for the flocking state (84.6%, $P = 0.0005$).

The morphological traits involved in delayed maturation varied as a function of breeding tactic. Delayed plumage maturation occurred in almost all colonial [21 species (95.5%), $n = 22$] and solitary breeders [86 species (94.5%), $n = 91$] but was less common in cooperative breeders [14 species (58.3%), $n = 24$]. Delayed maturation associated with changes in iris or bare part coloration, but not in plumage, were therefore more common in cooperative breeders ($\chi^2 = 25.3$, $P < 0.0001$).

## DISCUSSION

I examined the association between various ecological traits indicative of competition for resources during the breeding or non-breeding season and the occurrence of delayed maturation in various traits including plumage, iris, beak and leg coloration. The pairwise phylogenetic analysis of a large sample of species from many families identified several correlates of delayed maturation in birds.

The occurrence of flocking during the non-breeding season increased the likelihood of delayed maturation. The results suggest that competition for resources in the non-breeding season, thought to be brought about by flocking, is an important correlate of the evolution of delayed maturation. In contrast, factors acting in the breeding season alone, such as female mimicry or breeding status signalling, need not be invoked at all in the many species that failed to show an overlap between delay and the onset of breeding activity. Flocking still remained a significant correlate of delayed maturation when no such overlap occurred. The results support the finding that several North American dichromatic passerine species with delayed plumage maturation nevertheless achieve full adult coloration before the first breeding episode, which implies that factors acting in the non-breeding season were probably more relevant in this subset of species (Rohwer and Butcher, 1988).

The relationship between delayed maturation and flocking rests on several assumptions about competition for food and aggression during the non-breeding season. Although the current body of evidence is quite suggestive, more empirical work is needed to examine these assumptions in delayed species. Manipulation of plumage traits in fully mature birds foraging in flocks has been shown to affect access to food as predicted by the status-signalling hypothesis in the non-breeding season (Senar, 1999). The plumage of young birds could be considered a similar badge of status that would help settle disputes for food in flocking species. In line with this hypothesis, adult siskins (*Carduelis spinus*) directed less aggression towards young males in transitional plumage (Senar *et al.*, 1998). Similarly, young Darwin's finches (*Geospiza fortis*) in transitional plumage avoided attacks by more dominant adults when feeding together (Grant, 1990). There is also some indication that differences in leg (Miskelly, 1981) or iris coloration (Craig, 1988), induced by delayed maturation, can be used to settle dominance struggles in birds of different ages.

The occurrence of delayed maturation increased in more dichromatic species. Plumage dichromatism is associated with more intense sexual selection (Dunn *et al.*, 2001), which would support the prediction that more intense competition for breeding resources can foster the evolution of delayed maturation (Lyon and Montgomerie, 1986). Although several studies have documented delayed plumage maturation in dichromatic species, the contribution of competition levels in the non-breeding season has often been overlooked (Rohwer and Butcher, 1988). The possibility exists that more dichromatic species are also more sociable in the non-breeding season. The proportion of dichromatic species that failed to flock in the non-breeding season was quite small, suggesting that the effects of breeding competition and flocking on maturation can be confounded in many species that show an overlap between delay and the onset of breeding activity. The same could be said for the lekking and cooperative breeding species considered here, which nearly all flocked in the non-breeding season. The scope for factors acting only in the breeding season thus appears limited.

Delayed maturation in plumage traits was less common in cooperative breeders than in other species, suggesting an increase in the use of iris or bare parts to signal status. In dabbling ducks, bright bill coloration is more prevalent in monomorphic species (Johnson, 1999), suggesting a shift in signalling from bright plumage coloration to bright bill coloration. Such a shift takes place presumably because advertising with a conspicuous trait such as plumage is more costly than advertising with the smaller, less conspicuous bill. Higher prevalence of delayed maturation in iris or bare parts in cooperative breeders may represent another instance of transference, suggesting as above that signals conveyed with plumage traits can be more costly. Because cooperative breeders often defend year-round territories, signalling subordinate status to neighbours using plumage traits could be disadvantageous in territorial encounters. Signals conveyed by iris or bare parts, which are probably perceived at a shorter distance, may be useful in the context of the family hierarchy without compromising territorial defence (Grant, 1990).

Colonial breeding species, which are often thought to experience more intense sexual selection, showed delayed maturation to a similar extent as non-colonial species. In other studies, size dimorphism, plumage dichromatism and the occurrence of extravagant feather ornaments, traits that are all thought to be related to the intensity of sexual selection, also showed little association with breeding density (Beauchamp, 1999; Cuervo and Møller, 2000). In addition, there is little evidence that opportunities for extra-pair copulations increase with breeding density (Westneat and Sherman, 1997). The idea that colonial breeding exacerbates competition for mates may not be as clear as once thought, hence the lack of a relationship with delayed maturation.

Two main challenges remain. First, it is important to document the costs and benefits of transitional appearance in young birds during the breeding and non-breeding season, since adaptive hypotheses for the evolution of delayed maturation make specific assumptions about the amount of competition for resources and the use of aggression. Second, future work should aim to tease apart the relative contribution of factors acting in the non-breeding and breeding season in species that show an overlap between delay and the onset of breeding activity.

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