

On the evolution of the occurrence of subadult plumage



The Painted Bunting is one of the well-studied species in which subadult plumage occurs

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Abstract

Young birds that do not achieve somatic maturation in the same year as they achieve sexual maturation, wear a plumage distinct from that of the definitive adult plumage during their first potential breeding year. This feature has got extensive attention in literature as 'delayed plumage maturation'. This paper argues that the occurrence of subadult plumage is a better name as it does not make any advanced assumptions on the evolutionary development of subadult plumage.

Although the occurrence of subadult plumage does not have to be adaptive, most hypotheses on the evolution of subadult plumage assume this trait to be adaptive. In studying the adaptiveness of a trait there are two major approaches. The within species approach considers the adaptiveness of the trait within a single species by relating variation in plumage colour to variation in fitness-related parameters (either natural variation (descriptive approach) or artificial variation (experimental approach)). The comparative approach compares the occurrence of subadult plumage in several species and uses the generality of the trait to get an indication of its adaptiveness. Comparative studies can either use phylogeny or not use phylogeny. The best understanding of the adaptiveness of subadult plumage will follow from the combined use of the comparative approach with phylogeny and of the experimental within species approach. The comparative approach with phylogeny is necessary to identify independent groups and suitable control groups, the experimental within species approach can actually prove whether something is adaptive or not.

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Introduction

Aim

This study deals with the phenomenon 'delayed plumage maturation', which has got broad attention in literature of the last few decades (see Hill 1996). More than giving an extensive review, the aim of this study is to discuss the different approaches possible in studying the evolutionary changes and the adaptiveness of this trait.

Methodology

Terminology of moult and plumages

The traditional concept of 'plumage' is that it describes the general appearance of a bird and that a bird can wear only one plumage at a time. Humphrey and Parkes (1959), while standardising moult and plumage terminology, have restricted the term 'plumage', however, to a single generation of feathers and introduce the terms 'aspect' and 'feather coat' to additionally describe a bird. 'Aspect' serves to describe the total appearance of a bird at a specific moment, whereas 'feather coat' is used in descriptions of aggregates of feathers, thus distinguishing groups of feathers that belong to different plumages.

Birds can renew their plumage by moulting. Moulting, as defined by Humphrey and Parkes (1959), is the shedding of feathers and the replacement of most or all of them by a new generation of feathers. A moult can either be 'complete' or 'partial'; in a complete moult all feathers of a plumage are replaced, whereas in a partial moult only specific portions of the bird's covering of feathers are renewed. Humphrey and Parkes have furthermore argued to name all moults according to the incoming plumage, always starting with the prefix 'pre'.

The number of moults and plumages a particular species has, is expressed per 'cycle'. A cycle is defined to run from a given plumage or moult to the next occurrence of the same plumage or moult. In most species, though not in all, a cycle takes one year. The number of moults and thus of plumages per cycle varies per bird species. When a species moults only once per cycle and thus has only one plumage per cycle, this plumage is called the basic plumage and the preceding moult is called the prebasic moult. This moult is almost always complete. When a bird species moults twice per cycle, the plumage following the complete moult is called the basic plumage (following the prebasic moult) and the second plumage is called the alternate plumage. This alternate plumage follows the, mostly partial, prealternate moult. If a bird species moults more than twice per cycle (either three or four times), the additional moults and plumages are called the presupplemental moults (A and B) and the supplemental plumages (A and B). These supplemental moults and plumages can either be placed before the alternate moult and plumage or after it. The terminology of moults and plumages is illustrated by figure 1, which shows the pattern of the plumage succession of the Scarlet Tanager (*Piranga olivacea*). The Scarlet Tanager moults twice per cycle and its plumages are thus called 'basic' and 'alternate'.

The occurrence of subadult plumage

Most juvenile birds moult directly through a complete first prebasic moult from their juvenile plumage to the definitive adult plumage. Alternatively, there is a considerably large group of bird species in which juvenile males need two moults to acquire the definitive adult plumage. Birds in this group have a partial first prebasic moult and do not obtain somatic maturity before their second (complete) prebasic moult, i.e. not before their second fall. Mostly, these birds have already become sexually mature long before this. This results in the situation in which some second-year birds (i.e. birds in their second calendar year) wear a plumage readily distinguishable from adult birds during their first potential breeding season. These second-year birds are called 'subadult birds'. The heterochrony (opposite of synchrony) in timing of somatic maturation in relation to the timing of sexual maturation in subadult birds, has achieved much attention in scientific literature throughout the second half of this century under the name 'delayed plumage maturation'. Delayed plumage maturation is not restricted to a specific order, even though early literature on this phenomenon concentrates almost exclusively on North American passerine birds (e.g. Selander 1965, Rohwer 1978, Rohwer *et al.* 1980, Procter-Gray and Holmes 1981, Studd and Robertson 1985, Lyon and Montgomerie 1986). According to Thompson (1991) subadult birds occur in at least seven orders and 11 families of non-passerine birds and in at least 21 families of passerines (see for references: Thompson 1991). These families "include species that are sexually monochromatic and dichromatic, that have various mating systems and migratory strategies, and that occur throughout the world in diverse habitats". Only in the last 15 years attention has been paid to the occurrence of subadult plumage in (groups of) bird species other than North-American passerines (e.g. Foster 1987, Järvi *et al.* 1987, Slagsvold and Saetre 1991, Hakkarainen 1993, Saetre *et al.* 1993, Chu 1994, Saetre and Slagsvold 1996). And although delayed plumage maturation is almost exclusively known for males, two species have been reported in which it occurs in females (the Hooded Warbler (*Wilsonia citrina*) and the Tree Swallow (*Tachycineta bicolor*); see Lozano and Handford 1995).

Rohwer *et al.* (1980), who are the basic reference in literature on delayed plumage maturation, have defined delayed plumage maturation as "males achiev[ing] obvious plumage maturity 1 year after their first potential breeding season". Thompson (1991) focuses more on the distinction between somatic and sexual maturity. He defines it as "the delayed acquisition of adult plumage by sexually mature birds". Hill (1996) points out the ambiguity of both the terms 'obvious plumage maturation' and 'sexually mature'. In many species second-year males are on average less brightly or distinctly coloured than adult males, though they are generally considered not to show delayed plumage maturation. Similarly many second-year males have smaller testes and produce less sperm than older males, though they are considered to be sexually mature. Hill therefore proposes a new definition of delayed plumage maturation: "The delayed acquisition of definitive nuptial plumage until after the first potential breeding season such that the subadult plumage has a pattern distinct from that of males in definitive plumage but not necessarily from that of females" (Hill 1996). Problem with this new definition of Hill and the term 'delayed plumage maturation' itself is that in describing the occurrence of a subadult plumage, an evolutionary direction is implicitly assumed (*delayed* plumage maturation). For this reason (more thoroughly discussed in the next paragraph), this study does not use the term delayed

plumage maturation. Instead the term 'the occurrence of subadult plumage' is used to describe the heterochrony in sexual and somatic maturation. Bird species that acquire their definitive plumage one year after their first potential breeding season are said to have a 'subadult plumage' in their second year. This subadult plumage has a pattern distinct from that of the definitive plumage of adults of the same sex but not necessarily from that of the other sex.

Heterochronic events in the occurrence of subadult plumage

In the current situation (graphically represented in figure 2), some bird species develop their definitive adult plumage in the same year as they become sexual mature (state 0), whereas some other species become somatic mature not before one year after they became sexual mature (state 1). By using the term 'delayed plumage maturation' for the occurrence of a subadult plumage in second-year males nearly all previous studies implicitly assume one specific heterochronic event in the evolution of subadult plumage (But see Björklund 1991, Chu 1994 and Hill 1996) to explain this current situation. 'Delayed plumage maturation' namely is the post-displacement (retardation) of somatic maturation from an ancestral situation in which the timing of sexual and somatic maturation used to be synchronic (all bird species state 0; figure 2c).

Alternative hypotheses on heterochronic events resulting in the observed current relations between the timing of sexual and somatic maturation, however, are possible as well. State 0, for instance, can also be the result of a pre-displacement of sexual maturation from an ancestral situation in which somatic maturation was achieved the year before sexual maturation (figure 2a). An alternative possibility that can explain the observed current relations, is the pre-displacement of somatic maturation in some birds from a situation in which the subadult plumage is the ancestral state (all birds state 1; figure 2b). A third alternative hypothesis can be that the observed heterochrony is the result of a displacement of sexual maturation rather than that of somatic maturation (figure 2d). In this case the ancestral state has been the synchronic timing of sexual and somatic maturation. The current occurrence of birds in state 1 can be explained from this ancestral state by the acceleration of sexual maturation. The acceleration of sexual and somatic maturation can explain the current occurrence of birds in state 0 in this situation.

As various heterochronic events are possible, it is of major importance to realise that the current situation, in which two states occur (0 and 1) can be derived from various ancestral states. To fully understand the occurrence of subadult plumage, it is necessary to get insight in its evolutionary development (Björklund 1991, Chu 1994, Hill 1996).

Phylogeny

One way of gaining insight in evolutionary developments is the use of phylogeny, the evolutionary relations between species (O'Hara 1988, Harvey and Pagel 1991, Felsenstein 1985). Through studies on phylogeny, the direction of evolutionary changes in the occurrence of subadult plumage can become clear. Moreover the way in which different species are related to a common ancestor can become clear and dependencies between them can be unravelled. This is important for determining the evolutionary change that lies at the origin of the occurrence of subadult plumage in

the species of interest and thus to determine suitable control groups to compare the species of interest with.

Figure 3 shows a made-up phylogenetic tree on the evolutionary relations between six species (A to F) concerning one specific trait. Let us assume this trait to be the occurrence of subadult plumage; species can either be in state 1 (species C, D and F, subadult plumage occurs) or in state 0 (species A, B and E, subadult plumage is absent). From this phylogenetic tree it can be interpreted that subadult plumage occurred in the common ancestor of the six species (state 1). In the evolution of species F from this ancestor, no change in the trait subadult plumage has occurred; the occurrence of subadult plumage in this species is said to be 'ancestral'. In the evolution of the species the species A and B, on the contrary, the trait subadult plumage has changed once (change I). The absence of subadult plumage in these two species is said to be a 'derived' trait; subadult plumage occurred in the common ancestor. In the evolution of species C and D two changes have occurred; first the occurrence of subadult plumage has been lost (I) and then it has been gained (II) again. Though the common ancestor of the six species was in state 1, the direct ancestor of species C and D was not and the occurrence of subadult plumage in these two species is said to be a derived trait (as is the absence of subadult plumage in species E). Thus although certain species share the same trait (for instance species A, B and E, which lack subadult plumage), this trait can be evolved in different ways, through different selective mechanisms. For this reason the question why subadult plumage is (or is not) absent in specific species should be split into as many questions as there are (more or less) independent groups of species (for instance one question concerning species A and B and one concerning species E), each of the different questions with its own suitable control species. When, for instance, interested in the absence of subadult plumage in species E, one is interested in change III. A suitable control group to compare this trait with would be species D, as the species D and E share the same origin. The absence of subadult plumage in species A and B, on the contrary, is not due to change III, but to change I (species F being the most suitable control group). Comparison with species D will not reveal the selective mechanism that has resulted in the absence of subadult plumage in the species A and B.

The hypotheses

Several hypotheses have been developed to explain the occurrence of subadult plumage in second-year males. Each of them is actually a composite of two hypotheses; one on the proximate mechanism of the occurrence of subadult plumage and one on the selective mechanism favouring the evolution it. The various hypotheses together with the accompanying proximate and selective mechanisms are summarised in table 1 (see also Lyon and Montgomerie 1986). The hypotheses are competitive and non-overlapping with respect to the proximate mechanism of subadult plumage they suppose, but not with regard to the selective mechanism favouring the occurrence of subadult plumage; the selective mechanism proposed by different hypotheses may be shared with other hypotheses.

Almost all studies on the occurrence of subadult plumage assume this trait to be adaptive (an adaptive trait improves survival and reproduction and has evolved through natural selection). Consequently almost all hypotheses on this subject try to explain the adaptiveness of it. Adaptation, however, is not the only mode of evolution (Harvey and Pagel 1991). A trait can also be maintained by genetic (or

developmental, allometric or mechanical) constraints, be the result of genetic drift or have been evolved due to selection on another, correlated, trait (Savalli 1995). Only little attention has been paid to non-adaptive modes of evolution; the moult constraint hypothesis (Rohwer and Butcher 1988) is the only hypothesis on the occurrence of subadult plumage that does not seek an adaptive explanation.

The hypotheses that do assume the occurrence of subadult plumage to be adaptive have some important assumptions in common. All assume second-year males to be in competitive disadvantage compared to adult males (for instance due to the lack of experience). Moreover the operational sex-ratio is assumed to be strongly male biased, resulting in intense male-male interactions. The adaptive hypotheses do not all share the same selective mechanism. The cryptic hypothesis assumes the occurrence of subadult plumage to enhance early survival, whereas the other three hypotheses assume it to increase the probability of breeding in their first potential year of breeding.

Moult constraint hypothesis

The moult constraint hypothesis proposes that first-year males are unable to attain the definitive breeding plumage by their first potential breeding season. Reason for this is either the lack of the energy needed for the required feather replacements or a genetic constraint, which has prevented the evolution of the required spring moult. According to this hypothesis, the subadult plumage of second-year males is a maladaptive trait, at least during the breeding season.

Cryptic hypothesis

According to the cryptic hypothesis (Selander 1965, Procter-Gray and Holmes 1981, Zack and Stutchbury 1992; also called the 'sexual selection hypothesis' or the 'delayed maturation hypothesis' (see Lyon and Montgomerie 1986)), the subadult plumage of second-year males serves to lower their risk of mortality and thus to increase their lifetime reproductive success. One of the main assumptions underlying this hypothesis is that birds in a bright plumage suffer a higher risk of mortality than birds in a more cryptic plumage, either by being more vulnerable to predation or by higher costs of intrasexual competition. As second-year males do not benefit as much from territorial signalling as do adult males (they are in competitive disadvantage compared to adult males), breeding attempts are more costly for them; they will have a lower return. Second-year males would therefore better reduce their reproductive investment and, by doing so, maximise their early survival. This idea is best presented by Procter-Gray and Holmes (1981): according to them 'not being bright' is "generally favoured when the costs of a bright plumage (intrasexual aggression / predation) exceed the mating benefits".

Why then do second-year birds wear a subadult plumage that is less cryptic than the juvenile plumage? According to Selander (1965), second-year males still wear an intermediate subadult plumage, because there are some benefits of a subadult plumage over a juvenile plumage. These benefits may be that subadult birds do have some chance on breeding, that subadult birds can gain experience in territorial and courtship behaviour or that subadult birds have some advantage in male-male encounters at feeding or roosting areas (Selander 1965).

Status signalling hypothesis

The status signalling hypothesis (Lyon and Montgomerie, 1986) suggests that second-year males wear a subadult plumage to reliably signal their subordinate status towards adult males. Main assumptions of this hypothesis are that adult males can distinguish second-year males both as males and as subordinates and that these second-year males are indeed treated less aggressively. Furthermore the females are assumed to choose mates on the basis of intrinsic male attributes (i.e. plumage brightness) rather than on extrinsic cues such as territory quality. The operational sex ratio is assumed to be strongly male-biased, resulting in intense male-male competition. Under these conditions a second-year male in a subadult plumage is no threat for adult males (it is only a minor competitor for females) and therefore aggressiveness in male-male interactions between adults and subadult birds is supposed to reduce. In this way honestly showing subordination can result in an increased probability of mating or in increased experience of high quality territories. The cost of honestly showing subordination by wearing a (dull) subadult plumage, however, is the reduced probability of obtaining a mate.

Female mimicry hypothesis

The female mimicry hypothesis (Rohwer *et al.* 1980, Rohwer 1983) suggests that second-year males benefit from reduced aggression in male-male interaction with adult males by mimicking females in appearance. For the second-year males, the reduced aggression results in an increased probability of breeding in their first potential year of breeding.

An important assumption underlying the female mimicry hypothesis is that females choose territories rather than male characteristics. Moreover adult males are assumed to settle on the breeding grounds prior to second-year males. By the time second-year males arrive on the breeding grounds, all high-quality habitats are already occupied. In mimicking females, second-year males are supposed to gain entry to the high-quality habitats already occupied by adult males. The benefit of entering these habitats might be the accumulation of site dominance or the gain of information (e.g. on the renewal and exploitation of food resources). The benefit of entering high-quality habitats is thought to be valid only the first few hours. Once the critical information is acquired, second-year males must sing and fight as vigorously as any other males to hold their place. By doing so they will be recognised as males.

Female mimicry is considered as a subdivision of agonistic sexual selection (i.e. intrasexual selection), in which deceit rather than brute force provides a competitive advantage. Ways other than deception by mimicked appearance known in female mimicry are deception by mimicked behaviour or by mimicked chemical signals (e.g. Thornhill 1979, Forsyth and Alcock 1990). Moreover female mimicry is not restricted to birds, but it is known from various other class of animals (see for references: Forsyth and Alcock 1990).

Juvenile mimicry hypothesis

According to the juvenile mimicry hypothesis (Foster 1987) second-year males mimic juveniles rather than females by wearing a subadult plumage; the juvenile characteristics are thought to be retained. By mimicking juveniles, second-year males benefit from reduced aggression in intrasexual competition with adults. These adult males are thought to be deceived by misrepresenting the preparedness of the second-year males to breed. Second-year males gain access to breeding sites and females and increase their probability of mating. Assumptions underlying this hypothesis are that

adult males can not distinguish between second-year males and juveniles and that aggression towards second-year males is reduced by the higher toleration of juveniles.

Although the five hypotheses share several assumptions, a specific assumption, not shared by any of the other hypotheses, can be formulated for each one. Critical assumption of the moult constraint hypothesis is that the occurrence of subadult plumage is maladaptive. Critical assumption of the cryptic hypothesis is that dull second-year males would suffer a higher risk of predation if they were brighter. Critical assumption of the status signalling hypothesis is that adult males can recognise dull second-year males both as males and as subordinates and treat them less aggressively as a result. Critical assumption underlying the female and the juvenile mimicry hypothesis is that adult males are unable to distinguish second year males from adult females and juveniles respectively.

Winter and summer hypotheses

Rohwer and Butcher (1988) have pointed out with good reason that early literature paid undue attention to adaptations to the breeding season. As all North American passerines that have a subadult plumage in their first potential breeding summer also have one in their first winter, it is indeed relevant to take the possibility into account that the subadult plumage is an adaptation to other seasons than the breeding season. Rohwer and Butcher illustrate the relevance of this remark by pointing at a group of 16 North-American passerine species in which males wear subadult plumages only during their first winter. In all of these species, subadult males undergo a complete body moult in spring which causes them to lose their subadult plumage and acquire a plumage during the breeding season that is very similar or identical to that of adult males. This indicates that subadult plumage in these species must be an adaptation to winter. Another argument with which they stress the importance of considering the possibility that subadult plumage is an adaptation to the winter season, is the fact that in none of the 42 species with extensive moult in spring, males remain or become female-like. If males of these species would have done so, it would have been strong support for the summer hypotheses. Now it slightly supports the idea that subadult plumage is an adaptation to the winter season.

Current literature follows the distinction of hypotheses in separate winter and summer hypotheses as made by Rohwer and Butcher (Thompson 1991, Hill, 1996). Two variants of the cryptic hypothesis, the status signalling hypothesis and the female mimicry are treated as separate hypotheses. This study, on the contrary, does not consider the season in which a specific selective mechanism functions important enough to distinguish two variants of each hypothesis. Seasonal aspects are at most recognised as subdivisions of the accompanying hypothesis. Rationale behind this is that the selecting mechanism involved is the major concern of the hypotheses. The specific period or season in which the selective mechanism is active is of subordinate importance. Separating hypotheses on the basis of the season in which the selective mechanisms are relevant would give rise to numerous new hypotheses.

Approaches of studying evolutionary changes

In discussing approaches of studying evolutionary changes and adaptiveness of traits, Harvey and Pagel distinguish two common approaches that are fundamentally different (Harvey and Pagel 1991). The first approach is used by population geneticists. They concentrate on genotypic variation of a specific trait in order to understand evolutionary changes in this trait ('kinematic approach'). The second approach, used by ecologists, concentrates on phenotypic variation in the trait of interest. Basic idea in this second approach of studying evolutionary changes is that traits have been evolved through natural selection to maximise fitness ('optimality modelling'). As literature on the occurrence of subadult plumage concentrates on the second approach, I will only discuss methods used in this approach.

In studying evolutionary changes on the base of phenotypic variation, distinction can be made between the within species approach and the comparative approach (Harvey and Pagel 1991). The within species approach considers the adaptiveness of a specific trait within a single species on the base of phenotypic variation. Two approaches can be distinguished within this approach, depending on the kind of phenotypic variation used. In the 'descriptive approach' natural variation already present in the trait is related to (certain aspects of) fitness, whereas in the 'experimental approach' phenotypic variation is applied to the trait artificially in order to understand the adaptiveness of it.

The comparative approach considers the adaptiveness of a specific trait through comparison between various (groups of) species. In this approach the generality of the occurrence of a specific trait is used to understand the adaptiveness of this trait, after correcting for dependency in the occurrence of the trait. Correlated evolution among characters or between characters and environments is seen as an evidence for adaptiveness of traits. Comparative studies can be subdivided in those that use phylogeny (Felsenstein 1985, O'Hara 1988) and those that do not use phylogeny. This subdivision is partly a temporal one, as phylogeny has only become available in the last decade. Studies using the phylogenetic relations between (groups of) species are either directional or non-directional (Harvey and Pagel 1991). Directional phylogenetic studies concentrate on the directions and rates of evolutionary changes between ancestors and descendants (down lineages over time). Non-directional phylogenetic studies analyse evolutionary changes across contemporary species (across different lineages). By the lack of a good fossil record the non-directional approach is used most often.

The various studies on the occurrence of subadult plumage can be subdivided with regard to the approach they use to study the adaptiveness this trait (see table 2). I will discuss some studies of each approach to illustrate the different approaches.

The within species approach

The descriptive approach

Järvi *et al.* test eight hypotheses on the occurrence of subadult plumage within the Pied Flycatcher (*Ficedula hypoleuca*) (Järvi *et al.* 1987). These hypotheses include two non-adaptive hypotheses ('neutral mutation hypothesis' and 'individual recognition hypothesis'). For each of the hypotheses they formulate assumptions and predictions. These assumptions and predictions are then tested by analysing the

observed variation in male plumage colour in relation to various fitness-related parameters (viz. age, body size, physical condition, survival rate, degree of aggressiveness (measured against a dummy), territorial quality, female mate choice, sex ratio of the adult in the population, and degree of reproductive success). As they are able to explain (some) variation in the parameters on the basis of variation in male plumage coloration, they reject both the non-adaptive hypotheses, thus assuming this variation to be adaptive. Two other hypotheses are rejected as well ('female mimicry hypothesis' and 'cryptic hypothesis'). From their study, they cannot reject the four hypotheses left (three intersexual selection hypotheses and one intrasexual selection hypothesis). Therefore, they suggest that the evolution of the observed variation in plumage coloration of male Pied Flycatchers can be explained by a combination of these four hypotheses.

Thompson uses Painted Buntings (*Passerina ciris*) to test the same five hypotheses as discussed in this paper (he, however, does distinguish winter and summer variants as separate hypotheses) (Thompson 1991). From each hypothesis he derives testable predictions regarding subadult male moults and plumages. He then determines the sequence of all moults and plumages and resulting changes in plumage colour, exhibited by male Painted Buntings from hatching to somatic maturity. From the observed sequence, he is able to reject three hypotheses. He can not reject the (winter) cryptic hypothesis and the (winter and summer) female mimicry hypothesis.

The experimental approach

Slagsvold and Saetre study critical assumptions of the female mimicry hypothesis through experiments in Pied Flycatchers (Slagsvold and Saetre 1991). To test whether adult males are actually deceived by the female-like plumage of second year males, they study behavioural responses of males and females to caged conspecifics with different grades of plumage colour. Furthermore they test whether this possible deceit actually results in the settlement of subadult males in the better habitats, by analysing the settling pattern of males in spring in relation to their plumage colour. They convincingly prove that adult males are indeed deceived and do consider subadult birds as females, as the most female-like subadult males are freed of aggression and are even approached with sexual display by the adult males. Their finding that female-like subadult males are allowed to settle closer to already-established males than dark-coloured males as well makes them suggest that there is an adaptive value of having subadult plumage colour.

Hakkarainen's study concentrates on two hypotheses (female mimicry hypothesis and status signalling hypothesis) on the occurrence of subadult plumage in the European Kestrel (*Falco tinnunculus*). He uses the descriptive approach to relate the quality of obtained habitats and breeding success to observed plumage colour variation in subadult birds. Furthermore he studies the ability of adult males to differentiate between adult females and subadult birds by showing them simultaneously in an aviary. As second-year males with a subadult plumage both obtain better breeding habitats and higher reproductive successes (than adult males that arrived simultaneously with the subadult birds), he suggests an adaptive value to subadult plumage. Moreover his experiments show that adult males are indeed successfully deceived by the subadult plumage of second-year males, supporting the female mimicry hypothesis rather than the status signalling hypothesis.

The comparative approach

Without phylogeny

Rohwer *et al.* (1980) 'test' the female mimicry hypothesis by relating the occurrence of subadult plumage to variation in the environmental variables 'spring arrival time', 'breeding-habitat quality' and 'operational sex-ratio' in North-American passerine bird species (Rohwer *et al.* 1980). Since they find most (5/6) of the predictions accompanying the female mimicry hypothesis confirmed, they regard this theory to be supported.

Lyon and Montgomerie discuss the likelihood of four hypotheses on subadult plumage by relating the occurrence of subadult plumage in North-American passerine bird species with variation in the environmental variable 'territory type' (either all-purpose (nest and food) or nest-only) (Lyon and Montgomerie 1986). They argue three of the hypotheses to lack supporting evidence. They develop a new hypothesis, the status signalling hypothesis and derive the prediction from it that subadult plumage is more prevalent when males defend nest-only territories. As they find a higher proportion of species with subadult plumage defend nest-only territories than of species without subadult plumage, they regard the status signalling hypothesis to be supported.

With phylogeny

In his study on a group of fringillid species, Björklund tests the assumption that the occurrence of subadult plumage is the result of a retardation of the development of adult plumages (Björklund 1991). By examination of two different phylogenetic trees (one based on appendicular myology and the other on DNA hybridisation) he finds that the occurrence of subadult plumage is an ancestral rather than a derived trait. Based on this finding he concludes that subadult plumage is not an adaptive trait in fringillid finches and that the question of interest should be why subadult plumage does not occur in several species in this group.

Hill studies 15 lineages of House Finches and tests the assumption that the occurrence of subadult plumage is an adaptive trait (Hill 1996). He examines a phylogenetic tree based on cladistic analysis and finds that the occurrence of subadult plumage was lost by the ancestral House Finch, but has been regained independently by the three taxa in which subadult plumage currently occurs. Thus he concludes that the occurrence of subadult plumage is an adaptive trait and that hypotheses concerning it are reasonable. He discusses the same hypotheses as Thompson (1991) and can not reject the (winter) cryptic hypothesis, the (winter) female mimicry hypothesis and the (summer) status signalling hypothesis.

In considering the adaptiveness of the occurrence of subadult plumage in Shorebirds, Chu finds that there is no adaptive explanation to it (Chu 1994). He finds the occurrence of subadult plumage to be mainly a consequence of retention of primitive moult patterns (in accordance with the moult constraint hypothesis).

Discussion

The within species approach: descriptive versus experimental

When comparing the descriptive approach with the experimental approach on the basis of literature on the occurrence of subadult plumage, two different general patterns come to the fore. In the descriptive approach the general schedule appears to be that predictions are derived from various hypotheses. These predictions are then tested by relating existing variation in plumage colour to variation in fitness-related parameters. When second-year males with subadult plumage appear to do better with regard to the fitness variables, the occurrence of subadult plumage is simply assumed to be adaptive. In the experimental approach the general pattern appears to be that a specific assumption underlying one or two hypotheses is examined. This assumption is tested by artificially applying variation in plumage colour. When second-year males with subadult plumage appear to have an advantage over second-year males without, the trait is assumed to be adaptive. One disadvantage of the descriptive approach is that this method often does not have enough distinctive power to reject hypotheses convincingly. As other variables than the trait of interest are not taken into account and as they are likely to vary as well, it is impossible to exclude correlating effects. Thus even though a relation between plumage colour and fitness-related parameters is found, no statements can be made with certainty regarding adaptiveness; the trait still can be non-adaptive, but correlated to another, adaptive, trait. Advantage of the experimental approach is that variation in plumage colour in the trait is likely to explain differences in fitness-related parameters, as variables other than the one of interest are kept constant. Thus differences in fitness can, with considerable certainty, be ascribed to the artificially applied variation in plumage colour. Disadvantage of the experimental approach, however, is that often only one or few hypotheses can be taken into account.

The comparative method: use phylogeny or not

Studies using the comparative approach but not using phylogeny, mainly do not use it by the lack of possibilities to do so; most recent comparative studies do use phylogeny. Without phylogeny, the main advantage of the comparative method appears to be that the generality of a specific trait is revealed. Comparative studies using phylogeny, however, succeed even better in accessing this information as they are able to identify *independent* evolutionary events. As shown in the study of Chu (1994) and that of Hill (1996), the occurrence of subadult plumage is independently derived in different species. Therefore the adaptive value of subadult plumage should also be examined in these species independently. With the use of phylogeny far better information is derived on the ancestral states of the trait. Indication whether an observed trait is ancestral or derived helps to understand the adaptive value of the trait.

The within species approach versus the comparative approach

From the phylogenetic comparative studies of Björklund (1991), Chu (1994) and Hill (1996), one essential advantage of considering evolutionary changes with the use of phylogenetic trees becomes clear. The phylogenetic studies show that even as the occurrence of subadult plumage is more rare than the absence of it, various basic questions are still possible. In considering the occurrence of subadult plumage, however, the basic question is often assumed to be: "Why do certain species have a subadult plumage". Alternative basic questions are not even considered. In his study

of fringillid finches Björklund (1991) finds that the relevant question for this group of species is why certain species do not show subadult plumage. According to his findings, it does not make sense to seek for adaptive explanations of the occurrence of subadult plumage by comparing fringillid finches with and without subadult plumage. Within this group of bird species, the absence of subadult plumage is the trait that is potentially adaptive. Chu (1994) concludes that in shorebirds the occurrence of subadult plumage is likely to be the derived trait, but it is likely to be non-adaptive. On the contrary, Hill (1996) finds that the assumption normally made in studies on subadult plumage (i.e. subadult plumage is adaptive), is legitimate to ask in the House Finches.

Although studies using the within species approach can measure the current adaptive value of subadult plumage, they share the disadvantage that they can not distinguish whether the adaptive function was there at the time of evolutionary change or that this function has been added afterwards. In other words studies using the within species approach can never be sure whether the current adaptive function of a trait is the reason why the trait has evolved or why the trait has been maintained. There, however, is a major advantage of the within species approach, not shared by the comparative approach. Experiments can be used to actually test whether or not a specific assumption is valid or not. Comparative studies can not do so. Even from phylogenetic trees, at most an indication can be derived. Comparative studies can not prove whether or not a trait is adaptive. Experiments in which only one trait is allowed to vary can actually prove the validity of an assumption (under the specific conditions of the experiment). The study of Slagsvold and Saetre for instance explicitly tests whether or not the assumption that adults are deceived by subadult plumages. From their findings it becomes clear that this assumption is valid. Comparative studies could never have proven the validity of this assumption.

Conclusions

Two of the possible approaches of studying the evolution of the occurrence of subadult plumage have a critical advantage, not shared by the other approaches. Phylogenetic studies have made clear that it is necessary to consider phylogenetic relations in order to determine the relevant evolutionary questions (and control groups). The major advantage of the phylogenetic approach is that the suitable control groups for a specific question of interest can be determined. Clear advantage of the within species approach is that assumptions and predictions can actually be tested. In contrast to the comparative approach, the experimental approach can actually prove whether or not a trait is adaptive. As these advantages are critical (i.e not shared with others), the best approach in studying the adaptiveness of the occurrence of subadult plumage would be:

- do phylogenetic research on the trait of interest in a specific group of bird species to determine independent groups of species,
- determine from this phylogenetic analysis the relevant evolutionary questions and the suitable control groups,
- develop hypothesis on the relevant questions from which explicit predictions can be derived
- use experiments to test the predictions

In this way, the combined use of the two approaches will result in the best understanding of the adaptiveness of the occurrence of subadult plumage.

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Tables

Table 1: The various hypotheses on the occurrence of subadult plumage, their proximate functions and the selective mechanism accompanying them.

hypotheses	proximate mechanism	selective mechanism
molt constraint hypothesis	none	genetic constraints
cryptic hypothesis	predation avoidance	increased early survival and lifetime reproductive success
status signaling hypothesis	reliable signaling of subordinate status	increased chance on breeding and reduction of aggression in male-male interactions
female mimicry hypothesis	mimicry of females	increased chance on breeding and female choice of territories
juvenile mimicry hypothesis	mimicry of juveniles	increased chance on breeding and female choice of territories

Table 2: Studies on subadult plumage in birds.

study	species	within species approach		comparative approach	
		descrip-tive	experi-mental	without phylogeny	with phylogeny
Björklund, 1991	Finches (Fringillidae)	0	0	0	1
Chu, 1994	Shorebirds (Charadriiformes)	0	0	0	1
Foster, 1987	Manakins (Chiroxiphia)	1	0	0	0
Hakkarainen <i>et al.</i> , 1993	Kestrel (<i>Falco tinnunculus</i>)	1	1	0	0
Hill, 1996	House Finches (Carpodacus)	0	0	0	1
Järvi <i>et al.</i> , 1987	Pied Flycatcher (<i>Ficedula hypoleuca</i>)	1	0	0	0
Lozano and handford, 1995	Tree Swallow (<i>Tachycineta bicolor</i>)	1	0	0	0
Lyon and Montgomerie, 1986	Passerines (Passeriformes)	0	0	1	0
Procter-Gray and Holmes, 1981	American Redstart (<i>Setophaga ruticilla</i>)	1	0	0	0
Rohwer, 1978	Red-winged Blackbirds (<i>Agelaius phoeniceus</i>)	0	1	0	0
Rohwer and Butcher, 1988	Passerines (Passeriformes)	0	0	1	0
Rohwer <i>et al.</i> , 1980	Passerines (Passeriformes)	0	0	1	0
Saetre <i>et al.</i> , 1993	Pied Flycatcher (<i>Ficedula hypoleuca</i>)	1	1	0	0
Saetre and Slagsvold, 1996	Flycatchers (Ficedula)	0	1	0	0
Selander, 1965	Blackbirds (Quiscalus)	0	0	1	0
Slagsvold and Saetre, 1991	Pied Flycatcher (<i>Ficedula hypoleuca</i>)	1	1	0	0
Studd and Robertson, 1985	Passerines (Passeriformes)	0	0	1	0
Thompson, 1991	Painted Bunting (<i>Passerina ciris</i>)	1	0	0	0

Figures

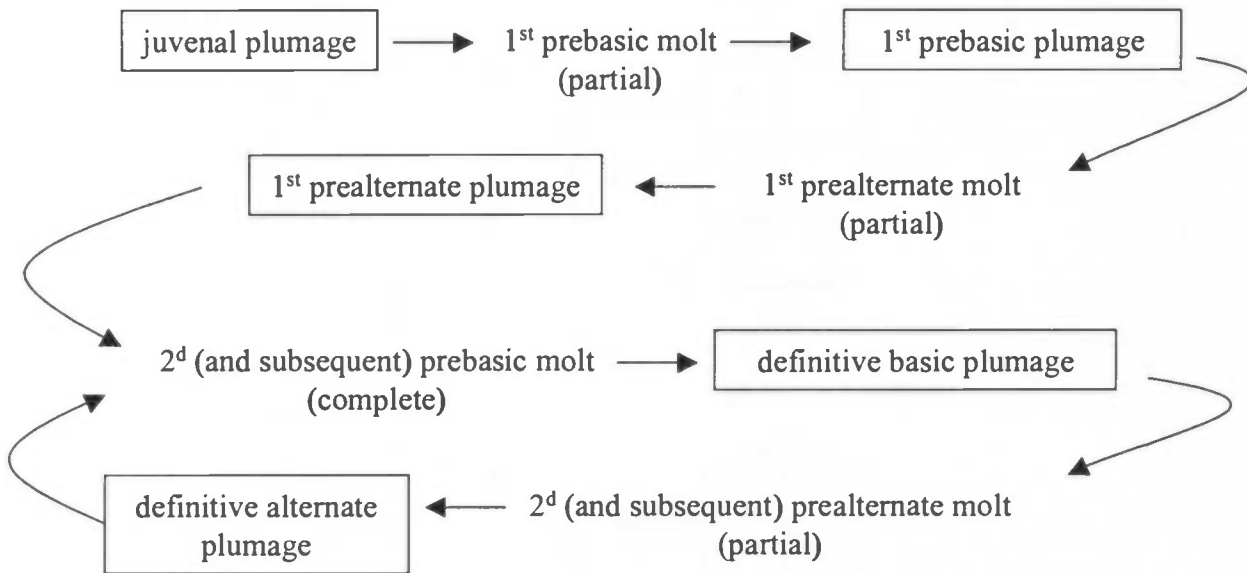


Figure 1: Pattern of plumage succession of the Scarlet Tanager (*Piranga olivacea*) (From: Humphrey and Parkes 1959). As for the Scarlet Tanager the first prebasic moult is partial, the first basic and alternate molt can be distinguished from the definitive adult basic and alternate plumage. Thus the Scarlet Tanager is one of the species in which subadult plumage occurs.



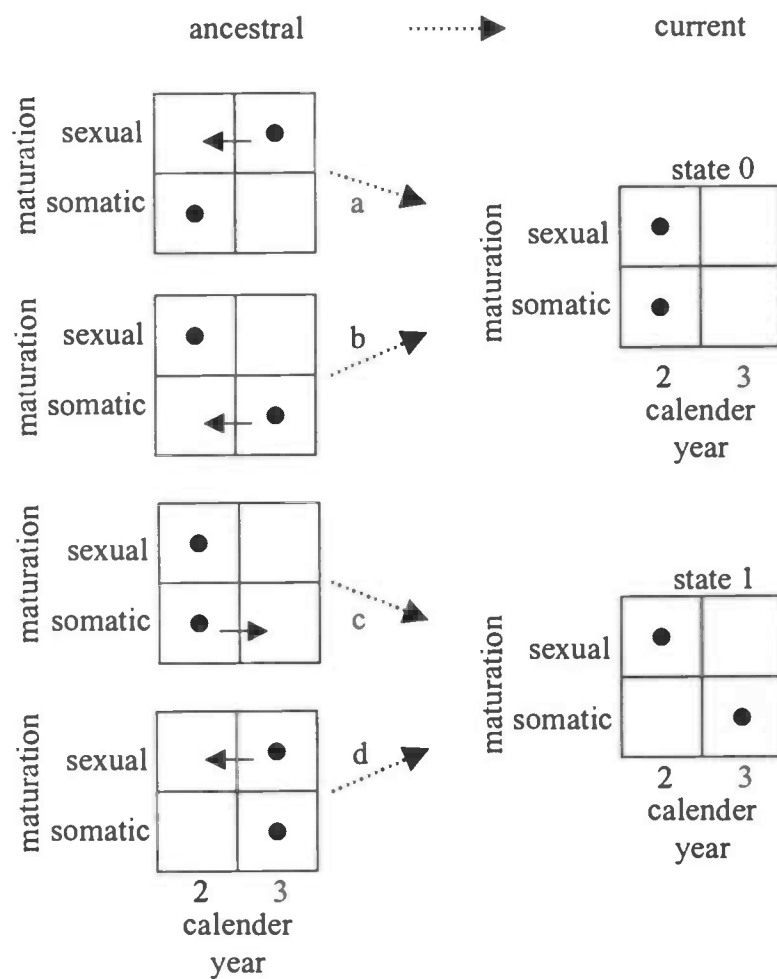


Figure 2: Graphical representation of possible heterochronic events concerning the occurrence of subadult plumage. The current relation between the timing of somatic maturation in relation to the timing of sexual maturation is shown on the right side of the figure. Bird species that become sexual and somatic mature in their first potential breeding year, do not show a subadult plumage (state 0), whereas bird species in which somatic maturation occurs the year after sexual maturation have a subadult plumage (state 1). On the left side of the figure four possible ancestral relations between the timing of sexual and of somatic maturation are shown. Straight arrows indicate the heterochronic events which can be underlying the current relation: a) acceleration of sexual maturation, b) acceleration of somatic maturation, c) retardation of somatic maturation, d) acceleration of sexual maturation.

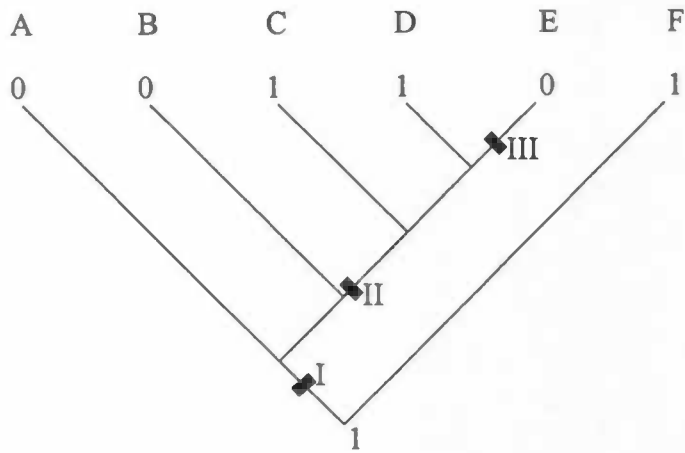


Figure 3: A made-up phylogenetic tree concerning a trait that can either be in state 0 or in state 1. Of the six different species included in the tree (species A to F), state 1 occurs in species C, D and F, whereas it does not occur in the other three species (state 0). In this phylogenetic tree, state 1 turns out to be the primitive state. On two occasions in the evolution of the six species state 1 is lost (change I and III: $1 \rightarrow 0$); on one occasion state 0 has evolved to state 1 (change II: $0 \rightarrow 1$).