BIOLOGICAL REVIEWS
Cambridge Philosophical Society
Biol. Rev. (2012), **87**, pp. 257–274.
doi: 10.1111/j.1469-185X.2011.00193.x

Delayed plumage maturation and delayed reproductive investment in birds

Gerard L. Hawkins[1,*], Geoffrey E. Hill[2] and Austin Mercadante[2]

[1] *Elias, Matz, Tiernan & Herrick, LLP, 11th Floor, 734 15th Street, N. W., Washington D.C. 20005, USA*
[2] *Department of Biological Sciences, 331 Funchess Hall, Auburn University, AL 36849, USA*

ABSTRACT

Delayed plumage maturation is the delayed acquisition of a definitive colour and pattern of plumage until after the first potential breeding period in birds. Here we provide a comprehensive overview of the numerous studies of delayed plumage maturation and a revised theoretical framework for understanding the function of delayed plumage maturation in all birds. We first distinguish between hypotheses that delayed plumage maturation is attributable to a moult constraint with no adaptive function and hypotheses that propose that delayed plumage maturation is a component of an adaptive life-history strategy associated with delayed reproductive investment. We then recognize three potential benefits of delayed plumage maturation: crypsis, mimicry and status signaling. Evidence suggests that delayed plumage maturation is not a consequence of developmental constraints and instead represents a strategy to maximize reproductive success in circumstances where young adults cannot effectively compete with older adults for limited resources, particularly breeding opportunities. A multi-factorial explanation that takes into account lifespan and the degree of competition for limited breeding resources and that combines the benefits of an inconspicuous appearance with the benefits of honest signaling of reduced competitiveness provides a general explanation for the function of delayed plumage maturation in most bird species. Delayed plumage maturation should be viewed as a component of alternative reproductive strategies that can include delay in both plumage and sexual development. Such strategies are frequently facultative, with individuals breeding prior to the acquisition of definitive plumages when conditions are favourable. Presumably, the benefits of delayed plumage maturation ultimately enhance lifetime reproductive success, and studying delayed plumage maturation within the context of lifetime reproductive success should be a goal of future studies.

Key words: life history, mate choice, mimicry, plumage colouration, predation, social status.

CONTENTS

* Address for correspondence (E-mail: ghawk@emth.com)

I. INTRODUCTION

Delayed plumage maturation is the delayed acquisition of a definitive colour and pattern of plumage until after the first potential breeding period in birds. The primary feature of delayed plumage maturation is that it results in a distinctive appearance for two or more age classes within a breeding population. Delayed plumage maturation is exhibited by both sexes of large-bodied bird species such as albatrosses, eagles, condors, gulls, jaegers, and alcids, as well as by one or both sexes of numerous small-bodied species, including many songbirds. Many well-studied migratory songbirds in North America and Eurasia exhibit delayed plumage maturation (Rohwer, Fretwell & Niles, 1980; Studd & Robertson, 1985; Lyon & Montgomerie, 1986), as do numerous tropical songbirds such as manakins, bowerbirds, asities, Darwin's finches, paradise flycatchers, Hawaiian honeycreepers, and monarch flycatchers (e.g. Prum & Razafindratsita, 1997; Doucet *et al.*, 2007). The scope of this phenomenon is not completely known as scientists are still finding new examples of delayed plumage maturation (Peterson, Navarro-Siguenza & Chen, 2003).

Delayed plumage maturation has been investigated for over four decades, but the literature is fragmented and has not been adequately integrated into modern conceptual frameworks of life-history theory, sexual selection, and social signaling. The leading hypotheses of delayed plumage maturation were all developed in the 1980s, and the primary focus of these hypotheses was on explaining delayed plumage maturation in the males of North American passerines (Rohwer *et al.*, 1980; Studd & Robertson, 1985; Lyon & Montgomerie, 1986; Rohwer & Butcher, 1988). This theoretical base for delayed plumage maturation was conceived at the same time as, and largely independent of, theories for the evolution of ornamental traits *via* sexual selection (e.g. Zahavi, 1975; Lande, 1981; Hamilton & Zuk, 1982; Arnold, 1983; Kodric-Brown & Brown, 1984). A basic understanding of feather colouration would have been achieved more efficiently if researchers had first tackled the question of the basic functions of different types of colour display (carotenoid colouration, melanin colouration, structural colouration) and then turned to circumstances in which expression of the colour displays was delayed (Hill, 2002). Since about 1991, studies of avian colouration have shifted away from delayed plumage maturation to more general studies of the function and evolution of colouration, which now rests on a solid foundation (Hill & McGraw, 2006*a*, *b*).

In this article we comprehensively review empirical studies of delayed plumage maturation and use current theories of sexual selection, social signaling, and life-history evolution to evaluate hypotheses for why some species of birds display delayed plumage maturation. Working from modern evolutionary and life-history theory, we present a simplified yet powerful theoretical framework for understanding delayed plumage maturation. We propose that delayed plumage maturation generally is an adaptive life-history strategy associated with delayed reproductive investment that has its source in the inability of subadults to compete with adults for limited resources, particularly breeding opportunities.

II. DEFINITION OF DELAYED PLUMAGE MATURATION

There is no universally accepted definition of the term "delayed plumage maturation," and the lack of a consistent definition of this term has led to confusion in the literature (Hill, 1996). To date, definitions of delayed plumage maturation have hinged most critically on the reproductive capacity of individuals and the distinctiveness between definitive and subadult plumages (Rohwer *et al.*, 1980; Studd & Robertson, 1985; Lyon & Montgomerie, 1986; Rohwer & Butcher, 1988; Thompson, 1991). Differences in interpretations of plumage distinctiveness and the importance of gonadal maturity have led to different opinions regarding which bird species exhibit delayed plumage maturation.

We define delayed plumage maturation as the delayed acquisition of definitive plumage colouration and pattern until after an individual's first potential breeding period. We use the term "subadult" to refer to an individual that has not acquired definitive plumage colouration and pattern by its first potential breeding period. Subadult plumage that results from delayed plumage maturation has a colouration or pattern that is consistently distinct from members of the same sex in definitive plumage. Using the moult terminology invented by Humphrey & Parkes (1959), delayed plumage maturation typically occurs by means of one or more prebasic and if applicable prealternate moults into a distinct subadult plumage. Delayed plumage maturation also may occur *via* the retention of juvenal wing and tail feathers in a partial first prebasic moult (Chu, 1994; Senar, Copete & Martin, 1998; Beauchamp, 2003). We consider this to be a less-interesting phenomenon because most birds have partial first prebasic moults, which traditionally have been attributed to energetic or time constraints and not selection on the colouration resulting from the retained juvenal feathers (Senar *et al.*, 1998).

(1) Degree of sexual development

Many species that exhibit delayed plumage maturation also have a comparable delay in gonadal maturation, and these species typically do not breed before they acquire definitive plumage. Examples of species that delay both acquisition of definitive colouration and development of mature gonads include albatrosses, eagles, condors, larger gulls, and jaegers. In other species, such as most sexually dichromatic North American passerines, males that exhibit delayed plumage maturation can breed in subadult plumages in favourable circumstances. Studies of delayed plumage maturation generally have focused on such reproductively capable species. Some authors have defined delayed plumage maturation as the delayed acquisition of definitive plumage by sexually mature birds (Thompson, 1991; Senar *et al.*, 1998), while others (Hill, 1996) have questioned this definition because first-year males of many passerine species have smaller testes and produce less sperm than older males and thus may not be "sexually mature" (Selander, 1965; Hill, 1994, 1996; Graves, 2004). Delayed sexual development can be part of a reproductive strategy in the same way as delayed plumage maturation, and defining delayed plumage maturation according to sexual development obscures some of the more interesting cases of long-term subadult breeding strategies.

(2) The distinctiveness of subadult plumages

Variability in expression of colour displays among birds in definitive plumage has created confusion in the literature as to what constitutes delayed plumage maturation. In most species with colourful feathers, there is variable expression of plumage colouration that is often related to individual age or condition (Dale, 2006; Hill, 2006). Age-related variation in colour quality describes species in which young birds acquire definitive or adult plumage but, on average, differ in colour quality or patch or stripe size from older adults of the same sex. Although older individuals have higher colour quality or a larger patch on average, any given yearling male might be more brightly coloured than an older male. Such age-related plumage colouration generally has not been considered to constitute delayed plumage maturation (Rohwer *et al.*, 1980; Studd & Robertson, 1985; Lyon & Montgomerie, 1986; Rohwer & Butcher, 1988).

A good example of condition-dependent feather colouration that is related to age is found in the U.S. subspecies of the house finch (*Carpodacus mexicanus frontalis*). Male house finches vary in expression of carotenoid-based plumage colouration from dull yellow to bright red, with yearling males (males in first basic plumage) being on average slightly drabber than older males (males in second and subsequent basic plumages) (Hill, 2002). Other examples of species that have age- or condition-related colour variation include the eastern bluebird (*Sialia sialis*) (Siefferman, Hill & Dobson, 2005), Harris's sparrow (*Zonotrichia querula*) (Rohwer, Ewald & Rohwer, 1981), chestnut-sided warbler (*Dendroica pensylvanica*) (King, DeGraaf & Griffin, 2001), and dark-eyed junco (*Junco hyemalis*) (Ketterson, 1979).

Species with delayed plumage maturation have age-specific variation in plumage colour or pattern. In these species subadults of one or both sexes have a distinctly different plumage pattern than that of adults of the same sex, with little or no overlap in colour expression. Examples of sexually dichromatic North American passerines in which males exhibit age-specific variation in plumage colour or pattern include the Cassin's finch (*Carpodacus cassini*), painted bunting (*Passerina ciris*), Baltimore oriole (*Icterus galbula*), and indigo bunting (*Passerina cyanea*) (Rowher *et al.*, 1980).

Distinguishing between age-specific variation in plumage colour or pattern and age-related variation in colour quality simplifies the classification of species into those with and without delayed plumage maturation, but even with this definition the plumage colouration of some species remains difficult to classify. In the cedar waxwing (*Bombycilla cedrorum*), for instance, both males and females acquire an increased amount of red waxy tips to their wings as they age and most first-year birds lack such tips (Mountjoy & Robertson, 1988). Perhaps because some waxwings develop waxy tips in their first year, the cedar waxwing has not been included in lists of North American passerine species which exhibit delayed plumage maturation, as set forth in Rohwer *et al.* (1980), Studd & Robertson (1985), Lyon & Montgomerie (1986), and Rohwer & Butcher (1988). Age-related differences in cedar waxwings, however, appear to facilitate age-assortative mating and allow younger birds honestly to signal their lower intrinsic resource-holding potential, thereby assisting them in remaining in flocks and possibly obtaining mates (Mountjoy & Robertson, 1988). Cedar waxwings thus may have similar costs and benefits associated with their first-year plumages as species that have more distinct subadult plumages. Thus, while restrictive definitions of delayed plumage maturation are convenient, the reality is that expression of delayed plumage maturation is a continuum that ranges from species in which subadults are totally dissimilar to adults of the respective sex in plumage colour and pattern to species in which subadults are only slightly dissimilar (Studd & Robertson, 1985; Senar *et al.*, 1998). This is perhaps most clear in the case of species, such as gulls, which have two or more distinct subadult classes which become increasingly adult-like as they age.

One problem with defining delayed plumage maturation based on the distinctive plumage of young birds is that the distinctiveness of colouration from a human perspective is not the same as distinctiveness from an avian perspective (Cuthill, 2006; Hill, 2010). Recent studies have shown that many species formerly considered monochromatic have distinct colour differences between males and females that are not discernable by humans but are perceptible by birds (Eaton, 2005). A recent study also shows that colour variation among males that is imperceptiable to humans may affect aggressive interactions (Alonso-Alvarez, Doutrelant & Sorci, 2004), and it has been suggested that age differences in ultraviolet colouration may benefit subadult males by avoiding adult aggression (Delhey & Kempenaers, 2006). Currently, there are few examples of age-specific differences in plumage colouration that are visible to birds but not perceptible to humans (Delhey & Kempenaers, 2006), but no systematic searches for such traits have been undertaken.

(3) Manifestation of delayed plumage maturation

Subadult plumages can resemble the plumages of adult males or adult females, or they can be distinct from these plumages. For example, first-year male Cassin's finches and painted buntings are essentially indistinguishable in appearance from females in definitive plumage (Rohwer *et al.*, 1980). First-year male great-tailed grackles (*Quiscalus mexicanus*) (Rohwer *et al.*, 1980) and lazuli buntings (*Passerina amoena*) (Rohwer *et al.*, 1980; Muehter, Greene & Ratcliffe, 1997; Greene *et al.*, 2000) typically have distinct subadult plumages that are similar to those of adult males in definitive plumage. First-year male orchard orioles (*Icterus spurious*) have a subadult plumage that is distinct from either males or females in definitive plumage (Enstrom, 1992*a*, *b*, 1993).

Expression of subadult plumages also can vary within a species. Within some species, such as the black-headed grosbeak (*Pheucticus melanocephalus*) (Hill, 1988*a*) and red-winged blackbird (*Agelaies phoeniceus*) (Rohwer *et al.*, 1980), subadult male plumages range from dissimilar to similar to males in definitive plumage (Studd & Robertson, 1985; Senar *et al.*, 1998). In some longer-lived birds, such as gulls, eagles, and tropical passerines like Darwin's finches, paradise flycatchers, Hawaiian honeycreepers, and monarch flycatchers, subadults of one or both sexes progress through a transitional series of different subadult plumages that become increasingly adult-like before they acquire adult plumage (Doucet *et al.*, 2007). In other species, such as bowerbirds and birds of paradise, males moult into the same subadult plumage for several years before acquiring adult plumage (Doucet *et al.*, 2007).

Depending on the species, delayed plumage maturation may be exhibited by one or both sexes. In long-lived, sexually monochromatic species such as albatrosses, eagles, condors, gulls, jaegers, and alcids, delayed plumage maturation typically is exhibited by both sexes. In North American passerines that exhibit delayed plumage maturation, typically only males of sexually dichromatic passerines exhibit delayed plumage maturation. In a few passerine species, with the most well-studied example being the sexually monochromatic tree swallow (*Tachycineta bicolor*), only females show delayed plumage maturation (Stutchbury & Robertson, 1987). In the tropics, where females often have relatively equal roles in territory defence and reproduction, delayed plumage maturation in females is more common and often is exhibited by both sexes (Stutchbury & Morton, 2001). Examples include many tropical tanager species, such as the black-cheeked ant-tanager (*Habia atrimaxillaris*), bay-headed tanager (*Tangara gyrola*), and the white-shouldered tanager (*Tachyphonus luctuosus*) (Stutchbury & Morton, 2001). In a few species, such as the house finch (Hill, 2002, 1996), white-crowned sparrow (*Zonotrichia leucophrys*) (Rohwer *et al.*, 1980), olive warbler (*Peucedramus taeniatus*) (Lowther & Nocedal, 1997), and scarlet robin (*Petroica boodang*) (noted in Berggren, Armstrong & Lewis, 2004), delayed plumage maturation is exhibited by males in some populations but not others.

(4) Delayed maturation in bare part colouration

Many bird species show delayed maturation in the colour of bare parts such as the eyes, bill, and legs (Hardy, 1974; Lawton & Lawton, 1986; Peterson, 1991). The principal hypotheses of delayed plumage maturation generally should be applicable to delayed maturation in bare parts, but there are important distinctions. Significantly, the colouration of bare parts can change more rapidly than the colour of plumage (Karubian *et al.*, 2011), and consequently there may be differing costs associated with delays in the maturation of plumage *versus* bare parts (Hill, Hood & Higgins, 2009).

III. HYPOTHESES—GENERAL

Progress towards a general understanding of the function of delayed plumage maturation has been confused and hampered by a profusion of named hypotheses, with at least 15 listed in Cucco & Malacarne (2000). Each of these hypotheses has been proposed as distinct, but many are in fact minor variations on prior explanations. We propose that hypotheses explaining delayed plumage maturation focus on two distinct levels of analysis: (1) whether or not delayed plumage maturation is an adaptive life-history strategy; and (2) what specific benefits subadult plumage imparts (Fig. 1). Thus, we recognize only two general hypotheses to explain the existence of delayed plumage maturation: the moult-constraint hypothesis and what we call the delayed-investment

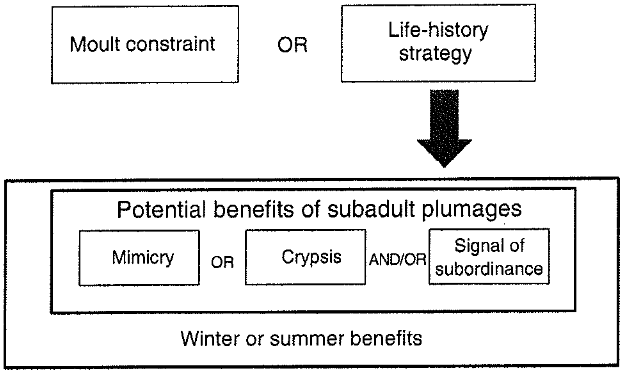

Fig. 1. The hierarchical association of hypotheses for the function of delayed plumage maturation that we recognize in this review. All hypotheses are either hypotheses of constrained development or delayed investment in full reproduction. Within the delayed-investment (breeding threshold) hypotheses, subadult plumage may be beneficial because it functions in mimicry, crypsis, or status signaling and each of these benefits may occur in either the breeding or non-breeding seasons.

hypothesis - which subsumes the breeding threshold hypothesis of Studd and Robertson (1985), the reduced investment hypothesis of Procter-Gray & Holmes (1981), and delayed-maturation hypotheses proposed by Selander (1965, 1972) and Ficken & Ficken (1967). All other hypotheses concern specific benefits of subadult plumage.

The moult-constraint hypothesis proposes that delayed plumage maturation is a non-adaptive developmental epiphenomenon. By contrast, the delayed-investment hypothesis proposes that delayed plumage maturation is a component of an adaptive life-history strategy associated with a strategy of delayed reproductive investment (Selander 1965, 1972; Ficken & Ficken, 1967; Procter-Gray & Holmes, 1981; Studd & Robertson, 1985). Studd & Robertson (1985) gave the clearest articulation of the idea that delayed plumage maturation is a life-history strategy in their "breeding threshold hypothesis". They proposed that when the probability of young passerines obtaining breeding resources in competition with older, experienced adults is low, then the young birds benefit by investing less in current reproduction and waiting until a subsequent breeding season or seasons to invest fully in reproductive effort. Although these birds do not fully delay gonadal maturation and delay breeding on a facultative basis, as suggested by Studd & Robertson (1985), their hypothesis also applies to longer-lived, larger birds in which delayed plumage maturation and a delay in gonadal maturation are components of a total delay in breeding. Under the delayed-investment hypothesis, younger birds delay the acquisition of definitive plumage until they can effectively compete for resources in breeding and nonbreeding contexts. By deferring the costs associated with bright plumages and totally or facultatively delaying breeding, these birds may have a greater chance of survival and thus a higher lifetime reproductive output. Such a strategy requires a reasonable expectation of future reproduction, and as a result delayed plumage maturation is more prevalent in species with longer average lifespans.

Under the delayed-investment hypothesis, there are three potential benefits of subadult plumage that might help young birds increase survival and ultimately reproduction (Fig. 1): (1) mimicry, (2) crypsis, and (3) status signaling. Below we consider these hypothesized benefits in more detail and assess the evidence to support each.

(1) A constraint or an adaptation?

(a) *Constrained moult*

The first consideration when assessing potential functions of subadult plumage is whether the delay in plumage development is an adaptation or a constraint. In the transition from a zygote to a fully mature adult, a bird must pass through a series of immature morphological stages. Under the moult-constraint hypothesis, subadult plumage is a necessary transitional developmental state between juvenal plumage and definitive plumage or the result of some other constraint on the development of an appropriate moult.

The moult-constraint hypothesis was proposed to explain delayed plumage maturation in males of sexually dichromatic North American passerines (Rohwer & Butcher, 1988). The possibility of a moult constraint exists because first-year birds in these species have subadult plumage in the winter and summer and a partial prealternate moult (Rohwer & Butcher, 1988). Such a pattern could be explained if first-year males are constrained in some manner from undergoing a prealternate moult that is as complete as that of older males. In such circumstances, a definitive plumage might be beneficial, but young birds are developmentally constrained from achieving it. Such a constraint could arise either through an inability to acquire sufficient resources needed for feather production or because of a phylogenetic constraint that prevents the evolution of a prealternate moult in the first year (Rohwer & Butcher, 1988). To date, no *ad libitum* feeding experiment of the type suggested by Rohwer & Butcher (1988) has been conducted to evaluate whether these passerines have subadult plumages as a result of a moult constraint, but given the ubiquity of subadult plumages in these species, it seems unlikely that delayed plumage maturation is due to a food constraint.

It also does not appear that the moult-constraint hypothesis is applicable to species that acquire one or more subadult plumages by means of a complete prebasic moult because these birds are not constrained by the absence of an appropriate moult from producing plumage with definitive colouration. It thus seems unlikely that the moult-constraint hypothesis can explain delayed plumage maturation in such species as albatrosses, eagles, condors, gulls, jaegers, and alcids, which generally acquire one or more subadult plumages by means of a complete prebasic moult. Similarly, it seems unlikely that the moult-constraint hypothesis can explain delayed plumage maturation in numerous tropical and subtropical birds, which, because of their longer lifespans, typically delay the acquisition of definitive plumage and breeding longer than temperate species (Stutchbury &

Morton, 2001). Examples of tropical or subtropical species in which a subadult undergoes a complete prebasic moult into another subadult plumage include the red-backed fairy-wren (*Malurus melanocephalus*) (Karubian, Sillett & Webster, 2008), 'elepaio (*Chasiempis sandwichensis*) (VanderWerf, 2001), akepa (*Loxops coccineus*) (Lepson & Freed, 1995); satin bowerbird (*Ptilonorhynchus violaceus*) (Collis & Borgia, 1993), Madagascar paradise flycatcher (*Terpsiphone mutata*) (Mulder, Ramiarison & Emahalala, 2002), and long-tailed manakin (*Chiroxiphia linearis*) (e.g. Doucet *et al.*, 2007).

A phylogenetic analysis of the evolution of delayed plumage maturation in shorebirds by Chu (1994) provided some support for the moult-constraint hypothesis. This analysis showed that distinct subadult plumages did not evolve because of selection for such plumages, but as an incidental consequence of three evolutionary novelties, depending on the species: (*i*) selection for distinctive juvenal plumage in taxa that had a partial first prebasic moult; (*ii*) selection for seasonal change in plumage appearance in taxa that had a partial first prealternate moult; and (*iii*) a reduction in the extent of the first prealternate moult in taxa that had seasonal change in plumage appearance. Chu (1994) suggested that his finding in shorebirds also may be applicable to passerines because many passerines have partial first prebasic moults. This analysis, however, cannot explain delayed plumage maturation in species that acquire one or more subadult plumages by means of a complete prebasic moult, and thus it does not provide a general explanation of delayed plumage maturation across species.

Although some studies have suggested the applicability of the moult-constraint hypothesis to explain delayed plumage maturation where they found only costs and no benefits to the subadult plumages (Enstrom, 1992*b*, 1993; Valle, De Vries & Hernández, 2006), none of these studies provided any specific evidence in support of such a constraint. Indeed, to date no study has demonstrated clearly that delayed plumage maturation in any species of bird is primarily attributable to a moult constraint.

(*b*) *Constrained sexual maturation*

In contrast to short-lived, small-bodied songbirds, which have been the focus of most studies of delayed plumage maturation, many long-lived, large birds such as albatrosses, eagles, condors, gulls, jaegers, and alcids exhibit distinctive subadult plumages for years after juvenal plumage is lost. These birds generally do not acquire definitive plumage until they commence breeding. One could argue that the years in which these birds have subadult plumages are simply years needed for growth and maturity of reproductive systems and hence that these birds are developmentally constrained from breeding and from the need for definitive plumages. As discussed below, however, general patterns of avian development support the view that in these long-lived, large species both gonadal maturity and plumage maturation reflect reproductive strategies rather than developmental constraints.

Virtually all bird species have the physiological potential to develop mature gonads and breed at one year of age. Small avian species reach adult size in less than one month after hatching and even large birds like the American white pelican (*Pelecanus erythrorhynchos*) reach adult size in fewer than 100 days (Welty & Baptista, 1988). By one year after hatching, which is typically the first potential breeding period, all but perhaps the very largest birds have fully mature organ systems, including such complex systems as the visual, neuro-musculature, and immune systems. It seems unreasonable to maintain that developmental constraints delay the maturation of the reproductive system in such species for years beyond the time needed to develop other complex organ systems. Indeed, many species of large waterfowl and gallinaceous birds, such as the Canada goose (*Branta canadensis*) and wild turkey (*Meleagris gallopavo*), develop fully functional reproductive systems and may breed in their first year (Selander, 1965). We are unaware of any evidence that indicates that any species of bird is developmentally constrained from acquiring definitive plumage and becoming reproductively capable by the first potential breeding season, which is not to say that every species adopts a reproductive strategy that results in fertility at this time.

(2) **Delayed plumage maturation as a reproductive strategy**

If all birds have the potential to develop functional gonads by their first potential breeding period at about one year of age, then failure to invest in gonadal development is a reproductive strategy. Indeed, delayed gonadal development and delayed plumage development are two forms of delayed reproductive investment and are complementary strategies. Birds that have a distinctive subadult plumage with no gonadal development are abandoning all chance of reproduction in the first year or years of their lives. Birds that have some gonadal development and a distinctive subadult plumage are likely forsaking most but not all chance of reproduction. Birds with substantially or fully developed gonads but still distinct subadult plumage are investing substantially in reproduction, but may still benefit from a distinct subadult plumage.

The males of many sexually dichromatic, North American passerines that have delayed plumage maturation typically have functional reproductive organs by the time they reach their first potential breeding season (Rohwer *et al.*, 1980). In these species, delayed plumage maturation typically is a component of a facultative delayed breeding strategy in which a subadult may breed when opportunities arise (Studd & Robertson, 1985). For small bird species with relatively high mortality (Lack, 1967; Klimkiewicz, Clapp & Futcher, 1983; Klimkiewicz & Futcher, 1989), a facultative delayed breeding strategy, in which reproductive effort is reduced but the ability to reproduce is retained, is an effective strategy when competition for breeding resources is intense (Studd & Robertson, 1985). This is because even in these circumstances limited investment in reproduction will sometimes lead to production of offspring and provide experience for breeding in subsequent years (Ficken & Ficken, 1967; Bruinzeel & van de Pol, 2004).

Although much of the research on delayed plumage maturation has focused on short-lived, small birds, some long-lived, large birds also may pursue a facultative delayed breeding strategy in the early years of their lives. A gull species that spends two years in subadult plumages before acquiring definitive plumage in the third year may be incapable of breeding in its first year, but it may pursue a facultative delayed breeding strategy in its second year, as was demonstrated in a study of the age of first breeding by female laughing gulls (*Larus atricilla*). This study found that no one-year-old females laid eggs, a slight majority of two-year-old females laid eggs and 88% of three-year or older females laid eggs (Dolbeer & Bernhardt, 2003). Thus, reproductive effort increased as reproductive opportunities improved and greater reproductive effort was associated with increasingly adult-like plumage.

(3) Evidence for reduced reproductive investment and increased survival and reproductive success

(*a*) *Lifespan*

If delayed plumage maturation is a strategy by young birds to avoid risks of competition, then there should be a relationship between lifespan and the occurrence of subadult plumages among species. Specifically, all else being equal, those species that have a subadult plumage should, on average, have a longer expected lifespan than those species that acquire definitive plumage in their first year. Based on a well-established correlation between adult body size and lifespan, Studd & Robertson (1985) tested this idea by comparing body size and plumage development. They found that dichromatic North American passerines with subadult male plumages tended to be larger, and thus longer lived, than dichromatic North American passerines that lack subadult male plumages. Subsequently, Montgomerie & Lyon (1986) maintained that there is little evidence that longer-lived birds are more likely to have a distinctive subadult male plumage when controlling for confounding variables. However, a more comprehensive study of delayed song maturation in 137 Western Palearctic songbirds found a strong correlation between delayed plumage maturation and longevity (Cucco & Malacarne, 2000). These studies focused on patterns within the Order Passeriformes, but delayed plumage maturation also is quite conspicuous in many long-lived, large birds, including albatrosses, eagles, condors, gulls, jaegers, and alcids, which supports a general relationship between lifespan and delayed plumage maturation.

The number of distinct, age-specific plumages exhibited by a species may depend on its potential lifespan (Studd & Robertson, 1985) and on the time required to reach the highest social class. Long-lived species and species with complex social hierarchies, such as the long-tailed manakin (Doucet *et al.*, 2007) and satin bowerbird (Collis & Borgia, 1993), tend to exhibit two or more subadult plumage classes, while short-lived species, such as many sexually dichromatic North American passerines, have only one subadult plumage class (VanderWerf & Freed, 2003).

(*b*) *Competition for limited breeding resources*

Lifespan frames the potential benefits of investment in current *versus* future reproduction, but the level of competition for breeding resources ultimately determines the costs and benefits of investing in reproduction in the first potential breeding season (Studd & Robertson, 1985). Competition for limited breeding resources can involve either potential mates or territories. Zack & Stutchbury (1992) demonstrated that relatively small but strong, consistent differences in territory quality can favour the evolution of delayed breeding in such diverse social systems as cooperatively breeding birds, migratory passerines, colonial-breeding gulls, and lek-breeding grouse and manakins. According to Zack & Stutchbury (1992), subadults in a wide variety of avian social systems frequently have the option to breed immediately on a lower quality territory but elect to delay breeding to associate with higher-quality territories. By associating with high-quality breeding sites, these males enhance their chances of acquiring those sites in future years and in so doing increase their lifetime reproductive success. This analysis is supported by a study of species in which subadult males hold no territories and instead drift around the breeding area during their first potential breeding season to assess territory quality and obtain information that will assist in territory acquisition in subsequent breeding seasons (Bruinzeel & van de Pol, 2004). Although some of these "floater" males succeed in establishing territories, they are almost always in lower-quality positions that are peripheral to the territories of adult males. Time spent by a subadult "floater" in an area, however, increases its familiarity with the area and its occupants and the likelihood that it ultimately will breed successfully in that area (Bruinzeel & van de Pol, 2004).

(*c*) *Reduced reproductive investment by subadults*

There is considerable evidence that young birds generally are competitively inferior to, and generally less successful breeders than, older birds (Wynne-Edwards, 1962; Saether, 1990; Forslund & Pärt, 1995; Muehter *et al.*, 1997). First-year male passerines typically have smaller testes than older males in both monogamous and polygamous species, and thus their sperm-producing capabilities and circulating levels of steroid hormones are typically lower than those of older males (Wright & Wright, 1944; Selander, 1965; Hill, 1994; Vleck & Brown, 1999; Yamagishi *et al.*, 2002; Graves, 2004). As part of a strategy of reduced investment in reproduction, first-year male passerines often exhibit less aggression than adult males, which can reduce the chances of pairing (Ficken & Ficken, 1967).

Possibly as a result of exhibiting reduced aggression and delayed migration in the spring, which may reflect a reduced investment in breeding (Hill, 1989) and/or an inability to compete effectively with adults for territories and food resources on the winter grounds (Rohwer, 1983; Marra, Hobson & Holmes, 1998), first-year male passerines that exhibit delayed plumage maturation obtain low-quality territories if they obtain territories at all (Ficken & Ficken, 1967;

Procter-Gray & Holmes, 1981; Hill, 1988*a*, *b*; Landmann & Kollinsky, 1995*a*; Lanyon & Thompson, 1986; Berggren *et al.*, 2004). Those subadult males that attempt to settle on high-quality territories often find themselves defeated in contests with dominant adult males (Huhta & Alatalo, 1993; Muehter *et al.*, 1997). Subadults also typically are at a disadvantage in obtaining mates, as was documented in studies of the orchard oriole (Enstrom, 1993) and red-backed fairy-wren (Karubian, 2002).

Because they compete relatively poorly for access to territories and mates, many subadult males do not engage in nesting behaviours and have no reproductive output in their first potential breeding season (Samson, 1976). When subadults engage in nesting behaviour, clutch initiation typically is later (Lanyon & Thompson, 1986; Saether, 1990), clutch size typically is smaller (Lyon & Montgomerie, 1986; Saether, 1990), and the number of young fledged per nest typically is less than adults (Grant, 1990; Saether, 1990; Landmann & Kollinsky, 1995*a*; Weggler, 2001). Dull subadult males also have been found to sire significantly fewer extrapair young than bright adult and subadult males (Webster, Varian & Karubian, 2008).

Despite a body of evidence documenting that young males are at a competitive disadvantage during their first or first few breeding seasons, some studies indicate that subadults can reproduce as successfully as adults when conditions are favourable, including studies of the Baltimore oriole (Flood, 1984), North Island robin (*Petroica longipes*) (Berggren *et al.*, 2004), tree swallow (Lozano & Handford, 1995), American redstart (*Setophaga ruticilla*) (Procter-Gray & Holmes, 1981) and saffron finch (*Sicalis flaveola*) (Palmerio & Massoni, 2009). Although these studies appear to be inconsistent with studies that demonstrate that subadults generally cannot compete effectively with adults for limited breeding resources, they indicate that subadults that have reached the requisite level of development may successfully breed when there are sufficient breeding resources available.

(*d*) *Enhanced survival and reproductive success*

As discussed in Section V.3, many studies indicate that delayed plumage maturation results in reduced aggression towards subadults by older conspecifics. Few studies demonstrate that reduced aggression from older conspecifics results in increased survival, however, and even fewer have attempted to assess the effects of reduced aggression on lifetime reproductive success and hence fitness (Lyon & Montgomerie, 1986; Karubian *et al.*, 2008). The lack of such studies undoubtedly is due to the difficulties associated with studying longevity and lifetime reproductive success in the wild.

An example of a study that found that delayed plumage maturation enhanced the survival of young birds is an investigation of the North Island robin, a forest passerine endemic to the North Island of New Zealand and nearby offshore islands (Berggren *et al.*, 2004). This study provided support for winter benefits of delayed plumage maturation by demonstrating that dull, female-like juveniles that were dyed to mimic darker adult males had a lower overwinter survival rate than control dull, female-like juveniles over a two-year period. A similar result was found in a study of the survival of subadults in two populations of the mute swan (*Cygnus olor*) in North America (Conover, Reese & Brown, 2000). In this study, the authors found that young swans that moulted into a drab brownish-grey subadult plumage were tolerated by their parents, whereas young swans that moulted directly into a white adult plumage were attacked by their parents and driven away at the onset of moult. Furthermore, young swans that moulted into drab plumage had higher survival rates from hatching to fledging and during their first two years of life than young swans that moulted directly into a white adult plumage, but swans that moulted into white adult plumage bred at a younger age. The authors concluded that the young swans were honestly signaling their age, and that the brownish-grey cygnets forego early opportunities to breed but increase the probability of surviving their first two years of life. Brownish-grey subadults thus acquire a longer period of parental care, suffer less aggression from older birds, and increase their survival but forgo the opportunity to breed at an early age.

A similar trade-off between survival and early reproduction was found to occur in subadults of the medium ground-finch (*Geospiza fortis*) by Grant (1990), as discussed in Section VI, and another study found that delayed plumage maturation enhanced reproductive success in the lazuli bunting, as discussed in Section V.3*b*.

IV. ECOLOGICAL CONDITIONS THAT PROMOTE DELAYED PLUMAGE MATURATION

If competition for limited breeding resources between subadults and adults is a principal condition of selection for delayed plumage maturation, then a key to understanding delayed plumage maturation is determining the ecological circumstances under which such competition is most likely to occur. All hypotheses of delayed plumage maturation except the moult-constraint hypothesis emphasize the importance of competition for limited resources such as food, mates, territories, and nest sites. Such competition generally is deemed to be most intense in species that have polygynous, leking, or cooperative breeding systems, species with sexually dichromatic plumages, and species that live in high population densities or forage in flocks.

(1) Delayed plumage maturation and competition for available resources

Early theorists noted that delayed plumage maturation is often found in species with high population densities (Orians, 1961; Wynne-Edwards, 1962; Selander, 1965; Ficken & Ficken, 1967). Delayed plumage maturation also was said to be more common in polygynous species and colonial or semi-colonial breeders (Orians, 1961; Wynne-Edwards, 1962; Selander, 1965; Ficken & Ficken, 1967). Species that exhibit delayed plumage maturation generally face intense competition for nest sites (Orians, 1961; Selander, 1965; Ficken & Ficken, 1967). As stated by one author based on his studies of marsh-nesting blackbirds, delayed plumage maturation in first-year males is "characteristic of species in which breeding sites are limited" (Orians, 1961, p. 308).

An extensive study by Beauchamp (2003) found a significant correlation between delayed maturation and flocking behaviour, plumage dichromatism, and certain social breeding systems. According to Beauchamp (2003), the occurrence of delayed plumage maturation in species that forage in flocks rather than solitarily supports the hypothesis that competition for food resources during the non-breeding season is associated with the development of delayed plumage maturation. Under this hypothesis, duller subadults will suffer less aggressive attention from older conspecifics in flocks than bright adults and thus benefit from greater access to food resources.

Sexually dichromatic species presumably experience more intense sexual selection than sexually monochromatic species (Badyaev & Hill, 2003), so the occurrence of delayed plumage maturation in sexually dichromatic species supports the prediction that more intense competition for breeding resources can foster the evolution of delayed plumage maturation. Although the relationship between delayed plumage maturation and sexual dichromatism has been noted before (e.g. Rohwer *et al.*, 1980; Lawton & Lawton, 1986; Lyon & Montgomerie, 1986), prior studies had not focused on whether sexually dichromatic species that exhibit delayed plumage maturation are more social, and thus encounter more competition, in the non-breeding season. In fact, according to Beauchamp (2003), the proportion of such species that failed to flock in the non-breeding season was quite small, and delayed plumage maturation in these species thus may be attributable to the effects of competition during the non-breeding season. Beauchamp (2003) also found that delayed plumage maturation was less common in cooperative breeders than in other species, but that cooperative breeders were more likely to experience delayed maturation in the colour of bare parts than other species.

(2) Delayed plumage maturation and sociality in birds

Lawton & Lawton (1986) also described in some detail the close relationship between delayed maturation and sociality in birds. They conducted an extensive comparative study of species in the Corvidae family and found that in many corvids sexually mature individuals retain juvenal plumage or bare-part colour for more than a year. Moreover, they found a higher incidence of neoteny (delayed morphological development in relation to physiological development) in social rather than nonsocial corvid species. These authors suggested that, as in the case for mammals (see Gould, 1977), neoteny reduces intraspecific aggression among age classes of birds and thereby facilitates the evolution of complex, stable social systems, especially in species with cooperative breeding systems and otherwise highly social species. Lawton & Lawton (1986) also observed that reduced aggression may allow for a prolonged period of direct parental care, which may facilitate the acquisition of foraging or breeding skills by observational learning while at the same time enabling a sexually capable subadult to take advantage of a potential breeding opportunity.

The analysis of Lawton & Lawton (1986) has been supported by several studies of delayed plumage maturation in tropical and subtropical species. For example, a study of delayed plumage maturation in male satin bowerbirds, which do not acquire full adult plumage until their seventh year, suggested that subadult plumages enable subadults to approach bowers and learn complex courtship display behaviours that are important in female choice (Collis & Borgia, 1993). A study of delayed plumage maturation in male long-tailed manakins, which move through several distinct, age-specific subadult plumages before acquiring adult plumage in their fifth calendar year, found that delayed plumage maturation similarly supported a complex social system by mediating aggression by adult males against subadults during a protracted period of queuing for status in a lek, and thus enhanced the stability of orderly male queues (McDonald, 1993). It also has been suggested that delayed plumage maturation in the asities (Philepittidae) similarly may have evolved to allow males to gain access and experience at male display sites (Prum & Razafindratsita, 1997), and that delayed plumage maturation in the akepa may have evolved in part to facilitate the learning that is necessary by subadults to compete with adults (Lepson & Freed, 1995). Recent studies of the cooperatively breeding red-backed fairy-wren (Karubian, 2008; Karubian *et al.*, 2011) similarly documented the relationship between sociality and delayed maturation in bare parts (colour of the bill). Lawton & Lawton's (1986) suggestion that delayed maturation may result in longer direct parental care was supported by studies of the North Island robin (Berggren & Low, 2006) and mute swan (Conover *et al.*, 2000).

Importantly, Lawson & Lawson (1986) also suggested that delayed maturation in plumage and bare parts may contribute to the evolution of new, more sociable species, particularly those in which the adults of one species, such as the yellow-billed magpie (*Pica nuttalli*), strongly resemble the juveniles of another species, such as the black-billed magpie (*Pica hudsonia*). This analysis of speciation in corvids was supported by a study of the black-crowned palm-tanager (*Phaenicophilus palmarum*) and the gray-crowned palm-tanager (*Phaenicophilus poliocephalus*), which concluded that the more sociable gray-crowned palm-tanager diverged from the black-crowned palm-tanager as a result of a delay in maturation (McDonald & Smith, 1994). The authors of this study predicted that there are likely to be many more examples, particularly among tanagers, where speciation has occurred as a result of shifts in developmental sequences resulting from delayed plumage maturation.

(3) Winter *versus* summer adaptations

We do not recognize a fundamental distinction between breeding adaptations and non-breeding adaptations of delayed plumage maturation (winter *versus* summer hypotheses) because delayed plumage maturation generally is an alternative reproductive strategy to increase lifetime reproductive success. Benefits in the form of enhanced survival in non-breeding contexts and survival and reproduction in breeding contexts all contribute to overall reproductive success. In appropriate competitive circumstances, each of the hypothesized functions of subadult plumage that we discuss - mimicry, crypsis, and status signaling - can be beneficial for largely the same reasons in either breeding or non-breeding contexts. Signaling subordinance should work in contests over winter food in the same way that it works in contests over mates in the spring. Moreover, non-breeding contexts frequently occur in the breeding season and breeding contexts sometimes occur in the non-breeding season (as when ducks pair on the winter grounds), making winter *versus* summer hypotheses even less relevant. In light of this, there appears to be little to be gained by trying to classify adaptive benefits seasonally. Because winter *versus* summer hypotheses have been the focus of a significant number of previous studies on delayed plumage maturation, however, we briefly review below the ideas that have been discussed, and have included in Table 1 and Fig. 2 information regarding studies that have distinguished between summer and winter hypotheses of delayed plumage maturation.

Early theorists generally considered delayed plumage maturation to be an adaptation for breeding (Rohwer *et al.*, 1980; Lyon & Montgomerie, 1986), but Rohwer & Butcher (1988) shifted the focus to benefits during the non-breeding season in sexually dichromatic, North American passerines. Indeed, Rohwer & Butcher (1988) found that the subadult plumage of no sexually dichromatic, North American passerine was unequivocally an adaptation to the first summer breeding season because all species that have a summer subadult plumage also have a winter subadult plumage and either have no spring moult or a partial spring moult. This pattern suggests that subadult plumages may be adaptive in winter because they reduce aggression from older conspecifics and thus allow them greater access to territories and food resources and, due to the high costs of an extensive spring moult, are retained in summer even if they are disadvantageous to breeding. We do not believe that Rohwer & Butcher (1988) contradicts our fundamental hypothesis that delayed plumage maturation is primarily related to a reduced investment in maturation associated with alternative (delayed) reproductive strategies because delayed plumage maturation in these species appears to be part of a life-history strategy to increase survival and the ability to breed on a facultatively delayed basis.

Rohwer & Butcher (1988) also identified certain sexually dimorphic, North American passerines that have a subadult plumage during the first winter but not the first summer because they undergo an extensive spring moult that produces a bright plumage or in a few cases acquire a bright plumage by wear. As a result, the first-winter subadult plumages of these birds cannot be viewed as a breeding adaptation, and they may be adaptive and subject to selection during the non-breeding season (Rohwer & Butcher, 1988; Senar *et al.*, 1998). Because these species acquire a bright plumage by the time they commence breeding in their first spring, they do not exhibit delayed plumage maturation. Presumably, a combination of these species' short lifespans and the availability of and competition for breeding resources has made it advantageous for them to acquire a definitive first summer plumage through an extensive first prealternate moult and to invest fully in breeding in their first potential breeding season. Whether these species' dull first-winter plumage is an adaptation or due to a constraint is unknown.

Other studies of species that have a subadult plumage in both the non-breeding and breeding seasons also suggest that benefits of subadult plumages may be attributable to non-breeding contexts. As noted above, Beauchamp (2003) concluded that delayed plumage maturation likely results primarily from competition for food resources during the non-breeding season. In addition, the above-noted study of the North Island robin by Berggren *et al.* (2004) found that delayed plumage maturation increased the survival of young birds before their first breeding season and concluded that summer-adaptation hypotheses of delayed plumage maturation for this species were implausible.

We agree that the benefits of subadult plumages may occur primarily in the non-breeding season in some species, and indeed expect that these benefits may be greatest, or at least most obvious, when a species is engaged in flocking and other social behaviours which result in greater proximity to and competition with adults for resources. Benefits may be less obvious in the breeding season because subadults engage in less direct competition with adults for resources. Moreover, for some longer-lived, large species of birds, reproduction is delayed for one or more years, presumably because of severe competition for limited breeding resources, and for these species delayed plumage maturation operates in a non-reproductive context in the early years.

In the case of the North Island robin, summer adaptive benefits may not be currently present because the population was reduced to low levels far below carrying capacity and all birds thus may now have adequate breeding resources. Studies of other, closely related Australasian species of robins, however, indicate that first-year males tend to occupy poorer-quality habitats than older males during the breeding season, which suggests both that delayed plumage maturation may be a summer adaptation in these species (Berggren *et al.*, 2004) and that delayed plumage maturation as a breeding strategy may be ancestral in this clade of robins. The pattern of delayed plumage maturation in male North Island robins, which take from two to three years to acquire the black adult plumage but start breeding in the first calendar year after hatching (Powlesland, 2002; Berggren & Low, 2006), indicates that delayed plumage maturation in this species does more than enhance first-winter survival by juveniles (Berggren & Low, 2006), and suggests that it has or had an adaptive benefit during the breeding season. When resources become abundant and competition decreases, however, then the benefits of delayed plumage maturation during the breeding season are lost.

Table 1. Summary of studies of delayed plumage maturation (DPM) with an interpretation of the hypotheses they support. Winter hypotheses represent an adaptation to the non-breeding period after prebasic moult but before breeding, and summer hypotheses represent an adaptation to the breeding season. (SS, status-signaling hypothesis; FM, female-mimicry hypothesis; C, cryptic hypothesis; JM, juvenile-mimicry hypothesis; MC, moult-constraint hypothesis; S, hypothesis is supported; PS, hypothesis is partially supported; I, available data are inconsistent with hypothesis; - , no data available)

	Assessment of DPM hypotheses									
	Winter			Summer						
Species with DPM	SS	FM	C	SS	FM	C	JM	MC	Method	Reference
Mute swan (*Cygnus olor*)	S	I	I	S	I	I	I	I	Behavioural observation	Conover *et al.* (2000)
King penguin (*Aptenodytes patagonicus*) (male and female)	-	-	-	S	I	-	-	-	Behavioural observation and moult analysis	Nicolaus *et al.* (2007)
Eurasian kestrel (*Falco tinnunculus*)	-	-	-	I	S	-	-	-	Behavioural observation	Hakkarainen *et al.* (1993)
Barn owl (*Tyto alba*) (male and female)	-	-	-	-	-	-	-	-	Moult analysis	Roulin (1999)
Velvet asity (*Philepitta castanea*)	-	-	-	S	-	-	-	-	Behavioural observation	Prum & Razafindratsita (1997)
Long-tailed manakin (*Chiroxiphia linearis*)	-	-	-	S	-	-	-	I	Moult analysis	Doucet *et al.* (2007)
	-	-	-	S	I	I	I	I	Model presentation	McDonald (1993)
	-	-	-	S	I	S	S	I	Behavioural observation	Foster (1987)
Lance-tailed manakin (*Chiroxiphia lanceolata*)	-	-	-	-	-	-	-	I	Moult analysis	DuVal (2005)
Satin bowerbird (*Ptilonorhynchus violaceus*)	-	-	-	S	-	-	-	-	Behavioural observation	Collis & Borgia (1993)
Red-backed fairy-wren (*Malurus melanocephalus*)	-	-	-	S	-	-	-	-	Behavioural observation	Karubian (2002)
	-	-	-	S	I	-	-	-	Behavioural observation and model presentation	Karubian *et al.* (2008)
	-	-	-	S	-	-	-	-	Behavioural observation	Webster *et al.* (2008)
'Elepaio (*Chasiempis sandwichensis*)	I	I	-	S	I	-	I	-	Model presentation	VanderWerf & Freed (2003)
	-	I	-	-	I	-	PS	I	Behavioural observation	Vanderwerf (2001)
North Island robin (*Petroica longipes*)	-	-	-	S	-	-	-	I	Moult analysis	Berggren & Low (2006)
	S	-	S	-	-	-	-	-	Behavioural observation	Berggren *et al.* (2004)
Cedar waxwing (*Bombycilla cedrorum*) (male and female)	-	-	-	S	I	I	-	-	Behavioural observation	Mountjoy & Robertson (1988)
Purple martin (*Progne subis*)	-	-	-	I	I	-	-	I	Model presentation	Stutchbury (1991)
	-	-	-	-	S	-	-	-	Behavioural observation	Brown (1984)
Tree swallow (*Tachycineta bicolor*) (female)	-	I	-	S	I	I	-	-	Model presentation	Stutchbury & Robertson (1987)
	-	I	-	S	I	-	-	-	Behavioural observation	Lozano & Handford (1995)
Pied flycatcher (*Ficedula hypoleuca*)	-	-	-	I	S	-	-	-	Model presentation and behavioural observation	Slagsvold and Saetre (1991); Saetre & Slagsvold (1996)
Pied flycatcher	-	-	-	I	I	-	I	-	Model presentation	Huhta & Alatalo (1993)
Red-flanked bushrobin (*Tarsiger cyanurus*)	-	-	-	S	-	-	-	-	Behavioural observation	Morimoto *et al.* (2006)
Medium ground-finch (*Geospiza fortis*)	-	-	-	S	I	I	-	-	Behavioural observation	Grant (1990)
Black-headed grosbeak (*Pheucticus melanocephalus*)	-	-	-	S	I	S	-	-	Behavioural observation	Hill (1994)
	-	-	-	S	-	-	-	-	Model presentation	Hill (1989)
	-	-	-	S	I	S	-	-	Behavioural observation	Hill (1988*a*)
	-	-	-	S	I	S	-	-	Behavioural observation	Hill (1988*b*)
Indigo bunting (*Passerina cyanea*)	S	I	I	I	I	I	I	I	Moult analysis	Rohwer (1986)
Painted bunting (*Passerina ciris*)	-	-	-	I	I	-	-	-	Behavioural observation	Lanyon & Thompson (1986)
	I	S	S	I	S	I	I	I	Moult analysis	Thompson (1991)
Orange-breasted bunting (*Passerina leclancherii*) (male and female)	S	I	I	S	I	I	I	-	Moult analysis	Thompson & Leu (1995)
Lazuli bunting (*Passerina amoena*)	-	-	-	S	I	-	-	-	Behavioural observation	Greene *et al.* (2000)
	-	-	-	S	-	-	-	-	Model presentation	Muehter *et al.* (1997)

Table 1. *(Cont.)*

Species with DPM	Winter SS	Winter FM	Winter C	Summer SS	Summer FM	Summer C	Summer JM	Summer MC	Method	Reference
American redstart (*Setophaga ruticilla*)	-	-	-	I	I	-	I	-	Model presentation	Procter-Gray (1991)
	-	-	-	-	I	S	-	-	Behavioural observation	Procter-Gray & Holmes (1981)
	S	-	S	I	I	I	I	-	Moult analysis	Rohwer *et al.* (1983)
Black redstart (*Phoenicurus ochruros*)	-	-	-	I	-	-	-	-	Model presentation	Schwarzová (2010)
	-	-	-	-	I	-	-	-	Behavioural observation	Weggler (2001)
	-	-	-	I	I	I	I	S	Behavioural observation	Landmann & Kollinsky (1995*a*)
	-	-	-	I	I	-	I	-	Model presentation	Landmann & Kollinsky (1995*b*)
	I	I	I	-	-	-	-	-	Behavioural observation	Cuadrado (1995)
Saffron finch (*Sicalis flaveola*)	-	-	-	I	-	-	-	-	Behavioural observation	Palmerio & Massoni (2009)
Orchard oriole (*Icterus spurius*)	-	-	-	I	I	I	I	-	Model presentation	Enstrom (1992*a*)
	I	I	I	-	-	-	-	I	Behavioural observation and moult analysis	Enstrom (1992*b*)
Baltimore oriole (*Icterus galbula*)	S	-	-	-	-	-	-	-	Moult analysis	Rohwer & Manning (1990)
	-	-	-	S	S	I	-	-	Model presentation	Flood (1984)
Red-winged blackbird (*Agelaius phoeniceus*)	-	-	-	S	S	-	-	-	Model presentation	Rohwer (1978)
House finch (*Carpodacus mexicanus*)	-	S	-	-	-	-	-	-	Behavioural observation	Brown & Brown (1988)
	I	S	S	S	I	I	I	I	Behavioural observation	Hill (1996)
Eurasian siskin (*Carduelis spinus*)	S	I	I	-	-	-	-	-	Behavioural observation	Senar *et al.* (1998)
Zebra finch (*Taeniopygia guttata*)	-	-	-	-	-	-	-	S	Behavioural observation	Leader & Nottebohm (2006)

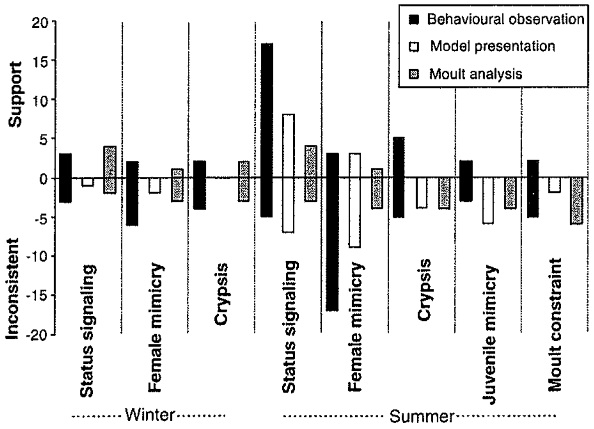

Fig. 2. A summary of the number of studies that have supported or failed to support hypotheses for the function of delayed plumage maturation, as indicated in Table 1. Studies which support the indicated hypothesis are portrayed above the line (positive numbers), while studies which fail to support these hypotheses are portrayed below the line (negative numbers). Studies are classified according to whether they are based on nonexperimental behavioural observations, model presentations, or analysis of moult.

V. HYPOTHESIZED BENEFITS OF SUBADULT PLUMAGES

If developmental constraints cannot explain delayed plumage maturation for most bird species and delayed plumage maturation is part of a strategy of delayed reproductive investment, then there must be benefits to having a subadult plumage rather than a definitive plumage in the early year(s) of development. The three hypotheses for how subadult plumage helps young birds defer the costs of reproduction are that subadult plumages aid in mimicry, crypsis, or signaling subordinance. We review below the logic of each of these hypotheses and then assess the evidence that supports or refutes each. Table 1 and Fig. 2 provide data on the studies that have found support for or lack of support for the various hypotheses.

(1) Mimicry hypothesis

(*a*) *Conceptual framework*

Rohwer *et al.* (1980) advanced the hypothesis that the female-like plumage worn by some males of sexually dichromatic, North American passerines in their first breeding season evolved as a deceptive signal of sex. According to this hypothesis, which is known as the female-mimicry hypothesis, first-year subadult males mimic the appearance of adult females and in so doing exploit the tendency of mature adult males not to attack females. Reducing male aggression through mimicry was proposed to enhance the chances of subadult males breeding in their first year as well as in subsequent years (Rohwer *et al.*, 1980). Female mimicry also may be advantageous to first-year males during the breeding season if adult males behave nonaggressively and allow access to food or other resources normally reserved for females. This increased access could give subadult males better proximity to females and thereby increase their opportunities for extra-pair copulations (Brown, 1984). Similarly, a female-like plumage may be advantageous to a subadult male in non-breeding contexts if it results in less aggression from conspecific adult males and greater access to food and other resources (Brown & Brown, 1988).

An alternative form of the mimicry hypothesis proposes that drab subadult plumage is an adaptation to mimic juvenal plumage rather than adult female plumage (Foster, 1987). The underlying assumption of this hypothesis is that adults display less aggression towards subadult males in a juvenal-like plumage than toward adult females (Thompson & Leu, 1995).

(*b*) *Assessement*

There is little empirical support for the mimicry hypotheses of delayed plumage maturation as an explanation for the subadult plumages of most species of birds, particularly for the testable prediction that territorial adult males cannot distinguish subadult males from females or juveniles. There are, however, at least a couple of birds in which yearling males do appear to mimic females. A study of the Eurasian kestrel (*Falco tinnunculus*) found that adult males were unable to distinguish between young males and adult females and that this inability enhanced the breeding ability of young males (Hakkarainen *et al.*, 1993). A subsequent study of the Eurasian kestrel refined this result by concluding that the female-mimicry hypothesis can be a mechanism that explains delayed plumage maturation in first-year males that had not moulted any of their juvenal feathers into adult feathers (Vergara & Fargallo, 2006).

Another species in which the female-mimicry hypothesis may be applicable is the pied flycatcher (*Ficedula hypoleuca*) as several studies of this species have shown that adult males have difficulty distinguishing between females and female-like males (Slagsvold & Saetre, 1991; Saetre & Slagsvold, 1992, 1996; Saetre, 1993). Among the many studies of pied flycatchers (see Huhta & Alatalo, 1993), however, subadult males are not always treated like females. Moreover, analysis of delayed plumage maturation in this species is complicated by the fact that adults vary from bright to dull in appearance and in the latter case overlap with the plumage of subadults. The results of other studies that claim to support the female-mimicry hypothesis, such as the study of the Baltimore oriole by Flood (1984) and the red-winged blackbird by Rohwer (1978), did not find that adult males were unable to distinguish subadult males from females. These latter studies involved species that have a variable subadult plumage which typically is more male-like or intermediate in appearance between the adult male and the adult female at the time of the possible onset of breeding. Thus, the results of these studies also appear to be explainable under the status-signaling hypothesis (see Section V.3).

A study of the moults and resulting plumages of first-year painted buntings found that during each of their three, first-year post-juvenal moults, subadult males grew plumage that was almost exclusively adult-female-like, rather than adult-male-like, which supports certain predictions of the female-mimicry hypothesis (Thompson, 1991). No study, however, has demonstrated that the female-like subadult male plumages in this species actually reduce aggression from conspecific adults in accordance with the female-mimicry hypothesis. Moreover, a study of the behaviour of subadult male painted buntings by Lanyon & Thompson (1986) found that they settled in inferior habitats relative to the more favourable edge habitat occupied by adult males. This result is not unexpected, however, because neither the female-mimicry hypothesis nor the other adaptive hypotheses of delayed plumage maturation predict that subadults will be as successful as adults in this regard (Rohwer, 1983).

The one definitive case of effective female mimicry concerns a lifetime, alternative reproductive strategy in the ruff (*Philomachus pugnax*), a Paleartic shorebird. A small percentage of male ruffs are smaller than typical males, approximately the size of females, and have a plumage colour and pattern that is unlike typical males but exactly like that of females (Jukema & Piersma, 2006). These "faeder" males both look and act like females, clearly and demonstrably using their female appearance to gain access to leks and opportunities to copulate with females (Jukema & Piersma, 2006). The sophistication of the deception perpetrated by "faeder" male ruffs is in contrast to anything observed in other bird species and underscores the weakness of claims of female mimicry in other species.

There also is little support for subadult plumage mimicking the plumage of juveniles. Rohwer *et al.* (1980) reported that in North America no subadult male passerine that exhibits delayed plumage maturation has a plumage that is more similar to juvenal plumage than to the adult female plumage. Moreover, in migratory passerines, there are no juveniles in the population until the earliest broods fledge, and thus the mimetic function of dull colouration is not possible until the second breeding attempt (Schwarzová, 2010). In light of the foregoing, mimicry of juveniles is rarely invoked to explain delayed plumage maturation notwithstanding that the underlying assumption that adults display less aggression to conspecific juveniles than other conspecific adults appears to be sound (Ligon & Hill, 2009).

(2) **Cryptic hypothesis**

(*a*) *Conceptual framework*

The cryptic hypothesis posits that young males can benefit by delaying the attainment of definitive plumage because a drab first-year plumage allows subadults to be less conspicuous towards predators and older conspecifics. Young males that delay attainment of definitive plumage have greater lifetime reproduction by avoiding mortality risks associated with attempting to breed when they are inexperienced young adults (Selander, 1965, 1972).

Selander (1965) conceived the cryptic hypothesis to explain delayed plumage maturation in promiscuous, polygnous blackbird species in which first-year males rarely breed, but this hypothesis is applicable to other species in which subadult males breed on a facultative basis. According to Selander (1965), (*i*) subadult males may take advantage of opportunities to breed when conditions involving competition with adult males for breeding resources permit, (*ii*) the experience gained by subadult males in territorial and courtship behaviour may benefit them when breeding in subsequent years, and (*iii*) an adult male-like subadult plumage may have some selective value in agonistic encounters at feeding or roosting sites (Selander, 1965). In essence, Selander (1965, 1972) proposed that males of certain blackbird species exhibit a general delay in physiological and morphological development as a result of a general inability to compete with adult males for limited breeding resources but that these birds may breed when low-cost opportunities are available.

Selander (1965, 1972) was not specific with respect to the mortality risks associated with bright plumages (e.g. risk from predators *versus* aggression from older conspecifics, costs of obtaining bright plumages), but he did note the enhanced risk to predators resulting from full development of the long tails of grackles. As a result, subsequent authors limited Selander's (1965, 1972) hypothesis to predation risk and termed it the cryptic hypothesis to distinguish it from other hypotheses that focused on intraspecific interactions (Lyon & Montgomerie, 1986). Although we view Selander's (1965, 1972) delayed-maturation hypothesis more broadly and as a precursor to the sophisticated breeding threshold hypothesis of Studd & Robertson (1985), because of the prevalence of the term "cryptic hypothesis" in the literature on delayed plumage maturation, we adopt this interpretation of Selander (1965, 1972) and subsume under the cryptic hypothesis all hypotheses in which birds delay the acquisition of definitive plumage to remain inconspicuous to predators and older conspecifics. Under this approach, the central idea of the cryptic hypothesis is that the benefit of subadult plumage is inconspicuousness.

(*b*) *Assessment*

Few studies have attempted to test directly the idea that the benefit of subadult plumage is increased inconspicuousness, undoubtedly in part because of the difficulties involved in studying how the enhanced crypsis provided by dull subadult plumages reduces predation risk and aggression from conspecific adults in the wild. Various studies that have attempted to evaluate the more general question of whether predation risk is associated with bright and cryptic plumages (such as Götmark, 1992, 1993, 1994, 1995, 1996, 1997; Götmark & Olsson, 1997; Slagsvold, Dale & Kruszewicz, 1995) have produced inconsistent results. These attempts to quantify the risks of conspicuous plumage perhaps can be summarized best by a study that involved a field experiment in which stuffed chaffinches (*Frinilla coelebs*) and pied flycatchers were exposed to Eurasian sparrowhawks (*Accipiter nisus*) on spring migration in Denmark (Götmark, 1993). In the case of the pied flycatcher, the hawks attacked the cryptic females more often than conspicuous males, while in the case of the chaffinch the hawks attacked the colourful males more often than the cryptic females (Götmark, 1993). These and other studies that have sought to determine the effects of bright and cryptic plumages on predation risk show that there is no simple relationship between colourful feathers and predation risk, and that factors such as search image and prey familiarity can affect predation risk as much as feather colouration.

In assessing the cryptic hypothesis, Rohwer *et al.* (1980) commented that this hypothesis likely could not provide a complete explanation for delayed plumage maturation because, among other things, the first-year males of all of the sexually dichromatic, North American passerines that exhibit delayed plumage maturation have plumages that more closely resemble adult female or adult male plumages than the more cryptic plumages of juveniles. As pointed out by Studd & Robertson (1985), this suggests that minimizing competition with older males is more important in these species than minimizing the risk of predation or avoiding entirely the costs of reproduction by delaying breeding.

We concur that the enhanced inconspicuousness to predators and older conspecifics provided by dull subadult plumages does not completely explain the benefits of delayed plumage maturation. Nevertheless, we find the logic of the cryptic hypothesis hard to dispute. The subadult plumages of most species of birds are less conspicuous than definitive plumages. Moreover, many species of birds wear bright definitive alternate plumages for breeding and drabber definitive basic plumages the rest of the year. There is no obvious alternative explanation for such a transition between bright and drab definitive plumages than benefits of increased crypsis (Hill, 2010). If drabber plumages benefit birds generally through crypsis, then drabber subadult plumages should certainly benefit young, inexperienced birds.

(3) Status-signaling hypothesis

(*a*) *Conceptual framework*

Under the status-signaling hypothesis proposed by Lyon & Montgomerie (1986), young males experience less aggressiveness from mature adult males during the breeding season because their subadult plumage is an honest signal of subordinate status. By honestly signaling their sex, age, and inexperience to older, experienced members of the same sex, subadults become less of a threat to challenge for mates and resources and consequently are subject to less aggression (Lyon & Montgomerie, 1986; Dale, 2006). By reducing the risks associated with such aggression in their first year, subadults of sexually dichromatic passerines can breed when low-cost opportunities are available and otherwise increase their chances of surviving to their second and subsequent breeding seasons, thereby increasing lifetime reproductive output (Lyon & Montgomerie, 1986).

Lyon & Montgomerie (1986) proposed that females in species with delayed plumage maturation choose mates primarily on the basis of the brightness of plumage rather than territory. They proposed mate choice based on plumage colouration as a critical assumption, arguing that if female choice was based on territory quality then adult males would have an interest in fending off all males on their territories (Lyon & Montgomerie, 1986; Rohwer & Butcher, 1988). Status signaling, however, has been shown to work in competition over resources as well as in the context of female choice (reviewed in Senar, 2006). By broadening the hypothesis to include honest signaling of subordinate status in the context of both mate choice and territory acquisition, delayed plumage maturation can be viewed as a signal that is part of a general strategy of reduced reproductive effort. Signaling subordinance also may provide benefits to subadults during the non-breeding season by reducing aggression from older conspecifics and thereby giving them greater access to territories and available food resources (Rohwer & Butcher, 1988).

(*b*) *Assessment*

Most studies of delayed plumage maturation support the status-signaling hypothesis, particularly the testable prediction that bright adult males correctly perceive dull subadult males as males but respond less aggressively to them (see Table 1; Dale, 2006; Senar, 2006). The reason that distinct subadult plumages reduce aggression against subadults by older conspecifics is that the subadult plumages honestly advertise inferior competitive ability. The general strategy of a subadult that exhibits delayed plumage maturation is to take on fewer risks and invest less in reproductive effort and, instead, to invest more in survival and maintenance. This strategy of reduced reproductive investment is honestly signaled through subadult plumage.

A principal benefit of delayed plumage maturation is that subadults generally encounter less aggression from older conspecifics than they would if they had a definitive plumage. Species in which adult males respond less aggressively to distinctively plumaged subadults of the same sex include the red-backed fairy-wren (Karubian *et al.*, 2008), red-flanked bushrobin (*Tarsiger cyanurus*) (Morimoto, Yamaguchi & Ueda, 2006), ‘elepaio (VanderWerf & Freed, 2003), mute swan (Conover *et al.*, 2000); Eurasian siskin (*Carduelis spinus*) (Senar *et al.*, 1998), lazuli bunting (Muehter *et al.*, 1997), satin bowerbird (Collis & Borgia, 1993), long-tailed manakin (Foster, 1987; McDonald, 1993), medium ground-finch (Grant, 1990), black-headed grosbeak (Hill, 1988*a*, *b*), Baltimore oriole (Flood, 1984), and red-winged blackbird (Rohwer, 1978). In these studies, reduced aggression from conspecific adults is not dependent on the type of colouration of the subadult plumage, which may be produced by carotenoid-based pigments, melanin-based pigments, or the microstructure of feathers. Rather, the key feature of subadult plumages that allows them to serve as a signal of subordinance is their distinctiveness from definitive plumages.

Status signaled through subadult plumage can lead to more complex interactions between subadult and adult males than simply reduced aggression. For example, studies of the purple martin (*Progne subis*) (Morton, Forman & Braun, 1990; Wagner & Morton, 1997) and lazuli bunting (Greene *et al.*, 2000) indicate that adult males tolerate certain subadult males as close neighbours even as they chase away other adult males in definitive plumage. These adult males then cuckold their young neighbours, fathering as many as 50% of the young in nests of these subadult males. The inexperienced subadults in these arrangements never cuckold their adult neighbours, and essentially trade paternity of some of the offspring in their nests for an opportunity to breed.

Although many studies of delayed plumage maturation have focused on interactions between adults and subadults, substantial plumage variation among subadults similarly can signal social status and reduce aggression in interactions between subadults. Thus, for example, in a species that has a variety of first-year, subadult male plumages ranging from bright to dull, bright subadult males may be both subordinate to adults and dominant to dull subadult males (e.g. Karubian *et al.*, 2008). Similarly, in species that have two or more subadult age classes, such as many long-lived birds, subadult plumages may function in interactions between adults and subadults, between classes of subadults and within a class of subadults (McDonald, 1989; Zack & Stutchbury, 1992). Age-specific subadult plumages typically allow each class of subadults to exert dominance over a lower class or classes while still being subordinate to adult males and any subadult class above it (Foster, 1987; VanderWerf & Freed, 2003; Doucet *et al.*, 2007).

Many studies indicate that delayed plumage maturation reduces intraspecific aggression, but studies of the American redstart (Ficken & Ficken, 1967; Procter-Gray & Holmes, 1981; Procter-Gray, 1991), European black redstart (*Phoenicurus ochruros*) (Cuadrado, 1995; Landmann & Kollinsky, 1995*b*; Schwarzová, 2010), and orchard oriole (Enstrom, 1992*a*, *b*) indicate that subadult plumages do not reduce aggression from conspecific adults in accordance with either the status-signaling or mimicry hypotheses. Indeed, a study of the orchard oriole found that the first-year subadult plumage actually increased aggression from adult males as they were more aggressive to first-year males in the breeding season than to adult males (Enstrom, 1992*a*). In addition to these studies, a study of delayed plumage maturation in the great frigatebird (*Fregata minor*), a large, sexually dichromatic seabird, found that subadult plumage did not reduce aggression from conspecific adults on the foraging grounds and thus was non-adaptive (Valle *et al.*, 2006). The value of subadult plumages to subadults of these species remains unexplained. Based on the delayed-investment hypothesis, however, the plumages exhibited by the subadults of these species are closely related to the degree of competition for limited resources, particularly breeding resources, and as a result it can be expected, for example, that the first-year males of short-lived species such as the American redstart and black redstart must face a high degree of competition for breeding territories and/or mates given their female-like subadult plumages. Moreover, where high-quality habitats are limited, aggressiveness by territorial males may be determined more by territorial quality than feather colour and quality, and females may not choose males primarily on the basis of feather colour and quality (Landmann & Kollinsky, 1995*b*). In the case of large, long-lived seabirds, intense competition for mates and breeding resources and the high cost of raising offspring likely explain why many of these birds delay the acquisition of definitive plumage for many years.

VI. FUTURE RESEARCH

Dozens of studies with the goal of explaining delayed plumage maturation have focused on the immediate benefits of subadult plumage in either a breeding or non-breeding context. If delayed plumage maturation is part of a life-time reproductive strategy, however, wherein birds trade reduced access to resources and reduced breeding opportunities early in life for greater opportunities later in life, then the benefits of subadult plumage can only really be assessed by measuring lifetime reproductive success. Because it is difficult to track individual birds through their lifetimes, such comprehensive studies have rarely been attempted.

A study by Grant (1990) is a model for the important insights that can be gained when lifetime reproductive success rather than short-term benefits are emphasized. Grant (1990) demonstrated that differing environmental conditions could affect selection for the number of years spent in subadult plumage in the medium ground-finch, a species of Darwin's finch on the Galapagos Islands. Males of this species acquire adult black plumage anywhere from two to six years of age, but they also can breed in the brown and streaked subadult plumage. By assessing long-term data sets that included the complete reproductive history of every bird in the study population, Grant (1990) was able to show that variability in the plumage colouration of young males was a result of a trade-off between (*i*) individuals that took longer to acquire the black adult plumage, which survived drought conditions significantly better than those that acquired adult plumage quickly, and (*ii*) individuals that acquired the black adult plumage quickly, which had significantly lower survival in drought conditions but had a reproductive advantage in their first breeding season because of female preference for this plumage. Grant (1990) noted that as a result of constantly changing environmental conditions, the length of the subadult plumage stage was constantly evolving.

In our view, this work is the model for future studies of delayed plumage maturation. Over the past three decades, field studies have adequately tested the immediate costs and benefits of subadult plumage. To acquire a more complete understanding of delayed plumage maturation, we need to understand the lifetime fitness consequences of delaying plumage development in a wide variety of species and not just short-lived, small passerines. Such studies will not be feasible in every species of bird, but in the circumstances in which such an approach can be pursued the insights gained will be substantial.

VII. CONCLUSIONS

(1) The explanation for delayed plumage maturation that arises from the now substantial literature is that subadult plumages generally are not the result of developmental constraints or lack of appropriate moults. Rather delayed plumage maturation is part of a strategy of reduced investment in competition with older individuals, often but not always in a reproductive context, in the first year or years of life.

(2) Comparative analyses that take into account lifespan, the availability of resources, and the costs of competition for resources indicate that a delay in reproductive investment evolves when there is high expectation for future reproduction, the competition for breeding resources is keen, and the costs of failed competition are large.

(3) Three functions have been proposed for distinctive subadult plumage: mimicry, crypsis, and status signaling. Mimicry is the least supported of the three hypothesized functions and seems an unlikely explanation for subadult plumage in most birds because definitive evidence for female mimicry exists in only one species. Crypsis is a likely benefit for drabber subadult plumages, but convincing tests of this idea are nearly lacking. Moreover, the general similarity of subadult plumages to adult plumages, as compared with more cryptic juvenal plumages, suggests that minimizing competition with adults is more important than minimizing the risk of predation. Avoiding aggression from older, more experienced conspecifics by honestly signaling subordinance through subadult plumage is the benefit of delayed plumage maturation that has received by far the most empirical support.

(4) In most bird species studied to date, males in subadult plumages are subject to less aggression from older conspecifics than males in definitive plumage. Crypsis and status signaling can be beneficial to young birds in both breeding and non-breeding contexts.

(5) Presumably, the benefits of delayed plumage maturation ultimately enhance the lifetime reproductive success of birds that pursue this strategy, and studying delayed plumage maturation within the context of lifetime reproductive success should be a goal of future studies.

VIII. ACKNOWLEDGEMENTS

We thank members of the Hill Lab for comments on an earlier version of the manuscript. During manuscript preparation G.E.H. was supported by National Science Foundation grant 0923088. G.L.H. would like to thank Guy Beauchamp and Sievert Rohwer for taking the time to review and comment on an early draft of this manuscript.

IX. REFERENCES

Alonso-Alvarez, C., Doutrelant, C. & Sorci, G. (2004). Ultraviolet reflectance affects male-male interactions in the Blue Tit (*Parus caeruleus ultramarinus*). *Behavioral Ecology* **15**, 805–809.

Arnold, S. J. (1983). Sexual selection: the interface of theory and empiricism. In *Mate choice* (ed. P. P. G. Bateson), pp. 67–107. Cambridge University Press, New York.

Badyaev, A. V. & Hill, G. E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics* **34**, 27–49.

Beauchamp, G. (2003). Delayed maturation in birds in relation to social foraging and breeding competition. *Evolutionary Ecology Research* **5**, 589–596.

Berggren, A., Armstrong, D. P. & Lewis, R. M. (2004). Delayed plumage maturation increases overwinter survival in North Island Robins. *Proceedings of the Royal Society of London Series B* **271**, 2123–2130.

Berggren, A. & Low, M. (2006). Sexual dichromatism in North Island Robins (*Petroica longipes*) is weakened by delayed plumage maturation in males and females. *Emu* **106**, 203–209.

Brown, C. R. (1984). Light-breasted Purple Martins dominate dark-breasted birds in a roost: implications for female mimicry. *The Auk* **101**, 162–164.

Brown, M. B. & Brown, C. R. (1988). Access to winter food resources by bright-versus dull-colored House Finches. *The Condor* **90**, 729–731.

Bruinzeel, L. W. & van de Pol, M. (2004). Site attachment of floaters predicts success in territory acquisition. *Behavioral Ecology* **15**, 290–296.

Chu, P. C. (1994). Historical examination of delayed plumage maturation in the shorebirds (Aves: Charadriiformes). *Evolution* **48**, 327–350.

Collis, K. & Borgia, G. (1993). The costs of male display and delayed plumage maturation in the Satin Bowerbird (*Ptilonorhynchus violaceus*). *Ethology* **94**, 59–71.

Conover, M. R., Reese, J. G. & Brown, A. D. (2000). Costs and benefits of subadult plumage in Mute Swans: testing hypotheses for the evolution of delayed plumage maturation. *The American Naturalist* **156**, 193–200.

Cuadrado, M. (1995). Female-like plumage does not reduce aggression from adult male Black Redstarts *Phoenicurus ochrurus* in winter. *Ardea* **83**, 431–434.

Cucco, M. & Malacarne, G. (2000). Delayed maturation in passerine birds: an examination of plumage effects and some indications of a related effect in song. *Ethology Ecology & Evolution* **12**, 291–308.

Cuthill, I. (2006). Color perception. In *Bird coloration, Volume I: mechanisms and measurements* (eds G. E. Hill and K. J. McGraw), pp. 3–40. Harvard University Press.

Dale, J. (2006). Intraspecific variation in coloration. In *Bird coloration, Volume II: function and evolution* (eds G. E. Hill and K. J. McGraw), pp. 36–86. Harvard University Press.

Delhey, K. & Kempenaers, B. (2006). Age differences in Blue Tit *Parus caeruleus* plumage colour: within-individual changes or colour-biased survival? *Journal of Avian Biology* **37**, 339–348.

Dolbeer, R. A. & Bernhardt, G. E. (2003). Age-specific reproduction by female Laughing Gulls (*Larus atricilla*). *The Auk* **120**, 531–535.

Doucet, S. M., McDonald, D. B., Foster, M. S. & Clay, R. P. (2007). Plumage development and molt in Long-tailed Manakins (*Chiroxipia linearis*): variation according to sex and age. *The Auk* **124**, 29–43.

DuVal, E. H. (2005). Age-based plumage changes in the Lance-tailed Manakin: a two-year delay in plumage maturation. *The Condor* **107**, 915–920.

Eaton, M. D. (2005). Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. *PNAS* **102**, 10942–10946; www.pnas.org/cgi/doi/10.1073/pnas.0501891102.

Enstrom, D. A. (1992*a*). Breeding season communication hypotheses for delayed plumage maturation in passerines: tests in the Orchard Oriole, *Icterus spurious*. *Animal Behaviour* **43**, 463–472.

Enstrom, D. A. (1992*b*). Delayed plumage maturation in the Orchard Oriole (*Icterus spurius*): tests of winter adaptation hypotheses. *Behavioral Ecology and Sociobiology* **30**, 35–42.

Enstrom, D. A. (1993). Female choice for age-specific plumage in the Orchard Oriole: implications for delayed plumage maturation. *Animal Behaviour* **45**, 435–442.

Ficken, M. S. & Ficken, R. W. (1967). Age-specific differences in the breeding behavior and ecology of the American Redstart. *The Wilson Bulletin* **79**, 188–199.

Flood, N. J. (1984). Adaptive significance of delayed plumage maturation in male Northern Orioles. *Evolution* **3**, 267–279.

Forslund, P. & Pärt, T. (1995). Age and reproduction in birds: hypotheses and tests. *Trends in Ecology and Evolution* **10**, 374–378.

Foster, M. S. (1987). Delayed maturation, neoteny, and social system differences in two manakins of the genus *Chiroxiphia*. *Evolution* **41**, 547–558.

Götmark, F. (1992). Anti-predator effect of conspicuous plumage in a male bird. *Animal Behaviour* **44**, 51–55.

Götmark, F. (1993). Conspicuous coloration in male birds is favored by predation in some species and disfavored in others. *Proceedings of the Royal Society of London Series B* **253**, 143–146.

Götmark, F. (1994). Does a novel bright colour patch increase or decrease predation? Red wings reduce predation of risk in European Blackbirds. *Proceedings of the Royal Society of London Series B* **256**, 83–87.

Götmark, F. (1995). Black-and-white plumage in male Pied Flycatchers (*Ficedula hypoleuca*) reduces the risk of predation from Sparrowhawks (*Accipiter nisus*) during the breeding season. *Behavioral Ecology* **6**, 2–25.

Götmark, F. (1996). Simulating a colour mutation: conspicuous red wings in the European Blackbird reduce the risk of attacks by Sparrohawks. *Functional Ecology* **10**, 355–359.

Götmark, F. (1997). Bright plumage in the magpie: does it increase or reduce the risk of predation? *Behavioral Ecology and Sociobiology* **40**, 41–49.

Götmark, F. & Olsson, J. (1997). Artificial colour mutation: do red-painted Great Tits experience increased or decreased predation? *Animal Behaviour* **53**, 83–91.

Gould, S. J. (1977). *Ontogeny and phylogeny*. Belknap Press of Harvard University Press.

Grant, B. R. (1990). The significance of subadult plumage in Darwin's Finches, *Geospiza fortis*. *Behavioral Ecology* **1**, 161–170.

Graves, G. R. (2004). Testicular volume and asymmetry are age-dependent in Black-throated Blue Warblers (*Dendroica caerulescens*). *The Auk* **121**, 473–485.

Greene, E., Lyon, B. E., Muehter, V. R., Ratcliffe, L., Oliver, S. J. & Boag, P. T. (2000). Disruptive sexual selection for plumage coloration in a passerine bird. *Nature* **407**, 1000–1003.

Hakkarainen, H., Korpimaki, E., Huhta, E. & Palokangas, P. (1993). Delayed maturation in plumage colour: evidence for the female-mimicry hypothesis in the kestrel. *Behavioral Ecology and Sociobiology* **33**, 247–251.

Hamilton, W. & Zuk, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

Hardy, J. W. (1974). Behavior and its evolution in Neotropical jays (*Cissilopha*). *Bird-Banding* **45**, 253–268.

Hill, G. E. (1988*a*). Age, plumage brightness, territory quality, and reproductive success in the Black-headed Grosbeak. *The Condor* **90**, 379–388.

Hill, G. E. (1988*b*). The function of delayed plumage maturation in male Black-headed Grosbeaks. *The Auk* **105**, 1–10.

Hill, G. E. (1989). Late spring arrival and dull nuptial plumage: aggression avoidance by yearling males? *Animal Behaviour* **37**, 665–673.

Hill, G. E. (1994). Testis mass and subadult plumage in Black-headed Grosbeaks. *The Condor* **96**, 626–630.

Hill, G. E. (1996). Subadult plumage in the House Finch and tests of models for the evolution of delayed plumage maturation. *The Auk* **113**, 858–874.

Hill, G. E. (2002). A red bird in a brown bag—the function and evolution of colorful plumage in the House Finch. Oxford.

Hill, G. E. (2006). Female mate choice for ornamental coloration. In *Bird coloration, Volume II: function and evolution* (eds G. E. Hill and K. J. McGraw), pp. 137–200. Harvard University Press.

Hill, G. E. (2010). *National Geographic bird coloration*. National Geographic, Washington, DC.

Hill, G. E., Hood, W. R. & Higgins, K. (2009). A multifactorial test of the effects of carotenoid access, food intake, and parasite load on production of ornamental feather and bill coloration in American Goldfinches. *Journal of Experimental Biology* **212**, 1225–1233.

Hill, G. E. & McGraw, K. J. (Eds) (2006*a*). *Bird coloration, Volume I: mechanisms and measurements*. Harvard University Press.

Hill, G. E. & McGraw, K. J. (Eds) (2006*b*). *Bird coloration, Volume II: function and evolution*. Harvard University Press.

Huhta, E. & Alatalo, R. V. (1993). Plumage color and male-male interactions in the Pied Flycatcher. *Animal Behaviour* **45**, 511–518.

Humphrey, P. S. & Parkes, K. C. (1959). An approach to the study of molts and plumages. *The Auk* **76**, 1–31.

Jukema, J. & Piersma, T. (2006). Permanent female mimics in a lekking shorebird. *Biology Letters* **2**, 161–164; doi:10.1098/rsbl.2005.0416.

Karubian, J. (2002). Costs and benefits of variable breeding plumage in the Red-backed Fairy-wren. *Evolution* **56**, 1673–1682.

Karubian, J. (2008). Changes in breeding status are associated with rapid bill darkening in male Red-backed Fairy-wrens *Malurus melanocephalus*. *Journal of Avian Biology* **39**, 81–86.

Karubian, J., Lindsay, W. R., Schwabl, H. & Webster, M. S. (2011). Bill coloration, a flexible signal in a tropical passerine bird, is regulated by social environment and androgens. *Animal Behaviour* **81**, 795–800.

Karubian, J., Sillett, T. S. & Webster, M. S. (2008). The effects of delayed plumage maturation on aggression and survival in male Red-backed Fairy Wrens. *Behavioral Ecology* **19**, 508–516; doi:10.1093/beheco/arm 159.

Ketterson, E. D. (1979). Status signaling in Dark-eyed Juncos. *The Auk* **96**, 94–99.

King, D. I., DeGraaf, R. M. & Griffin, C. R. (2001). Plumage coloration and reproductive success in male Chestnut-sided Warblers. *The Wilson Bulletin* **113**, 239–242.

Klimkiewicz, M. K., Clapp, R. B. & Futcher, A. G. (1983). Longevity records of North American birds: Remizidae through Parulinae. *Journal of Field Ornithology* **54**, 287–294.

Klimkiewicz, M. K. & Futcher, A. G. (1989). Longevity records of North American birds supplement 1. *Journal of Field Ornithology* **60**, 469–494.

Kodric-Brown, A. & Brown, J. H. (1984). Truth in advertising: the kinds of traits favoured by sexual selection. *The American Naturalist* **124**, 309–323.

Lack, D. (1967). *The natural regulation of animal numbers*. Clarendon Press, Oxford.

Lande, R. (1981). Models of speciation by sexual selection of polygenic traits. *Proceedings of the National Academy of Sciences, USA* **78**, 3721–3725.

Landmann, A. & Kollinsky, C. (1995*a*). Age and plumage related territory differences in male Black Redstarts: the (non)-adaptive significance of delayed plumage maturation. *Ethology Ecology & Evolution* **7**, 147–167.

Landmann, A. & Kollinsky, C. (1995*b*). Territory defence in Black Redstarts, *Phoenicurus ochruros*: effects of intruder and owner age? *Ethology* **101**, 121–129.

Lanyon, S. M. & Thompson, C. F. (1986). Site fidelity and habitat quality as determinants of settlement pattern in male Painted Buntings. *The Condor* **88**, 206–210.

Lawton, M. F. & Lawton, R. O (1986). Heterochrony, deferred breeding and avian sociality. *Current Ornithology* **3**, 187–222.

Leader, N. & Nottebohm, F. (2006). Delayed plumage maturation in socially isolated juvenile Zebra Finches, *Taeniopygia guttata. Animal Behaviour* **72**, 113–121

Lepson, J. K. & Freed, L. A. (1995). Variation in male plumage and behavior of the Hawaii Akepa. *The Auk* **112**, 402–414.

Ligon, R. A. & Hill, G. E. (2009). Do adult Eastern Bluebird, *Sialia sialus*, males recognize juvenile-specific traits? *Animal Behaviour* **77**, 1267–1272.

Lowther, P. E. & Nocedal, J. (1997). Olive Warbler (*Peucedramus taeniatus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/310doi:10.2173/bna.310; accessed on 19 May 2011.

Lozano, G. A. & Handford, P. T. (1995). A test of an assumption of delayed plumage maturation hypotheses using female Tree Swallows. *The Wilson Bulletin* **107**, 153–164.

Lyon, B. E. & Montgomerie, R. D. (1986). Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? *Evolution* **40**, 605–615.

Marra, P. P., Hobson, K. A. & Holmes, R. T. (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**, 1884–1886.

McDonald, D. B. (1989). Correlates of male mating success in a lekking bird with male-male cooperation. *Animal Behaviour* **37**, 1007–1002.

McDonald, D. B. (1993). Delayed plumage maturation and orderly queues for status: a manakin mannequin experiment. *Ethology* **94**, 31–45.

McDonald, M. A. & Smith, M. H. (1994). Behavioral and morphological correlates of heterochrony in Hispaniolan palm-tanagers. *The Condor* **96**, 433–446.

Montgomerie, R. D. & Lyon, B. E. (1986). Does longevity influence the evolution of delayed plumage maturation in passerine birds? *The American Naturalist* **128**, 930–936.

Morimoto, G., Yamaguchi, N. & Ueda, K. (2006). Plumage color as a status signal in male-male interaction in the Red-flanked Bushrobin, *Tarsiger cyanurus. Journal of Ethology* **24**, 261–266.

Morton, E. S., Forman, L. & Braun, M. (1990). Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. *The Auk* **107**, 275–283.

Mountjoy, D. J. & Robertson, R. J. (1988). Why Are waxwings "waxy?" Delayed plumage maturation in the Cedar Waxwing. *The Auk* **105**, 61–69.

Muehter, V. R., Greene, E. & Ratcliffe, L. (1997). Delayed plumage maturation in Lazuli Buntings: tests of the female mimicry and status signalling hypotheses. *Behavioral Ecology and Sociobiology* **41**, 281–296.

Mulder, R. A., Ramiarison, R. & Emahalala, R. E. (2002). Ontongeny of male plumage dichromatism in Madagascar Paradise Flycatchers *Terpsiphone mutate. Journal of Avian Biology* **33**, 342–348.

Nicolaus, M., Le Bohec, C., Nolan, P. M., Gauthier-Clerc, M., Le Maho, Y., Komdeur, J. & Jouventin, P. (2007). Ornamental colors reveal age in the King Penguin. *Polar Biology* **31**, 53–61.

Orians, G. H. (1961). The ecology of blackbird (*Agelaius*) social systems. *Ecological Monographs* **31**, 285–312.

Palmerio, A. G. & Massoni, V. (2009). Reproductive biology of female Saffron Finches does not differ by the plumage of the mate. *The Condor* **111**, 715–721.

Peterson, A. T. (1991). Geographic variation in the ontogeny of beak coloration of Gray-breasted Jays. *The Condor* **93**, 448–452.

Peterson, A. T., Navarro-Siguenza, A. G. & Chen, G. (2003). Delayed plumage maturation in Asian thrushes, genus *Turdus. Forktail* **19**, 152–153.

Powlesland, R. G. (2002). Delayed plumage maturation in the male North Island robin (*Petroica longipes*). *Notornis* **49**, 263–265.

Procter-Gray, E. (1991). Female-like plumage of subadult male American Redstarts does not reduce aggression from other males. *The Auk* **108**, 872–879.

Procter-Gray, E. & Holmes, R. T. (1981). Adaptive significance of delayed attainment of plumage in male American Redstarts: tests of two hypotheses. *Evolution* **35**, 742–751.

Prum, R. O. & Razafindratsita, V. R. (1997). Lek behavior and natural history of the Velvet Asity (*Philepitta castanea:* Eurylaimidae). *The Wilson Bulletin* **109**, 371–392.

Rohwer, S. (1978). Passerine subadult plumages and the deceptive acquisition of resources: test of a critical assumption. *The Condor* **80**, 173–179.

Rohwer, S. (1983). Testing the female mimicry hypothesis of delayed plumage maturation: a comment on Procter-Gray and Holmes. *Evolution* **37**, 421–423.

Rohwer, S. (1986). A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. *The Auk* **103**, 281–292.

Rohwer, S. & Butcher, G. S. (1988). Winter *versus* summer explanations of delayed plumage maturation in temperate passerine birds. *The American Naturalist* **131**, 556–572.

Rohwer, S., Ewald, P. W. & Rohwer, F. C. (1981). Variation in size, appearance, and dominance within and among the sex and age classes of Harris' Sparrows. *Journal of Field Ornithology* **52**, 291–303.

Rohwer, S., Fretwell, S. D. & Niles, D. M. (1980). Delayed maturation in passerine plumages and the deceptive acquisition of resources. *The American Naturalist* **115**, 400–437.

Rohwer, S., Klein, Jr., W. P. & Heard, S. (1983). Delayed plumage maturation and the presumed prealternate molt in American Redstarts. *The Wilson Bulletin* **95**, 199–208.

Rohwer, S. & Manning, J. (1990). Differences in timing and number of molts for Baltimore and Bullock's Orioles: implications to hybrid fitness and theories of delayed plumage maturation. *The Condor* **92**, 125–140.

Roulin, A. (1999). Delayed maturation of plumage coloration and plumage spottedness in the Barn Owl (*Tyto alba*). *Journal of Ornithology* **140**, 193–197.

Saether, B. E. (1990). Age-specific variation in reproductive performance in birds. *Current Ornithology* **7**, 251–283.

Saetre, G-P. (1993). Sex recognition by male Pied Flycatchers in a population with little sexual dimorphism in plumage colour. *Ornis Scandinavica* **24**, 158–160.

Saetre, G-P. & Slagsvold, T. (1992). Evidence for sex recognition from plumage colour by the Pied Flycatcher, *Ficedula hypoleuca. Animal Behaviour* **44**, 293–299.

Saetre, G-P. & Slagsvold, T. (1996). The significance of female mimicry in male contests. *The American Naturalist* **147**, 981–995.

Samson, F. B. (1976). Territory, breeding density, and fall departure in Cassin's Finch. *The Auk* **93**, 477–497.

Schwarzová, L. (2010). Aggressive behavior in subadult and adult Black Redstarts: status-signaling strategy? *Journal of Ethology* **28**, 45–52.

Selander, R. K. (1965). On mating systems and sexual selection. *The American Naturalist* **99**, 129–141.

Selander, R. K. (1972). Sexual selection and dimorphism in birds. In *Sexual selection and the descent of man 1871–1971* (ed. B. Campbell), pp. 180–230. Aldine, Chicago.

Senar, J. C. (2006). Color displays as intrasexual signals of aggression and dominance. In *Bird coloration, volume II: function and evolution* (eds G. E. Hill and K. J. McGraw), pp. 87–136. Harvard University Press.

Senar, J. C., Copete, J. L. & Martin, A. J. (1998). Behavioral and morphological correlates of variation in the extent of the post-juvenile molt in the Siskin *Carduelis spinus. Ibis* **140**, 661–669.

Siefferman, L., Hill, G. E. & Dobson, F. S. (2005). Ornamental plumage coloration and condition are dependent on age in eastern bluebirds *Sialia sialis. Journal of Avian Biology* **36**, 428–435.

Slagsvold, T., Dale, S. & Kruszewicz, A. (1995). Predation favours cryptic coloration in breeding male Pied Flycatchers. *Animal Behaviour* **50**, 1109–1121.

Slagsvold, T. & Saetre, G.-P. (1991). Evolution of plumage color in male Pied Flycatchers (*Ficedula hypoleuca*): evidence for female mimicry. *Evolution* **45**, 910–917.

Studd, M. V. & Robertson, R. J. (1985). Life span, competition, and delayed plumage maturation in male passerines: the breeding threshold hypothesis. *The American Naturalist* **126**, 101–115.

Stutchbury, B. J. (1991). The adaptive significance of male subadult plumage in Purple Martins: plumage dyeing experiments. *Behavioral Ecology and Sociobiology* **29**, 297–306.

Stutchbury, B. J. & Morton, E. S. (2001). *Behavioral ecology of tropical birds.* Academic Press.

Stutchbury, B. J. & Robertson, R. J. (1987). Signaling subordinate and female status: two hypotheses for the adaptive significance of subadult plumage in female Tree Swallows. *The Auk* **104**, 717–723.

Thompson, C. W. (1991). The sequence of molts and plumages in Painted Buntings and implications for theories of delayed plumage maturation. *The Condor* **93**, 209–235.

Thompson, C. W. & Leu, M. (1995). Molts and plumages of Orange-breasted Buntings (*Passerina leclancherii*): implications for theories of delayed plumage maturation. *The Auk* **112**, 1–19.

Valle, C. A., De Vries, T. & Hernández, C. (2006). Plumage and sexual maturation in the Great Frigatebird *Fregata minor* in the Galapagos Islands. *Marine Ornithology* **34**, 51–59.

VanderWerf, E. A. (2001). Two-year delay in plumage maturation of male and female 'Elepaio. *The Condor* **103**, 756–766.

VanderWerf, E. A. & Freed, L. A. (2003). 'Elepaio subadult plumages reduce aggression through graded status-signaling, not mimicry. *Journal of Field Ornithology* **74**, 406–415.

Vergara, P. & Fargallo, J. A. (2006). Delayed plumage maturation in Eurasian kestrels: female mimicry, subordination signaling or both? *Animal Behaviour* **74**, 505–1513.

Vleck, C. M. & Brown, J. L. (1999). Testosterone and social and reproductive behavior in *Aphelocoma* jays. *Animal Behaviour* **58**, 943–951.

Wagner, R. H. & Morton, E. S. (1997). Sexual selection for delayed size maturation in a bird exhibiting delayed plumage maturation. *Journal of Avian Biology* **28**, 143–149.

Webster, M. S., Varian, C. W. & Karubian, J. (2008). Plumage color and reproduction in the Red-backed Fairy-wren: why be a dull breeder? *Behavioral Ecology* **19**, 517–524; doi:10.1093/beheco/arn015.

Weggler, M. (2001). Age-related reproductive success in dichromatic male Black Redstarts *Phoenicurus ocruros*: why are yearlings handicapped? *Ibis* **143**, 264–272.

Welty, J. C. & Baptista, L. (1988). *The life of birds.* Fifth edition. Saunders College Publishing, New York, New York.

Wright, P. L. & Wright, M. H. (1944). The reproductive cycle of the Red-winged Blackbird. *The Condor* **45**, 46–59.

Wynne-Edwards, V. C. (1962). *Animal dispersion in relation to social behavior.* Oliver and Boyd, Edinburgh.

Yamagishi, S., Asai, S., Eguchi, K. & Wada, M. (2002). Spotted-throat individuals of the Rufous Vanga *Schetba rufa* are yearling males and presumably sterile. *Ornithological Science* **1**, 95–99.

Zack, S. & Stutchbury, B. J. (1992). Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behavior* **123**, 194–219.

Zahavi, A. (1975). Mate selection—a selection for a handicap. *Journal of Theoretical Biology* **53**, 205–214.

(Received 2 September 2010; revised 24 June 2011; accepted 29 June 2011; published online 27 July 2011)