

Delayed plumage maturation in birds and the significance of condition-dependent parental care

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Abstract Several hypotheses have suggested that delayed plumage maturation (DPM) in male birds evolves to increase crypsis or to deter adult aggression towards inexperienced young males. Here, we present novel extensions of a game theory modeling framework to investigate the evolutionary mechanisms of DPM in a bird population. We reveal that increasing either the maximum survival rate or predation risk can promote the evolution of DPM. Longer life span and transferrable physical condition between breeding years show a significant mutual promotion effect on DPM evolution, and would also enable the evolution of DPM in some species with no reproductive output in year one. Our models indicate that sufficiently high investment on adult plumage is essential for the evolution of DPM, which is consistent with some previous empirical studies. Finally, we highlight the significance of condition-dependent male parental care and provide new insight into how sexual conflict over parental care between parents may influence the evolution of DPM in birds. Our results should help researchers better test the DPM delayed-investment strategy hypothesis with empirical data.

Keywords Delayed plumage maturation · Predation risk · Life span · Adult plumage investment · Parental care

Introduction

Delayed plumage maturation (DPM) is the delayed acquisition of adult plumage color and pattern until after an individual's first potential breeding season in birds (Rohwer et al. 1980; Lyon and Montgomerie 1986; Hawkins et al. 2012). DPM is most frequent among passerine species (e.g., Rohwer et al. 1980) with new discoveries being made across a range of different bird families (Peterson et al. 2003). Since the 1980s, two general categories of hypotheses have been proposed to explain the adaptive significance of DPM (Cucco and Malacarne 2000; Hawkins et al. 2012; Vergara et al. 2013): the “*molt-constraint hypothesis*” where first-year individuals are constrained from undergoing a pre-alternate molt, and the “*delayed-investment hypothesis*,” in which DPM is a key component of an adaptive delayed reproductive investment strategy that enables sub-adults to achieve benefits in some manner to compensate for possible breeding disadvantages.

While the delayed-investment strategy hypothesis has received considerable examination, there has been little empirical evidence for the molt-constraint hypothesis (Hawkins et al. 2012). We suggest that considering DPM as an avian life-history strategy that balances the trade-off between survival and reproduction is necessary, since sub-adult birds may have to invest more energy in their survival to guarantee future breeding success. Studd and Robertson (1985) developed a simple delayed breeding model to explore the relationship between the life span and mortality risk of birds attributed to first-year breeding. However, fitness trade-offs were assumed to be independent of traits possessed by other individuals, which makes the model less suitable for exploring evolution

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related to sexual advertisements since the “selection” and “contests” among individuals should be essential in a true sexual selection viewpoint (Andersson 1994). Game theory modeling (Maynard Smith 1982) is ideally suited to explore the evolution of such phenomenon since evolutionary contests are analyzed as “strategies,” and mathematical models are used to then predict the resulting prevalence of all competing strategies.

Biologists widely agree that delayed maturation is a strategy to reduce the costs of the first-year reproduction in order for a male to get to later breeding seasons when its reproductive potential is higher (Martin 1995; Hawkins et al. 2012). A number of theoretical models have addressed this in the context of age-dependent sexual signals or sexual advertisements. Through combining life-history theory and game theory models, Kokko (1997) first developed an age-dependent model where individual males could allocate resources to signaling or to increasing condition at each age for mates. Increasing investment by males in sexual advertisement over years was an evolutionarily stable strategy (ESS) under broad conditions (Kokko 1997). Proulx et al. (2002) found that better condition older males would allocate more efforts to advertisement due to more limited future opportunities for reproduction. Rands et al. (2011) explored the evolution of sexual ornaments that can grow and be kept for many years, and found that higher quality males should delay ornament growth until close to breeding. More recently, Adamson (2013) explored the evolutionary origins of age-dependent sexual traits through numerical simulations using a haploid population genetic model and found that reduced adult mortality facilitates sexual selection by favoring the evolution of age-dependent sexual signals under weak selection.

In this study, we model the evolutionary adaptation of DPM in birds via the delayed-investment strategy hypothesis. We build on the original age-dependent game theory modeling framework developed by Kokko (1997), and create novel extensions. Our aim is to examine two primary questions: (1) How does DPM evolve in bird populations? (2) What other factors play important roles in promoting the evolution of DPM? For our first question, we extend the previous modeling framework of Kokko (1997) by considering five additional factors: (1) The life-history traits of different populations are related to the surrounding environments (e.g., the abundance of foods and nest sites, frequency of extreme weathers, and density of predators), which may strongly influence the evolutionary outcomes; (2) Life span normally varies significantly among DPM species; (3) Due to the life experience gained through years, the resources obtained should be different between sub-adult and adult males; (4) The size or pattern of adult plumages varies among species, and consequently, plumage investment effort will differ; (5) Sub-adults may also not breed or have adult plumage (Hawkins et al. 2012), as has been shown for some seabirds (Lawton and Lawton 1986) and manakin species (McDonald 1989).

For our second question, we include in our model previous proposed effects from earlier DPM studies (reviewed by Hawkins et al. 2012) to explore the evolutionary outcomes. We categorize these effects as follows: (1) avoiding predation, e.g., through the cryptic effect (Selander 1965) and (2) increasing the resources gained due to less aggression from adults, thus easier access to food or other essential resources (Hill 1989; Hawkins et al. 2012), e.g., female mimicry (Rohwer et al. 1980; Foster 1987) or signaling the status to adult males (Lyon and Montgomerie 1986). Furthermore, we highlight the importance of condition-dependent parental care effects (Kokko 1998; Badyaev and Hill 2002), a factor that has previously been studied in many birds (Sasvári and Hegyi 2001), but has yet not been considered or discussed in the evolution of avian DPM.

The model

Basic assumptions

Following Kokko (1997), we assume an infinite population. Males can obtain a certain “baseline condition” of q_i , where i represents male age. Here, we consider the baseline condition differing among ages. Since adults should gain more of the available resources than yearling sub-adults due to the life experience gained, e.g., greater foraging experience (Marchetti and Price 1989), q_1 is assumed to be equal or smaller than q_i ($i > 1$). Males vary in sexual advertisement strategy (i.e., plumage color and pattern), and the effort at age i is a_i ($0 \leq a_i \leq 1$, Kokko 1997). In this model, the strategy representing the advertisement effort in birds is assumed as continuous, given the variation in plumage investment (Owens 2006) and degree of delayed maturation known among bird species (Berggren et al. 2004). The “baseline condition” is therefore allocated between reproduction (i.e., to express the sexual advertisement traits, A_i) and survival (i.e., to maintain body physical condition, C_i) (Kokko 1997):

$$A_i = \begin{cases} a_i q_i & (i = 1) \\ a_i (\mu C_{i-1} + q_i) & (i > 1) \end{cases} \quad (1)$$

$$C_i = \begin{cases} (1 - a_i) q_i & (i = 1) \\ (1 - a_i) (\mu C_{i-1} + q_i) & (i > 1) \end{cases} \quad (2)$$

where $\mu \in [0, 1]$ represents the fraction of physical condition transferred from the previous year (Kokko 1997). Note that here, we do not include the parameter of fraction of sexual trait transferred (Kokko 1997) because birds would undergo a complete molt each year.

In order to assess the life-history trade-off between survival and reproduction, we modify the functions of survival rate (s) and fecundity (f) from Kokko (1997) in this study. We use the following equations for survival rate and fecundity:

$$s_i = m[1 - \varepsilon \cdot \exp(-C_i)], \quad (3)$$

$$f_i = E[\exp(dA_i) - 1], \quad (4)$$

where m represents the maximum survival rate, d scales the female preference for the sexual trait, and E represents the state of the environment due to the competition by all other males, which is equal for all males, and changes whenever the advertisement strategies used by the population also changes (Kokko 1997). We assume that the physical condition directly determines the male individual's capacity for competition and to avoid predation in the population, which subsequently determines survival rate. Male sexual advertisement traits can be directly assessed by the females, thus determine the fitness gained from reproduction.

Generally, the survival rate is known to be related to environmental conditions and biotic effects such as conspecific competition and predation. Consequently in Eq. 3, we can treat m as being related to the environmental conditions. For example, in more severe environments, individuals in the population will be more likely to die due to more scarce food resource and/or more frequent extreme weather (e.g., low temperature or prolonged rainfall). For the second part of Eq. 3, we can consider it as the individuals' competitive capability derived from physical condition. Individuals in stronger physical condition are more competitive, are able to get more resources, and thus have higher survival rates.

Finally, we add another parameter of ε (>0) to Eq. 3 to scale the predation risk. Survival rate should decrease under more severe predation risk, but individuals with better physical condition can also avoid predation more effectively. As shown in Fig. S1a, survival rate will fall under more severe predation risk, but could still achieve the maximum value of m . In order for $s_i \geq 0$, we derive the following inequality from Eq. 3: $\varepsilon \leq \exp(C_i)$. The minimum value of C_i should be $q_1(1 - a_2)$, which represents the physical condition of sub-adult individuals with fully developed plumage. Then, ε would need to satisfy the condition of $\varepsilon \leq \exp(q_1(1 - a_2))$.

For the fecundity equation (Eq. 4), Kokko (1997) assumed that males could reproduce even if they invest no energy in sexual advertisement traits, i.e., $f_i > 0$ when A equals zero. Here, we rewrite the fecundity equation so that males can select the option of not breeding in the first year with no further energy investment on plumage (i.e., $f_i = 0$ when $a_1 = 0$). Males may therefore save all energy for future breeding but lose all the benefits of first-year breeding. In summary, we propose three potentially available strategies in our model: DPM, non-DPM, and DPM without breeding.

Dynamic and evolutionary stable strategy (ESS)

We follow the ESS seeking process described by Kokko (1997) to derive the stable strategy set of $\{a_i\}$ (detailed description can be found in the Supplementary materials). Since we aim to model DPM in birds, we assume that the plumage investment for adult males is fixed, i.e., set a_i ($i > 1$) as a constant, and then seek the value of a_1 for ESS. To assess the importance of life span on the evolutionary outcomes, as proposed by Studd and Robertson (1985), we calculate the ESS solutions for populations with different age classes (2, 3, and 5) for comparison.

Models including crypsis, mimicry, status signaling, and condition-dependent parental care

We rewrite the Eq. 3 to include the cryptic effect from the male immature plumage at age 1 (Fig. S2):

$$s'_1 = m[1 - \varepsilon \cdot \exp(-C_1)] \left[\frac{\alpha \cdot \exp\left[-e_1 \left(a_1 - \frac{a_2}{2}\right)\right]}{1 + \exp\left[-e_1 \left(a_1 - \frac{a_2}{2}\right)\right]} - 0.5\alpha + 1 \right]$$

where α represents the maximum magnitude of the cryptic effect. Then, $s'_1 \in [s_1(1 - 0.5\alpha), s_1(1 + 0.5\alpha)]$ depends on the value of a_1 . Here, survival rate is assumed to be negatively related to a_1 due to crypsis. In order to keep $s'_1 < 1$, α should be equal or smaller than $\frac{2}{m} - 2$. e_1 represents the sensitivity (i.e., shape) of the survival rate with changing value of a_1 .

To explore the effects of mimicry or status signaling, we assume that sexual advertisement in the first year entails an accelerating cost to the male individuals through the baseline condition decreasing, i.e., gaining fewer resources (Fig. S3). Specifically, q_1 is rewritten as the following:

$$q'_1 = q_1 + \left[\frac{\exp\left[-e_2 \left(a_1 - \frac{a_2}{2}\right)\right]}{1 + \exp\left[-e_2 \left(a_1 - \frac{a_2}{2}\right)\right]} - 0.5 \right] \beta$$

where $\beta \in [0, q_2 - q_1]$ is a constant which scales the maximum magnitude of the changing baseline condition, and e_2 represents the sensitivity (i.e., shape) of the baseline condition with decreasing a_1 . We can find that $q'_1 \in [q_1 - \beta, q_1 + \beta]$.

Finally, we assess the effect of condition-dependent parental care. Normally, males with better physical condition can afford higher quality parental care (Préault et al. 2005), such as better nest-defending capability and higher provisioning rate. We therefore relax the assumption that parental care is at a certain fixed level.

Consequently, we rewrite the fecundity function (Eq. 4) as follows:

$$f'_i = E[\exp(dA_i) - 1] \left[\frac{\gamma}{1 + \exp[-e_3(C_i - v)]} - 0.5\gamma + 1 \right]$$

The last part of the function represents the parental care effect (Fig. S4), where $\gamma \in [0, 1]$ scales the maximum effort of male parental care, v equals the median value of C when a_1 varies from 0 to a_2 , and then $f'_i \in [f'_i(1 - 0.5\gamma), f'_i(1 + 0.5\gamma)]$. Similar as e_1 and e_2 , e_3 is a constant and represents the sensitivity of the response. Parental care is divided into care provided by the female and the male. Female parental care is assumed to be homogeneous, so the investment effort can be treated as a constant (i.e., $1 - 0.5\gamma$), while male parental care differs according to their physical condition (i.e., $\frac{\gamma}{1 + \exp[-e_3(C_i - v)]}$, which is always smaller than γ).

Results

Modeling outputs of the evolutionary stability of DPM

We find that the ESS of investment on plumage in the first year is strongly related to maximum survival rate and predation risk (Fig. 1). Increasing either the maximum survival rate or predation risk can promote the evolution of DPM (Fig. 1). Life span (L) plays a significant role in the evolution of DPM, with a longer life span showing an obvious positive effect (Fig. 1). When life span is quite limited (e.g., $L=2$ or 3), DPM without breeding will have no chance to become evolutionary stable under a certain range of predation risk and maximum survival rate. However, all three potential strategies (i.e., DPM, non-DPM, and DPM without breeding) can evolve if L is set to 5 (Fig. 1c). This suggests that the DPM strategy in avian populations is more likely to evolve when individuals have a longer life span.

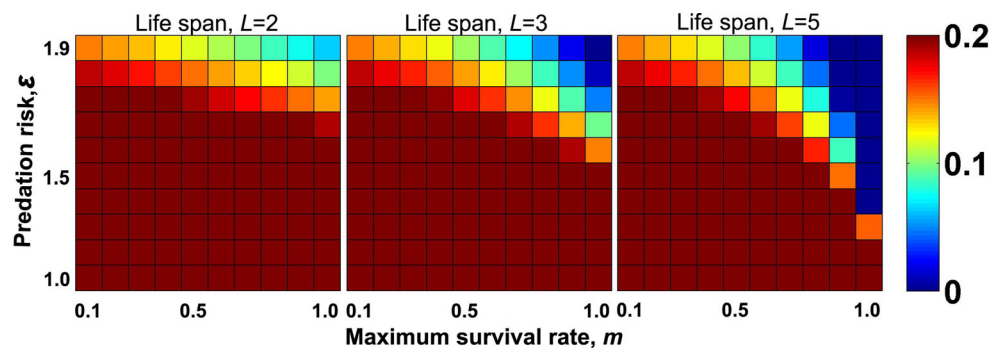


Fig. 1 The evolutionary stable plumage advertisement strategy at age 1 (a_1) under different maximum survival rates (m , ranging from 0.1 to 1.0), predation risk (ε , ranging from 1.0 to 1.9), and life span ($L=2, 3$, and 5). The evolutionary stable value of a_1 is indicated as different colors ranging from dark blue (0) to dark red (1). Increasing either the maximum survival rates or predation risk can enable the evolution of delayed

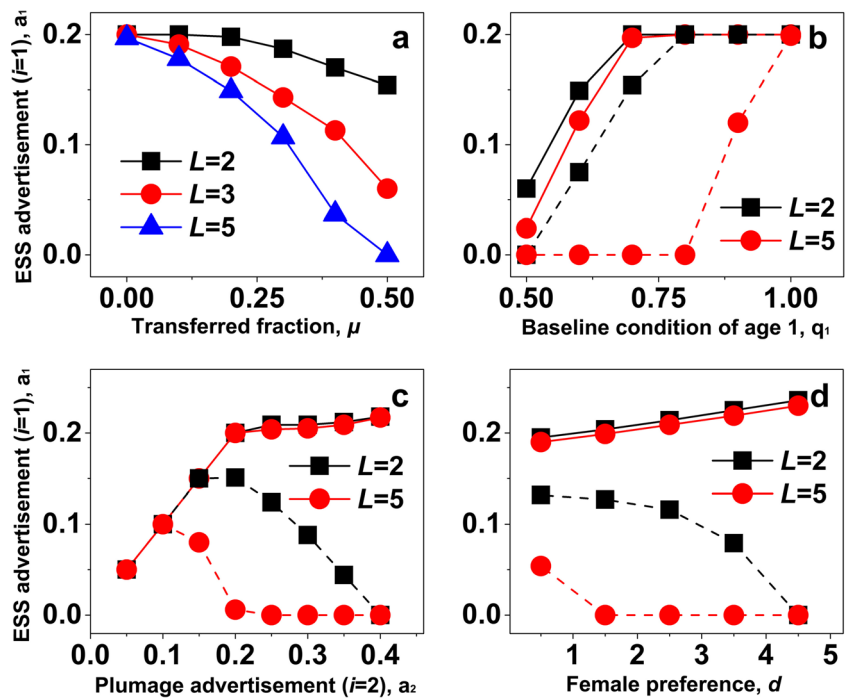
maturation (i.e., $a_1 < a_2$, the grid with color other than dark red), especially under longer life span. The other parameters are as follows: transferred fraction of physical conditions between years (μ)=0.5, female preference (d)=2, baseline condition of age 1 (q_1)=0.9, baseline condition of age 2 (q_2)=1.0, and adult plumage advertisement (a_2)=0.2

Generally, larger values of the transferred fraction of the male's physical condition (μ) would be favored by DPM individuals (Fig. 2a). In addition, there are mutual promotion effects between μ and L (Fig. 2a): the evolutionary stable plumage advertisement effort of age 1 (a_1) shows a more rapid decline if the species has relatively longer life span, and conversely, the differences of the evolutionary stable value of a_1 among life spans shows an increasing trend under larger transferred fraction. Subsequently, we calculate the ESSs with different baseline conditions of age 1 (q_1 , Fig. 2b), adult plumage advertisement effort (a_2 , Fig. 2c), and female preference coefficient (d , Fig. 2d) under two different values of μ and L . We find that if $\mu=0.5$, the evolutionary stable advertisement effort of age 1 will decline when q_1 reduces or a_2 increases (when $a_2 > 0.1$) or d increases. Our model results show quite different trends if μ is set to 0, especially while considering the effect of a_2 or d . Specifically, if $a_2 \leq 0.15$, the population will evolve to be non-DPM (i.e., $a_1 = a_2$), and if $a_2 > 0.15$, the population will evolve to be DPM, with a_1 showing a slight increasing trend (Fig. 2c). Increasing female preference has the opposite effect on the evolutionary stable value of advertisement effort of age 1, i.e., it will always increase rather than decline when μ is set to 0 compared to when μ is set to 0.5 (Fig. 2d). A longer life span has a positive effect in all three scenarios even if μ equals zero (Fig. 2b–d).

Modeling outputs considering crypsis, mimicry, status signaling, and condition-dependent parental care

We calculate the ESS results using a series of maximum value of three effects (i.e., α , β , and γ) and find that increasing any of these variables can promote the evolution of DPM (Fig. 3). The evolutionary stable advertisement effort of age 1 declines while increasing maximum value of any of the three effects (Fig. 3). Moreover, we find that relatively more sensitive responses (i.e., larger values of e_1 , e_2 , and e_3) enable the population to become evolutionary stable under even smaller

Fig. 2 The evolutionary stable plumage advertisement strategy at age 1 (a_1) under different transferred fractions of physical conditions between years (μ) (a), baseline conditions of age 1 (q_1) (b), adult plumage advertisement (a_2) (c), and female preference (d) (d). Life span (L) is set to 2 and 5 for comparison. The results connected by *solid line* in (b), (c), and (d) are calculated when physical conditions are not transferable (i.e., $\mu=0$), while those connected by *dashed line* are calculated when $\mu=0.5$. The other parameters are the following: $m=0.9$, $\varepsilon=1.45$ in (a) and (b); $m=0.9$, $\varepsilon=1.7$ in (c) and (d); $q_1=0.7$ in (a); $a_2=0.25$ in (d). The remained parameters are set the same as Fig. 1



values of α , β , and γ (Fig. 3). Specifically, if γ is set to 1, i.e., the female parental care effort is 0.5 and the male parental care effort is $\frac{1}{1+\exp[-e_3(C_i-\gamma)]}$, DPM without breeding ($a_1=0$) can evolve in the population when $e_3=8$ or $e_3=15$. Due to conserving more energy from allocating less investment in plumage by DPM sub-adult males, their female mates may gain benefits from receiving similar or even better male parental care than the older males would have provided.

Discussion

How does DPM evolve?

DPM as a life-history strategy is common in male birds, but there remains no clear consensus as to the evolutionary function of DPM (Bentz and Siefferman 2013). In fact, DPM may represent a flexible strategy that may vary between

populations in different regions (Hill 1996a), or even among different individuals in the same population (Hill 1988; Greene et al. 2000). Our models show that the evolution of DPM is sensitive to variation in prevailing environmental conditions. To maintain high survival rates, males may have to give up the potential of greater chances of reproducing under more severe predation risk (Fig. 1). Individuals with no delayed plumage would suffer from higher mortality under increased predation risk, which may exceed any benefits gained from a higher potential reproduction opportunity in the first year. This would then enable the evolution of DPM.

Our modeling results also reveal the importance of resource competition effects in the population (Fig. 1), as indicated by Studd and Robertson (1985). Sub-adult individuals with a greater degree of delayed plumage should have relatively stronger physical condition than the others, and then should be more competitive. While maximum survival rate (m) increases, differences in survival rates between individuals with high and low physical condition will also increase (Fig. S1c).

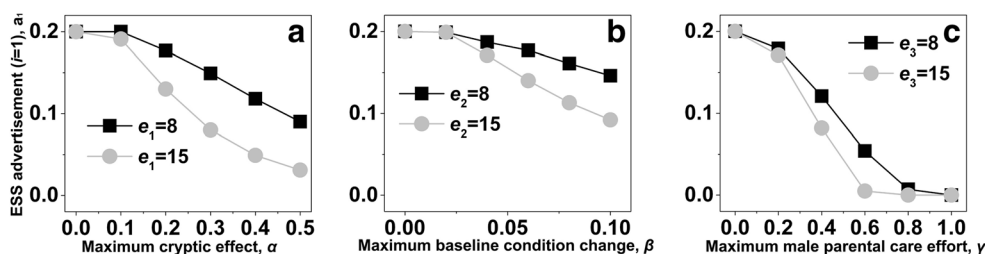


Fig. 3 The evolutionary stable plumage advertisement strategy at age 1 (a_1) while considering the cryptic effect (a), available resource effect (b), and condition-dependent parental care effect (c). The maximum cryptic effect (α) ranges from 0.0 to 0.5, maximum baseline condition change (β)

ranges from 0.0 to 0.1, and maximum male parental care effort (γ) ranges from 0.0 to 1.0. We select two levels of sensitivity (i.e., e_1 , e_2 , and e_3 are set to 8 and 15) for comparison. The other parameters are as follows: $m=0.8$, $\varepsilon=1.5$, $\mu=0.5$, $d=2$, $q_1=0.9$, $q_2=1.0$, and $a_2=0.2$

This suggests that DPM sub-adult individuals should have even higher survival rates relative to the individuals with no delayed plumage. DPM individuals could therefore gain benefits through higher survival rates at age 1 and better be able to transfer physical condition into the following year, outweighing the costs associated with lower likelihood of reproducing at age 1. We can therefore conclude that DPM will be more likely to evolve among males in relatively higher quality habitats (i.e., have higher maximum survival rate) through greater competition.

Our modeling approach reveals that considering the fitness consequences of DPM throughout an individual's life span is essential for a more complete understanding of DPM (Figs. 1 and 2). Although the relationship between life span and DPM was challenged by Montgomerie and Lyon (1986), more recent and comprehensive studies in many taxa supported this conclusion (Hawkins et al. 2012). Since individuals with less advertisement effort at age 1 could generally conserve more energy for physical condition, more individuals can survive to adulthood, longer life span can enable the fitness gained after reaching adulthood to be weighted through reproducing more times (Fig. 2a). Proulx et al. (2002) had modeled the situations with longer male life spans potentially through considering lower adult mortalities and indicated that males could benefit from reducing their signaling advertisement under increased future reproductive opportunities (see also in Adamson 2013). We suggest that a longer life span may play a more important role in promoting DPM evolution indirectly through intensifying the effects while changing the other factors. Therefore, in this study, we assess the effects of all the other factors under different life spans to indicate the importance of longer life span (Fig. 2). Specifically, if the physical condition is not transferable ($\mu=0$), i.e., the adult survival and fecundity rates are the same among individuals with different advertisement efforts at age 1, a longer life span still shows a positive effect on DPM evolution (Fig. 2a). While the physical condition can be transferred ($\mu>0$), individuals with less advertisement effort at age 1 will have a better baseline condition after reaching adulthood, and gain more benefits from higher survival rates and larger number of offspring under longer life span. Life span and transferred fraction therefore show a mutual promotional effect (Fig. 2a). The other effects of baseline condition of age 1 (Fig. 2b), adult plumage advertisement (Fig. 2c), and female preference (Fig. 2d) also show clear dependence on both life span and transferability of physical condition. Longer life span and transferrable physical condition between breeding years also enable the evolution of DPM in some birds with no reproductive output in year one (Fig. 1). This finding is consistent with the empirical studies that some manakins that adopt this strategy show quite long life spans (>10–14 years, Snow and Lill 1974), as do some seabird species (Schreiber and Burger 2002).

If the baseline condition of age 1 (q_1) is reduced, the fitness of sub-adult male individuals will decline more drastically for individuals with more advertisement effort at age 1 (Fig. S1d). This means that the sub-adult individuals with less delayed plumage will suffer from relatively higher costs under smaller value of q_1 , promoting the evolution of DPM (Fig. 2b). For the effect of adult advertisement effort (a_2), we find that relatively higher investment is essential for the evolution of DPM (Fig. 2c). This implies that a DPM strategy will be more likely to evolve in the species with costly adult plumage (e.g., bright and colorful plumage). This phenomenon had already been detected in populations of house finch (*Carpodacus mexicanus*) where adult males that exhibit DPM have more ornamented and costly adult plumage (Hill 1996a, b). In our model, we also find that if a_2 is too large and the physical condition is not transferable, increasing a_2 will negatively impact the adult individuals' physical condition, increasing the likelihood of mortality for that individual (Promislow et al. 1992). Since the life-span fitness of DPM individual should be strongly dependent on the individual's level of reproduction after reaching adulthood, a higher mortality rate will therefore have a negative effect on the evolution of DPM strategy (Fig. 2c).

Increasing female preference (d) means that individuals with less advertisement effort at age 1 will generally lose more potential reproductive benefits at age 1. However, if the physical condition is transferable, those individuals can compensate through higher productivities and survival rates after reaching adulthood. Increasing life span can also effectively neutralize the fitness loss of early adulthood and promote the evolution of DPM (Fig. 2d).

The effect of condition-dependent male parental care

We demonstrate that including the effect of condition-dependent male parental care can also promote the evolution of DPM strategy (Fig. 3c). This strategy is preferential for bird species that rely more on parental care provided by males (i.e., larger value of γ). Although sub-adult male DPM individuals suffer from lower access to females than non-DPM ones, individuals with better physical condition can improve their survival and that of their offspring from better parental care. Parental care is often described as any parental expenditure that increases the offspring's likelihood of survival and reproduction at a cost of restricting the parents' ability to invest in other components of fitness (Trivers 1972; Clutton-Brock 1991). This care can be expressed at different stages of the reproductive cycle such as egg guarding, preparation of nest, incubation, food provisioning, and nest protection. Other studies have demonstrated age-dependent and/or color-dependent parental care (Saetre et al. 1995; Badyaev and Hill 2002; Pr eault et al. 2005). Older male birds are characterized by more superior foraging ability (Heise and Moore 2003; Gomes et al. 2009) that allows them to improve their

provisioning rates to a greater extent than younger, less experienced males (Limmer and Becker 2009) can. However, Palmerio and Massoni (2009, 2011) found no difference in either parental care or offspring growth of sub-adult and adult male saffron finches (*Sicalis flaveola*), with the growth rates of nestlings also similar. McGraw et al. (2001) even found that young male house finch actually feeds at a higher rate than older males.

As shown in our model, although the total baseline condition is less than that of adult, sub-adult may achieve similar benefits through reduced cost in plumage investment; this may even enable the physical condition of sub-adults to exceed that of adults, but further empirical evidence is required. Palmerio and Massoni (2011) used the residuals of the regression of body weight on tarsus length as a measure of body condition, but this approach has been criticized by some authors (e.g., Schulte-Hostedde et al. 2005). Appropriate measurements for body condition have yet to be explored that could verify our modeling results concerning the effect of condition-dependent parental care, and we suggest that this should be prioritized in future studies. When compared to the effects of avoiding predation and gaining more resources, the influence of condition-dependent parental care should be more complex since itself is strongly dependent on the relative effort of male to female parental care (determined by the value of γ). Generally, each parent should prefer to shift more of the costly parental care of the offspring onto its mate (Trivers 1972), resulting in conflict between them. The evolution of DPM is therefore related to the resolution of sexual conflict over parental care between two parents. This gives new insight into the evolution of DPM that requires testing with empirical evidence in the future.

Summarizing, although DPM had been studied for over four decades, a conceptual framework for understanding the evolution of this strategy using modern evolutionary and life-history theory had only been recently advocated (Hawkins et al. 2012). Here, we use novel extensions of the age-dependent game theory modeling framework developed by Kokko (1997) to demonstrate that the DPM strategy could evolve based on the lifelong trade-off between survival and reproduction (Fig. 1). The evolutionary stable plumage advertisement strategy at age 1 is dependent on a series of external and internal factors, such as environmental conditions, transferred fraction of physical condition, life span, male adult plumage investment, baseline condition of age 1, and female preference. Our model also reveals the important effect of condition-dependent parental care, which can clearly promote the evolution of DPM (Fig. 3). Other empirical studies have proposed other mechanisms for the evolution or maintenance of DPM in bird populations, e.g., Greene et al. (2000) showed that different degrees of delayed maturation can be maintained in a lazuli bunting (*Passerina amoena*) population through extra-pair copulations. Further modeling studies incorporating

such factors are required to enhance our understanding of age-dependent sexual advertisement strategy in birds.

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