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**Seasonality, environmental predictability and
the avian annual cycle**

**Szezonalitás, környezeti prediktabilitás és a
madarak éves ciklusa**

Egyetemi doktori (PhD) értekezés

Tökölyi Jácint

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1.

Seasonality, environmental predictability and the avian annual cycle

Introduction

In the vast majority of habitats on Earth environmental conditions show temporal variability. These environmental changes can be simple or very complex, ranging from predictable diurnal cycles through the regular alternation of warm and cold or wet and dry seasons to the much less predictable patterns observed in deserts or in areas influenced El Niño effects.

Organisms living in periodically changing environments may be exposed to contrasting selective forces at different parts of the cycle. For example, conspicuous coloration or behavior may be advantageous during the mating season when it increases the probability of finding a mate, but conspicuousness is clearly disadvantageous during the non-breeding season, when it leads to a greater probability of being detected by predators or parasites without providing any benefits (Piersma and Drent 2003). Animals can adapt to such variable selective forces by partitioning their life history events to different parts of the cycle (McNamara and Houston 2008). As a result, the most costliest activities such as reproduction are generally performed during the period with highest food availability, whereas other periods are spent on maintenance, such as molt, migration to benign wintering sites or hibernation (McNamara and Houston 2008).

To cope with the changing conditions animals need to adjust their morphology, physiology and behavior to the environment; this phenotypic flexibility (Piersma and Drent 2003) may lead to dramatic changes in the appearance or morphology of animals. For example males of many bird species switch from a dull winter plumage to a colorful nuptial one in spring. Similarly, organs such as gonads, intestines or even parts of the brain can be regressed for extended periods (Piersma and Drent 2003): gonads in birds and bats shrink several hundred-fold outside the breeding season (Murton and Westwood 1978), the hippocampus of food-hoarding birds increases in size during autumn and decreases in spring (Smulders et al. 1995) and a wide range of physiological changes occur in birds during migration (Piersma and Drent 2003; Gwinner 1990).

When environmental changes are at least partly predictable, animals can rely on their endogenous rhythms to be in the right physiological state at the right time. However, if the environment is unpredictable then animals need to respond flexibly to the changing conditions. Examples of such flexibility occur both in highly variable environments and in more seasonal areas. Desert frogs, for instance, spend many months buried in ground and emerge only after heavy rainfall (Wells 2007). Similarly, birds regrowing gonads at temperate latitudes can accelerate or delay the process depending on the actual conditions (Murton and Westwood 1978).

Despite this flexibility, responding instantaneously to the changing conditions is often difficult, because physiological responses may require considerable time. Birds, for instance, although able to modulate the regrowth of their reproductive organs, need at least 4-6 weeks to reach reproductive condition from a state of completely regressed gonads (Murton and Westwood 1978). In such cases the animals face the following problem: they can only respond quickly to the changing conditions if they are prepared, maintaining physiological preparation, on the other hand, is costly; for example large gonads in birds and bats, in addition to the potential metabolic costs add extra weight to the animal which can compromise flight and lead to elevated predation risk (cf. Lind et al. 1999).

The outcome of this trade-off will ultimately depend on at least two factors: (1) the characteristics of the environment, such as the degree of predictability, the consistency of environmental changes and (2) the properties of the physiological

system, such as the response time or the costliness of maintaining preparedness.

The effects of variability on the timing of life history events have been studied previously both in plants and animals (e.g. Philippi and Seger 1989). However, relatively little attention has been paid to animals making sequential decisions in complex, variable environments. Most previous theoretical approaches considered relatively simple stochastic environments. This is unfortunate, because environmental variability can be much more complex (e.g. variability due temperature or rainfall can manifest itself in isolation or in combination with the other), and these need to be taken into account to obtain a better understanding of behavior in realistic environments.

My aims in this thesis are twofold. First, to describe a theoretical framework developed to model the effect of complex environmental variation on animals making sequential decisions during the course of the annual cycle. Second, as physiological systems may be affected differently by temporal variation in environmental conditions, two case studies are described that investigate adaptation to seasonal environments with implications to environmental variability.

Specifically, I investigate the following problems:

- Opportunistic breeding: in environments where food availability is highly unpredictable (such as in deserts, alpine habitats, etc.) animals behave opportunistically; that is, because it is not possible to predict the changes in food availability, animals start reproducing only after the onset of a favorable period. Based on observations of birds in unpredictable environments it was supposed that these animals maintain the reproductive system partially activated throughout the year (summarized in Morton 2009), so that they can start breeding shortly after rainfall. In this way, these birds don't have to pay the cost of high reproductive readiness for extended periods, while still being able to respond relatively quickly. To investigate this problem in a theoretical framework, we developed an optimal annual routine model of avian gonad regulation that can be used to investigate optimal reproductive readiness in environments differing in predictability and seasonality (Chapter 3).
- Reproductive plasticity in seasonal environments. In seasonal environ-

ments animals face a similar problem if the onset of spring varies from year to year (i.e. maintaining reproductive readiness is costly, but if the animals are not prepared they risk missing the peak in food availability). Using the above model I investigate the optimal level of reproductive readiness and plasticity in seasonal environments with different levels of year-to-year variability in the onset of spring. Second, I use the optimal strategies calculated for the different environments to predict the response of birds to rapid environmental change (Chapter 4).

- Breeding phenology and migratory behavior. The trade-off between maintaining preparedness and missing breeding opportunities can be applied to migratory birds that leave their breeding grounds during winter: the farther a bird migrates the less likely it is that it can respond quickly to conditions on the breeding ground. On the other hand, staying at northern latitudes during the winter results in higher mortality probably in most species. Based on this trade-off it can be predicted that conditions selecting for higher reproductive readiness could lead to the evolution of shorter migration distances. Assuming that year-to-year variability in environmental conditions is probably higher early in spring than later, birds breeding early may be exposed to stronger selection to stay close to the breeding grounds. This relationship is further complicated by the fact that migration can also affect breeding phenology (e.g. because of life history trade-offs or time constraints). We investigated these hypotheses in a phylogenetic comparative study of the migratory behavior and breeding phenology of finches and allies from the Western Palearctic and North America (Chapter 5).
- Seasonal color change. Many temperate zone birds have differently colored plumage in summer and in winter. The change from the drab winter plumage to the bright nuptial coloration can occur by different mechanisms, of which the two most common are color change by prenuptial molt or the abrasion of cryptic feather tips. In each case, the birds cannot directly determine the degree of color change: molt is costly in terms of time and energy (e.g. Pap et al. 2007); therefore, the degree to which a bird can renew its plumage in spring can depend on the actual environmental con-

ditions. Similarly, although color change by abrasion can be regulated to some degree by preening (Møller and Erritzøe 1992), it also depends on the environment (e.g. from UV radiation). Therefore, variation in the environmental conditions may affect the degree of color change. As a result, the evolution of color change mechanisms might be affected by variation in the environmental conditions, as well as the species-specific benefits of color change. We investigated this hypothesis in a phylogenetic comparative study of the finches and allies (Chapter 6).

Methods

- The annual routine model developed to study reproductive readiness investigates weekly decisions of a female bird during many years. Each week, the animal decides on the (1) modulation of reproductive organs (maintain, increase, decrease) and (2) reproduction (i.e. whether to start, keep or desert a brood). The modelled organism can only reproduce if it has fully developed gonads and reproduction is considered successful only if the young are provided with food until fledging. Maintaining gonads in a highly developed state and providing food for the young has metabolic and predation costs. These costs, relative to the reproductive success of the bird will determine the optimal sequence of decisions in a given environment. We investigate the optimal levels of reproductive readiness under different patterns of food availability; in this way it is possible to simulate different patterns of variability (e.g. the length of only the bad or only the good period, or both may be variable) (Chapter 3).
- Using this model it is possible to investigate optimal behavior in environments where food availability varies seasonally but there is year-to-year variability in the onset of spring. By applying this approach, the optimal levels of reproductive readiness can be determined in environments with different levels of seasonality and variability. Knowing the optimal strategy in turn enables us to predict the response of birds to rapid environmental change (Chapter 4).

- To investigate factors affecting the evolution of migration, we analysed the relationship between migratory behavior and breeding phenology in 134 species of songbirds (the finches and their allies) from North America and the Western Palearctic. First, we collected data on breeding phenology (the start and length of the breeding season). Second, we quantified migration distance based on distribution maps. We analysed the relationship between these factors in statistical models controlling for the non-independence of data points due to the phylogenetic relationships of species, while simultaneously controlling for potentially confounding factors, such as adult body mass or winter diet. To clarify the relationship between the traits we used directional tests (Pagel and Meade 2006) which can be used to find out whether evolutionary changes in one trait are contingent upon the other or vice versa (Chapter 5).
- To analyse factors affecting seasonal color change, we first determined the occurrence of color change by molt or abrasion in 150 species of songbirds (the finches and their allies). Second, we collected data on different ecological, life history and social traits, such as winter diet, timing of breeding, winter flocking behavior and intensity of sexual selection. We used phylogenetic comparative methods to determine which traits affect the occurrence of molt, abrasion or the combined use of both strategies (Chapter 6).

Results

- Consistent with our predictions, we found that maintaining intermediate levels of reproductive readiness is an optimal strategy in highly variable environments in some cases, but not in others. The optimal level of readiness depends on several other factors, such as: (1) the length of the favorable period - if the good period is long enough to finish a brood with high probability, birds will maintain their gonads more developed, even if this is costly; (2) the amplitude of environmental fluctuations - when fluctuations are small, there is relatively more food during bad periods and maintaining high readiness is not so costly; (3) longevity - short-lived birds

invest more into current reproductive attempts and generally show higher levels of reproductive readiness than long-lived birds; (4) the time required to reach fully developed gonads - the less time is required to reach full preparation, the lower the reproductive readiness is, because birds can respond more quickly. In addition, our results show that even a very small degree of predictable seasonal variation in food availability (in addition to the unpredictable variations) can lead to the entrainment of breeding and the segregation of the breeding and non-breeding seasons (Chapter 3).

- In seasonal environments the increased variability in the onset of spring leads to higher levels of reproductive readiness at the end of the winter; that is, if the animals cannot predict the expected start of the favorable period, they maintain higher levels of reproductive readiness for an extended period. However, this pattern is also affected by several other factors: (1) under density-dependence the seasonality of the environment affects winter survival rate: low seasonality leads to high survival rate which selects for lower reproductive investment; as a result physiological preparedness and response to environmental change is lower in environments with low seasonality. (2) The temporal distribution of food availability is important: if food availability is uniform during the summer then it is optimal to start a brood as soon as possible. On the other hand, if there is less food early in spring than later, then the optimal strategy is to start breeding around the peak in food availability. Therefore, in such environments the birds will not start reproduction even if the spring starts earlier (Chapter 4).
- Analysis of the migratory behavior of finches and allies in phylogenetic context reveals that migration is strongly related to the onset and length of the breeding season. Furthermore, this relationship is not confounded by body mass or winter diet, factors that are known to affect migratory behavior. Directional tests indicate that evolutionary transitions in phenology determine transitions in migratory behavior and not vice versa: long distance migration is more likely to evolve in taxa with a short, late breeding season, whereas short distance migration is more likely to evolve in taxa with a long, early breeding season (Chapter 5).

- Analysis of the seasonal color change mechanisms revealed that color change by molt and by abrasion is determined by different factors: the former is more likely to occur in insectivorous species with a late breeding season, whereas the latter is more common in species with winter flocking behavior. The two strategies also occur together, especially in species with high levels of polygyny. (Chapter 6).

Conclusions

Variability in environmental conditions can have strong effects on the behavior of animals. Environmental fluctuations can be complex but they are ubiquitous and therefore need to be taken into account to have a fuller understanding of the behavior of animals inhabiting such environments.

This thesis makes two main contributions in this respect. First, the optimal annual routine model presented here provides a theoretical framework to investigate the effects of environmental variability for animals that make sequential decisions in complex environments. This approach can provide novel predictions for the effect of environmental variability on animal behavior which are becoming increasingly testable with the advent of long-term ecological and climatic data. Although this model was developed with timing of reproduction in mind, environmental variability may affect other behaviors as well, and these can be investigated using the approach present here. For example, in a recent study Jetz and Rubenstein (2010) found that communal breeding is more common in species living in variable environments; this interesting link between climate and social behavior provides a new twist that requires further theoretical and empirical analysis.

Understanding the effects of environmental variability is clearly important as one of the predicted effects of recent climate change is an increase in the variability of environmental conditions (e.g. Morris et al. 2008). The model presented here suggests that several components of the environment may affect the optimal levels of plasticity (Chapter 4). These factors will ultimately determine how animals respond to rapid environmental changes. Although long-term ecological studies indicate a widespread phenological response to the increase

in temperature (Walther et al. 2002), relatively little is known about the role of microevolutionary processes and phenotypic plasticity in determining these responses. Quantifying plasticity might be a fruitful approach in discerning these mechanisms, given that it is probably much easier to measure plasticity than microevolution.

Second, analysing different physiological or behavioral systems (i.e. migration and seasonal color change) revealed that seasonal changes are probably more widespread and more significant than previously thought (Chapter 6). Furthermore, the components of the annual cycle have a stronger affect on each other, and their evolution appears to be tightly linked (Chapters 5 and 6). Thus, although the problem of physiological preparedness can be generalized and studied using theoretical approaches, seasonal changes in physiology and behavior are determined by multiple components, and each of these may have a different effect on the response of organisms to variable conditions. Therefore, it is important to investigate each of them.

By describing the relationship between breeding phenology and migration we have made the first step to determine the relationship between these two important components of the birds' annual cycle (Chapter 5). Previous studies already established the effect of migration on the evolution of molt strategies (Svensson and Hedenström 1999; Barta et al. 2008); our study expands this relationship to the breeding season (and thereby to the whole annual cycle). Thus, breeding phenology appears to be an important factor in the evolution of life history strategies in birds as it can affect migratory behavior, and indirectly the molt strategy of a species. More studies are required in different taxonomic groups to unequivocally ascertain these relationships.

Comparative analysis of the seasonal color change strategies revealed that the combined strategy (i.e. both molt and abrasion) occurs with a higher probability in species where coloration presumably has a strong impact on the mating success of birds (i.e. polygynous species) (Chapter 6). This strategy may ascertain that the birds reach full coloration in spring even if conditions are unfavorable. Plumage color in birds was considered a static signal that can only change during molt; however recent studies increasingly indicate that there are considerable seasonal variations in color (e.g. Delhey et al., 2010). Nonetheless, even if plumage

coloration varies with time, it probably cannot change rapidly enough to track quick changes in the environment. It is possible therefore that in highly variable environments more dynamic signalling traits may be optimal (e.g. song). This hypothesis could be tested in future studies by expanding the investigation of signal variability to multiple signals of tropical and desert-dwelling species.

In conclusion, seasonality and predictability have a complex effect on the behavior of animals. The models presented here provide a theoretical background to analyze these problems and predictions from these theoretical approaches help us analyze the problems in a phylogenetic or empirical context. The insight gained from these studies will ultimately help us understand the behavior of animals living in unpredictable environments and to make predictions on the expected response of animals to environmental change.

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2.

Szezonális, környezeti prediktabilitás és a madarak éves ciklusa

Bevezető

A Föld természetes élőhelyeinek többségében a környezeti paraméterek időben változnak. Ezek a környezeti változások sokféle formát ölthetnek, a periodikus napszaki ciklusoktól kezdve a hideg és meleg vagy az esős és száraz évszakok váltakozásán át a sokkal kevésbé kiszámítható környezeti változásokig, mint amilyen megfigyelhető például félsivatagos környezetben a ritka esőzések következtében vagy a sokéves ciklusokon átívelő El Niño hatások által érintett területek esetében.

A periodikusan változó környezetekben élő állatok eltérő szelekciós hatásnak vannak kitéve a ciklus különböző fázisaiban; így például a feltűnő viselkedés előnyös lehet a szaporodási időszakban a párválasztás szempontjából, viszont hátrányos azon kívül, mivel növeli a predációs veszélyt anélkül, hogy bármilyen előnyt nyújtana (Piersma and Drent 2003). Az ehhez hasonló változó szelekciós hatásokhoz az állatok úgy alkalmazkodhatnak, hogy élettevékenységeiket a ciklus különböző szakaszaira időzítik (McNamara and Houston, 2008). Ennek eredményeképp például az éves ciklus során az energetikailag költséges utódnevelési

időszak rendszerint a legmagasabb táplálékelérhetőségű periódusra esik, míg az év többi részében az állatok a túlélésük szempontjából fontos tevékenységeket végzik, mint például vedlés, kedvezőbb területekre való vándorlás vagy hibernáció (McNamara and Houston, 2008)

Ahhoz, hogy ezek a ciklikus változások megvalósulhassanak, az élőlények belső felépítésének, fiziológiai szabályozásának és viselkedésmintázatainak is változásokon kell átesniük, melyek gyakran drámai formát öltenek. Ilyen például számos madárfajnál a téli rejtőszínezet átváltozása díszes nyári tollruhába, a szaporítószervek erőteljes zsugorodása a költési időszakon kívül madaraknál és denevéreknél (Murton and Westwood 1978), vagy a hippokampusz hipertrófiája táplálékrejtő madárfajoknál az őszi környékén, amikor a téli tartalékokat halmozzák fel (Smulders et al. 1995), nem beszélve arról a számos fiziológiai változásról ami a hibernációval vagy éppen a vonulással jár együtt (Gwinner 1990; Piersma and Drent 2003).

Amikor a környezet változása többé-kevésbé szabályos, az élőlények belső ritmusukra hagyatkozva előre felkészülhetnek a környezeti változásokra; ezáltal érhető el, hogy a megfelelő időben a megfelelő fiziológiai állapotba kerüljenek. Ugyanakkor, hogyha a környezeti tényezők kevésbé kiszámíthatóak, sokkal nehezebb előre felkészülni a környezeti változásokra. Ilyen esetekben a flexibilis viselkedés teszi lehetővé, hogy az állatok az éppen aktuális körülményekre gyorsan reagáljanak. Ilyen flexibilitásra számos példa ismert, pl. sivatagi békáknál, melyek az év nagy részét a föld alatt, hibernálva töltik és csak nagyobb esőzéseket követően bújnak elő (Wells 2007). Sok esetben azonban a gyors reakciónak korlátai vannak, mivel a fiziológiai állapotváltozások rendszerint időigényes folyamatok. A madarak szaporítószerveinek esetében pl. 4-6 hétre van szükség amíg azok elérik a funkcionális méretet, mely sokszor több százszorosa lehet a télen, regresszált állapotban levő szervek méretének (Murton and Westwood 1978).

Ilyenkor az élőlények a következő cserekapcsolattal találják magukat szemben: csak akkor tudnak biztosan szaporodni, hogyha hosszú távon fenntartják a fiziológiai készségüket, ezáltal a kedvező környezeti változásokra azonnal tudnak reagálni. A készség fenntartása ugyanakkor költséges: madaraknál és denevéreknél például a megnövekedett szaporítószervek a metabolikus költségek mellett a repülést akadályozhatják, ami jelentősen csökkentheti ragadozók elől

való menekülési képességüket (Lind et al. 1999).

Ezen cserekapcsolatok kimenetelét feltételezhetőleg két tényező határozza meg: egyrészt a környezet sajátosságai: pl. mennyire kiszámítható vagy milyen hatása van a különböző környezeti változásoknak a táplálékelérhetőségre; másrészt a fiziológiai rendszer tulajdonságai: mennyi időt vesznek igénybe a fiziológiai állapotváltozások, vagy mennyire költséges a készültség fenntartása, stb.

A környezeti variabilitás döntési folyamatokra gyakorolt hatását részletesen vizsgálták elméleti szempontból néhány, viszonylag egyszerű időzítési probléma esetében, mint például a csírázás és a virágzás időzítése (Philippi and Seger 1989). Hasonlóképp, a változó környezetben élő állatok ökofiziológiáját több modellszervezet esetében tanulmányozták (pl. Hau 2001). Mindezek ellenére kevés átfogó ismerettel rendelkezünk a környezeti variabilitás viselkedésre gyakorolt hatásáról. Ennek okai többfélék: (1) az elméleti modellek többsége viszonylag egyszerű környezeti változásokat feltételez; ugyanakkor a valós környezetekben a variabilitás több forrásból adódhat (pl. csapadék, hőmérséklet, stb.), aminek következtében a variabilitás mértéke és formája igen sokféle lehet, a részben kiszámítható környezettől a teljesen véletlenszerűig; ezeket a finom különbségeket figyelembe kell venni ahhoz, hogy a valós környezethez alkalmazkodott élőlények viselkedését megérthessük. (2) A környezeti tényezők variabilitásának kvantifikálásához hosszútávú adatsorokra van szükség a különféle környezeti paramétereiről, ezek azonban csak napjainkban kezdenek elérhetővé válni. (3) Az ökofiziológiai vizsgálatok jelentős részét mérsékelt égövi fajokon végezték, ahol a környezeti tényezők variabilitása (a szabályszerű szezonális változásokhoz képest) viszonylag csekély (Hau 2001). Sokkal kevesebb ismerettel rendelkezünk a trópusi/szubtrópusi élőlények fiziológiájáról, jóllehet ezek sok esetben lényegesen eltérhetnek a mérsékelt égövi fajokétól. Ugyanakkor mérsékelt égövi fajok esetében is hiányosak a variabilitás hatásairól és következményeiről szerzett ismereteink.

A fentiek alapján jelen disszertációban céljaim a következők: egyrészt kidolgozni egy olyan elméleti megközelítést, amely lehetővé teszi a környezeti variabilitás hatásainak vizsgálatát komplex környezetekben, másrészt vizsgálni az éves ciklus során fellépő, különféle fiziológiai/viselkedésbeli szezonális változásoknak a mechanizmusát és evolúciós következményeit. Specifikusan, az alábbi

kérdésköröket vizsgálom:

- Opportunistikus szaporodási rendszerek. A táplálékelérhetőség nagyfokú kiszámíthatatlansága esetén (mint amilyen előfordulhat sivatagokban, magashegységekben, de bizonyos növények terméshozásának kiszámíthatatlansága miatt bárhol máshol is) az élőlények opportunistikusan viselkednek, azaz mivel nem tudják előre megjósolni a környezeti változásokat, csak azok bekövetkezte után kezdhetnek szaporodni. Korábbi, empirikus megfigyelések alapján feltételezték, hogy ezek az állatok félkész állapotban tartják szaporodási rendszerüket, ezáltal viszonylag gyorsan tudnak válaszolni a környezeti változásokra, ugyanakkor nem kell elviseljék a teljes készütség költségeit (Morton 2009). Ennek a kérdésnek a vizsgálatára kidolgoztunk egy optimális éves rutin modellt a madarak szaporítószerveire alkalmazva, melynek segítségével az optimális készütségi szintet vizsgálni lehet különféle környezeti scenáriók alapján (3. fejezet).
- Viselkedésbeli plaszticitás szezonális környezetben. Az opportunistikus szaporodási rendszerű állatokhoz hasonló problémával állnak szemben az élőlények szezonális környezetben, hogyha a tavasz kezdete nem kiszámítható, hanem évről-évre változik. A fenti modellt felhasználva vizsgálom, hogy milyen mértékű szaporodási készütség, illetve viselkedési plaszticitás várható ezeknél az állatoknál szezonális környezetben, hogyha a tavasz kezdete különböző mértékű prediktabilitást mutat. Ismerve a plaszticitás mértékét, lehetővé válik megvizsgálni azt, hogy a különböző környezetekben hogyan tudnak az élőlények a gyors környezetváltozásra reagálni. Ez fontos lehet pl. a gyors klímaváltozás hatásainak megértésében (4. fejezet).
- Költésfenológia és vonulás közötti kapcsolat. A fiziológiai felkészültséghez hasonló evolúciós hatása lehet a vonulásnak is: a költőhelytől távol levő madarak nem tudnak azonnal reagálni az ott bekövetkezett környezeti változásokra. Minél közelebb van egy madár a költőterületéhez, annál gyorsabban reagálhat, ugyanakkor jobban ki van téve a hideg északi tél viszontagságainak. Ez alapján elképzelhető, hogy a magas készütségre szelektáló tényezők (pl. a költés időzítésének variabilitása) befolyásolhatják a vonulási stratégiák evolúcióját. A költés időzítése feltételezhetőleg na-

gyobb variabilitást mutat a korán fészkelő, hosszú költési szezonnal rendelkező fajoknál, tehát a fenti hipotézis alapján ezeknél a fajoknál várható rövidebb vonulási távolság. Ezt a problémát bonyolítja a tény, hogy a vonulás visszahathat a költési paraméterekre (pl. a túlélés és szaporodás közötti cserekapcsolat, vagy időbeli korlátok miatt). Ezeket a kérdéseket vizsgáltuk a Nearktiszban és Nyugat-Palearktiszban előforduló pintyfélék és rokonaik vonulási rendszereinek és költésfenológiájának filogenetikai vizsgálatával (5. fejezet).

- A szezonális színváltozás mechanizmusait befolyásoló tényezők. Számos mérsékelt égövi madárfajnál a téli, rejtőszínezetű tollruha sokkal kevésbé feltűnő, mint a nászruha. Ez a színváltozás több úton valósulhat meg, elsősorban a testtollak vedlése vagy a nászruhát takaró rejtőszínezetű tollcsúcsok lekopása révén. Mindegyik mechanizmus sajátossága, hogy a madarak nem tudják direkt módon teljesen meghatározni a színváltozás mértékét: a tollak kicserélése vedlés útján idő- és energiaigényes (Pap et al. 2007), ezért annak mértéke, hogy egy madár a költési időszak előtt mennyire tudja megújítani tollazatát az aktuális táplálékélérhetőségtől függ. Ugyanakkor a kopással való színváltozás (jöllehet tolláskodással szabályozható egyes testrészeken, Møller and Erritzøe 1992), szintén függ a környezeti tényezőktől (pl. az UV sugárzás mértékétől), vagyis a környezeti variabilitás nagyban befolyásolhatja az elért színváltozás mértékét. Ennek következtében a szezonális színváltozás, illetve a színváltozás mechanizmusainak evolúciója függhet egyrészt a környezeti paraméterektől, másrészt a színváltozás előnyeitől, ami fajok között eltér. Ennek a kérdésnek a vizsgálatára egy filogenetikai vizsgálatot végeztünk a pintyeket és rokonaikat felhasználva, amelyben megvizsgáltuk a vedléses illetve kopásos színváltozással összefüggő ökológiai és szociális tényezők szerepét ezen stratégiák evolúciójában (6. fejezet).

Módszerek

- Az általunk kidolgozott éves rutin modellben heti felbontásban vizsgáljuk az állatok optimális viselkedését. Az optimális viselkedést a döntésekkel járó fitness nyereség illetve a belőlük származó költségek határozzák meg. Minden héten az állatnak az alábbi döntési lehetőségei vannak: (1) a szaporítószervek méretének szabályozása (fenntart, megnövel, csökkent) illetve (2) döntés a szaporodásról (költség elkezdése, fiókák etetése, fiókaetetés abbahagyása). A modellezett élőlény csak akkor kezdhet el szaporodni, hogyha szaporítószervei maximálisan kifejlődtek, és fiókái csak akkor válnak életképesse, hogyha meghatározott ideig táplálja őket. Mind a szaporítószervek fenntartásának, mind pedig a fiókanevelésnek energetikai és predációs költségei vannak. Ezen költségek, a várható reprodukív nyereséghez viszonyítva meghatározzák, hogy egy adott állat számára egy adott környezetben mi az optimális döntés (vagyis melyik döntés maximalizálná az állat fitnessét). Az optimális viselkedést különböző környezeti táplálékeloszlás mellett vizsgáljuk; ennek célja az, hogy különféle variabilitású környezeteket próbáljunk létrehozni (pl. elképzelhető olyan variabilitás, melyben jó és rossz időszak hétről hétre teljesen véletlenszerűen változik, más esetben az egyik vagy másik mutathat bizonyos mértékű prediktabilitást; 3. fejezet).
- Az előbbi modellt felhasználva, a táplálékeloszlás módosításával lehetővé válik az optimális viselkedés modellezése olyan környezetben, ahol a táplálékeloszlás szezonálisan változik, viszont a tavasz kezdetének időpontja évről-évre eltérő lehet. Ennek segítségével vizsgálható, hogy ilyen szezonális környezetben milyen hatással bír a környezet (specifikusan a tavaszkezdet) variabilitásának mértéke az optimális viselkedésre. Különböző variabilitású és szezonális környezetekben vizsgáljuk az optimális fenotipikus plaszticitást, majd ismerve az egyes környezetekben optimális stratégiákat megvizsgáljuk, hogy milyen viselkedés várható hirtelen környezetváltozás (a tavasz átlagnál korábbi kezdete) esetén (4. fejezet).
- A vonulás evolúcióját befolyásoló tényezők vizsgálatához 134 Nearktisz-

ban és Nyugat-Palearktiszbán fészkelő énekesmadár (pintyek és rokonaik) esetében elemeztük a vonulási viselkedés és a költési szezon paramétereire közötti összefüggést. Ehhez először összegyűjtöttük az említett fajokról irodalomban elérhető költésfenológiai vizsgálatokat, mely alapján meghatározható a költési szezon kezdete és hossza, valamint elterjedési térképekről megbecsültük az egyes fajok vonulási távolságát. A költésfenológiai paraméterek összefüggését a vonulási távolsággal többváltozós statisztikai modellekkel vizsgáltuk, kontrollálva a testtömegre, téli táplálék-típusra és a fajok közötti filogenetikai kapcsolatra. Az összefüggések pontosabb megértéséhez direkcionális tesztek alkalmaztunk, amely lehetővé teszi annak meghatározását, hogy melyik jelleg evolúciós változása határozza meg a másik jelleg változását (5. fejezet).

- A szezonális színváltozás vizsgálatokor 150 énekesmadárfaj (pintyek és rokonaik) esetében irodalmi források alapján meghatároztuk, hogy van-e színváltozás vedléssel vagy kopással, majd különféle ökológiai, életmenet és szociális jellegekről, mint például a táplálék típusa, költési szezon időzítése, téli csapathoz tartozás, szexuális szelekció intenzitása gyűjtöttünk adatokat. Filogenetikai kapcsolatokra kontrollált statisztikai modellekkel vizsgáltuk, hogy mely tényezők vannak összefüggésben a vedléses vagy kopásos színváltozás, illetve ezek kombinációjának jelenlétével (6. fejezet).

Eredmények

- A feltételezéseknek megfelelően modellünkben kimutatható, hogy az átmeneti készülségi szint optimális stratégia lehet nagy variabilitású környezetekben. Ez a mintázat azonban távolról sem általános, az optimális készülségi szintet több tényező befolyásolja, mint például: (1) a kedvező periódus hossza - hogyha a jó időszak prediktálható módon elég sokáig tart ahhoz, hogy a fiókákat ki lehessen röptetni, akkor érdemes magasabb készülségi állapotban várni a jó időszak kezdetét, még ha ez költséges is; (2) a környezeti fluktuációk mértéke - hogyha ez nem annyira magas, akkor a kedvezőtlen időszak alatt is viszonylag sok táplálék van, és a készülség

fenntartása nem annyira költséges; (3) a mortalitási ráta - rövid életű madarak többet fektetnek a szaporodásba, ezért rendszerint magasabb készülségi állapotot tartanak fenn, mint a hosszúéletűek; (4) a maximális készülségi szint eléréséhez szükséges idő - minél kevesebb idő szükséges a teljes készülség eléréséhez, annál alacsonyabb a készülségi szint, mivel az állatok gyorsabban tudnak reagálni. Emellett eredményeink azt mutatják, hogy már nagyon kismértékű szezonális változás a táplálékkelérhetőségben (a véletlenszerű változások mellett) elegendő ahhoz, hogy a szaporodási időszak a szezonális táplálékcsúcsra korlátozódjon (3. fejezet).

- Szezonális környezetekben a tavasz kezdetének megnövekedett variabilitása az esetek többségében magasabb készülségi szinttel jár, vagyis hogyha az állatok nem tudják prediktálni a tavasz kezdetének várható idejét akkor magasabb készülségi szintet tartanak fenn a tél vége felé. Ez azonban több tényezőtől is függ: (1) denzitásfüggő táplálékkelérhetőség mellett a környezet szezonális befolyásolja az állatok téli túlélését: minél alacsonyabb a szezonális befolyás, annál magasabb a túlélés; ez a cserekapcsolat a túlélés és szaporodás között alacsonyabb szaporodási befektetéshez vezet. Ennek következménye a kisebb fiziológiai felkészültség és gyengébb válasz a környezeti variabilitásra. (2) a táplálékkelérhetőség időbeli eloszlása befolyásolja, hogy mikor optimális elkezdni a szaporodást; hogyha a táplálékkelérhetőség egyenletes, akkor a korai költés optimális, ellenben ha kora tavasszal kevesebb táplálék van mint nyáron, akkor érdemes később kezdeni. Emiatt ilyen környezetben a madarak nem kezdenek el költeni akkor sem, ha a tavasz korán kezdődik, tehát a hirtelen környezetváltozásra adott válaszuk csekély (4. fejezet).
- A vonulási rendszerek filogenetikai analízise kimutatta, hogy a pintyeknél és rokonaiknál a vonulási távolság összefüggésben van a költési szezon kezdetével és annak hosszával: a hosszútávú vonulók később kezdenek költeni, és költési szezonjuk rövid. Ez az összefüggés független volt olyan tényezők hatásától, mint pl. a testtömeg vagy téli táplálék, amelyekről ismeretes, hogy a vonulási stratégiát erősen befolyásolhatják. A directionális teszt eredményeiből kitűnik, hogy a vonulási stratégiákban meg-

figyelhető evolúciós átmenetek a költési fenológia állapotától függenek; a hosszútávú vonulás nagyobb valószínűséggel alakul ki későn költőknél, és fordítva, a korán költő és hosszú költési szezonú fajoknál gyakoribb a rövidtávú vonulás kialakulása (5. fejezet).

- A szezonális színváltozás két mechanizmusának filogenetikai vizsgálata kimutatta, hogy a vedléssel és kopással történő színváltozás jelenlétét más-más tényezők határozzák meg. A vedléssel történő színváltozás elsősorban későn költő fajoknál és rovarrevőknél fordul elő, míg a kopás a télen csapatosan élő fajoknál gyakoribb. A két stratégia együttesen is előfordul, leginkább olyan fajoknál, ahol magas a poligínia gyakorisága (6. fejezet).

Következtetések

A környezeti tényezők jelentős hatással vannak az élőlények viselkedésére. Ezek a hatások nagyon összetettek lehetnek, ami miatt tanulmányozásuk sok esetben nehéz, és számos megválaszolatlan kérdés van még hátra. A különböző környezeti tényezőkről gyűjtött nagy felbontású, hosszútávú adatsorok korábban nem tapasztalt mértékben forradalmasíthatják az ökológia és evolúció határtudományait.

Jelen disszertáció két ponton járul hozzá ennek a folyamatnak az elősegítéséhez. Az itt bemutatott optimális éves rutin modell egy olyan, eddig még nem alkalmazott elméleti háttérrel nyújt a környezeti variabilitás hatásainak vizsgálatához, mely lehetővé teszi az összetetten változó környezetben élő állatok szekvenciális döntéseinek jobb megértését. Ez a megközelítés újszerű predikciókat ad a környezeti variabilitás és a viselkedés közötti összefüggésre, amelyek az egyre inkább elérhetővé váló környezeti adatsorok felhasználásával tesztelhetővé válnak. Bár a modellünk a költésidőzítés kérdéseire lett kifejlesztve, a környezeti variabilitás más viselkedésformákra is kihat, ami ezzel a megközelítéssel vizsgálhatóvá válik. Így például egy recens vizsgálatban Jetz and Rubenstein (2010) összevetette a madarak kooperatív szaporodási rendszerének előfordulását az elterjedési területük klimatikus variabilitásával és azt találták, hogy variábilisabb környezetben gyakoribb a kooperatív költés. Ez a kapcsolat a szociális

viselkedés és a klímavariabilitás között egy olyan érdekes, új fordulat, amelynek megértése további elméleti és empirikus vizsgálatokat igényel.

A környezeti variabilitás hatásairól szerzett ismereteink abból a szempontból is fontosak lehetnek, hogy a globális klímaváltozás egyik lehetséges következménye a megnövekedett klimatikus variabilitás (Morris et al. 2008). Az itt bemutatott modell alapján a környezet jelentős mértékben befolyásolhatja a viselkedésbeli flexibilitást (4. fejezet), ami végső soron meghatározza, hogy az állatok milyen mértékben képesek reagálni a gyors környezetváltozásra. Bár a hosszútávú fenológiai vizsgálatok alapján az élőlények reakciója a növekvő hőmérsékletre általánosnak tűnik (Walther et al. 2002), keveset tudunk az adaptáció és a fenotipikus plaszticitás szerepéről ennek a folyamatnak a meghatározásában. A plasztikus viselkedés alaposabb vizsgálata feltételezhetőleg jelentős szerepet fog játszani a két mechanizmus szétválasztásában, tekintve, hogy az esetek többségében valószínűleg egyszerűbb mérni, mint a mikroevolúciós folyamatokat.

Másrészt, a különféle fiziológiai és viselkedési rendszerek elemzésével sikerült kimutatni, hogy a szezonális változások általánosabbak, mint azt korábban feltételezték (6. fejezet), valamint hogy az éves ciklus komponensei jelentős mértékben kihatnak egymásra (5. és 6. fejezet). Tehát, bár a fiziológiai készség problémája elméleti szempontból általánosítva vizsgálható, a fiziológiai és viselkedési rendszerek szezonális változásai valójában több mechanizmust foglalnak magukba, amelyek mindegyike más-más módon befolyásolhatja a változó környezetekhez való alkalmazkodást. Éppen ezért lényeges, hogy ezeket a rendszereket külön-külön is megvizsgáljuk.

A vonulási stratégiák és költésfenológia közötti összefüggés elemzésével megtettük az első lépéseket a madarak két fontos élettévékenysége közötti összefüggés feltárása felé (5. fejezet). Korábbi vizsgálatokból már ismert volt a vonulás szerepe a vedlési stratégiák evolúciójában (Svensson and Hedenström 1999; Barta et al. 2008), az általunk végzett vizsgálat kiterjeszti ezt a kapcsolatot a költésre is (vagyis gyakorlatilag a teljes éves ciklusra). Eszerint tehát a költésfenológiának lényeges szerepe lehet a madarak életmenetstratégiáinak evolúciójában, hiszen a vonulást, és ezen keresztül a vedlést is befolyásolhatja. Ezen összefüggések megerősítéséhez további vizsgálatokra lesz szükség, lehető-

leg más taxonómiai csoportokon is.

A szezonális színváltozáson végzett összehasonlító vizsgálat alapján kiderült, hogy az összetett színváltozási stratégia (vedlés + kopás) nagyobb valószínűséggel fordul elő azon fajoknál, ahol a színezetnek feltételezhetőleg jelentős szerepe van a párválasztásban (poligín fajok; 6. fejezet). Ez a stratégia biztosíthatja, hogy a színváltozás gyorsan bekövetkezzen a tavasz kezdetén, bármilyenek is a környezeti viszonyok. A madarak díszes tollazatát sokáig statikus jelzéseknek gondolták, a részletesebb vizsgálatok azonban egyre gyakrabban mutatnak ki időbeli változást a tollazatban (pl. Delhey et al. 2010). Azonban bármennyire is változik a tollak színe kopással, fakulással vagy vedléssel, egy nagyon gyorsan változó, variábilis környezetben az ilyen úton történő színváltozás nem tudja követni a környezeti változásokat, és feltételezhető hogy ezekben a környezetekben a dinamikusabban szabályozható jelzések használata optimális (pl. ének). Ennek kiderítéséhez a szezonálisan változó jelzések vizsgálatát érdemes lenne kiterjeszteni trópusi és sivatagi fajokra is.

Összefoglalásképp, a környezeti szezonalitásnak és variabilitásnak komplex, számos tényezőtől függő hatása lehet az élőlények viselkedésére. Az általunk kifejlesztett modell egy elméleti háttérrel biztosít ezen kérdések vizsgálatához, a modellből származó predikciók pedig segíthetnek abban, hogy a feltételezéseinket filogenetikai vagy empirikus kontextusban vizsgálhassuk. Az így nyert ismeretek nem csak a különféle környezetekben előforduló állatok viselkedésének megértésében segítenek, hanem lehetővé teszik az élőlények környezetváltozásra adott válaszában előrejelzését is, ami a napjainkban zajló globális változások idején különösen fontos lehet.

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3.

Study I: Timing of avian reproduction in unpredictable environments

Abstract

Organisms living in periodically varying environments adjust their life history events to the changes in food availability. When these changes are not entirely predictable animals face a trade-off between maintaining physiological preparedness (which can be costly) and being unprepared (which decreases the chances of successful reproduction). To investigate this problem, we developed an optimal annual routine model of gonad regulation in birds. Most birds regress their reproductive organs during non-breeding periods, but to start breeding again they need to have functional gonads. Maintaining the gonads in this state is costly, but because it takes time to achieve this state, if gonads are not functional the bird may miss a possible breeding opportunity. We explore the resolution of this trade-off in environments where favorable periods can occur at any time of the year and variability in the length of good and bad periods can be altered. Consistent with empirical studies of reproductive behavior in unpredictable environments, we find that birds maintain the gonads partially activated during unfavorable conditions in many cases. However, gonad regulation may differ strikingly depending on the consistency of the good and bad periods. Furthermore, seasonal changes in food availability lead to the entrainment of reproduction and the segregation of the

breeding and non-breeding season, even if the magnitude of seasonality is small compared to the degree of environmental fluctuations. These results indicate that several aspects of the environment need to be taken into account to understand reproductive behavior in unpredictable environments. Given that the trade-off between the costs and benefits of maintaining physiological preparedness is not limited to birds, our results have implications for understanding behavioral flexibility in other organisms as well.

Keywords: phenotypic flexibility, annual routine, gonadal cycle, breeding season, opportunism.

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Introduction

In periodically changing environments animals organise their major life history events to match the regular changes in food availability. Proper timing is very important because the costs and benefits of performing a given action (e.g. migration, molt) vary over the year (Lack 1968; Perrins 1970; Houston and McNamara 1999; Barta et al. 2006, 2008; McNamara and Houston 2008; Wingfield 2008); in particular, reproductive success often depends on appropriate timing of breeding (e.g. Brinkhof et al. 1993; Visser and Verboven 1999). To cope with the changing environmental circumstances, animals have to adjust their state, resulting in reversible changes in body mass, internal morphology and physiology (Piersma and Drent 2003). If the environment is at least partly predictable, animals can use their internal biological rhythms to tune the timing of these changes to the environment. On the other hand, if information on the future is restricted (i.e. the environment is unpredictable) then animals need to be flexible and behave opportunistically (Bronson 1989; Zann et al. 1995; Hahn et al. 1997; Barea and Watson 2007; Robin et al. 2009).

Examples of temporal or spatial opportunism occur in a wide range of organisms: in anurans for instance, most species inhabiting arid or semiarid regions use ephemeral rain pools for reproduction (Wells 2007). These animals remain inactive for several months each year, but the entire population starts reproducing almost instantaneously after rainfall (Wells 2007). Opportunistic breeding is also frequent in birds, especially in the Australian avifauna, where food availability depends very strongly on rainfall and the birds can breed only during periods with high food availability (for an overview, see Robin et al. 2009). Similarly, small mammals inhabiting the tropics and commensal rodents associated with humans, such as house mice (*Mus musculus*) and Norway rats (*Rattus norvegicus*) generally have a very flexible reproductive system with the possibility of year-round reproduction, depending on actual food availability (Bronson 1989).

Opportunistic breeding implies that animals need to respond very quickly to changes in the environment. In some cases this is achieved relatively easily, as in the desert anurans (see above). In other cases, however, responding instantaneously to the changing environment is not as simple, because starting reproduc-

tion may require a suite of lengthy physiological preparations. For example, some female true seals (family Phocidae) do not feed during weaning but rely entirely on stored fat reserves to raise offspring (they are capital breeders; Stephens et al. 2009); accumulating these reserves takes time. Similarly, most birds regress their gonads outside the breeding period (Murton and Westwood 1978), presumably to reduce body mass and hence decrease the metabolic costs of flight (Dawson and Sharp 2007) or the risk of predation (cf. Lind et al. 1999). From this regressed state it may take several weeks or months before the reproductive organs are again fully functional (Murton and Westwood 1978). Because gonads have to be fully developed in order to reproduce, birds need to start regrowing their gonads well before the time of highest food availability to ensure that the energetically expensive egg-laying and chick-rearing periods fall within the time window of abundant food sources. Here we use birds as an example to investigate how lengthy physiological preparation influences the timing of important life history events in unpredictable environments. Our study can, however, provide insight for other organisms where such preparation is required.

In stable seasonal environments the reactivation of gonads in spring is triggered by long-term predictive information from the environment, mainly photoperiodic cues (e.g. Wingfield et al. 1992; Dawson and Sharp 2007). This enables birds to develop their reproductive organs in anticipation of the favorable season. In contrast, when the environment is stochastic and hence there is unpredictable variation in the onset of the favorable season, animals face a twofold problem, because they (i) cannot fully anticipate the expected start of the reproductive season (it is stochastic) and (ii) cannot respond immediately to changes in the environment (because physiological development takes considerable time). Hence, in such environments there is a trade-off between (i) reactivating reproductive organs earlier, which incurs the cost of maintaining the gonads during unfavorable periods and (ii) delaying reactivation, which increases the chance that periods with high food availability will be missed. The consequences of missing the peak of suitable food are especially serious in birds whose offspring require specialized, protein-rich food, because these species cannot easily buffer the effect of environmental variability e.g. by providing milk (Zann et al. 1995; Barea and Watson 2007).

As a result of this trade-off, birds living in highly variable environments are thought to maintain their reproductive system in a partially regressed state (Immelmann 1973; Morton 2009), and observations of Australian opportunistic breeders provide some support for this prediction (e.g. Immelmann 1973; As-theimer and Buttemer 1999; Morton 2009; but see Perfito et al. 2007). However, even if the favorable period can start at any time of the year, the fitness benefit of staying prepared during periods with low food availability (and as a result the level of preparedness during these periods) may differ between environments. Thus, all else being equal, a longer period of continuous preparedness incurs a higher cost of maintaining gonads between two consecutive breeding periods. Similarly, the fitness benefit of staying prepared and starting reproduction quickly after the onset of the good period is higher when the good period is shorter, because in this case only individuals with high levels of preparedness can successfully complete a reproductive attempt. These relationships should also depend on the food availability during the unfavorable period: if food availability is low then staying prepared is more costly; accordingly, most temperate zone birds regress their gonads completely during winter, e.g. there is a 200-fold decrease in gonad size in starlings *Sturnus vulgaris* (Murton and Westwood 1978; Dawson and Sharp 2007), whereas gonads are maintained at a relatively high level in some tropical species (Bosque et al. 2004; but see Wikelski et al. 2003 for contrasting patterns of gonad regulation in tropical birds).

Past theoretical studies of evolution in stochastic environments mainly focussed on life history adaptations such as reproductive investment (e.g. Schaffer 1974; Schultz 1991), and the evolution of risk-spreading (bet-hedging) strategies (e.g. Cohen 1966; Philippi 1993; McNamara 1995). Studies of bet-hedging provided comprehensive analyses of several timing problems, such as the timing of germination in desert plants (e.g. Philippi 1993), the use of diapause in insects (e.g. McNamara 1994), or timing of maturation (e.g. Tuljapurkar and Wiener 2000). However, much less is known about the importance of unpredictability for the optimal timing of life history events when sequential decisions are made in complex environments.

Our aim in this paper is to develop an optimal annual routine model to investigate the timing of reproduction in unpredictable environments when breeding

requires lengthy physiological preparation. Using this approach, we extend the framework of annual routine models developed to analyse optimal behavior in seasonal environments (Houston and McNamara 1999; McNamara et al. 2004; Barta et al. 2006, 2008) by including year-to-year variation. We assume that the animal knows the current level of food availability but has incomplete knowledge about future conditions. First, we explore the regulation of reproductive organs and timing of reproduction in environments differing in the length and predictability of bad and good periods, assuming that these periods can occur at any time of the year and food availability is aseasonal. Second, by acknowledging that unpredictable environments may have a seasonal pattern of food availability (e.g. because of seasonal variation in temperature), we also explore cases where mean food availability changes during the course of the year and there are fluctuations around the mean. Because a large proportion of tropical and near-tropical ecosystems show considerable variation in environmental conditions (Wingfield et al. 1992; Hau 2001; Shine and Brown 2008), this approach is necessary to understand the reproductive behavior of animals inhabiting environments with lower seasonality.

The model

The behavior of the modelled organisms is followed over an annual cycle divided into $T = 52$ decision epochs (i.e. $t = 0, 1, 2, \dots, T$ weeks). Time 0 is the first week of the year, time T is exactly one year later and is also time 0 of the next year. An animal is characterized by four state variables: development status of reproductive organs o ($0 \leq o \leq o_{max}$), brood age a ($0 \leq a \leq a_{max}$), experience e ($0 \leq e \leq e_{max}$) and food level f . At the start of each week, the bird simultaneously modulates the size of reproductive organs (*increase*, *decrease* or *maintain* gonad size) and chooses a breeding option: *subsist* (do not start a brood, or desert brood if there is one), *start* a brood or *care* for the young. The bird has to balance its energy expenditure with its energetic gain over a week (McNamara et al. 2008, also see below).

The environment

All aspects of the environment except food are constant over time. Food availability varies over the course of the year, its variation being determined by two sources. First, the mean amount of food, $g(t)$, changes seasonally over the year according to the equation:

$$g(t) = A + \epsilon \left[1 + \sin \left(\pi \frac{t - 13}{26} \right) \right]. \quad (3.1)$$

Here A controls the overall amount of food in the environment and ϵ sets the degree of seasonality; larger values of ϵ determine higher seasonality, that is, the difference between winter and summer food availability is higher.

Second, the actual amount of food, $g_F(t)$, fluctuates around the mean, $g(t)$. We consider two possibilities: food availability can be either high ($F = G$) during good periods or low ($F = B$) during bad periods. If food availability is high then the actual amount of food available for an individual is $g_G(t) = g(t) + \delta$, $0 \leq \delta < A - \epsilon$. If food availability is low, the amount available is $g_B(t) = g(t) - \delta$. Hence δ gives the amplitude of fluctuations in the environment. The parameter A is adjusted until the population growth rate is 1, thus we assume that the per capita amount of food available is density dependent (for details see McNamara et al. 2008).

Transitions from bad to good food and vice versa can happen all year round with the following restriction. After a transition (e.g. from bad to good) the food must stay at its current level (e.g. at good) for a given amount of time (the minimum duration of the period, D_F , $F = B, G$) before it can switch back (e.g. to bad). After the minimum length of time has elapsed the transition occurs with a given probability per week which causes uncertainty about when the period of a given food condition actually ends. By changing the probability of the transition the average length and variability of the duration of a given food condition can be controlled; low probability results in long mean duration with high variance, while high transition probability means short average length with low variance in the duration of a given condition (for details see Appendix 3.A).

The minimum duration of the period, D_F , captures the consistency of a given environmental condition. Low D_F corresponds to a situation with low consis-

tency, like in the Arctic where a sudden snowstorm can instantaneously terminate a favorable period which has just started. Apart from these extremes climatic conditions often show a higher degree of consistency; for example rainfall may cause vegetation growth and this can predictably provide good living conditions for a considerable period of time after the rain. This can be modelled by long D_F .

To increase tractability we consider only a low ($D_F = 1$ week) and a high ($D_F = 11$ weeks) consistency situation in most cases investigated. In both situations the probability governing the transition at the end of the minimum period is set in such a way that the average duration of a given food condition is the same (~ 20 weeks) in both situations. If $D_F = 11$, i.e. the consistency is high, the individuals have enough time to perform at least one breeding attempt (see below). Given these two situations we consider four environments: (i) both good and bad periods are characterized by low consistency ($D_B = 1, D_G = 1$), (ii) both good and bad periods are characterized by high consistency ($D_B = 11, D_G = 11$), (iii) low consistency bad periods alternate with high consistency good periods ($D_B = 1, D_G = 11$), and vice versa (iv) high consistency bad periods alternate with low consistency good periods ($D_B = 11, D_G = 1$).

Behavior and state dynamics

Gonad size. The state variable o ($0 \leq o \leq o_{max}$), gives the developmental status of the reproductive organs. The animal can only start a brood if $o = o_{max}$ but reproductive organs can be regressed after that (i.e. care of brood is possible with $o < o_{max}$). Let the animal's reproductive organ be in status o_t at the beginning of week t . The animal can either *increase* the size of its gonads, $o_{t+1} = o_t + 1$, if $o_t < o_{max}$, *decrease* it, $o_{t+1} = o_t - 1$, if $o_t > 0$, or *maintain* it in the same status, $o_{t+1} = o_t$. Having the organ in status o costs $\Delta(o) = c_o o$ amount of energy (maintenance cost) per week, where c_o is a parameter of the model (Table 3.1).

Reproduction. If an animal does not have a brood at the beginning of week t ($a_t = 0$) and it has fully developed gonads ($o_t = o_{max}$) it can start breeding, $a_{t+1} = 1$, or subsist ($a_{t+1} = 0$). If the animal has a brood at the beginning of week t ($1 \leq a_t < a_{max}$), it can either continue to care for the brood, $a_{t+1} = a_t + 1$

or desert it ($a_{t+1} = 0$). If the parent dies between t and $t + 1$, the brood also dies. If the brood reaches the maximum age, $a_t = a_{max}$, the parent abandons the young at the beginning of week t , and the brood becomes independent ($a_{t+1} = 0$). We assume that the newly fledged young have zero experience (see below), the status of their reproductive organs is zero, and they experience the same environmental conditions as their parents at the time of abandonment.

For simplicity, we assume that brood size is fixed, which is a reasonable assumption for several avian taxa with invariant clutch sizes, such as shorebirds (Charadriodea and Scolopacoidea; del Hoyo et al. 1996) or the pigeons and doves (Columbidae; del Hoyo et al. 1997).

Experience. Foraging efficiency increases with experience (e); newly fledged animals have $e = 0$. Experience tends to increase with age towards its maximum value (e_{max}); if a bird has experience e at the start of week t , it is still e at $t + 1$ with probability $1 - p_e$, and is

$$e' = \min(e_{max}, e + 1) \quad (3.2)$$

at $t + 1$ with probability p_e .

The actual energetic intake rate of the bird will depend on its experience, thus:

$$\gamma_F(e, t) = g_F(t)\theta^{e_{max}-e}. \quad (3.3)$$

The parameter determining the foraging efficiency of the young, θ , has a value between 0 and 1, thus we assume that juveniles with less experience ($e < e_{max}$) are less efficient foragers than adults, and that energy intake increases with experience.

Energy balance. For simplicity, we assume that the bird's weekly intake must cover its weekly energy expenditure (for details, see McNamara et al. 2008). If the proportion of time spent foraging during that week is u , then u must satisfy the balance equation

$$\gamma_F(e, t)u = C + c_f u. \quad (3.4)$$

Here, the left hand side denotes the energy intake of a bird during a whole week and the right-hand side denotes energy expenditure. The parameter c_f determines how energy expenditure of foraging scales with the proportion of time spent foraging. C is the metabolic cost associated with gonad size and breeding; for a subsisting individual, this is just

$$C = c_b + c_o o, \quad (3.5)$$

where c_b is the basal metabolic expenditure, while c_o gives how energetic expenditure scales with reproductive organ size.

Starting a brood or caring for young has an additional metabolic cost of c_{start} and γ_b , respectively, therefore C is incremented by c_{start} or γ_b for birds deciding to start a brood or continue to care for an existing brood.

Sources of mortality. The bird can die because of predation or starvation. Predation hazard depends on the proportion of time spent foraging; the more time a bird spends foraging, the more exposed it is and the less time it has to watch out for predators. Moreover, if there are times of the day when foraging is more risky (in terms of predation hazard), a bird that forages for only a small part of the day can avoid the more risky periods, whereas a bird that forages for the whole day cannot. To capture this accelerating effect of foraging activity on predation hazard, the probability of mortality per week which is unrelated to starvation is determined as a quadratic function of u :

$$M(u) = p_b + p_m u^2. \quad (3.6)$$

Here, p_b is the background mortality, which is unaffected by the state of the animal or its behavior, and p_m is the mortality parameter associated with the time spent foraging.

Starvation occurs if the bird cannot balance its weekly energy expenditure; i.e. it needs to forage for more time than is available. We assume that u is the proportion of an average week that is required for foraging. However, because of variation in environmental conditions the bird sometimes has less and sometimes has more time available than average. To represent this, the probability of

starvation is taken to be

$$S(u) = 1 - 1/(1 + u^L). \quad (3.7)$$

Here, L is a large value (200 in the present model), so that the probability of starvation increases sharply from 0 to 1 around $u = 1$ (cf. McNamara et al. 2008).

Determination of the optimal strategy and the expected behavior

The optimal strategy is a rule that specifies the dependence of the actions taken on the state variables and time of year. This strategy maximises asymptotic growth rate of numbers of descendants and is calculated by dynamic programming, working backwards from the future and iterating to convergence (McNamara 1991, Houston and McNamara 1999). Details of this procedure are described in Appendix 3.B.

To obtain the realized behavior of birds we first calculated the steady state distribution of a large population of individuals following the optimal strategy. To do so, we follow the population forwards in time, at each time t calculating the distribution over states at time $t + 1$ in terms of the distribution at time t . The process is continued for several years until the state distribution settles down (Houston and McNamara 1999).

After the state distribution has been calculated, we use Monte Carlo simulations to study the realized behavior of the modelled birds. The initial state distribution of the birds in the simulation is the steady state distribution derived from the forward runs at week 0. When the birds reproduce, the offspring are entered into the population as new individuals, whereas birds that have died are removed. However, only data from adult birds (i.e. birds with $e = e_{max}$) was used to quantify reproductive readiness.

Table 3.1: *The model's parameters and their baseline values.*

Parameter	Symbol	Value
Probability of changing experience class	p_e	0.025
Parameter determining the foraging efficiency of inexperienced birds	θ	0.7
Basal metabolic expenditure	c_b	0.15
Metabolic cost of foraging	c_f	0.3
The metabolic cost associated with the reproductive organs	c_o	0.01
The metabolic cost of starting a brood	c_{start}	0.9
Gross intake needed to provide nestling	γ_b	0.9
Background mortality	p_b	0.0005
Mortality parameter associated with time spent foraging	p_m	0.005
Maximum organ size	o_{max}	5
Maximum experience	e_{max}	2
Maximum brood age	a_{max}	7
Brood size	n_{brood}	1
Minimum length of the good period	D_G	
Minimum length of the bad period	D_B	

Results

Aseasonal environments To explore the effect of year-round unpredictability on the reproductive behavior of birds we performed a series of runs in environments where variation in environmental conditions is determined solely by fluctuations in food availability (i.e. there are no regular seasonal changes in food availability; $\epsilon = 0$). In these aseasonal environments there is no distinct breeding season; reproduction occurs continuously throughout the year (for $\delta = 0$) or

breeding follows the fluctuations in food availability (for $\delta > 0$), independent of the time of year. We first investigated how the size of reproductive organs changes with the environmental conditions by plotting mean gonad size over favorable periods of a fixed length of 20 weeks followed by an unfavorable period of the same length (which is the average length of both periods). A summary of the key predictions of the model is given in Table 3.2.

The investigation of the actual trajectories of gonad size over time reveals the following patterns (Fig. 3.1). When the length of the good period is highly consistent birds have enough time to complete a breeding attempt during each good period ($a_{max} < D_G$). To be able to exploit this possibility, however, they have to be prepared at the beginning of the good period. Therefore, reproductive readiness is high during the bad period (Fig. 3.1a, b) except when there is no chance that the good period starts next week (i.e. during the first part of a highly consistent bad period; Fig. 3.1a). The level of environmental fluctuations, δ , influences the birds' behavior during the good periods. When the level of fluctuations is low ($\delta \leq 0.25$) birds breed only once per good period and then keep their reproductive organs deactivated. In contrast, when the level of fluctuations is high, birds keep breeding, and hence maintain large gonads, over all of the good period. This is a consequence of density dependence, which leads to lower survival rate in juveniles when environmental fluctuations are large. This, in turn, selects for increased reproductive investment in the adults (see Appendix 3.C).

When the consistency of the good periods is low, birds cannot successfully breed in each good period. To compensate for this loss of breeding opportunity, they have to use all the available time suitable for breeding, i.e. they have to keep their gonads ready for breeding during the whole good period, independently of δ (Fig. 3.1c, d). During the bad periods the birds behave similarly to the cases where the consistency of good periods is high, i.e. they are prepared for breeding when there is a chance that the good period will start next week. There is, however, one exception; birds keep their gonads regressed over the bad period when both the good and bad periods are characterized by low consistency and the level of environmental fluctuations is high (Fig. 3.1d). Under this condition the advantage of being prepared during the bad period is lowered because of the high uncertainty in the length of the good period. Furthermore, the cost of keeping

gonads activated is also high because of the relatively low level of food during bad periods caused by density dependence and the large difference between bad and good periods (cf. McNamara et al. 2008). This cost is lower for the case when the bad period is highly consistent (Fig. 3.1c) because the period during which birds should be prepared (i.e. when good period can start) is shorter on average in this case.

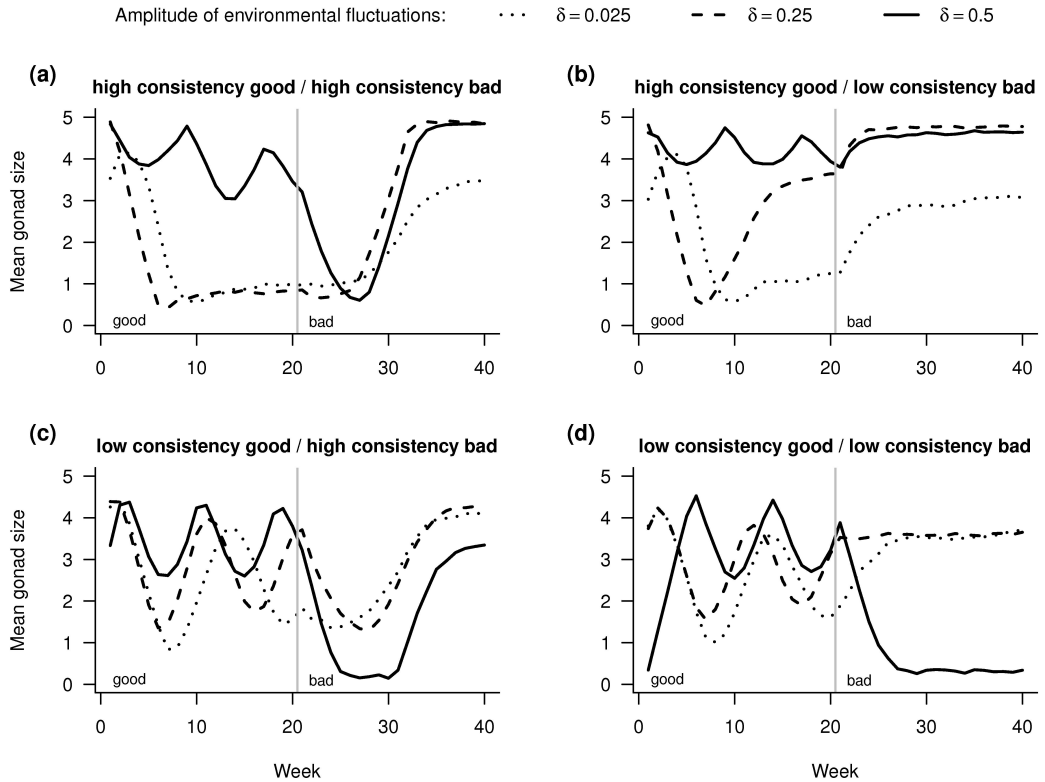


Fig. 3.1: Changes in mean gonad size in aseasonal environments ($\epsilon = 0$) during a simulated period consisting of a 20-week good period followed by a 20-week bad period in the four environments differing in the consistency of the bad and good periods, at increasing amplitudes of environmental fluctuations (δ). The vertical grey line demarcates the transition from high to low food availability. All other parameters are set to their baseline values (see Table 3.1).

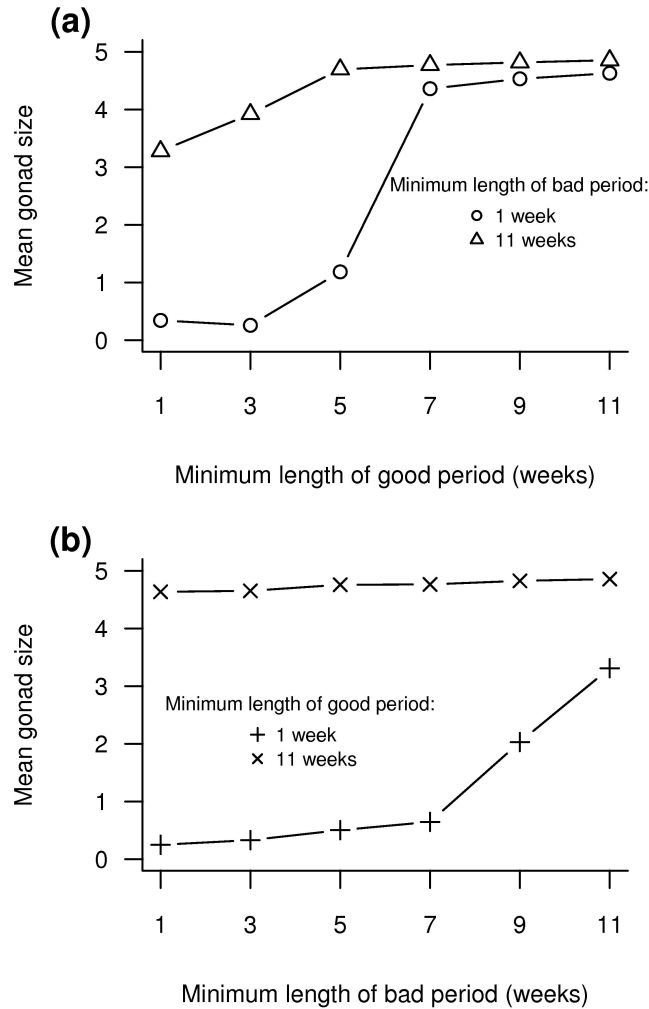


Fig. 3.2: The effect of transforming either the good (a) or the bad period (b) from low to high consistency at high levels of environmental fluctuations ($\delta = 0.5$) on reproductive readiness. In the first case (a), the minimum length of the bad period was held fixed (either at 1 week or 11 weeks) while increasing the length of the good period from 1 to 11 weeks. In the second case (b) the same was done with the role of the bad and good periods reversed. The effect of the different environmental conditions on the reproductive readiness of birds was evaluated by calculating the mean gonad size at the end of a 20 week bad period.

To see the effect of environmental consistency in more detail, the minimum length of both the good and the bad period was gradually increased from 1 to 11 weeks, while holding the minimum length of the other period constant, thereby

creating environments with intermediate levels of consistency (Fig. 3.2). The pattern of reproductive readiness in these environments is consistent with the previous conclusions: gonads are fully developed during periods of low food availability when good periods last long enough for birds to complete a brood with high probability (Fig. 3.2). The largest effect of changing the consistency of either the good or the bad period on the optimal level of reproductive readiness is observed when the minimal length of the other period is small (Fig. 3.2).

Seasonal environments To investigate the effect of environmental fluctuations when food availability also has a seasonal trend, we computed the optimal behavior in environments with seasonality ranging from $\epsilon = 0.05$ to $\epsilon = 0.5$ and fluctuations in food availability with a magnitude ranging from $\delta = 0.025$ to $\delta = 0.25$ (i.e. for each value of ϵ , δ was increased from 0.025 to 0.25). We chose this range of parameters so that the difference between the highest food availability in summer and the lowest amount in winter is not very large, because a large difference would result in very high winter mortality rates and an average life span of less than 1 year. With the chosen parameters, the largest difference between summer maximum and winter minimum is $2\epsilon + 2\delta = 1.5$, which is of a magnitude similar to previous annual routine models (Barta et al. 2006, 2008; McNamara et al. 2008).

In contrast to the aseasonal environments where reproduction can occur at any time of the year, the breeding and nonbreeding seasons in seasonal environments are segregated. This entrainment occurs at all values of ϵ , i.e. even at very low seasonality ($\epsilon = 0.05$). The breeding season is short and gonad regulation shows a seasonal pattern where reproductive organs are increased during the middle of the year but regressed at other times (Fig. 3.3a). Broods are initiated only during good periods that start around the middle of the year; however, if environmental conditions remain unfavorable during this period the birds skip breeding. As a result, the average number of brood fledged per year in these environments is low (Appendix 3.C).

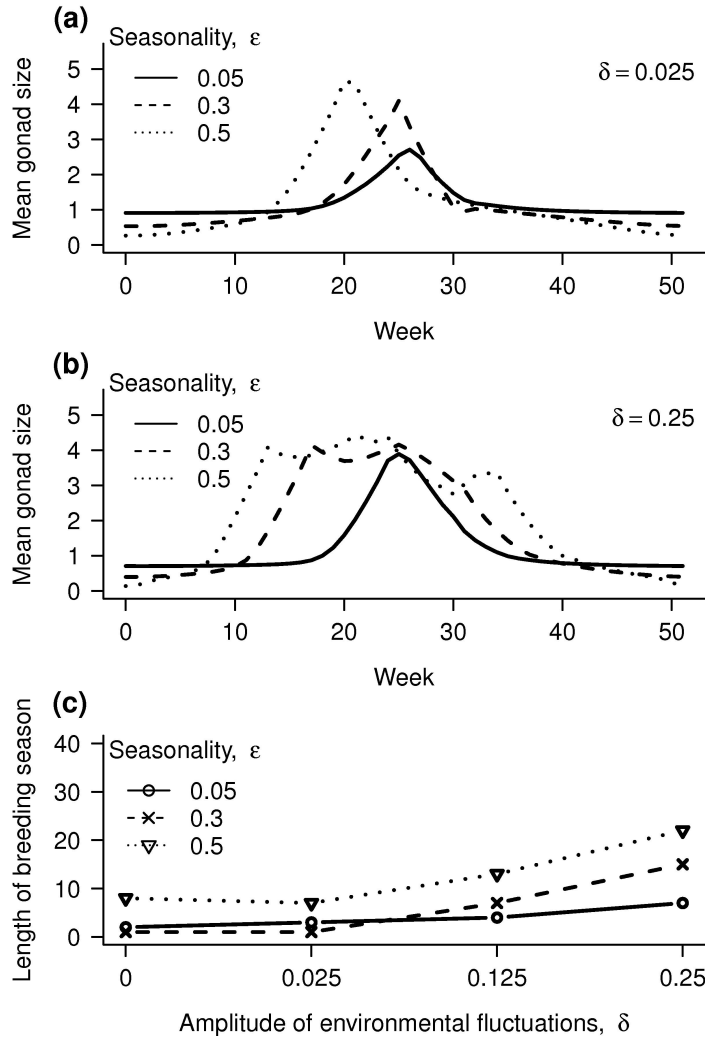


Fig. 3.3: Gonad regulation during the annual cycle and length of the breeding season in seasonal environments with different levels of environmental fluctuations in high consistency good / high consistency bad environments. In these seasonal environments, breeding occurs only in the middle of the year and gonads are upregulated only during this period (a). Gonads are maintained in a high development state for longer when there are environmental fluctuations (b, $\delta = 0.25$ in this case). The length of the breeding season (defined as the number of weeks in which at least 0.1% of the population initiates a brood) increases with the amplitude of the fluctuations (c). The behavior of the birds is similar in the other three environments (i.e. high consistency good / low consistency bad, low consistency good / high consistency bad and low consistency good / low consistency bad).

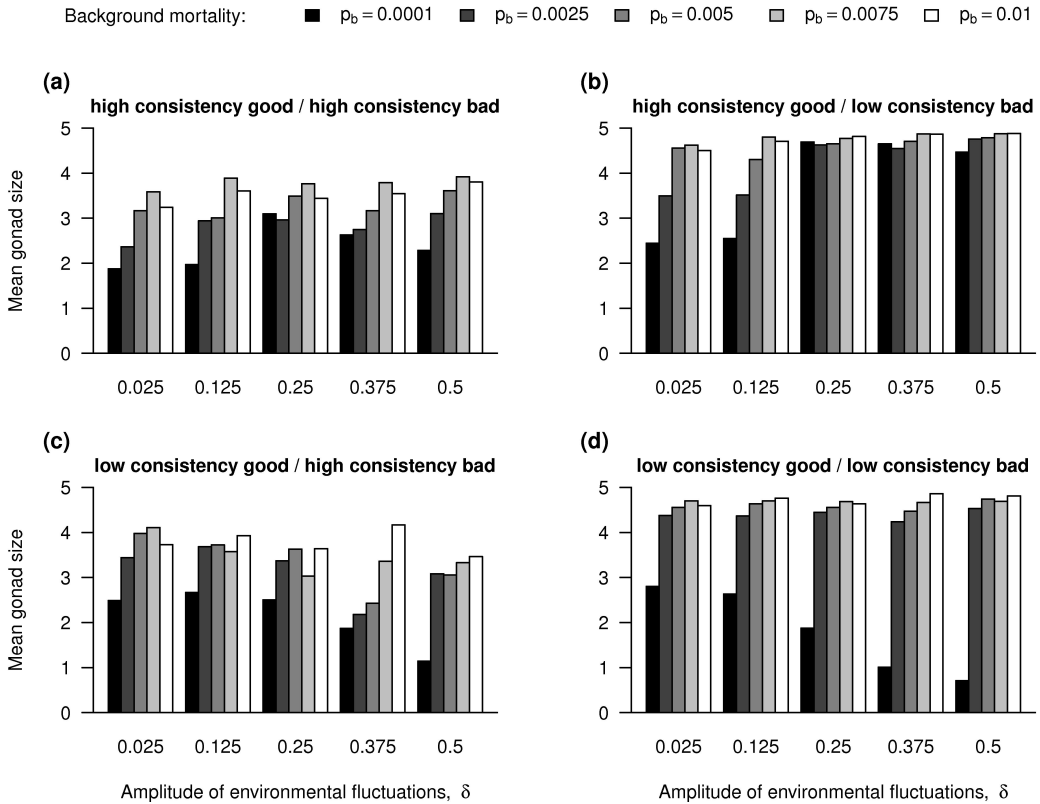


Fig. 3.4: The effect of background mortality rate on the optimal level of reproductive readiness (mean gonad size during bad periods) in aseasonal environments ($\epsilon = 0$). Mean gonad size was calculated for all adult birds, irrespective of the time elapsed since the end of the last good period, thus the presented values reflect the average level of preparedness of the population during bad periods.

In seasonal environments where the amplitude of environmental fluctuations (δ) is larger, gonads are kept activated for a longer time (Fig. 3.3b) and the breeding season lasts longer (Fig. 3.3c). This is explained by the fact that when the fluctuations are high, winter mortality also increases causing less intense competition for food during the summer. The consistency of environmental conditions has only a minor effect on the modulation of reproductive organs (results not shown), because the birds initiate reproduction after unpredictable surges in food availability that occur during the middle of the year even if the length of these favorable periods is highly unpredictable.

The effects of background mortality In the results presented above the annual survival rate is relatively high (around 0.9 when $\delta > 0$; Appendix 3.C). To investigate gonad regulation in short-lived birds, we increased the background mortality from $p_b = 0.0001$ to $p_b = 0.01$. For $p_b = 0.01$ annual survival rate is around 0.55; because survival is uncertain, the reproductive value of current breeding attempts increases and the optimal behavior differs in several aspects from the baseline case. In aseasonal environments short-lived birds in general show higher levels of reproductive readiness. This difference is most pronounced when the consistency of both the good and bad periods is low; here long-lived birds maintain low or intermediate levels of preparedness, but for $p_b > 0.0001$ birds maintain their gonads close to the maximal size (Fig. 3.4). In seasonal environments the main effect of the increased background mortality is that the breeding season becomes longer because the birds try to breed even when food availability is lower. When seasonality is low ($\epsilon = 0.05$), background mortality is high ($p_b = 0.01$) and there are large fluctuations in food availability ($\delta = 0.25$), the birds breed almost year-round (Fig. 3.5c).

Sensitivity analyses

To see how the cost of maintaining reproductive readiness (c_o) or the time required to become fully prepared (o_{max}) affects the patterns of gonad regulation, we made a series of runs where the values of these parameters was altered (Appendix 3.D). The results from these analyses indicate that the effect of environmental variability is similar under a wide range of parameter values; however, mean reproductive readiness during bad periods decreases when the metabolic cost associated with the gonads is higher or the time required to become fully prepared is shorter (Appendix 3.D).

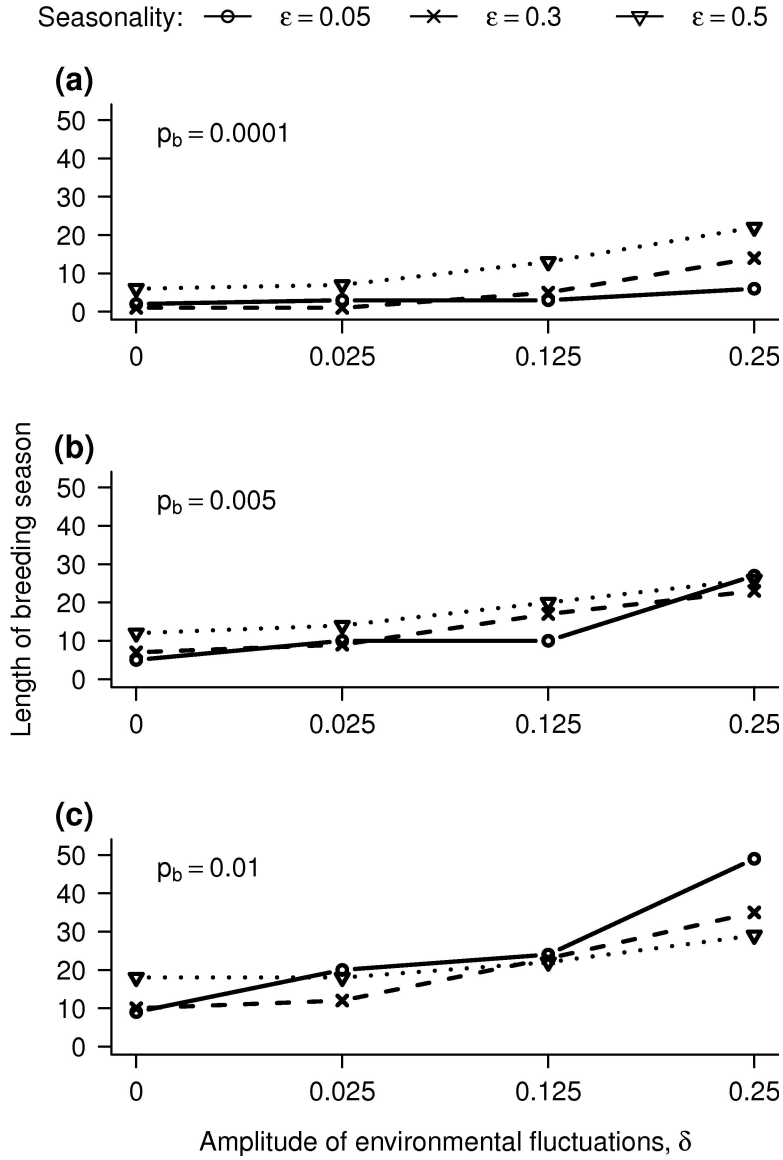


Fig. 3.5: The length of the breeding season in seasonal environments with fluctuations in food availability under three different background mortality rates: low ($p_b = 0.0001$, a), medium ($p_b = 0.005$, b) and high ($p_b = 0.01$, c) background mortality. The length of the breeding season was measured as the number of weeks in which at least 0.1% of the population initiates a brood.

Discussion

Life history models originally focussed on annual decisions, often taking the only state of an organism to be its age or its size. However, many life history trade-offs are mediated by physiological state variables that vary on a variety of timescales (McNamara and Houston 1996, 2008; Zera and Harshman 2001; Harshman and Zera 2007). These variables include energy reserves, parasite load, hormone levels, feather condition and oxidative damage. Such variables are not easily taken into account in models based on annual decisions. To capture the appropriate physiology, models which consider a sequence of decisions over the course of a year are needed. Recent models (e.g. Houston and McNamara 1999; Barta et al. 2006, 2008; McNamara et al. 2008) have incorporated such detail. The models explicitly take seasonality into account, but assume that all years are the same. Here for the first time we have built a model that includes year-to-year variation as well as seasonality. Our model involves decisions about both reproductive behavior and the associated reproductive physiology. This combination of physiology and behavior in a complex environment is a crucial feature of realistic life history models.

An important aspect of our model is that it is not possible to change physiology (gonad size) instantaneously. As a result there is a tension between maintaining the gonads in readiness and saving energy by reducing gonad size after reproduction. Distinct life-history stages emerge from the optimal response to this tension. Thus in addition to unifying physiology, behavior and ecology, our framework provides a formal derivation of life-history stages as envisaged by Jacobs and Wingfield (2000) and Wingfield (2008).

In our model, all individuals are subject to the same year-to-year variation. The population is also structured. Thus the correct fitness measure is the dominant Lyapunov exponent of the appropriate projection matrix (Metz et al. 1992). Finding an optimal strategy in our setting is extremely complex (cf. McNamara 1997). Fortunately, when fluctuations primarily affect reproductive success and organisms are long lived, it is reasonable to approximate fitness by the mean growth in descendant numbers (Haccou and McNamara 1998). Optimal strategies then can be found using dynamic programming (McNamara and Houston

1996, 2008; Houston and McNamara 1999), as we have done here.

A key result emerging from this model is that, despite the uniform distribution of favorable and unfavorable periods during the course of the year, opportunistic breeding schedules and the regulation of reproductive organs in unpredictable environments may be strikingly different depending on several factors, such as: (i) the length of the favorable period - if the good period is long enough to finish a brood with high probability, birds will maintain their gonads in a more developed state even if this is costly; (ii) the amplitude of environmental fluctuations - when fluctuations are small, there is relatively more food during bad periods and maintaining high readiness is less costly; (iii) longevity - short-lived birds invest more into current reproductive attempts and generally show higher levels of reproductive readiness than long-lived birds; (iv) the time required to reach fully developed gonads - the less time is required to reach full preparation, the lower the reproductive readiness is, because birds can respond more quickly to changes in the environment.

One strategy that opportunist breeders were thought to employ to cope with temporal variability in food resources was to maintain the reproductive system only partially regressed during the whole year, thereby minimizing the time required to fully activate the gonads (Immelmann 1973; Morton 2009). This conclusion is largely based on observation of Australian desert birds that may start reproductive activities (courtship and nest building) within hours after a heavy rainfall (Immelmann 1973; Hahn et al. 2008; Morton 2009), suggesting that the reproductive system of these birds could be activated within very short time. Although reports of such extremely flexible breeding may not be representative (Zann et al. 1995; Hahn et al. 2008), inspection of the gonads of birds known to breed year-round showed that a partially activated reproductive system does occur in some species (Astheimer and Buttemer 1999, Perfito et al. 2007). However, not all opportunistic breeders maintain the reproductive system activated year-round: red crossbills (*Loxia curvirostra*) and white-winged crossbills (*L. leucoptera*), which also have a very flexible breeding schedule regress their gonads and have low levels of circulating reproductive hormones during parts of the year when molting occurs (Hahn 1998; Deviche and Sharp 2001). Small ground-finches (*Geospiza fuliginosa*) that breed after unpredictable rainfalls in

the Galápagos archipelago also regress their gonads entirely between two favorable periods (Hau et al. 2004). Thus, while breeding in temporally unpredictable environments has only been investigated in detail in a few cases, even these show interspecific differences in the regulation of the reproductive system.

Our results suggest that maintaining the gonads in a partially developed state during periods with high food availability is indeed an optimal strategy under some conditions, but not in others. Thus, we found that gonads are maintained at an intermediate level when the amplitude of environmental fluctuations is not large. By contrast, optimal reproductive readiness in environments with high levels of environmental fluctuations is much more variable, with both completely regressed and fully developed gonads observed in environments differing in the consistency of the bad and good periods. Higher levels of environmental fluctuations result in more food being available during favorable periods, resulting in high reproductive success. Because food is density dependent, competition for food increases if the number of young produced or their survival rate is higher. All else being equal, this will result in a decrease in food availability, ultimately leading to lower levels of reproductive readiness during bad periods. Such effects of the amplitude of environmental fluctuations may explain why some species can maintain relatively large gonads during unfavorable periods, whereas others regress their gonads completely.

The optimal gonad size during bad periods also depends on the reproductive advantage of staying prepared and starting a brood as soon as possible after the onset of a good period. Thus, when favorable periods are expected to last long enough to complete a breeding attempt with high probability, high levels of preparedness may be optimal even during periods of low food availability. In contrast, when breeding attempts may be terminated by unpredictable reversals to bad food conditions, the birds use a different strategy, namely, they only start increasing their gonads when a favorable period has begun, and breeding attempts are finished only if the favorable conditions last long enough. Such high uncertainty in the outcome of breeding attempts has been observed for example in king penguins (*Aptenodytes patagonicus*) that try to breed a second time after a successful breeding attempt, despite the fact that fledging rate of chicks born later is extremely low (Brodin et al. 1998). Unpredictable surges in food availabil-

ity during chick provisioning, coupled with a relatively low cost of reproduction could explain why penguins frequently start broods despite such high failure rates (Brodin et al. 1998). Taken together, variation in the length of the favorable period could have a strong impact on optimal breeding schedules in unpredictable environments and quantifying breeding failures could be helpful in understanding reproductive decisions of birds inhabiting these environments.

In some environments, unpredictable variation in food supply may not be uniform during the course of the year. For example, even if food availability depends largely on rainfall, a winter rain may not yield as much food as a summer rain, if there is seasonality in temperature. In the zebra finch breeding may occur at virtually any time of the year in the arid interior of Australia (Zann et al. 1995; Perfito et al. 2007), where rainfall is unpredictable and seasonality in temperature is relatively small. However, breeding is more synchronized, and is much less likely to occur during the winter at a site in southern Australia, where temperature seasonality is higher (Perfito et al. 2007). While precipitation is also more predictable at this second site, the difference in the predictability of breeding was much larger than differences in rainfall patterns (Perfito et al. 2007). Our model predicts that, when food conditions are unpredictable but actual food availability depends on time of year, birds start reproducing during unpredictable surges in food only if these occur at a specific time of year (during the period with the highest long-term average food). This effect may occur even if annual variation in food availability is small compared to the degree of fluctuations, especially in long-lived birds as it is particularly important for such birds to avoid breeding at suboptimal times (McNamara et al. 2004). As a result, seasonal patterns in reproductive behavior may be observed even in highly variable environments with continuous, marked fluctuations in food availability, provided there are small but consistent differences in food availability between different parts of the year. This entrainment of breeding irrespective of the degree of environmental fluctuations may explain why so many tropical and subtropical species show seasonality in reproduction, even though the amplitude of seasonal changes is believed to be small and their year-to-year predictability is low (Moreau 1950; Murton and Westwood 1978; Hau 2001; Wikelski et al. 2003). Our model also predicts that birds do not initiate reproduction when environmental conditions during the long-

term seasonal maximum are unfavorable. Thus, reproductive behavior in seasonal environments with unpredictable variation in food availability differs from seasonal environments with no variability in that there is a relatively high frequency of reproductive year-skipping.

Table 3.2: *The effect of changing key parameters on the optimal behavior - main predictions of the model.*

Parameter	Predictions
Aseasonal environments	
Consistency of good periods (D_G)	Reproductive readiness during bad periods is high when D_G is long enough to finish a brood. Brood desertion is frequent when D_G is small.
Consistency of bad periods (D_B)	If D_B is large, gonads can be regressed between successive good periods.
Amplitude of environmental fluctuations (δ)	If δ is large, the number of brood attempts per good period increases; gonads size is large throughout good periods. Reproductive readiness during bad periods decreases with increasing δ .
Metabolic cost of gonads (c_o)	Reproductive readiness during bad periods decreases with increasing c_o .
Maximum gonad size (o_{max})	Gonad recrudescence starts earlier and reproductive readiness is higher on average during bad periods when o_{max} is larger.
Background mortality (p_b)	Higher levels of reproductive readiness when p_b is high.
Seasonal environments	
Amplitude of environmental fluctuations (δ)	Gonads are activated for a longer period when δ is high.
Background mortality (p_b)	Length of breeding season increases with p_b .

In conclusion, the optimal pattern of breeding and gonad state in unpredictable environments appears to depend on several aspects of the environment, such as the amplitude of environmental fluctuations, the consistency of environmental conditions and whether there are any differences in food availability at different times of the year. Moreover, there are considerable differences in the reproductive behavior of long-lived and short-lived birds, which is reflected in the patterns of gonad regulation and reproductive readiness. Taking these factors into account may be necessary to obtain a fuller understanding of the breeding behavior of birds living in variable environments. Lastly, although our model was developed with birds in mind, where gonad regulation is a prolonged process, the effect of various environmental factors proved to be important even when maximum gonad size was lower and consequently the time required for preparation was shorter. Thus, our conclusions should apply to other organisms living in unpredictable environments if their reproduction requires physiological preparation, even if the transitions in reproductive condition occur more rapidly.

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Appendix 3.A Fluctuations in food availability

To implement changes in food conditions, we introduce the state variable f (food level), which characterizes the expected amount of food available to the animal, $g(f, t)$. The levels are ordered, and we assume that there are n_B levels with low food availability ($1 \leq f \leq n_B$) and n_G levels with high food availability ($n_B < f \leq n_B + n_G$). The transition between these levels occurs probabilistically; food level changes from week to week with probability $p_{change}(f, t)$ or remains the same ($f_{t+1} = f_t$) with probability $1 - p_{change}(f, t)$. If it changes, then

$$f_{t+1} = \begin{cases} f_t + 1, & \text{if } f_t < n_B + n_G \\ 1, & \text{if } f_t = n_B + n_G. \end{cases} \quad (3.A.1)$$

That is, food level increases from $f = 1$ until reaching the highest level with bad food conditions (n_B), then jumps to the first level with good food conditions ($n_B + 1$), increases until reaching the highest food level ($n_B + n_G$) and falls back to 1.

Highly consistent periods were obtained by setting the number of food levels

(n_B or n_G) to 11. The transition probability, $p_{change}(f, t)$, was set to 1 when $f \neq n_B$ and $f \neq n_B + n_G$ and to 0.1 otherwise. For environments with low consistency, the number of food levels (n_B or n_G) is 1 and $p_{change}(f, t) = 0.05$. Note that with this formulation $D_B = n_B$ and $D_G = n_G$.

Appendix 3.B Dynamic programming equations

Let $V_n(e, a, o, f, t)$ denote the reproductive value of an individual in state $\{e, a, o, f\}$ at the beginning of week t , n years before the target year. Then we define $V_n^e(e, a, o, f, t, action1, action2)$ in terms of reproductive value at time $t + 1$ as

$$V_n^e(e, a, o, f, t, action1, action2) = (1 - p_e)V_n(e, a_{action1}, o_{action2}, f, t + 1) + p_e V_n(e', a_{action1}, o_{action2}, f, t + 1) \quad (3.B.1)$$

Here *action1* refers to reproductive action (*subsist*, *start*, *care*), *action2* refers to the modulation of reproductive organs (*increase*, *maintain*, *decrease*), e is defined by Eq. 3.2, $a_{action1}$ is defined as

$$a_{action1} = \begin{cases} 0, & \text{if } action1 \text{ is } subsist \\ 1, & \text{if } action1 \text{ is } start \\ a + 1, & \text{if } action1 \text{ is } care. \end{cases} \quad (3.B.2)$$

Desertion occurs when the bird has a brood and *action1* is *subsist*. and $o_{action2}$ is determined as

$$o_{action2} = \begin{cases} o + 1, & \text{if } action2 \text{ is } increase \text{ and } o < o_{max} \\ o - 1, & \text{if } action2 \text{ is } decrease \text{ and } o > 0 \\ o, & \text{otherwise.} \end{cases} \quad (3.B.3)$$

An animal performing *action1* and *action2* receives a payoff $H_{action1, action2}$, defined as:

$$H_{action1,action2} = (1 - M(u) - S(u))V_n^e(e, a, o, f, t, action1, action2), \quad (3.B.4)$$

where u satisfies the balance equation (eq. 3.4) for an animal being in state $\{e, a, o, f, t\}$ and performing $action1$ and $action2$. $M(u)$ and $S(u)$ are determined by eq. 3.6 and eq. 3.7, respectively.

The bird simultaneously chooses a reproductive action and modulates the size of its gonads. The available behavioral options depend on the state of the animal, as follows:

if $a = 0$ and $o = 0$,	$\{subsist, increase\}, \{subsist, maintain\}$;
if $a = 0$ and $o < o_{max}$,	$\{subsist, increase\}, \{subsist, decrease\},$ $\{subsist, maintain\}$;
if $a = 0$ and $o = o_{max}$,	$\{subsist, decrease\}, \{subsist, maintain\},$ $\{start, decrease\}, \{start, maintain\}$;
if $0 < a < a_{max}$ and $o = 0$,	$\{subsist, increase\}, \{subsist, maintain\},$ $\{care, increase\}, \{care, maintain\}$;
if $0 < a < a_{max}$ and $o < o_{max}$,	$\{subsist, increase\}, \{subsist, decrease\},$ $\{subsist, maintain\}, \{care, increase\},$ $\{care, decrease\}, \{care, maintain\}$;
if $0 < a < a_{max}$ and $o = o_{max}$,	$\{subsist, decrease\}, \{subsist, maintain\},$ $\{care, decrease\}, \{care, maintain\}$;
if $a = a_{max}$ and $o = 0$,	$\{subsist, increase\}, \{subsist, maintain\}$;
if $a = a_{max}$ and $o < o_{max}$,	$\{subsist, increase\}, \{subsist, decrease\},$ $\{subsist, maintain\}$;
if $a = a_{max}$ and $o = o_{max}$,	$\{subsist, decrease\}, \{subsist, maintain\}$.

The payoffs for these actions is calculated using Eq. 3.B.4. When the brood is abandoned, the parent receives a reward equal to the reproductive value of the young, i.e. $V_n(0, 0, 0, f, t)$. We set brood size at fledging to one and assume that the young have the food level of their parents f .

To calculate the optimal strategy and the reproductive value at time t , we use the 'errors-in-decision-making' approach (McNamara et. al 1997), that is, we first compute the reproductive payoff for all combinations of behavioral actions

for a given bird in a given state, then calculate the weighted mean of these payoffs. To illustrate this procedure, consider the case when the bird has no brood and its gonads are at the minimum size ($a = 0$ and $o = 0$), then it cannot start a brood and the only available options are to increase or maintain the size of its gonads. Let

$$H_{a=0, o=0}^{max} = \max(H_{subsis\text{t}, increase}, H_{subsis\text{t}, maintain}). \quad (3.B.5)$$

Then for each combination of behavioral decisions (i.e *subsis\text{t}*, *increase* and *subsis\text{t}*, *maintain*) we calculate

$$\rho_{a=0, o=0}^{subsis\text{t}, action2} = Er\left(\frac{H_{a=0, o=0}^{max} - H_{subsis\text{t}, action2}}{H_{a=0, o=0}^{max}}\right), \quad (3.B.6)$$

using the error function, $Er(x)$, with K as a measure of the extent of error:

$$Er(x) = \frac{1}{1 + Kx}. \quad (3.B.7)$$

The optimal policy is given by

$$\pi_{a=0, o=0}^{subsis\text{t}, action2} = \frac{\rho_{a=0, o=0}^{subsis\text{t}, action2}}{\sum_{action2} \rho_{a=0, o=0}^{action2}}. \quad (3.B.8)$$

The weighted mean payoff is then calculated as

$$V_n(e, a, o, f, t) = \pi_{a=0, o=0}^{subsis\text{t}, increase} H_{subsis\text{t}, increase} + \pi_{a=0, o=0}^{subsis\text{t}, maintain} H_{subsis\text{t}, maintain}. \quad (3.B.9)$$

For other combination of states ($1 \leq a \leq a_{max}$ and/or $o = o_{max}$), the optimal policy and reproductive value are determined similarly, with the appropriate behavioral options (see table above). To calculate the reproductive value and optimal policy for all states and for all t , we need the terminal reward

$$V_0(e, a, o, f, 52) = 1, \quad (3.B.10)$$

and the wrap-around condition (cf. Houston and McNamara 1999)

$$V_n(e, a, o, f, 52) = \hat{V}_{n-1}(e, a, o, f, 0), \quad (3.B.11)$$

where $\hat{V}_{n-1}(e, a, o, f, 0)$ is a renormalisation of $V_{n-1}(e, a, o, f, 0)$ so that

$$\max[\hat{V}_{n-1}(e, a, o, f, 0)] = 1 \quad (3.B.12)$$

Computations are stopped when

$$\sum |\hat{V}_{n+1}(e, a, o, f, 0) - \hat{V}_n(e, a, o, f, 0)| < 10^{-6}. \quad (3.B.13)$$

Here, the summation runs over all possible combinations of state values.

References

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Appendix 3.C Additional results: survival and reproduction

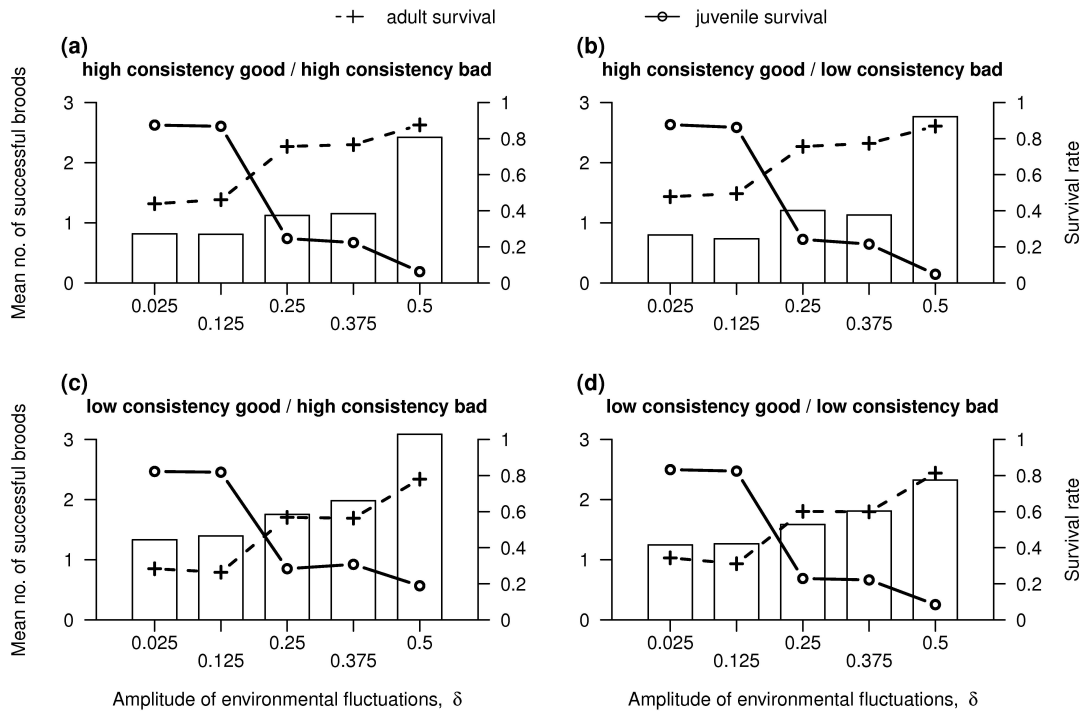


Fig. 3.C.1: Adult and juvenile survival rate (the probability that a young bird survives one year after fledging) and mean number of successful broods per year per individual in aseasonal environments differing in the consistency of the good and bad periods and the amplitude of environmental fluctuations. The number of broods fledged per year increases with fluctuation level in all environments, but the increase seems to accelerate under high consistency good periods and it is more even under low consistency good periods. Adult survival increases, while juvenile survival decreases with the degree of environmental fluctuations. These patterns arise as a consequence of the degree of difference between the high and low food availability and density dependence. If this difference (2δ) is small then the bad period is benign so juvenile survival is high. Consequently, many individuals survive until the good periods which results in intense competition for food during breeding. This, in turn, leads to high adult mortality. On the other hand, when the difference is large many individuals die during the bad periods leading to less severe competition during good periods and so higher adult survival.

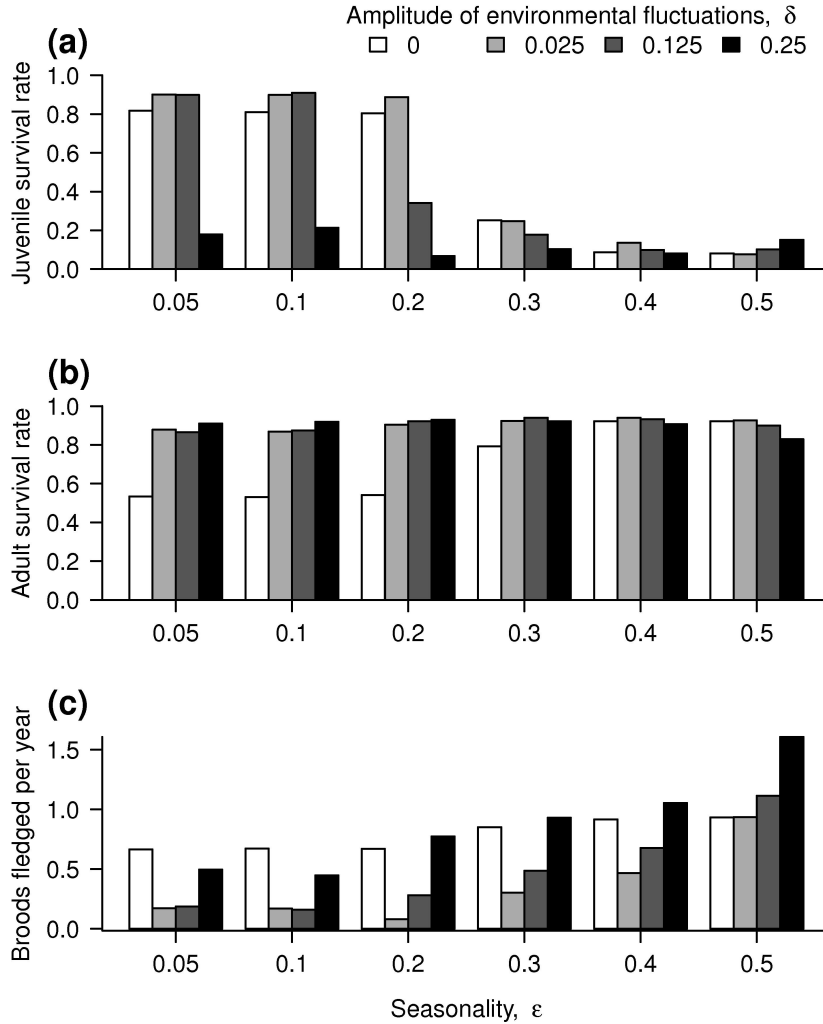


Fig. 3.C.2: Juvenile survival rate (a), adult survival rate (b) and mean number of successful broods per year per individual (c) in seasonal environments with fluctuating food availability differing in the degree of seasonality (ϵ) and the amplitude of environmental fluctuations (δ). Juvenile survival rate decreases with seasonality, whereas adult survival increases. Environmental fluctuations with a small amplitude in general lead to a decreased reproductive effort compared to environments with no fluctuations, because the birds will skip breeding in years when the environmental conditions are unfavorable. The number of broods fledged increases with the amplitude of environmental fluctuations with the largest effects observed at high seasonality. The figures show results from the high consistency bad / high consistency good environments; survival rate and annual fecundity are similar in the other three environments.

Appendix 3.D Additional results: sensitivity to the choice of critical parameters

To see how metabolic cost of the gonads affects behavior, we repeated the calculations for different values of c_o . A high cost of maintaining gonads leads to lower average gonad sizes (Fig. 3.D.1). This effect is larger in environments with low consistency, where maintaining large gonads is riskier because of the uncertainty in the success of the brood. However, the effect of environmental consistency in aseasonal environments and the importance of seasonality in seasonal environments is not affected qualitatively (results not shown). This is because food availability is density dependent, and increasing or decreasing the cost of large reproductive organs will result in changes in mortality, which affects food availability such that when mortality is high, food availability to the survivors increases, and vice versa.

To investigate how the time required to become fully prepared might affect optimal behavior, we made a series of calculations where maximum gonad size (o_{max}) was either increased or decreased. To separate the effect of preparation time from the metabolic cost of gonads, the parameter c_o was also changed, by setting its value to $c_o = 0.05/o_{max}$. As a result, the metabolic cost of having fully developed gonads was the same in all cases ($o_{max}c_o = 0.05$, the baseline value). We found that for larger parameter values ($o_{max} > 1$) the pattern of gonad regulation is only little affected by preparation time, but the lower o_{max} is, the less time it takes to reach full gonad size and the birds can keep their reproductive organs regressed for longer (Fig. 3.D.2). When maximum gonad size is 1, the birds can enter breeding condition within a week, and it is not necessary to stay prepared. Accordingly, gonads are generally regressed when $o_{max} = 1$.

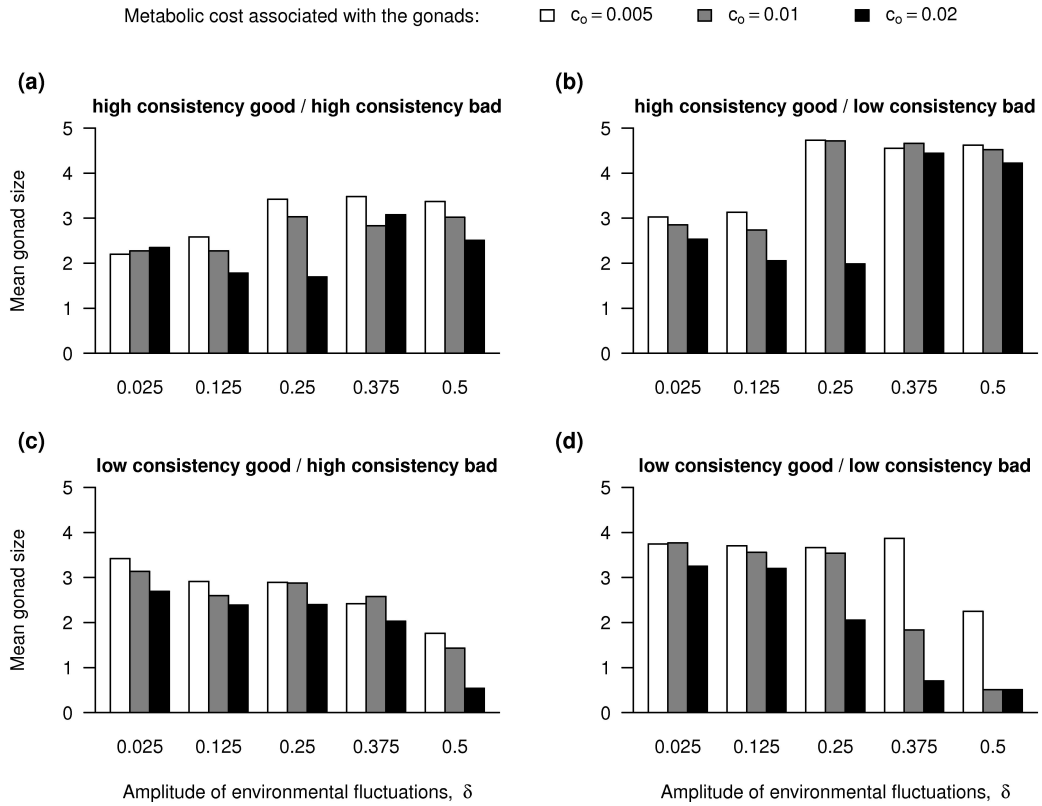


Fig. 3.D.1: *Reproductive readiness in aseasonal environments ($\epsilon = 0$), as reflected by the mean gonad size of birds experiencing bad conditions. The amplitude of environmental fluctuations was increased from $\delta = 0.025$ to $\delta = 0.5$ in the four environments differing in the consistency of the bad and good periods, at three different parameter values of c_o , the metabolic cost associated with the gonads. Mean gonad size was calculated for all adult birds, irrespective of the time elapsed since the end of the last good period, thus the presented values reflect the average level of preparedness of the population during bad periods.*

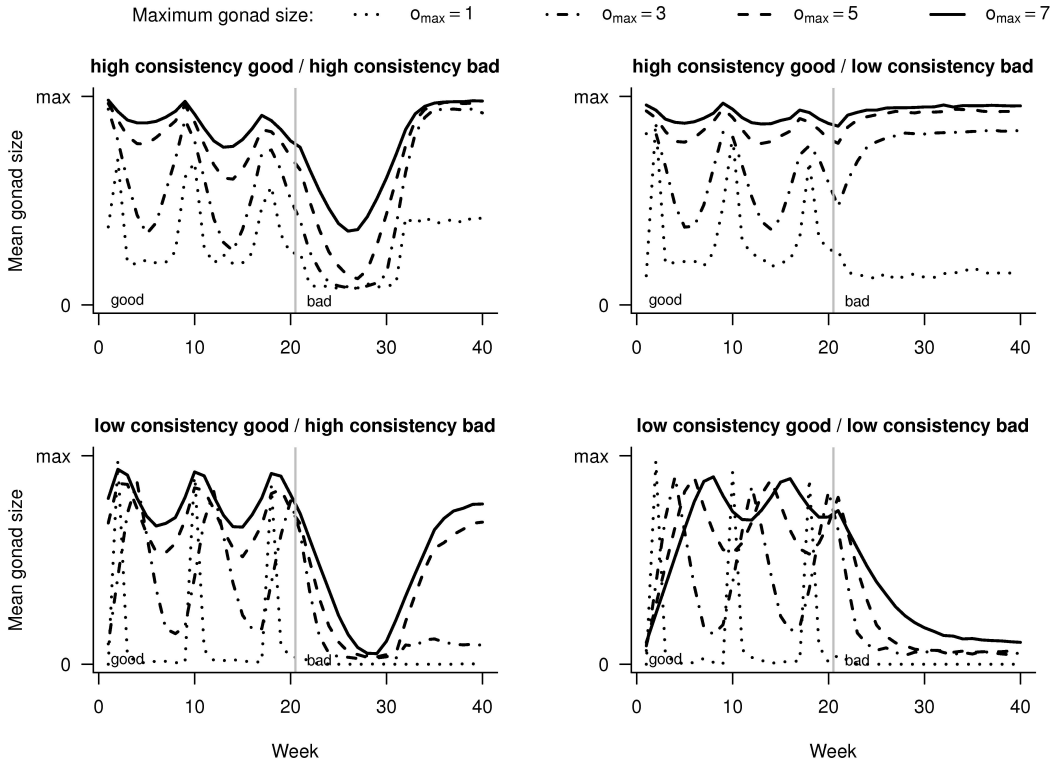


Fig. 3.D.2: Changes in mean gonad size in aseasonal environments ($\epsilon = 0$) during a simulated period consisting of a 20-week good period followed by a 20-week bad period in the four environments differing in the consistency of the bad and good periods, for different values of maximum gonad size (o_{\max}). The vertical grey line demarcates the transition from high to low food availability. Results are shown for $\delta = 0.5$ (large fluctuations in food availability); all other parameters are set to their baseline values (see Table 3.1).

4.

Study II: Reproductive plasticity and response of birds to environmental change

Abstract

Behavioral flexibility enables animals to adjust their life history decisions to unpredictable events thereby increasing reproductive success and population persistence in variable environments. However, to attain flexibility, the animals have to stay prepared, which can be costly. This costliness of plasticity can ultimately constrain the animals' ability to respond to environmental changes, such as the advancement of spring due to recent changes in global climate. Here, we analyze a model of avian annual routines to find the optimal levels of reproductive readiness in seasonal environments. Our results indicate that flexibility is generally higher in environments with pronounced year-to-year variability in the onset of spring if food availability during summer is uniform. When there is a peak in food availability during mid-summer, reproduction becomes entrained to this peak and reproductive flexibility is low under most conditions. Thus, the response of birds to sudden changes in the environment is constrained in low-variability environments, but also in environments with high year-to-year variability in the onset of spring if the peak of food availability is stable. Birds that cannot respond to

the earlier onset of spring by advancing their breeding season suffer a decrease in reproductive success. The amount of this reproductive loss is most marked at high seasonality where the reproductive value of the offspring depends tightly on appropriate timing.

Keywords: breeding phenology; annual cycle; spring predictability; climate change

Introduction

Temporal variation in environmental conditions like temperature or rainfall results in periodic changes in the limiting resources for most animals. In long-lived organisms such periodic changes result in the segregation of life history events such that the costliest activities (generally reproduction) occur during the periods with high food availability, whereas the periods with less food are spent on maintenance activities, such as molting, migration to benign wintering sites or hibernation (e.g. Murton and Westwood 1978, Bronson 1989, McNamara and Houston 2008).

The segregation of breeding and non-breeding activities during the annual cycle implies that the animals' body must perform different functions at different times of the year (Wingfield 2008). To fulfill these functions at the appropriate time, body composition, physiological systems and the behavioral repertoire of the animals must change with the seasons. Some of the most spectacular of these changes include the development of the nuptial plumage in spring and a more cryptic plumage in autumn (Tökölyi et al. 2008), the recrudescence of gonads in spring and their collapse in autumn (Murton and Westwood 1978), the differential activation of various immune functions during summer and winter (Buehler et al. 2008, Martin et al. 2008, Pap et al. 2010) or the increase in hippocampus volume in food hoarding birds around the time of food storage (Smulders et al. 1995), not to mention the range of physiological changes that are associated with migration or hibernation (e.g. Gwinner 1990; Boyer and Barnes 1999; Piersma and Lindström 1997).

Most of these seasonal changes involve significant alterations in physiology and therefore cannot be performed instantaneously (e.g. several weeks may be required to complete molt or gonad recrudescence). As a consequence, the organism has only limited opportunities for instantaneous responses to sudden, unpredictable changes in environmental conditions (because it may be unprepared or engaged in a different action). The recent increase in temperatures due to climate change provides one example of such a relatively quick change in the environment; the increasing temperatures lead to the advancement of plant phenology and the peak in insect abundance, resulting in a mismatch between the birds' in-

ternal timing and the optimal breeding dates (e.g. Walther et al. 2002). Although the birds respond to these changing conditions by starting reproduction earlier, the degree of compensation is highly variable between populations and species (e.g. Both et al. 2006, Végvári et al. 2010) and the lack of a quick response in some populations can lead to a decrease in reproductive success and consequently to population decline (Both et al. 2006, Møller et al. 2008).

A flexible reproductive schedule would increase reproductive success and improve population level responses to changes in the environmental conditions such as the advancement of spring (Charmantier et al. 2008, Husby et al. 2010). Flexibility implies quick physiological and behavioral responses to unpredictable changes in environmental conditions. For example, migratory birds could stay closer to the breeding grounds during winter, thereby minimizing the time required to reach the breeding site once conditions become favorable there in spring (Alerstam and Högstedt 1980, Tökölyi and Barta 2010). Similarly, birds may enter reproductive condition earlier and maintain larger gonads during winter and early spring so that they can start breeding more quickly if conditions improve (Murton and Westwood 1978). However, maintaining high reproductive readiness may entail serious fitness costs, resulting e.g. from the elevated metabolic expenditure and the increased predation hazard of birds in reproductive condition (such as high conspicuousness, higher body mass due to large gonads, and an increase in mate-searching activity and aggressive interactions). As a consequence, high levels of reproductive readiness should be observed only in environments where these costs are outweighed by the fitness benefits of a flexible reproductive system.

The outcome of this trade-off (i.e. the optimal level of reproductive plasticity) may strongly depend on the characteristics of the environment. Most importantly, animals that evolved in highly variable environments are more likely to benefit from having a flexible reproductive system, because they are more likely to gain from this flexibility, whereas in a predictable environment high levels of preparedness have no additional benefits. However, the optimal level of plasticity may be affected by several other factors as well. For example, if food availability is density-dependent, the enhanced reproductive success resulting from a flexible breeding schedule may not outweigh the costs associated with maintaining this

system in species with high adult survival rate, because these animals are selected for low levels of reproductive investment (e.g. McNamara et al. 2004, McNamara et al. 2008). A further consequence of the density-dependence of food is that if annual survival is high and competition for food is strong, breeding may become entrained to the period of the year with the highest food availability (resulting in a lack of reproduction outside this period despite the relatively high food availability; McNamara et al. 2004, 2008). Thus, if there is a distinct peak in food availability during summer and reproduction becomes entrained to this peak then reproductive flexibility is expected to be low.

Despite the importance of behavioral flexibility in predicting population responses to changes in the environmental conditions (Charmantier et al. 2008, Husby et al. 2010), little is known about the factors that determine the optimal levels of reproductive plasticity. Here, we use an annual routine model of gonad regulation of birds to describe the optimal levels of reproductive plasticity in seasonal environments differing in seasonality, peakedness and year-to-year variability in the onset of spring. In addition, we use this model to predict the response of birds following the optimal strategy to a simulated early onset of spring.

The model

Our annual routine model is based on the approach introduced by Houston and McNamara (1999). Briefly, we model the optimal behavior over an annual cycle. Each year consists of 52 decision epochs (weeks, t). Each week, the bird decides whether to increase, decrease or maintain its reproductive organs and whether to start a brood, care for the young or abandon them. These decisions are based on the time of year (t), the food available during that week as well as the state of the animal, which is represented by the state variables gonad size (o), brood age (a) and experience (e).

Food availability Food availability is low during winter and high during summer (Fig. 4.1a). Transitions from winter to summer occur probabilistically during spring (i.e for $t < 25$), and the reverse transition happens in autumn (Appendix

4.A). The favorable period (summer) has an average length of ~22 weeks (with a minimum of 20 weeks), but its starting date is variable (i.e. it may differ from year to year). By using different sets of transition parameters the degree of year-to-year variability in the onset of spring can be altered: if the probability of transition to summer is low for an extended period then year-to-year variation in the onset of spring is high. In contrast, if the probability of transition is high during a short period, the same phenology can be expected in most years (Fig. 4.1 b,c; Appendix 4.A).

We assume (for the baseline case) that food availability during winter, $g_W(t)$, is uniform and equals A , which is the minimum food available during the year. This value is set by finding computationally the value for which the population growth rate equals 1 (i.e. food availability is density-dependent; see McNamara et al. 2008 for a theoretical justification of this procedure).

Food availability during summer, $g_S(t)$, is determined by the following equation:

$$g_S(t) = A + \delta + \omega_S \left[1 + \sin \left(\pi \frac{t - 13}{26} \right) \right]. \quad (4.1)$$

Here, the parameter δ determines the minimum difference between the periods with low and high food availability whereas the parameter ω_S determines whether food availability during summer is uniform ($\omega_S = 0$) or changes with time ($\omega_S > 0$). In the latter case, the peak of food availability is during the middle of the year (i.e. at $t = 26$).

The overall seasonality in food availability (ϵ ; the difference between winter minimum and summer maximum) is $\delta + 2\omega_S$; the peakedness of the food distribution is determined by the relative magnitude of ω_S compared to the overall seasonality (i.e. by the fraction ω_S/ϵ ; Fig. 4.1a).

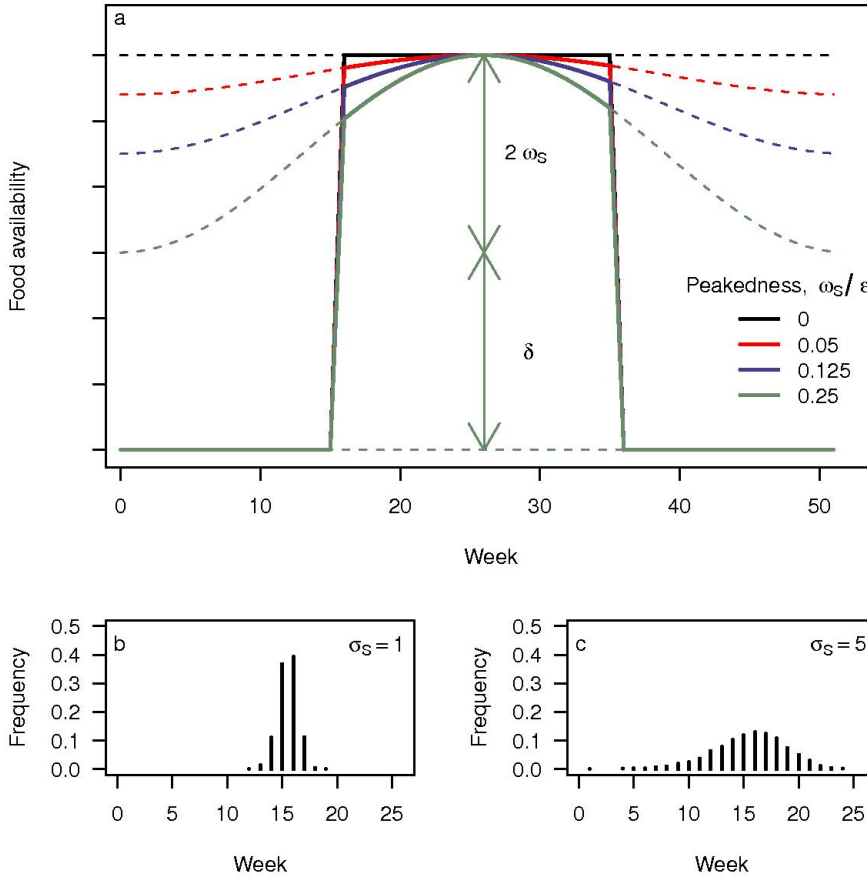


Fig. 4.1: Food availability during the annual cycle in environments with different peakedness (a); the solid lines show the actual change in food during the annual cycle in sample years when the onset of spring occurs on $t = 16$. Dashed lines indicate the expected distribution of food during periods with low and high food availability. The seasonality of these environments (ϵ) is determined by the two parameters δ and ω_S , whereas peakedness depends on their relative magnitude. The arrows are shown for the case when peakedness is large ($\omega_S/\epsilon = 0.25$). The lower panels show the frequency distribution of the onset of spring in environments with low and high year-to-year variability in the onset of spring (b and c, respectively).

Gonad size, o . The size of reproductive organs can take values between 0 and o_{max} . Each week, the bird decides to either maintain, increase or decrease the size of its gonads by one unit. Larger gonads are assumed to increase metabolic

expenditure both directly (through the energy required to maintain the increased tissue mass) and indirectly (due to the elevated flight costs of the larger body mass); therefore, we assume that having gonads of size o has a metabolic cost of $c_o o$, where c_o determines the magnitude of metabolic costs associated with large gonads.

Brood age, a . Birds without a brood ($a = 0$) can start one if they have fully developed gonads ($o = o_{max}$); starting a brood requires an amount of energy c_{start} . If the bird has a brood ($a > 0$ but $a < a_{max}$) it can either care for the brood or desert it. In the first case, the parent bird has to invest an amount of energy γ_b , in which case the brood will survive until the next week ($a_{t+1} = a_t + 1$). If the bird decides not to care for the young then the young will die ($a_{t+1} = 0$). Finally, if the brood survives until it is fully developed ($a_t = a_{max}$), then the offspring are assumed to become independent from their parents ($a_{t+1} = 0$). For simplicity, we assume that brood size is fixed at $n_{brood} = 2$ (for an investigation on optimal brood size in seasonal environments, see McNamara et al. 2008).

Experience, e . Newly born individuals are inexperienced ($e = 0$). The experience class of a bird that is not fully experienced increases from time t to time $t + 1$ ($e_{t+1} = e_t + 1$) with probability p_e , and remains the same ($e_{t+1} = e_t$) with probability $1 - p_e$. The experience class of a fully experienced bird ($e = e_{max}$), on the other hand, does not change. Experience determines the foraging efficiency of the bird, so that the energy intake rate, $\gamma(e, t, F)$, of a more experienced bird is higher:

$$\gamma(e, t, F) = g(t, F)\theta^{e_{max}-e}, \quad (4.2)$$

where θ is the parameter determining the effect of experience on the intake rate of the bird and F denotes food conditions (i.e. high or low food; Chapter 2).

Energy balance We assume that there is a basal metabolic expenditure (c_b) which is independent of the animal's state or behavior. In addition, maintaining the gonads and reproduction has additional metabolic costs (C). For a bird without a brood this is just the metabolic cost associated with the gonads ($C = c_o o$);

for a bird starting a brood or caring for the young this value is incremented by the cost of these activities, c_{start} and γ_b , respectively. In order to avoid starvation the bird has to balance these metabolic requirements by spending a certain proportion of its time foraging (foraging intensity, u). That is, u must satisfy the balance equation

$$\gamma(e, t, F)u = c_b + c_f u + C. \quad (4.3)$$

where the parameter c_f determines how energy expenditure of foraging scales with foraging intensity (i.e. we assume that foraging with high intensity requires more energy because of the sustained activity of the bird).

Sources of mortality If the weekly energy requirement cannot be balanced by the energy intake (even if foraging at maximum intensity), the bird will face an increased risk of death because of starvation. The probability of starvation, $S(u)$, is determined as

$$S(u) = 1 - 1/(1 + u^{200}). \quad (4.4)$$

That is, starvation risk increases sharply (but not deterministically) from 0 to 1 around $u = 1$ (for details see McNamara et al. 2008).

Mortality may be caused by predation as well; we assume that there is a background mortality that is independent of the behavior of the bird. In addition, predation hazard increases with foraging intensity (due to e.g. the increased activity and the resulting higher exposure times of the foraging birds). We assume that the probability of mortality per week that is unrelated to starvation is given by

$$M(u) = p_b + p_m u^2, \quad (4.5)$$

where p_b is the background mortality and p_m is the mortality parameter associated with the time spent foraging (cf. Houston et al. 1993; McNamara et al. 2008).

Determination of the optimal strategy

A strategy specifies the dependence of behavior on state and time of year. The optimal strategy maximises the asymptotic growth rate of the number of descendants. We find this strategy using an iteration based on dynamic programming (cf. Houston and McNamara 1999). Details of this procedure and the dynamic programming equations are described in Appendix 3.B. We use Monte Carlo simulations to study the realized behavior of the modelled birds that follow the optimal strategy. The model's parameters and their baseline values are listed in Appendix 4.B.

Results

To systematically explore the effect of seasonality, peakedness and year-to-year variability, we first increased seasonality from low ($\epsilon = 0.05$) to high ($\epsilon = 1.2$), and for each value of ϵ we increased the peakedness of the environment from $\omega_S/\epsilon = 0$ (i.e. food availability uniform during the summer) to $\omega_S/\epsilon = 0.25$, in which case food availability around the onset of spring is on average ~20% lower than during the height of the summer (Fig. 4.1a). To evaluate the effect of year-to-year variability in the onset of spring, we consider two cases: in the first case, year-to-year variability is low ($\sigma_S = 1$) and spring starts on the same week almost every year (Fig. 4.1 b). In the second case, year-to-year variation in the onset of spring is high ($\sigma_S = 5$), and spring may start within a period of ~20 weeks (Fig. 4.1 c). The mean starting date of spring is 15.5 in both cases. Further, we explore the effects of background mortality on the optimal levels of reproductive plasticity. Lastly, an alternative scenario in which food availability during winter is not uniform is described in Appendix 4.C.

The timing of breeding in different environments

The mean laying date of the first broods depends on seasonality, the peakedness of the environment and the interaction of these. When food availability is uniform during summer ($\omega_S/\epsilon = 0$) the breeding season starts shortly after the onset of spring (Fig. 4.2a). The mortality of the parents caused by reproduction and

parental activities in this case does not depend on the time when the brood is initiated (because food availability does not change during the summer), but the reproductive value of the young decreases with time (because young fledged late have less time to gain experience before the winter). As a consequence, the optimal time to breed is early in the season. By contrast, if there is a peak in food availability then it is better for the parent to start a brood later, when food availability is higher. This will result in the entrainment of reproduction to the peak at low seasonality where adult survival is high and competition for food during the breeding season is very strong, but not at high seasonality (Fig. 4.2a).

The average length of the breeding season is largest when $\omega_S/\epsilon = 0$ (Fig. 4.2b). Moreover, when food availability during summer is uniform, the breeding season is longer at low than at high seasonality: broods are initiated over an interval of ~ 17 weeks at low seasonality ($\epsilon = 0.05$), compared to a period of ~ 10 weeks at high seasonality ($\epsilon = 1.2$; Fig. 4.2b). The reason for this is that the reproductive value of the young declines more sharply with time at high seasonality (young fledged late in the season have much lower chances to survive the winter at high seasonality, where food availability during winter is lower). Therefore birds at high seasonality start reproduction early in the season whereas breeding is more asynchronous at low seasonality. However, as entrainment occurs at low seasonality when $\omega_S > 0$, the breeding season becomes shortened in these cases (Fig. 4.2b).

The mean laying date and the average length of the breeding season is very similar in environments with low and high year-to-year variability in the onset of spring.

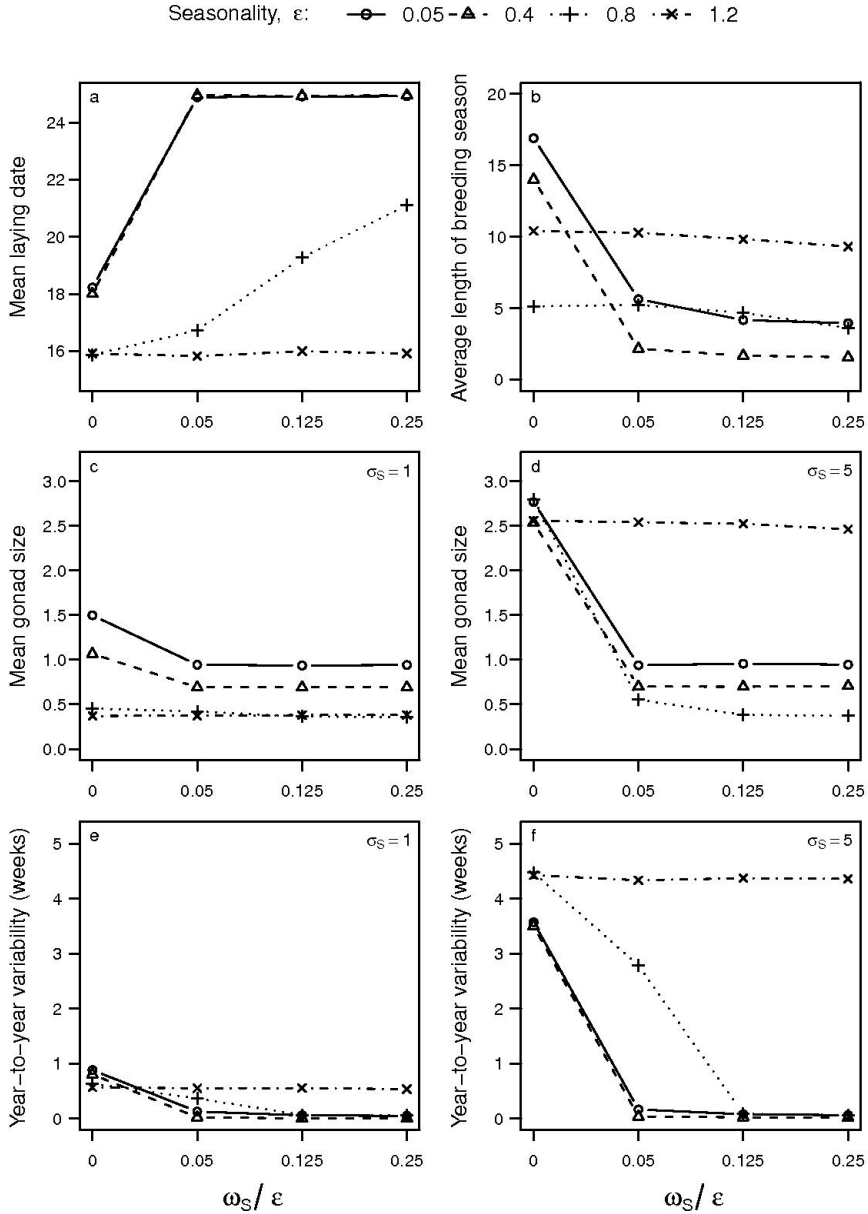


Fig. 4.2: Mean laying date (a) and the average length of the breeding season (b) in environments differing in seasonality and peakedness. The length of the breeding season is defined as the interval between the earliest and latest week in a given year in which at least 0.1 percent of the population initiates a brood. Variability in the onset of spring was set to $\sigma_S = 5$ (i.e. high variability). The middle and bottom panels show reproductive plasticity, as reflected by mean gonad size at $t = 10$ (c,d) and year-to-year variability in mean laying dates (SD of yearly means; e,f) in environments differing in seasonality, peakedness and year-to-year variability in the onset of spring.

Reproductive plasticity

To measure the plasticity of breeding schedules, we recorded year-to-year variability in the mean laying date of first broods; that is, we measured the mean laying date of first broods every year during a period of a 100 years and use the standard deviation of this dataset as an approximation of year-to-year variability in breeding. We also measured reproductive readiness before the start of the breeding season as mean gonad size at $t = 10$. In environments with low year-to-year variability ($\sigma_S = 1$), reproductive organs are kept regressed before the start of the breeding season (Fig. 4.2c); gonads are more regressed at high seasonality because food availability during winter is lower. The mean laying date of the first broods is similar in most environments, and there is virtually no year-to-year variability in reproductive behavior (Fig. 4.2e). By contrast, reproductive readiness is more pronounced and year-to-year variability in laying is higher when the environment is more variable (Fig. 4.2d, f). However, this applies only to environments where food availability during summer does not depend on the time of year ($\omega_s = 0$) or seasonality is high ($\epsilon = 1.2$). In all other cases (i.e. when breeding is entrained), reproductive plasticity is low (Fig. 4.2d, f), despite the high variability in the onset of spring.

Response to environmental change

To evaluate the response of birds with different reproductive plasticity to changes in the environment, we set the spring to start 3 weeks earlier than the average in Monte Carlo simulations of populations following the optimal strategy. We measured reproductive advancement by calculating the difference between the mean laying date when spring starts at $t = 13$ (early spring) and at $t = 16$ (average spring). We also estimated the reproductive success of these birds by calculating number of offspring (per adult) that survives until the end of the year.

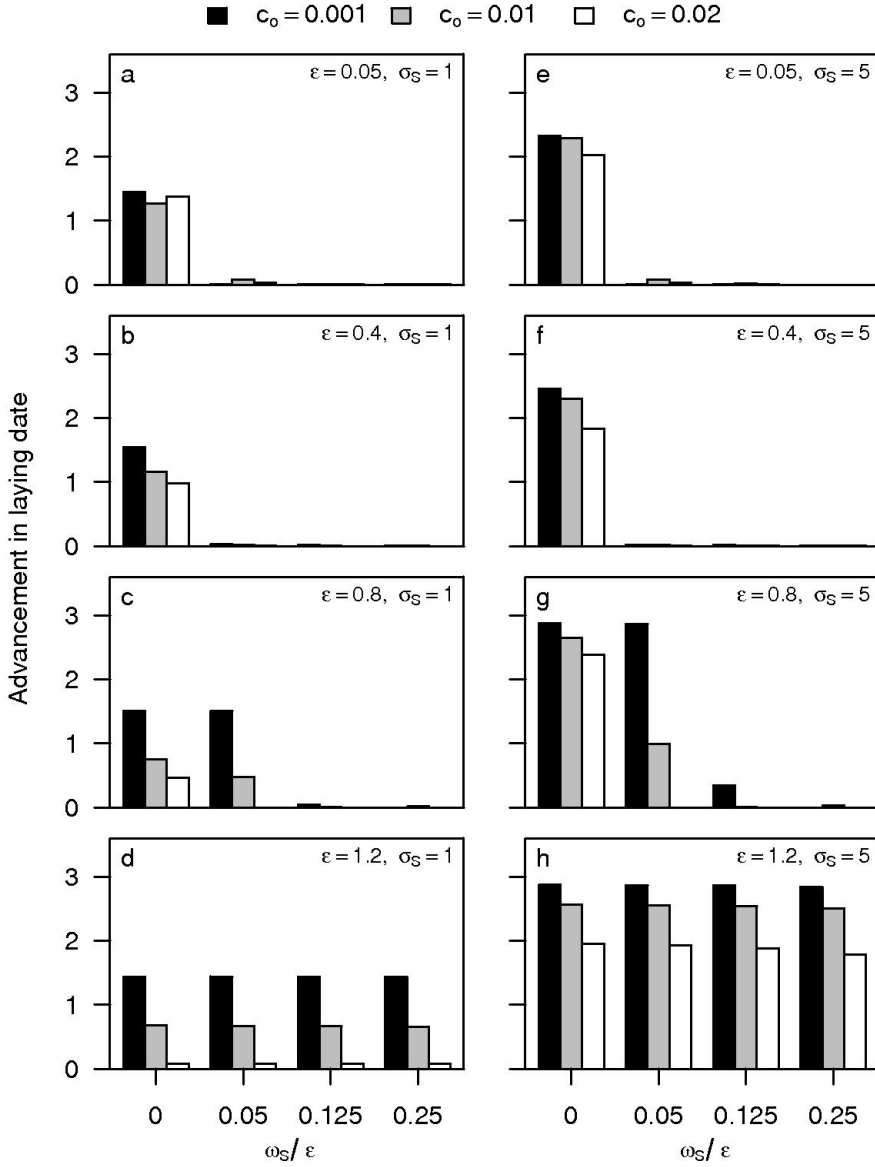


Fig. 4.3: Advancement in mean laying dates when the spring starts 3 weeks earlier than on average. An advancement in laying of three weeks shows complete compensation, whereas values close to 0 imply no advancement.

In general, strategies optimal in low variability environments show very weak responses to the simulated early spring. An advancement of ~ 1.5 week is ob-

served at high seasonality when the cost of maintaining the gonads is low ($c_o = 0.001$); at lower seasonality, an advancement of 1-1.5 weeks is only observed when food availability during the summer is not peaked (i.e. reproduction is not entrained; Fig. 4.3). The response of birds following policies from environments with high year-to-year variability in the onset of spring is more pronounced. In environments where food availability is uniform during the summer, reproductive advancement is very strong (almost 3 weeks), although it decreases for larger values of c_o , because staying prepared is more costly in this case. Birds do not breed earlier when food availability is peaked and seasonality is relatively low, but at large seasonality reproduction starts earlier both in the environments with uniform and a peaked summer food availability.

Breeding is much more likely to match the environmental conditions when the spring starts late (results not shown), because the birds are generally fully prepared by the average starting date of the spring and start to breed immediately after the onset of spring. The only exceptions to this are the environments where breeding is confined to the middle of the year (i.e. at $\epsilon \leq 0.4$ and $\omega_S > 0$); in these cases breeding starts at the same time irrespective of the onset of spring.

The effects of background mortality

To see the effect of background mortality on the optimal levels of reproductive plasticity, we manipulated the background mortality rate (p_b) by increasing its value from $p_b = 0.0001$ to $p_b = 0.001$. As shown in Fig. 4.4, the response of birds to environmental change is more pronounced when background mortality is high (i.e. in short-lived birds). When background mortality is low, the birds invest less into reproduction, hence reproductive readiness in early spring is lower, which explains the lower responsiveness of these birds. As a result, the fitness consequences of early onset of spring are somewhat higher in long-lived than in short-lived birds (Fig. 4.4).

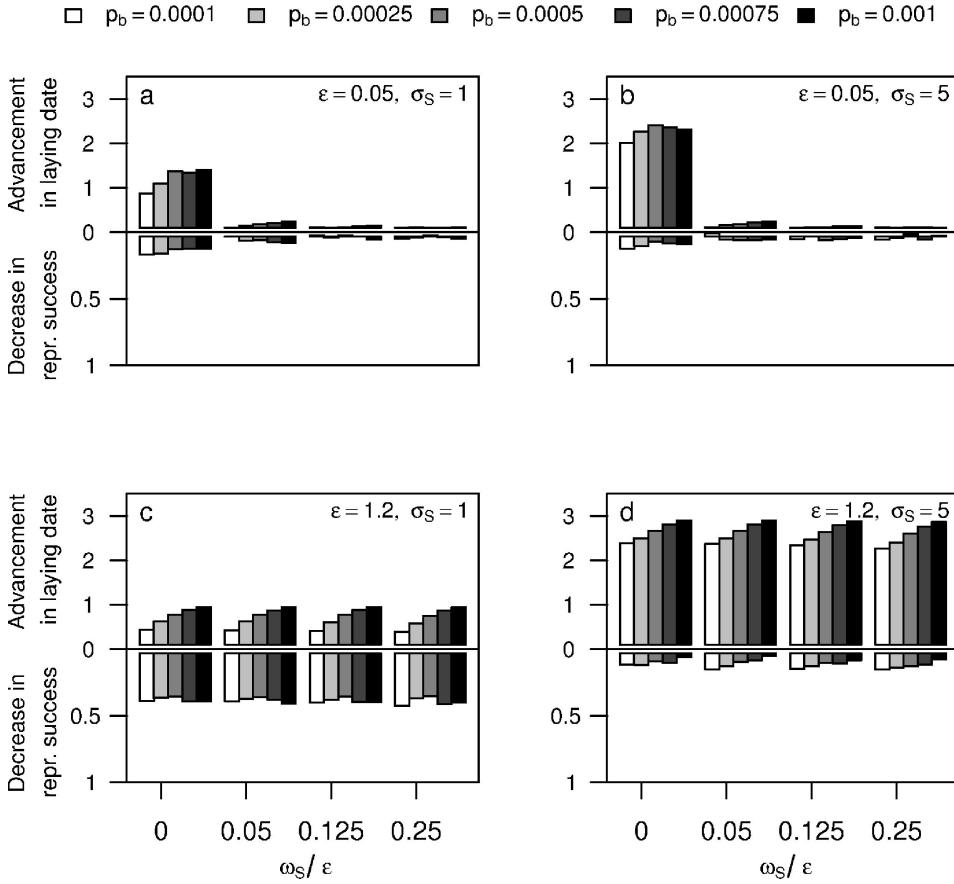


Fig. 4.4: The effect of background mortality (p_b) on the response of birds to environmental change and the fitness consequences of early onset of spring in environments differing in seasonality (ϵ) and variability in the onset of spring (σ_S). The advancement in laying is measured as the difference between the mean laying dates of a simulated early ($t = 13$) and average ($t = 16$) onset of spring. The fitness consequences of early onset of spring were calculated as the decrease in reproductive success in a simulated early spring scenario relative to an average onset of spring. Reproductive success was measured as the average number of young that survive until the end of the year (i.e. at $t = 52$) divided by the number of adults that were in the population at the start of the year (i.e. at $t = 1$).

The early onset of spring has a relatively small effect on reproductive success at low seasonality (Fig. 4.4 a,b). This can be explained by the fact that at low seasonality food availability during winter is relatively high. Juvenile survival is high and is only weakly affected by the fledging date; thus, even if the adults

cannot compensate for the early onset of spring, their reproductive success will not decrease substantially. This is not the case at high seasonality, where juvenile survival rate depends very strongly on fledging date: the earlier a bird becomes independent (relative to the start of the winter) the more time it has to gain experience while food availability is still high. Therefore, if the parents cannot compensate for the early onset of spring at high seasonality, their reproductive success will decrease (Fig. 4.4c).

Discussion

Analysis of the annual routine model presented here reveals that the optimal level of reproductive plasticity depends on multiple aspects of the environment in which the birds evolved, such as its variability, seasonality and peakedness, as well as on the longevity of the birds. Although this model cannot capture the full complexity of the annual cycle of birds (e.g. neither migration nor molt are included), the problem of gonad regulation is very general and is likely to apply to both migratory and resident species (Murton and Westwood 1978).

Birds inhabiting environments with high variability in the onset of spring are predicted to show high levels of reproductive flexibility, as manifested by the increased gonad size before the breeding season and high year-to-year variability in the timing of breeding. Although maintaining high levels of reproductive readiness is costly (especially early in the season; Jonzén et al. 2007), these costs can be outweighed by the higher reproductive success of individuals that start reproducing and fledge their young earlier (e.g. Visser and Verboven 1999). This is in general agreement with the observation of large differences in reproductive plasticity of birds under different ecological conditions (e.g. Wingfield et al. 1992, Schoech and Hahn 2008). For example, both observational (Murton and Westwood 1978) and experimental (Schoech and Hahn 2008) evidence indicates that birds breeding at high latitudes have less flexible breeding schedules and much weaker responses to unpredictable events than temperate birds. Based on our results, this difference is probably the consequence of the higher predictability of these arctic environments (cf. Alerstam and Högstedt 1980), which selects for a relatively rigid timing mechanism and low levels of reproductive readiness before

the onset of the breeding season. Furthermore, it is unlikely that such a pattern could be the result of differences in seasonality or the length of the summer between arctic and temperate environments, because we have found no decrease in flexibility at high seasonality. Thus, theoretically, arctic birds in general should show high levels of reproductive plasticity if the onset of spring were variable because the winter is harsh (i.e. food is very seasonal) and the reproductive value of broods fledged early is very high.

An important finding of this study is that high variability in the onset of spring in itself does not always lead to more flexible breeding schedules; if there is a peak in the food availability during the breeding season, the birds face conflicting selection pressures (Lack 1968, Perrins 1970, McNamara et al. 2004): their own survival is maximized if they breed during the peak of food availability but the reproductive value of their offspring is highest early in the season. The resolution of this trade-off is relatively simple if food availability during summer is uniform, because in this case adult survival does not depend on the timing of breeding, and the birds are selected to start as early as possible, resulting in a flexible timing of reproduction. On the other hand, if there is a large enough peak in food availability, reproduction becomes entrained to this peak (McNamara et al. 2008) and reproductive flexibility is low. It is important to emphasize that the food peak in our model is not affected by year-to-year variations: the highest amount of food during the annual cycle is available during the middle of the year, irrespective of when the spring started. This is a realistic scenario if food availability depends on temperature, which, in the temperate zone peaks at about the same time every year (during midsummer). The alternative scenario in which the peak varies from year to year resembles the case in our model where food availability during summer is uniform ($\omega_S = 0$), because in both of these cases the amount of food available depends only on the date of the onset of spring.

Flexibility of avian reproductive schedules has implications for understanding the response of animals to environmental change and vice versa (Coppack and Pulido 2004). Studies of phenological responses to recent changes in climate and the resulting advancement of the onset of spring may help us understand the factors that underlie the evolution of high (or low) reproductive flexibility. Although most of the large scale analyses involve arrival dates of migratory birds (and there

is evidence that timing of breeding is more flexible than timing of arrival to the breeding grounds; Both et al. 2005), they can be instructive in understanding the flexibility of annual routines under different conditions. Thus, an advancement in arrival date to the breeding grounds has been found (among others) to be more likely in species breeding early in spring (Tryjanowski et al. 2005), and those having shorter migration distances (e.g. Rubolini et al. 2007, Végvári et al. 2010, but see Jonzén et al. 2006). These differences are generally explained by the fact that migratory birds are unable to predict the advancement of spring on their breeding grounds from the distant wintering areas (e.g. Both et al. 2005); however, differences in reproductive flexibility may also play a role, because short-distance migrants are breeding earlier in the season than long-distance migrants (Tökölyi and Barta 2010) and environmental conditions are generally more variable early in spring than later. Thus, species breeding early in the season may face more pronounced year-to-year variability which could have resulted in the evolution of more flexible breeding schedules.

On the other hand, information on reproductive flexibility can be also used to understand the response of birds to the earlier onset of spring. Most importantly, our model predicts that (assuming that reproductive readiness is costly) a lack of response to the advancement of spring will be observed under a wide range of ecological conditions, even in non-migratory birds. Indeed, such a lack of response has been observed in a few cases in non-migratory populations (summarized in Coppack and Pulido 2004). Unfortunately, measuring or even approximately assessing reproductive flexibility in different populations is not an easy task; using information from food supplementation experiments (Schoech and Hahn 2008) or measuring year-to-year variability in laying dates from long-term breeding biology studies or nest card programs could provide useful information to predict phenological responses to the advancement of spring.

In addition to describing phenological responses, the modelling approach described here enables us to measure the fitness consequences of environmental change. This is especially important given that birds have been shown to suffer population decline as a consequence of spring advancement due to global changes in temperature (Both et al. 2006; Møller et al. 2008). However, little is known about the factors that might affect the degree of these population declines. An

ability to to compensate for the advancement of spring has been shown to mitigate the negative effects of environmental change (Møller et al. 2008), however, our model predicts that even with the same degree of compensation, the fitness consequences may be different depending on the seasonality of the environment. Thus, long lived birds living at high seasonality are most likely to experience negative effects of environmental change.

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Appendix 4.A The environment

The environment is modelled as an ordered set of food levels, f , included in the birds' state. Food availability on these levels can be either low or high. There is a single level with low food availability ($D_L = 1$), whereas the number of levels with high food availability (D_H) is 20. By specifying the transition probabilities among these levels, a seasonal environment can be created, with low winter and high summer food availability. Thus, the transition probability from low to high food availability $p_{change}(f, t)$ is determined in the first part of the year ($0 \leq t \leq 24$) by the cumulative distribution function of the normal distribution with a mean μ_S and a standard deviation σ_S ; these two parameters determine the mean and standard deviation of the expected onset of spring. For each environment differing in variability in the start of spring the parameter μ_S is chosen such that the mean transition date will be identical in these environments (average transition date 15.5). The probability of transition from bad to good food conditions at week 25, $p_{change}(1, 25)$, is set to 1 to ensure that spring will start every year, and $p_{change}(1, t) = 0$ for $t > 25$, thus transition from low to high food availability cannot occur for $t > 25$.

After reaching the first level with high food availability, f increases one level deterministically until reaching the highest level with high food availability (D_H); from this stage, food level falls back to $f = 1$ with probability $p_{change}(D_H, t) = 0.5$. Thus, the favorable period has a minimum length of 20 weeks, which may be longer by an average of two weeks; however, the length of the summer does not depend on the time when it started. This is important to distinguish the effect

of a variable timing of spring from the differences in the length of the season that may be associated with a variable onset of spring.

Appendix 4.B The model's parameters and their base-line values.

Parameter	Symbol	Value
Probability of changing experience class	p_e	0.025
Parameter determining the foraging efficiency of inexperienced birds	θ	0.7
Basal metabolic expenditure	c_b	0.15
Metabolic cost of foraging	c_f	0.3
The metabolic cost associated with the reproductive organs	c_o	0.01
The metabolic cost of starting a brood	c_{start}	0.8
Gross intake needed to provide nestling	γ_b	0.9
Background mortality	p_b	0.0005
Mortality parameter associated with time spent foraging	p_m	0.005
Maximum organ size	o_{max}	5
Maximum experience	e_{max}	2
Maximum brood age	a_{max}	7
Brood size	n_{brood}	2
Parameter determining the change in food availability with time during summer	ω_S	-
Minimum difference between winter and summer food availability	δ	-
Minimum food available during the year	A	-
Seasonality	ϵ	-

Appendix 4.C Alternative scenario - food availability during winter is not uniform

In the baseline case we assumed that food availability during winter does not change with time. In reality, this may not be true in all environments; food availability is likely to be lower during mid-winter than either in early autumn or late spring in many cases. This, in turn can potentially affect the optimal levels of plasticity because if food availability starts to increase before the onset of spring, the birds could start developing their gonads earlier. To test this idea, we created environments where food availability during winter varies in a sinusoidal pattern (similarly, and with the same amplitude as during summer; Fig. 4.C.1). Results from this analysis indicate that, as predicted, the increase in food during late winter leads to more developed gonads (i.e. higher levels of reproductive readiness) before the start of the breeding season for intermediate values of peakedness (Fig. 4.C.2 b), although the difference compared to the baseline case is not large. On the other hand, when peakedness is large, reproductive readiness is low; this is because overwinter survival in these environments is substantially higher than in the baseline case (because more food is available during winter than in the baseline case), resulting in more intense competition for food and ultimately lower levels of reproductive readiness. However, these differences do not have a strong effect on the year-to-year variability of reproduction, which shows the same patterns as in the baseline case (Fig. 4.C.2 c, d).

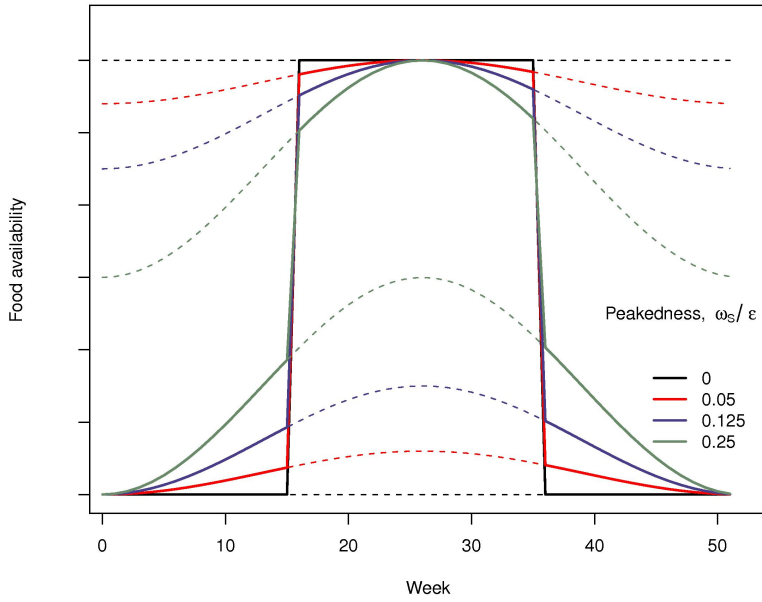


Fig. 4.C.1: *Food availability during the annual cycle in environments with different peakedness, in the case when food availability during winter is not uniform. The solid lines show the actual change in food during the annual cycle in sample years when the onset of spring occurs on $t = 16$. Dashed lines indicate the theoretical distribution of food during periods with low and high food availability.*

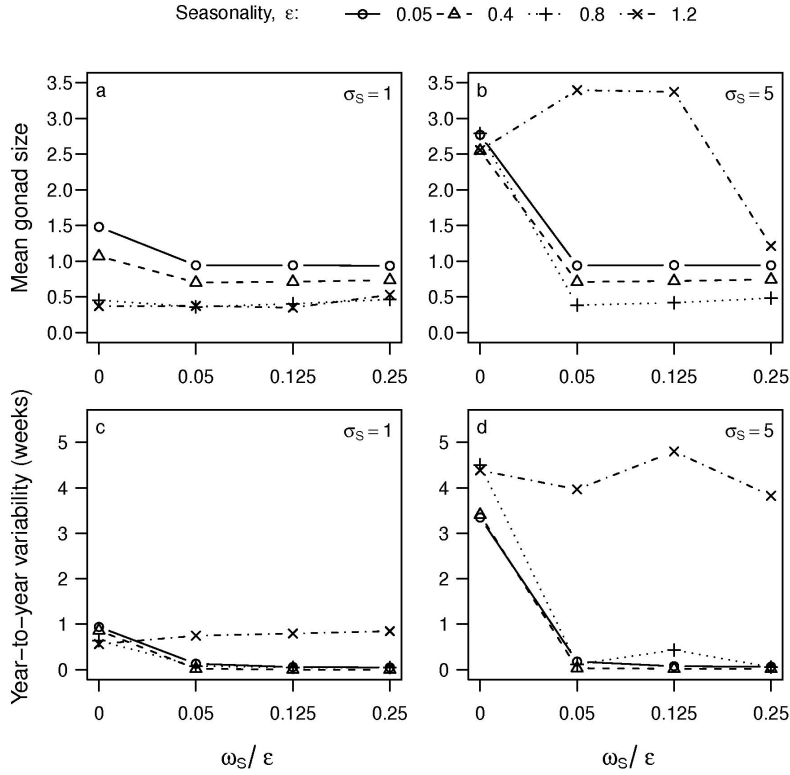


Fig. 4.C.2: *Reproductive plasticity, as reflected by mean gonad size on $t = 10$ (a, b) and year-to-year variability in mean laying dates (SD of yearly means; c, d) in environments differing in seasonality, peakedness and year-to-year variability in the onset of spring. Food availability during winter in these environments is not uniform (see Fig. 4.C.1).*

5.

Study III: Breeding phenology determines evolutionary transitions in migratory behavior in finches and allies

Abstract

The breeding season of long-distance migratory birds often starts later and is shorter than in resident or short-distance species breeding at the same latitude, but the reason for this is unclear. Here we investigate the association between migration distance and breeding phenology in a group of passerine birds, the finches and their allies, using phylogenetic comparative methods. We confirm that migration distance is related to aspects of the species' breeding phenology after controlling for the effect of potentially confounding variables. Directional phylogenetic analyses suggest that evolutionary transitions in migration distance are determined by the breeding phenology. A relatively long migration distance is more likely to evolve in birds with a late, short breeding season, whereas transitions to short distance migration are more likely to occur in lineages with an early, long breeding season. These results suggest that migration distance is constrained by breeding phenology and not vice versa. Thus, breeding phenology may be an important ultimate factor shaping the evolution of migratory strategies.

Keywords: bird migration, annual cycle, life history, time allocation, spring predictability.

Tökölyi, J., Barta, Z.: Breeding phenology determines evolutionary transitions in migratory behavior in finches and allies. Oikos, 2011, 120(2): 184-193

Introduction

The migratory behavior of birds nesting in the temperate zone is often strikingly correlated with aspects of their breeding phenology (Kipp 1943, Böhning-Gaese et al. 2000, Bruderer and Salewski 2009, García-Peña et al. 2009). Long distance migrants start to breed later and/or have a shorter breeding season than short distant migrant or resident species breeding in several groups of birds, including raptors (Newton 2008), shorebirds (García-Peña et al. 2009) and passerines (Bruderer and Salewski 2009), among others. However, despite the widespread recognition of this phenomenon, the reason why the breeding phenology of long distance migrants differs so markedly from less migratory species breeding on the same latitude is not clear.

Possible explanations linking breeding phenology to migratory behavior largely fall into four classes. First, life history trade-offs between fecundity and mortality have been invoked in connection with this phenomenon, based on the observation that the shorter breeding season of long distance migrants is often associated with fewer number of broods per year, hence a lower annual fecundity (Mönkkönen 1992, Martin 1995, Böhning-Gaese et al. 2000, Bruderer and Salewski 2009). Life history theory predicts that in a population of constant size, differences in reproductive effort should be associated with different mortality rates. The reason for this is that under density dependence, any increase in reproductive investment (and hence fecundity) will intensify competition, resulting in a decrease in survivorship. High survival rates increase competition likewise, and this leads to less resources available for reproduction, ultimately selecting for lower reproductive rates (Ricklefs 1980, Martin 1995, McNamara et al. 2008, Bruderer and Salewski 2009). Thus, if the non-breeding period affects annual survival rate and there is density dependence, then the behavior of birds during the reproductive period and the non-breeding season should coevolve to reflect this trade-off (Bruderer and Salewski 2009). Overwinter survival rates are thought to be higher in long distance migrants than in species spending the winter at northern latitudes (Greenberg 1984, Sherry and Holmes 1995, Møller 2007). On the other hand, annual fecundity is directly related to the length of the breeding season because the number of broods per year and the probability of raising replacement

broods after failed brood attempts is probably higher when the breeding season is longer. Therefore, the fecundity-mortality trade-off could possibly result in a correlation between migration distance and the length of breeding season because migration distance is related to overwinter survival, whereas the length of the breeding season is related to annual fecundity (the “life history hypothesis”).

Second, the migratory behavior adopted by a given population of birds may depend directly on breeding phenology. The “time allocation hypothesis” (Greenberg 1980) proposes that with a relatively short breeding season, the benefits of wintering at a more distant site with better survival prospects may be higher, because the birds can spend more time at the favorable wintering site. The higher costs of long distance movements, according to this scenario, are more likely to be outweighed by the higher survival rate on the distant wintering grounds for birds that spend more time there. Furthermore, the cost of migration could be lower for individuals migrating relatively late in the spring because they can exploit the higher food availability at that time and experience more favorable conditions during migration than birds migrating early in spring, and this lowered cost of migration could ultimately lead to longer migration distances (Bell 1996, 1997).

Third, predictability of environmental conditions on the breeding site could also affect migratory behavior (the “spring predictability hypothesis”, Alerstam and Högstedt 1980). If conditions on the breeding grounds do not change from year to year, birds can rely on their internal clock to arrive in spring at the earliest time when breeding becomes possible. Conversely, if the onset of spring is unpredictable, individuals wintering closer may predict weather conditions on the breeding grounds more accurately and respond more quickly than individuals migrating longer distances (Alerstam and Högstedt 1980). Given that weather conditions early in spring tend to be more variable than later (e.g. Newton 2008), one would predict that early breeders benefit more from staying close to the breeding grounds and have shorter migration distances.

Fourth, migratory behavior could also affect directly the breeding phenology. Moving between the wintering and breeding grounds takes time, and some long distance migrants may need several weeks to complete the journey (e.g. Alerstam 1990). Moreover, there is a considerable mortality cost associated with migration

(e.g. Sillett and Holmes 2002), and this presumably exerts a strong selection pressure on the birds to time their migration in a way that maximizes survival (e.g. by migrating late in spring and early in autumn; Bell 1996, 1997). This, in turn may affect the time available for other activities during the annual cycle, including reproductive activities, such as the number of broods per year (Bruderer and Salewski 2009), the length of the fledging period (Meiri and Yom Tov 2004), or parental activities (García-Peña et al. 2009). Thus, long distance migrants may reorganize their annual cycle and/or their reproductive behavior such that their reproductive cycle will fit into a short summer period while simultaneously maximizing survival rate during migration (by migrating under more favorable conditions). On the other hand, short-distance migrants and residents may be less constrained by time, and could therefore freely extend their breeding season. Notice that this hypothesis does not involve life history trade-offs because there is no change in reproductive effort *per se*, but it is the partition of the various reproductive activities that differs (e.g. it is possible to decrease the time spent on parental activities but increase the effort during that time, resulting in no net difference in reproductive investment). We refer to this as the “migration time hypothesis”.

All these alternatives predict a correlation between migratory behavior and aspects of the breeding phenology. Therefore, we have designed this study to discriminate among the possible alternatives. We collected data on the breeding phenology and migratory behavior of a group of passerine birds (the finches and allies of the Western Palearctic and the Nearctic), and employed directional phylogenetic tests (Pagel 1994, Pagel and Meade 2006), which provide a framework to analyze the temporal order and contingency of evolutionary transitions. Given a phylogenetic hypothesis among a set of species and two traits with binary states, the method developed by Pagel (1994) determines the rate of transition among the possible combination of states. Based on these rates it is possible to determine which of the two traits is more likely to change spontaneously and whether changes in one trait are contingent upon the background state of the other. Our predictions for these directional tests were as follows: (1) if the relationship between migration and breeding phenology is mediated by life history trade-offs, then evolutionary transitions in migratory behavior should be contin-

gent on breeding phenology, and vice versa, transitions in the length of the breeding season should also be contingent on migratory behavior. (2) If either the “time allocation” or the “spring predictability hypothesis” is correct, the prediction is that transitions in migratory behavior are contingent upon breeding phenology (length of breeding season and start of breeding, respectively). (3) Lastly, if the “migration time hypothesis” is true, then both the start and the length of the breeding are predicted to be contingent upon migratory behavior.

Methods

Data collection

We investigated the relationship between migratory behavior and breeding phenology in the finches and their allies, a taxonomically diverse group of small to medium-sized passerines, including the families *Parulidae* (New World warblers), *Thraupidae* (tanagers), *Emberizidae* (American sparrows, Old World buntings, etc.), *Cardinalidae* (cardinals), *Icteridae* (orioles and blackbirds) and *Fringillidae* (finches). Finches are an ideal group to investigate this problem, because they include species with a wide range of migratory behavior, including residents, short distance and long distance migrants, but the group is relatively homogenous with respect to body size and the mode of migration (they all migrate by flapping flight), thus extreme differences in the cost of migration are unlikely to bias the analyses.

Crossbills (genus *Loxia*) and cowbirds (genus *Molothrus*) were not included in this study, because the breeding season in these species cannot be determined in the same way as for the other species. Crossbills are opportunistic breeders and can breed year-round, often moving large distances between different breeding locations (Cramp and Perrins 1994, Poole 2005). Cowbirds on the other hand are brood parasites that lay in the nest of other species and their offspring are raised by foster parents (Poole 2005); as a consequence, reproductive investment per offspring is much lower in cowbirds and this could affect both the outcome of life history trade-offs and the timing of breeding differently than in other species (i.e. cowbirds can leave immediately after egg laying). The final dataset contained

134 species.

Data on breeding phenology was collected from several ornithological monographs and the references therein. For most species, phenology data were available from several locations; in each case, the geographical coordinates where the study was performed, the start and end of the laying period and the sample size (number of nests) was recorded. In a few cases (10 species), the dates were only given as part of the month, i.e. “early”, “mid” or “late” period of a month and we therefore substituted them with the 5th, 15th and the 25th day of the month, respectively. The length of the breeding season was simply taken as the difference between the end and start dates.

Data on the start and length of the breeding season originated partly from field studies of breeding biology and partly from museum collections and nest card programs encompassing larger geographic regions (U.S. states, Canadian provinces or European countries). In this latter case, we took the midpoint of the species’ distribution in that specific region, assessed from distribution maps in Cramp and Perrins (1994) and Poole (2005) to the nearest 0.5 decimal degree. Note however, that we did not include regions with a latitudinal span larger than 10 degrees, thus the lowest precision for any latitude data is about 5 degrees, and it is <<5 degrees in most of the cases.

Sampling intensity might introduce a bias in assessing breeding phenology, because more effort typically increases the probability that very early or very late nests are discovered. Therefore, only data based on a sample size of at least 20 nests were included in the analyses, and if more than one data point was available for a given species, we selected the one with the largest sample size. However, to maximize variation in migration distance within the sample, we also checked our results on a different dataset in which we selected the northernmost record for all species (i.e. the northernmost of all records available for a species that are based on ≥ 20 nests).

Another possible source of bias in recording breeding phenology is that different aspects of the breeding cycle may be reported. Thus, some studies report laying dates (laying of first eggs in the nest) whereas others report egg dates (dates on which viable eggs were found; McNair 1987, Peck and James 1987), and these may result in breeding periods with different start and length. To see

whether this affected our phenology variables, we used the original dataset with 496 records (with a median of 3 records per species) to compare data originating from laying dates and egg dates. The two type of data indeed showed differences (Appendix 5.A), suggesting that the origin of phenology data needs to be taken into account in the analyses (see the Results section).

Migratory behavior was quantified by calculating the minimum geographical distance between the point of origin of the phenological data and the wintering range, from digitized distribution maps. We used the maps provided by Ridgely et al (2007) for North American species and digitized the distribution of European species in our sample by hand, following range maps in Cramp and Perrins (1994). The resulting variable is the minimal distance a bird has to migrate to reach the winter quarters (where the breeding and wintering ranges overlap at the study location, the variable was set to 0). Although this measure may not represent the true migration distance of a species, (e.g. if some populations migrate to the southern end of the wintering range), we do not expect any systematic bias in this variable and assume that interspecific differences in the minimal migration distance reflect true differences in the degree of migratoriness. This assumption is supported by the very strong correlation between the minimum migration distance and the distance between the latitudinal midpoint of the breeding and wintering ranges (an approximation of the species-specific migratory behavior; Spearman's rank correlation, $r_s=0.865$, $p<0.001$, $n=134$). In addition, this variable has the important advantage of being specific to the population whose breeding phenology has been recorded.

Interspecific variation in migration distance may be affected by several other factors, such as the breeding latitude or the ability of the birds to survive harsh winter conditions. Species breeding at more northern latitudes experience harsher winters and have to migrate longer distances to enjoy the same winter conditions as birds breeding at more southern latitudes and these are more likely to be migratory (Newton 2008). In addition, birds of larger sizes can cope better with cold, because heat loss is lower compared to small animals (Bergmann's rule) and an ability to forage on seeds may also facilitate spending the winter at higher latitudes. To account for these confounding factors, we compiled data on adult body mass (the mean of male and female mass, from Dunning (2008) and winter

diet, i.e. granivorous (composed primarily of seeds, 0) or insectivorous (mostly insects, 1) from Cramp and Perrins (1994) and Poole (2005), and controlled for these variables in multivariate analyses.

Breeding habitat may also confound the relationship between migration and phenology, because long distance migrants may differ in habitat use from short distance migrants and residents (Martin 1995, Böhning-Gaese and Oberrath 2003). Neotropical long distance migrants breeding in North America are more likely to inhabit forested environments, whereas Trans-Saharan migrants in the Western Palearctic are more likely to breed in open habitats, compared to short distance or resident species in these areas. To account for any possible bias arising from these differences, we recorded the continent where the breeding phenology was studied (North America or Europe) and following Böhning-Gaese and Oberrath (2003), we assessed the type of breeding habitat based on a gradual scale ranging from closed to open habitats. Typical breeding habitat types reported in Cramp and Perrins (1994) and Poole (2005) were scored for each species on a scale from 1 to 7, as follows: 1 – closed forest; 2 – open forest; 3 – forest edge; 4 – gardens, orchards, urban areas; 5 – shrubland; 6 – open area with single trees or shrubs; and 7 – open area without trees or shrubs. If a species was reported to typically breed in more than one type of habitat, the score of these habitat types was averaged.

Comparative analyses

To find out whether the relationship between migration distance and breeding phenology is not the result of the confounding effects of breeding latitude, adult body size, winter diet, breeding habitat or continent, we performed multivariate analyses where we controlled for these confounding variables. Second, we ran directional phylogenetic tests between migratory behavior and the explanatory variables that were significantly related to migration distance in the multivariate analyses.

Before performing the multivariate analyses, we checked whether phylogenetic correction was needed by calculating Pagel's lambda statistic for phylogenetic signal, using the *geiger* package in the R statistical environment (Harmon et

al. 2008, R Development Core Team 2008). Pagel's lambda is a measure of the phylogenetic structure in the data; a value close to zero indicates phylogenetic independence, while larger values indicate that closely related species are more similar to each other than expected by chance (Pagel 1997, 1999). Significance was estimated by comparing the log-likelihood of a model with the maximum likelihood estimate of lambda for a given trait to the log-likelihood of a model where lambda was set to zero, using likelihood ratio tests. All traits showed significant phylogenetic signal (Table 5.1).

Table 5.1: *Lambda statistics for phylogenetic signal for the variables investigated. Branch lengths were set to unity.*

Variable	Lambda	Likelihood ratio	<i>P</i>
Migration distance	0.21	48.40	<0.001
Length of breeding season	0.08	44.07	<0.001
Start of breeding season	0.05	8.86	0.003
Breeding latitude	0.82	44.42	<0.001
Adult body size	0.56	107.16	<0.001
Winter diet	0.93	90.50	<0.001
Breeding habitat	0.92	82.72	<0.001

The relationship between migration distance, breeding phenology and the potentially confounding variables was tested using phylogenetic generalized least squares (PGLS) in R's *ape* package (Paradis 2006). The PGLS method accounts for the nonindependence of the data points arising from their phylogenetic relationship by incorporating a matrix of covariances among the species into the model (Martins and Hansen 1997, Pagel 1997, 1999). This matrix can be adjusted to reflect the degree of phylogenetic autocorrelation in the data by incorporating the maximum likelihood estimate of Pagel's lambda (Freckleton et al. 2002). Migration distance, the dependent variable, was square-root transformed prior to the analyses, as the distribution of this variable was highly skewed due to the large number of non-migratory species in the sample. Although this transformation did not result in a normally distributed variable, the residuals of the

PGLS models were normally distributed (Shapiro-Wilk tests of normality are reported along with the models). Breeding latitude, winter diet, start of breeding, length of breeding season, adult body mass, breeding habitat and continent were introduced as explanatory variables.

To find out the direction of evolutionary transitions and to corroborate the results of the PGLS analyses, we applied Pagel's test (Pagel 1994, Pagel and Meade 2006), using the software BayesTraits (available at <http://www.evolution.rdg.ac.uk/BayesTraits.html>). To test the correlated evolution of two binary traits on a phylogenetic tree, this method uses reversible-jump Markov chain Monte Carlo to estimate support for the hypothesis of correlated evolution between the two traits by searching among possible models conforming either to independent or correlated evolution. The dependent and independent models can be compared by means of the Bayes factor, i.e. by calculating $2[\log_e(\text{harmonic mean of log likelihood of the dependent models}) - \log_e(\text{harmonic mean of the log likelihood of the independent models})]$. A Bayes factor greater than 2 indicates positive evidence for the correlated model, greater than 5 is strong and greater than 10 is very strong evidence (Pagel and Meade 2006). Each model consists of up to eight different parameters describing the rate of transition among the four possible combination of states. The posterior distribution of these transition rate parameters are simultaneously estimated by the reversible-jump Markov chain Monte Carlo algorithm. Alternative evolutionary hypotheses (such as the temporal order and contingency of evolutionary changes) can be tested by comparing critical pairs of these parameters (e.g. by looking at the posterior probability that a given parameter is zero). If transitions in one character depend on the background of the other character, then evolutionary changes in the first are contingent upon the second character (the contingent changes test). For example, if the rate parameter for the $(0,0) \rightarrow (1,0)$ transition is higher than zero, but the rate parameter for the $(0,1) \rightarrow (1,1)$ transition is assigned a value of zero with high posterior probability, then this means that transitions in the first trait (from 0 to 1) are more likely when the background state of the other character is 0. For the analyses we have used an exponential hyperprior (0 100), which allows the estimation of the rate transition parameters from the data. The Monte Carlo algorithm was run for 10^7 iterations, with a sampling frequency of 100 iterations. The first 10^6 iterations were discarded, because the

harmonic means of the log-likelihood generally did not stabilize before this. For further details on this method, see Pagel and Meade (2006) and the BayesTraits manual (available at <http://www.ams.reading.ac.uk/zoology/pagel>).

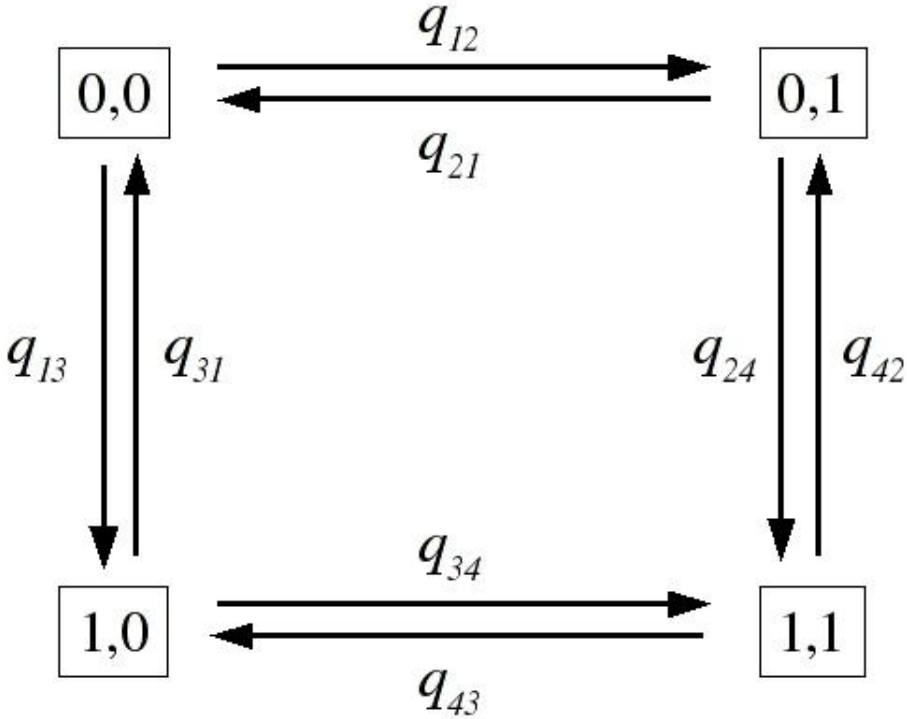


Fig. 5.1: Schematic representation of the transition rate parameters (q_{ij}) estimated by the directional tests. The numbers in the boxes represent the four possible combinations of two binary traits. The first number represents the state of migratory behavior whereas the second stands for the state of either of the three explanatory variables: start of breeding season, length of breeding, adult body size or winter diet. The parameters q_{ij} denote the rate of transition among these combination of states.

The drawback of the correlated changes test in our case is that it cannot account for the confounding effects of other variables. Thus, while two traits can be shown to conform to correlated evolution, it cannot be ruled out that transition

in both traits happened because of transition in a third variable. Here, both migration distance and breeding phenology depend on breeding latitude, and transitions in the breeding range of a species may simultaneously affect both traits. To circumvent this problem, we calculated residuals between migration distance and breeding latitude and subsequently scored species with positive residuals (i.e. migration distance longer than expected for that latitude) as long distance migrants (1) and short-distance migrants (0) otherwise. The problem with taking residuals is that this categorization may depend on the species included in the analysis, or the latitude from which their migration distance is calculated. To quantify this error, we repeated the calculation of the residuals using random points from within the breeding range of the species and the minimum migration distances from these coordinates. That is, for every focal species, we selected random points for all other species, but kept the original values for the focal species, calculated residuals and scored the focal species as long-distance or short distance migrant based on the residuals. This procedure was repeated 1000 times for each species. In this way, we were able to determine the rate of error of our initial categorization for each species (i.e. the number of times a species will be scored differently if the values of the other species changes). We found that our categorization is robust for most species, but 15 species received a different score at least one time (a rate of error > 0). Therefore, we have repeated the directional analyses by excluding these species.

The start of breeding, length of breeding season and body mass are all continuous variables, but the correlated changes test can only be performed on binary variables. Therefore, we dichotomized these variables using their median as the cutoff value. Thus, a species was scored as a late breeder (1) if it starts breeding after 7th May and early breeder (0) otherwise; species with a breeding season longer than 69.5 days were scored as having a long breeding season (1), all others were scored as having a short breeding season (0). The median body mass in our sample was 19.55 g; species with a body size larger than this value were scored as being large (1), those with a smaller value as small (0). As this categorization may potentially introduce a bias, we repeated the analyses using two different cutoff values, the 40 and 60 percentiles of body mass, start and length of the breeding season.

The phylogenetic relationship among the species was represented by a composite phylogeny assembled from recent molecular studies. As the phylogenetic information was obtained from different studies performed on different gene sequences, we were not able to use branch length information. Therefore, we generated branch lengths in two ways: first, we set all branch lengths to unity (conforming to a punctuational model of evolution); second we repeated both the multivariate and the directional tests by transforming branch lengths using Grafen's method, which is similar to a gradual model of evolution (Grafen 1989, Paradis 2006).

Results

Both the start of breeding and the length of the breeding season were significantly related to migration distance and these relationships remained significant when we controlled for the potentially confounding effects (Table 5.2a, b). Migration distance increased with breeding latitude and decreased with adult body size, but it was not related to breeding habitat or continent (Table 5.2a, b). Winter diet had a significant effect in the full models, but in the minimal models it was only significant when the start of the breeding season, but not its length, was introduced as the explanatory phenology variable (Table 5.2a, b). The relationship between migration distance and the five significant explanatory variables is depicted in Fig. 5.2. When the start and length of breeding season were introduced in the same model with breeding latitude, body mass and winter diet as covariates, the start of breeding season was not significantly associated with migration distance, whereas all other variables had a significant effect, suggesting that the length of the breeding season may be more important than its starting date. However, given the very strong correlation between the two phenology variables (Spearman's rank correlation, $r_s = -0.78$, $P < 0.001$), multicollinearity may be a problem when these two variables are introduced into the same model and therefore the possibility that the start of breeding may also have an effect (in addition or instead of the length of the breeding season) cannot be excluded.

The PGLS analyses were repeated by including sample size (number of nests) and type of phenology data (laying dates or egg dates) as covariates, in addition to

the six explanatory variables. However, neither sampling intensity nor the type of phenology data were significantly associated with migration distance, thus interspecific differences in sampling should not affect our results. Backward elimination of the nonsignificant predictors based on largest P -value resulted in the same minimum adequate model (Crawley 2007) as in the first models where these two variables have not been included, therefore they are not reported separately.

Table 5.2: *Full and minimal phylogenetic generalized least squares models for explaining migration distance (km, square-root transformed) by (a) start of breeding season (julian day) or (b) length of breeding season (days), together with additional explanatory variables: breeding latitude (degrees North), adult body size (g), winter diet (granivorous/insectivorous), breeding habitat (for categorisation, see text) and continent (Europe/North America). Minimal models were obtained by eliminating nonsignificant predictors from the full model in a backward stepwise manner based on the largest P -value. Branch lengths were set to unity.*

(a)

Source of variance	Full model: β (SE)	t (P)	Minimal model: β (SE)	t (P)
Start of breeding season	0.126 (0.053)	2.390 (0.018)	0.142 (0.050)	2.850 (0.005)
Breeding latitude	1.182 (0.188)	6.288 (<0.001)	1.077 (0.170)	6.321 (<0.001)
Adult body size	-0.239 (0.086)	-2.776 (0.006)	-0.244 (0.088)	-2.782 (0.006)
Winter diet	11.617 (4.661)	2.492 (0.014)	10.853 (4.662)	2.328 (0.022)
Breeding habitat	0.456 (0.793)	0.575 (0.566)	-	-
Continent	-8.963 (6.018)	-1.489 (0.139)	-	-

Shapiro-Wilk test on the normality of residuals for the full model: $W = 0.993$, $P = 0.725$; for the minimal model: $W = 0.988$, $P = 0.318$.

(b)

Source of variance	Full model: β (SE)	t (P)	Minimal model: β (SE)	t (P)
Length of breeding season	-0.154 (0.038)	-4.043 (<0.001)	-0.172 (0.036)	-4.732 (<0.001)
Breeding latitude	1.124 (0.166)	6.786 (<0.001)	1.010 (0.152)	6.639 (<0.001)
Adult body size	-0.262 (0.085)	-3.118 (0.002)	-0.296 (0.088)	-3.372 (0.001)
Winter diet	9.042 (4.568)	1.980 (0.050)	-	-
Breeding habitat	0.333 (0.765)	0.437 (0.663)	-	-
Continent	-9.279 (5.757)	-1.612 (0.110)	-	-

Shapiro-Wilk test on the normality of residuals for the full model: $W = 0.993$, $P = 0.791$; for the minimal model: $W = 0.989$, $P = 0.362$.

We found strong support for the correlated evolution of migratory behavior and breeding phenology (Bayes factor for migratory behavior – start of breeding 27.01, migratory behavior – length of breeding season 26.12). Furthermore, the correlated evolution between migratory behavior and adult body size and migratory behavior and winter diet were also supported (Bayes factor 8.32 and 13.30, respectively). The transition rate parameters strongly supported the hypothesis that breeding phenology determines migratory behavior (Table 5.3); transitions to long migration distance are more likely from short breeding seasons ($q_{13} \gg q_{24}$) and transitions to short migration distance are more likely from a long breeding season ($q_{42} \gg q_{31}$). Similarly, evolutionary transitions in migratory behavior are contingent upon the start of breeding: transitions to long migration distance are more likely from a state of late breeding ($q_{24} \gg q_{13}$) and transitions to short migration distance are more likely from a state of early breeding ($q_{31} \gg q_{42}$).

The transition rate parameters for the correlated evolution between migration and body mass and migration and winter diet both showed a pattern opposite to that observed in the case of breeding phenology. Both adult body size and

winter diet were found to be contingent upon migratory behavior; thus, based on the transition rate parameters a large body size is more likely to evolve in short distance migrants ($q_{12} \gg q_{34}$) and transitions to a granivorous diet are more likely from a state of short-distance migration ($q_{21} \gg q_{43}$).

The PGLS analyses and the directional tests (both Bayes factors and the transition rate parameters) were qualitatively similar if the branch lengths were transformed according to Grafen's method. Moreover, the results were virtually identical when using the northernmost data points (Appendix 5.B), and were not affected by the exclusion of species with a rate of error greater than 0 in the scoring of migratory behavior. Using the 40 or 60 percentiles as cutoff points to dichotomise the variables resulted in qualitatively similar results, with two exceptions (Appendix 5.C). In the analyses using the 60 percentiles to dichotomise the length of breeding season, three transition rate parameters were assigned a value of zero with a relatively high posterior probability: q_{24} , q_{31} and q_{34} . That is, transitions in migratory behavior are still contingent upon the length of the breeding season, but it also appears that a very long breeding season is more likely to evolve in short distance migrants ($q_{12} \gg q_{34}$). Second, in the directional test using the 40 percentiles to dichotomize body size, two rate parameters were assigned a value of zero with high posterior probability: q_{13} and q_{34} (Appendix 5.C), indicating that not only is a large body size more likely to evolve from a state of short distance migration, but also that a long distance migration is less likely to evolve from a very small body size. However, support for this test was relatively weak (Bayes factor 3.31).

Discussion

Consistent with previous studies, we found that interspecific variability in the migratory behavior of the finches and their allies is associated with aspects of their breeding phenology. Results from the directional analyses showed that transitions from a relatively short to a relatively long migration distance are more likely when the breeding season is short and starts late, whereas the reverse transition is more likely when the breeding season is long and starts early. Although we acknowledge the difficulties associated with categorizing continuous variables

into discrete traits, the results were relatively robust to different categorizations. Furthermore, while the coevolution between migratory behavior and breeding phenology may involve complex interactions between the traits, with both components affecting the other, we found a robust pattern in support of the hypothesis that the evolution of migratory behavior is affected by the breeding phenology of the species.

The results from the directional tests provided only weak support for the hypothesis that time constraints arising from longer migration distances affect the breeding phenology, as transitions in the start and length of the breeding season were not found to be contingent upon migratory behavior (except when we used the 60 percentiles as cutoff points for the length of breeding season). Thus, while a long migration distance may lead to less parental investment in male shorebirds (García-Peña et al. 2009) or select for shorter postembryonic developmental periods (Meiri and Yom Tov 2004), it does not lead, in general, to shorter breeding seasons or a later onset of breeding in the finches and their allies. These differences are not surprising, as the three traits are fundamentally different aspects of reproductive behavior and each may be affected differently by time constraints. In particular, as the length of the breeding period in this study probably reflects the number of brood attempts per year (either from multiple broods or replacement broods), it may have a greater effect on reproductive success than either parental care or the length of the postembryonic developmental period. The reproductive value of second broods or replacement broods in small passerines is probably large, given their relatively short life span (Møller 2007), so it might not be advantageous to give up the opportunity to raise these broods, if the environmental conditions enable it.

Table 5.3: Mean \pm SD and Z-scores of the transition rate parameters, estimated from the directional tests. Migratory behavior is the first variable in all cases, and length of breeding season, start of breeding season, adult body size and winter diet were the second character, respectively. All variables are dichotomous (see the Methods section for scoring species). Parameters which were assigned a value of 0 with high posterior probability (high Z-scores), suggesting that the given transition occurs with very low probability, are shown in bold. The meaning of the parameters is clarified in Figure 5.1.

Parameter	Length of breeding season		Start of breeding season		Adult body size		Winter diet	
	Mean \pm SD	Z-score	Mean \pm SD	Z-score	Mean \pm SD	Z-score	Mean \pm SD	Z-score
q12	0.56 \pm 0.43	0.00	0.41 \pm 0.09	0.00	0.19 \pm 0.08	0.00	0.05 \pm 0.02	0.04
q13	0.47 \pm 0.20	0.02	0.00 \pm 0.02	0.99	0.09 \pm 0.06	0.20	0.14 \pm 0.13	0.00
q21	0.39 \pm 0.12	0.00	0.42 \pm 0.13	0.00	0.16 \pm 0.07	0.00	0.22 \pm 0.13	0.00
q24	0.02 \pm 0.06	0.92	0.41 \pm 0.10	0.00	0.20 \pm 0.14	0.00	0.12 \pm 0.12	0.16
q31	0.01 \pm 0.06	0.93	0.42 \pm 0.10	0.00	0.10 \pm 0.04	0.00	0.26 \pm 0.13	0.00
q34	0.39 \pm 0.12	0.00	0.42 \pm 0.12	0.00	0.00 \pm 0.02	0.93	0.07 \pm 0.04	0.05
q42	0.46 \pm 0.20	0.03	0.00 \pm 0.02	1.00	0.21 \pm 0.14	0.00	0.06 \pm 0.03	0.00
q43	0.55 \pm 0.43	0.00	0.41 \pm 0.09	0.00	0.14 \pm 0.06	0.00	0.00 \pm 0.01	0.92

Our results do not support the hypothesis that the association between migratory behavior and breeding phenology is the result of life history trade-offs affecting these traits simultaneously. First, while arguments based on life history theory may explain the lower number of annual broods and the corresponding shorter breeding season in long distance migrants, they cannot account for the later start of the breeding season in these species. Second, if the fecundity-mortality trade-off would be responsible for the observed correlation between migration and breeding phenology, we would expect that evolutionary transitions in the length of the breeding season depend on the background state of migratory behavior (i.e. transition rates to a short breeding season higher in relatively long distance migrants *and* transition rates to long breeding season higher in short distance migrants), a prediction not supported by our results. This is not to say that differences in annual survival due to contrasting migration strategies cannot lead to differences in reproductive investment, because selection can affect other reproductive traits as well, e.g. clutch size (Martin 1995, Böhning-Gaese et al. 2000). However, our results make it unlikely that the shorter breeding season is the consequence of the high annual survival rate of long distance migrants, which selects for fewer broods per year (and hence a shorter breeding season). Furthermore, the fact that not all species migrate long distances (although this would supposedly increase their annual survival rate; Greenberg 1980, Bruderer and Salewski 2009), suggests that additional factors may operate which select for shorter migration distances in some species.

The most likely scenario based on our results is that reproductive phenology is determined by ecological factors, such as the species-specific type of food exploited during breeding. Reproduction in birds is an energy-demanding process and selection should act to maximally match the timing of reproduction with the peak of food availability (Lack 1968, Perrins 1970). The length and timing of this peak in food availability is likely to differ among different types of habitat, but differences may exist within habitats as well, if birds breeding at the same location rely on different types of food to feed their nestlings. The reproductive phenology in turn may determine the costs and benefits of migration, constraining migration distance such that only species with a short, late-starting breeding season can afford to migrate long distances while species with an extended

breeding season can travel only short distances. The evolutionary explanation for this phenomenon could be that species with a relatively long breeding season 1) have to migrate under less favorable weather conditions early in spring and late in autumn, and 2) can spend less time on the wintering grounds, both factors decreasing the benefit of migrating long distances (Greenberg 1980, Bell 1996, 1997). In addition, a long breeding season is likely to start early in spring, when environmental conditions tend to show a higher year-to-year variability. This, in turn, could increase the benefit of staying close to the breeding grounds, as individuals can respond more quickly to improving or deteriorating conditions and have a higher fecundity as a result (Alerstam and Högstedt 1980). Unfortunately, we could not clearly discriminate among these possible mechanisms; the length of the breeding season appeared to be more important in multivariate analyses, but the start and length of breeding season were very strongly correlated. Furthermore, as most of our data points are based on data collected from multiple years, a longer breeding season may result from high year-to-year variability. Lastly, our measure of spring predictability (the start of breeding) is only indirect; unfortunately, very few long term breeding data for our species were available to enable a more thorough analysis. It is not unlikely, however, that all these mechanisms act in concert to shape the migratory behavior of a species.

The origin and evolution of avian migration has attracted much interest and several hypotheses have been proposed to explain it (for recent reviews and discussions see for example Rappole and Jones 2002, Alerstam et al. 2003, Helbig 2003, Salewski and Bruderer 2007). For example, the phylogenetic study of Outlaw and Voelker (2006) suggests that the increasing seasonality of the breeding environments (through the expansion of breeding ranges from southern latitudes to temperate and boreal areas) played a key role in the evolution of migratory behavior in the pipits and wagtails (*Motacillidae*). Similarly, other studies have emphasized the importance of expanding breeding ranges for the origin of migratory behavior (e.g. Joseph et al. 1999, Böhning-Gaese 2005, Milá et al. 2006). It is likely however, that other factors may also affect the outcome of this colonization, because closely related species, supposedly with similar biogeographical history, often show contrasting migratory behavior. For example, in a molecular phylogenetic study, Outlaw et al. (2003) have shown that the 5 species of *Catharus*

trushes breeding in North America most likely originate from Central or South America, and migration most likely evolved in this clade by the expansion of the breeding range, while the wintering range changed relatively little. Yet the wintering range of one of the species (*C. guttatus*), extends far more to the north than the supposed center of origin of this taxon, suggesting that the migration distance was subsequently shortened in this species (Outlaw et al. 2003). On the other hand, some species do not evolve migratory behavior after a northward range shift, the European Collared Dove (*Streptopelia decaocto*) being a well-known example. Thus, the expansion from the tropics does not always result in long distance migration. Our results imply that the breeding phenology may explain at least partly the outcome of these range shifts, with long distance migration evolving only when breeding phenology does not constrain it. This is in accordance with current views that regard the evolution of migration as a consequence of birds exploiting the seasonal flush of food at higher latitudes for breeding yet returning to more benign environments to increase survival, but refines this scenario by highlighting ecological conditions that could determine whether the birds keep returning to these ancestral areas or adapt to the year-round occupation of the new breeding areas.

Migratory behavior was negatively associated with adult body size and migration distance was shorter in species with a granivorous winter diet. The directional analyses revealed that transitions in adult body size and winter diet are contingent upon migratory behavior, with a large adult body size and a granivorous diet being more likely to evolve from a state of a relatively short migration distance. Thus, in the finches and their allies, body mass and winter diet do not appear to constrain migratory behavior, but rather, these trait adapt to increase the survival chances of birds spending the winter at high latitudes (see Pravosudov et al. 2007 for a similar conclusion on brain size).

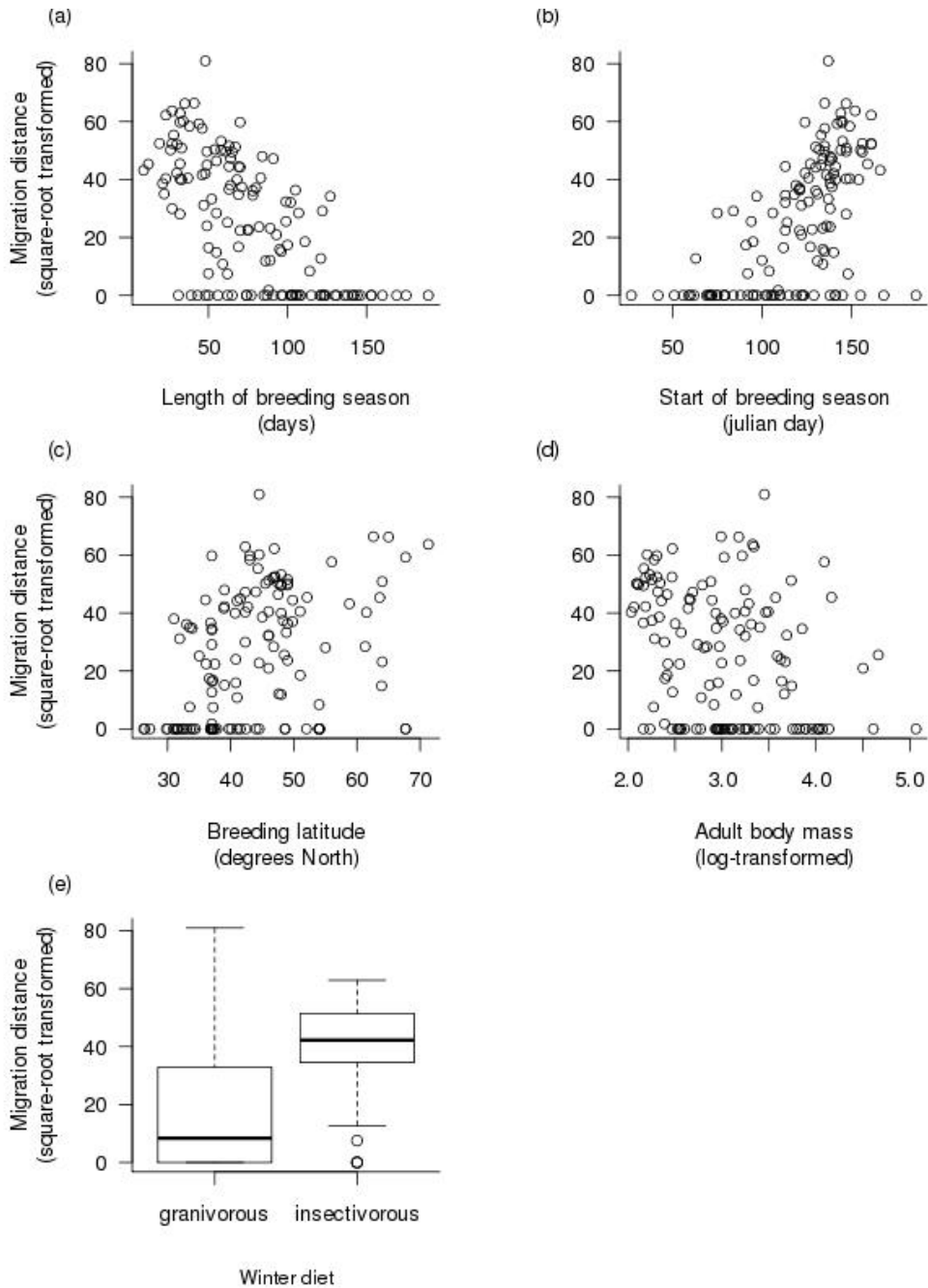


Fig. 5.2: Relationship between migration distance (km, square root transformed) and five explanatory variables: start (a) and length of breeding season (b), breeding latitude (c), adult body size (log-transformed for better visualization) (d) and winter diet (e). The outlier with the longest migration distance is the Bobolink (*Dolichonyx oryzivorus*); excluding this species does not affect the results.

Although the present study was restricted to the finches and allies, the relationship between phenology and migration could apply to other taxonomic groups as well. However, other factors, the cost of migration in particular, will certainly affect the outcome of the coevolution between migration and breeding phenology (Greenberg 1980). For example, swallows and martins (family *Hirundinidae*) breeding at temperate latitudes have an extended breeding season yet migrate long distances (Bruderer and Salewski 2009). As these birds are highly adapted for aerial life and can forage while in flight during migration, moving between the summer and winter quarters may be less costly for these species (both in terms of mortality and time) and a longer migration distance may be possible even with an extended breeding season. In addition, the relationship between breeding phenology and migration may apply not only to interspecific comparisons, but also to differences in the migratory behavior of populations of the same species. Both the “time allocation” and the “spring predictability” hypotheses have been applied to explain leap-frog migration (the pattern in which northern populations of a species migrate longer distances than the southern ones; Alerstam and Högstedt 1980, Greenberg 1980, Bell 1996, 1997). Although alternative explanations for leap-frog migration do exist (and indeed are more commonly accepted; Greenberg 1986, Drent and Piersma 1990), our results provide phylogenetic comparative evidence that breeding phenology may also play an important role in shaping migration strategies.

Acknowledgments

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Appendix 5.A Sampling bias

Differences in sampling may affect the start and length of the breeding season and thereby confound the relationship between breeding phenology and migration. First, sampling intensity might introduce a bias because more effort typically increases the probability of very early or very late nests to be discovered. Second, some studies report laying dates, whereas others report the dates on which viable eggs were found. Assuming identical sampling effort, earliest egg dates should not differ considerably from earliest laying dates, but the latest egg dates should be later than the latest laying dates, because the former incorporate the incubation period as well. However, egg collectors may have concentrated their efforts to specific part(s) of the breeding cycle (McNair 1987), thus the difference between the two types of data are not straightforward. To check that the two type of phenology data are indeed different and whether any kind of correction is needed, we used the original dataset with all phenology data (n=496 records for 134 species, with a median of 3 records per species) to build generalized estimating equation (GEE) models. GEEs are extensions of generalized linear models (Liang and Zeger 1986, Hardin and Hilbe 2003) that can be used for correlated data (ie. multiple data points from a single species in our case). GEE models were constructed using the *geepack* package in the R statistical environment (Yan and Fine 2004, R Development Core Team 2008), with an exchangeable correlation structure that assumes multiple observations within clusters (species) to be equally correlated. Start and end date of the breeding season were separately used as independent variables, location (the latitude where the phenology was recorded), sample size (number of nests) and type of the data (laying date or egg date) were introduced as explanatory variables, and species as a grouping factor. These analyses showed that the end date of the breeding season does not differ significantly at the 5% level between egg dates and laying dates (after controlling for sample size and location), but that the starting date in the case of egg dates is significantly later compared to laying dates. Furthermore, sample size is negatively correlated with the start and end dates such that earlier dates were recorded for larger sample sizes). Although this is what we would expect for the start date, the direction of the relationship in the case of end

dates is strange. It turns out however, that this relationship is not significant when one data point with extremely large sample size, 500 000 nests of Tricolored Blackbirds (*Agelaius tricolor*), is excluded.

To summarize, the start of breeding season is affected by both sampling intensity and the type of phenology data, whereas the end of the breeding season is not affected by these factors.

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Appendix 5.B Results from the dataset with the northernmost phenology records.

For all species where phenology data with a sample size of at least 20 nests was available from several locations, we selected the northernmost record and computed the minimum migration distance from these coordinates. Records matching these criteria were available for 54 out of 134 species. The median breeding latitude in this sample was 47.3 degrees North and the median migration distance 1137.5 km, compared to 42.55 degrees North and 642.5 km in the original sample in which data was selected based on the largest sample size. In this appendix we present the results of the multivariate analyses using this dataset with either the start (a) or the length of the breeding season (b) included as the explanatory phenology variable and the results of the directional tests (c).

(a)

Source of variance	Full model: β (SE)	t (P)	Minimal model: β (SE)	t (P)
Start of breeding season	0.187 (0.065)	2.887 (0.005)	0.210 (0.062)	3.323 (0.001)
Breeding latitude	0.935 (0.179)	5.226 (<0.001)	0.838 (0.168)	4.984 (<0.001)
Adult body size	-0.200 (0.083)	-2.399 (0.018)	-0.212 (0.087)	-2.440 (0.016)
Winter diet	11.601 (4.717)	2.459 (0.015)	10.113 (4.776)	2.118 (0.036)
Breeding habitat	0.681 (0.813)	0.838 (0.404)	-	
Continent	-9.034 (5.592)	-1.616 (0.109)	-	

Shapiro-Wilk test on the normality of residuals for the full model: $W = 0.990$, $P = 0.422$; for the minimal model: $W = 0.980$, $P = 0.043$.

(b)

Source of variance	Full model: β (SE)	t (P)	Minimal model: β (SE)	t (P)
Length of breeding season	-0.173 (0.046)	-3.774 (<0.001)	-0.193 (0.044)	-4.420 (<0.001)
Breeding latitude	0.941 (0.162)	5.811 (<0.001)	0.829 (0.153)	5.435 (<0.001)
Adult body size	-0.234 (0.082)	-2.839 (0.005)	-0.283 (0.089)	-3.166 (0.002)
Winter diet	10.699 (4.618)	2.317 (0.022)	-	
Breeding habitat	0.792 (0.796)	0.995 (0.322)	-	
Continent	-10.101 (5.358)	-1.885 (0.062)	-	

Shapiro-Wilk test on the normality of residuals for the full model: $W = 0.988$, $P = 0.277$; for the minimal model: $W = 0.979$, $P = 0.036$.

(c)

Parameter	Length of breeding season		Start of breeding season		Adult body size		Winter diet	
	Mean±SD	Z-score	Mean±SD	Z-score	Mean±SD	Z-score	Mean±SD	Z-score
q12	0.46±0.17	0.00	0.63±1.10	0.00	0.20±0.10	0.00	0.05±0.02	0.00
q13	0.43±0.13	0.02	0.07±0.21	0.79	0.10±0.07	0.17	0.40±1.10	0.00
q21	0.42±0.11	0.00	1.10±2.85	0.00	0.20±0.09	0.00	0.30±0.22	0.00
q24	0.02±0.07	0.92	0.49±0.30	0.12	0.41±1.86	0.00	0.13±0.20	0.18
q31	0.00±0.03	0.98	0.55±0.44	0.06	0.10±0.04	0.00	0.45±1.12	0.00
q34	0.42±0.13	0.00	1.09±2.83	0.00	0.00±0.02	0.93	0.05±0.03	0.04
q42	0.44±0.12	0.01	0.02±0.07	0.91	0.42±1.86	0.00	0.05±0.02	0.00
q43	0.45±0.20	0.00	0.63±1.10	0.00	0.11±0.05	0.01	0.00±0.01	0.90

Bayes factors: migratory behavior – length of breeding season: 18.07; migratory behavior – start of breeding season: 24.41; migratory behavior – adult body size: 8.46; migratory behavior – winter diet: 19.49.

Appendix 5.C Results from the analyses with alternative dichotomization of the variables

Mean \pm SD and Z-scores of the transition rate parameters, estimated from the directional tests. In these tests, migratory behavior was the first variable in all cases. The length of breeding season, start of breeding season and body size were the second character, respectively, and these variables were dichotomized with either the 40 (a) or the 60 percentiles (b) as cutoff points. The 40 and 60 percentiles were as follows: 62 and 82.8 days for the length of the breeding season, 30th April and 15th May for the start of the breeding season, 17.2 and 23 grams for adult body size respectively. Migratory behavior was dichotomized by regressing breeding latitude over migration distance and setting it to 1 for species with positive residuals and to 0 for species with negative residuals.

(a)

Parameter	Length of breeding season		Start of breeding season		Adult body size	
	Mean \pm SD	Z-score	Mean \pm SD	Z-score	Mean \pm SD	Z-score
q12	0.46 \pm 0.27	0.00	0.50 \pm 0.56	0.00	0.15 \pm 0.08	0.00
q13	0.45 \pm 0.21	0.00	0.01 \pm 0.03	0.96	0.06 \pm 0.06	0.37
q21	0.37 \pm 0.09	0.00	0.51 \pm 0.57	0.00	0.06 \pm 0.03	0.00
q24	0.00 \pm 0.02	0.99	0.40 \pm 0.11	0.00	0.22 \pm 0.37	0.00
q31	0.01 \pm 0.07	0.96	0.42 \pm 0.17	0.02	0.06 \pm 0.03	0.01
q34	0.45 \pm 0.40	0.00	0.41 \pm 0.23	0.01	0.04 \pm 0.03	0.38
q42	0.37 \pm 0.10	0.02	0.01 \pm 0.05	0.92	0.23 \pm 0.37	0.00
q43	0.44 \pm 0.40	0.00	0.34 \pm 0.12	0.00	0.14 \pm 0.07	0.00

Bayes factors: migratory behavior – length of breeding season: 18.79; migratory behavior – start of breeding season: 23.18; migratory behavior – adult body size: 3.31.

(b)

Parameter	Length of breeding season		Start of breeding season		Adult body size	
	Mean±SD	Z-score	Mean±SD	Z-score	Mean±SD	Z-score
q12	2.44±10.95	0.00	0.38±0.09	0.00	0.17±0.06	0.00
q13	0.34±0.20	0.07	0.00±0.03	0.98	0.11±0.06	0.07
q21	2.19±10.86	0.00	0.61±0.40	0.00	0.17±0.06	0.01
q24	0.10±0.12	0.43	0.57±0.33	0.00	0.20±0.20	0.00
q31	0.07±0.09	0.56	0.38±0.11	0.02	0.11±0.05	0.01
q34	0.20±0.19	0.32	0.57±0.52	0.00	0.01±0.03	0.90
q42	0.75±0.77	0.06	0.01±0.07	0.96	0.20±0.20	0.00
q43	1.09±1.10	0.01	0.58±0.51	0.00	0.18±0.06	0.00

Bayes factors: migratory behavior – length of breeding season: 30.89; migratory behavior – start of breeding season: 19.06; migratory behavior – adult body size: 6.53.

6.

Study IV: Seasonal color change by molt or by the abrasion of feather tips: a comparative study

Abstract

Many birds undergo seasonal changes in plumage coloration by pre-breeding molt, abrasion of cryptic feather tips, or both. Seasonal dichromatism is thought to result from optimizing coloration to the conflicting demands of different life-cycle periods: sexual selection for conspicuousness being substantial during the mating season while selection for camouflage and for social signals may act in all seasons. Furthermore, energetic and time demands may constrain the extent of molt, thereby limiting color change. We investigated the relative importance of several factors in shaping this variation in a songbird clade using phylogenetic comparative methods. We found that pre-breeding molt relates most strongly to breeding onset and winter diet, demonstrating that both time and food availability constrain feather replacement. Feather abrasion was best predicted by winter flocking behavior and secondarily by open habitats, implying that exposure to predators and the simultaneous need for social signaling may favor the expression of partially obscured ornaments in the non-breeding season. The combined occurrence of pre-breeding molt and feather abrasion was associated with polyg-

ynous mating system, suggesting that species under strong sexual selection may employ both strategies of color change to ensure the full expression of breeding coloration.

Keywords: molt constraints - plumage coloration - predation risk - sexual selection - social signaling.

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Introduction

Bird species show a striking diversity in the extent to which their coloration varies seasonally. For example, great tits (*Parus major*) remain in their colorful plumage throughout the year, with only faint fading to their yellow breast (Figuerola & Senar, 2005), whereas white-tailed ptarmigan (*Lagopus leucurus*) change gradually from a fully white to a finely patterned gray-brown appearance between winter and summer (Poole, 2005). Seasonal dichromatism may arise by at least two different means: (i) the partial or complete replacement of feathers during a second, pre-breeding molt, or (ii) the abrasion of differently colored, usually dull feather tips, exposing the underlying, usually bright feather parts. Pre-breeding molt is common in many avian taxa ranging from waterfowl through shorebirds to passerines, whereas color change by feather abrasion appears to be a characteristic of songbirds (Møller & Erritzøe, 1992, Figuerola & Senar, 2005). In some songbird families the two strategies occur concurrently, and closely related species often differ in the strategies adopted (Perrins, 1994, Poole, 2005). The reasons for this interesting interspecific variability are, however, scantily studied (Hamilton & Barth, 1962, Froehlich, Rohwer & Stutchbury, 2004).

The coloration of birds' plumage is supposed to simultaneously fulfill several roles during the birds' life, often being under opposing selection pressures. For instance, plumage color might serve as camouflage against predators and at the same time as advertisement towards female and male conspecifics (Andersson, 1994). The relative importance of these roles, however, are assumed to change over the annual cycle of birds: display is usually important mainly during the breeding season, while defense against predators may be crucial all over the year. A possible adaptation to this temporal variation in costs and benefits of plumage coloration can be the shift between breeding and non-breeding plumages. However, such shifts may not be achievable without any constraint, since molt (one of the major devices behind plumage change) is costly in terms of energy, time, compromised thermoregulation and flight ability (e.g. Murphy & King, 1999, Swaddle & Witter, 1997, Sanz *et al.*, 2004). The relative significance of these costs and benefits in shaping the interspecific variation in the extent and type of seasonal color change are poorly understood.

In this study we investigate the environmental and life-history correlates of both means of seasonal dichromatism in a diverse set of songbird species, the finches and their allies, in which both the pre-breeding molt and the abrasion of dull feather tips is common (Perrins, 1998, Poole, 2005). We use phylogenetic comparative methods to examine whether the covariation between seasonal color-change strategies and various environmental and life-history factors fit the frameworks set by four main hypotheses.

First, the need to present sexually attractive plumages in the breeding season may select for seasonal color change by either strategy. On the one hand, if the expression of feather ornaments is highest in freshly molted feathers, as plumage coloration may gradually deteriorate after molt (McGraw & Hill, 2004, Figuerola & Senar, 2005, Delhey *et al.*, 2006), then it should be advantageous to molt just before the breeding season. On the other hand, feathers may be structurally adapted to uncover colorful ornaments by the abrasion of dull feather tips (Willoughby, Murphy & Gorton, 2002). As the benefits of bright, colorful plumage are expected to increase with the intensity of sexual selection, we expect pre-breeding molt and/or abrasion to be more common in species with more intense sexual selection, i.e. with higher frequency of polygyny or stronger sperm competition, than in species with less intense sexual selection.

Second, predation may select for cryptic winter plumage, thus seasonal color change may be more common in species that are more exposed to predators. Since the rate of predation on adults of small passerines is greater in open habitats than in closed habitats (Götmark & Post, 1996, Møller, Nielsen & Garamszegi, 2006), we predict more prevalent pre-breeding molt and/or abrasion among species living in open habitats than in species occupying closed habitats.

Third, Hamilton & Barth (1962) suggested that dull non-breeding plumages reduce the levels of aggression between flock members in gregarious species. Accordingly, they demonstrated the frequent occurrence of seasonal dichromatism in species forming nomadic winter flocks in two taxa with pre-breeding molt (Hamilton & Barth, 1962). However, more recent research showed that colorful ornaments may be adaptive in flocking species by serving as status signals (Rohwer, 1975, Senar, 1999). The ability to signal differences in dominance or aggressiveness is beneficial since participants may assess the expected outcome of

fight and thus may avoid the costs of physical interaction (Rohwer, 1975). Furthermore, coverable badges may be used as status signals that are exposed only when birds are highly motivated to fight for resources (Hansen & Rohwer, 1986). Color badges that are partially covered by cryptic feather tips may function in such a manner in certain species (Veiga, 1996). Thus the hypothesis based on social signaling predicts that seasonal color change especially by abrasion should be more common in species with than without non-breeding flocking behavior.

Finally, the costs of molt may constrain the incidence or extent of color change (Rohwer & Butcher, 1988). Previous comparative studies found that migratory status or migration distance is related to the timing and frequency of molts per year (Svensson & Hedenström, 1999, Figuerola & Jovani, 2001). These findings suggest that migration or the factors associated with it may be important also for explaining interspecific variation in pre-breeding molt. Resident species, for example, might trade off pre-breeding molt for early breeding due to time constraints (Froehlich *et al.*, 2004). Winter diet was also shown to influence molt; the availability of protein-rich food (insects) appearing crucial for the nutritional demands of feather replacement (Froehlich *et al.*, 2004). However, diet and migratory status may covary as food availability during the winter is likely to depend on geographical latitude. Furthermore, migratory status may influence molt by reasons other than the aforementioned constraints of time and food, e.g. the need for high-quality feathers during long-distance migration may necessitate a pre-migratory molt. Therefore, the effects of nutritional and time constraints and other migration-related costs on pre-breeding molt remain entangled. Here we examine the relative roles of breeding onset, winter diet and migration distance in shaping the interspecific variation of pre-breeding molt. We predict that pre-breeding molt is more common and/or more extensive in species that begin breeding later, rely on more insectivorous diets and migrate longer distances, than in species with the opposite characteristics. We also predict that the effect of winter diet on pre-breeding molt depends on the latitude of the non-breeding habitat, because the availability of plant material during winter probably increases towards southern latitudes, whereas insects are scarce in tropical wintering habitats in the dry season that often coincides with the time of pre-breeding molt (Froehlich *et al.* 2004). Finally, we also tested whether migratory status is re-

lated to color change by abrasion, since abrading feathers may decrease flight efficiency (Schreiber *et al.* 2006), thus abrading feather tips might be selected against in long-distance migrants.

Methods

Pre-breeding molt and feather abrasion

We collected data on the extent of pre-breeding molt and the occurrence of abrading feather tips for European and North American species of the songbird clade of Fringillidae, Passeridae and Motacillidae (Barker *et al.*, 2004) from Perrins (1998) and Poole (2005). We included species for which data were available on at least one of the two color-change strategies ($n = 150$).

We used two measures of pre-breeding molt. First, we recorded whether pre-breeding molt occurred in a species, including species with partial pre-breeding molts. Second, we scored the extent of pre-breeding molt on a 1-6 scale as follows: 1 - no feathers, 2 - head, 3 - head and throat, 4 - head, throat and breast, 5 - head, throat, breast and some other feathers, and 6 - all body feathers molted. We scored only adult males because first-year birds and females often molt differently, and one can expect the effect of sexual selection to be strongest on males. Only molt that occurs in late winter and/or early spring was considered, in order to distinguish true pre-breeding molt from delayed post-breeding molt that occurs in some species (Svensson & Hedenström, 1999).

The occurrence of feather abrasion was recorded for a species if plumage descriptions noted that coloration changes from fall to spring through abrasion or wear. Care was taken to discriminate feather abrasion from fading, a third alternative way for color change, resulting from the degradation of feather pigments (Blanco *et al.*, 2005). Data were insufficient to score the extent of abrasion on the body.

Pre-breeding molt and abrasion are not mutually exclusive, as several species in our dataset use both strategies of seasonal color change ($n = 26$, 17.3% of our species). To explain the simultaneous occurrence of the two strategies, we scored species as 1 if they had both pre-breeding molt and abrasion („combined

strategy”), and 0 if they had only one or no color-change strategy.

Although Froehlich *et al.* (2004) reported that pre-breeding molt was not associated with color change in some species, this observation was based on human vision which may miss part of variation in coloration that is visible to birds (Cuthill, 2006). Similarly, they considered only sexually dichromatic species, but this categorization again was human-assigned and may not be relevant to birds (Eaton, 2005). Here we did not attempt to judge the extent of seasonal or sexual dichromatism. Also, we did not score whether males are „dull” or „bright” in winter (as done by Froehlich *et al.*, 2004), because these terms depend seriously on the light environment, the background habitat and the visual system of the receiver (Butcher & Rohwer, 1989, Endler, 1990, Cuthill, 2006). We applied a single criterion of human vision to both pre-breeding molt and feather abrasion: we scored each as “present” only when the given species appeared seasonally dichromatic to the human eye. However, our conclusions remained unchanged when we included a few additional species that have pre-breeding molt but no seasonal changes visible to humans (results not reported). Note also that since plumage color may gradually deteriorate after molt (McGraw & Hill, 2004, Figuerola & Senar, 2005, Delhey *et al.*, 2006), pre-breeding molt that replaces faded feathers with fresh ones might change coloration even if the molted plumage pattern remains the same.

Correlates of color change

All data were collected from Perrins (1998) and Poole (2005) if not stated otherwise. We used two well-established measures of the strength of sexual selection. First, social mating system was scored as monogamous (less than 5% of the males polygynous), weakly polygynous (5-15% of males) or strongly polygynous (>15% of males; Pitcher, Dunn & Wittingham, 2005). Second, as a measure of sperm competition we obtained data on testis size (corrected for body mass) from Pitcher *et al.* (2005). We scored winter habitat as open (e.g. desert, grassland) or closed (e.g. forest, woodland; McNaught & Owens, 2002); winter flocking behavior as solitary (territorial or living in pairs) or gregarious (living in flocks); and late winter diet as granivorous, insectivorous or mixed (vegetable matter and in-

sects in approximately equal proportion) based on descriptions in the references. The onset of breeding is given in units of 10-day intervals, where interval 1 is the first part of January and interval 22 is the first part of August. Species were then assigned to these categories based on the approximate start of the egg-laying period assessed from annual cycle diagrams. Using distribution maps, we classified species as residents if their summer and winter distributions overlapped completely, and otherwise as migrants. Migration distances were estimated similarly to Svensson & Hedenström (1999) from the summer and winter distribution midpoint values of longitudes and latitudes according to the formula described by Imboden & Imboden (1972).

Phylogenetic analyses

To investigate the relationships between color-change strategies and potential explanatory variables, we employed two comparative approaches. First, for binary dependent variables (occurrence of pre-breeding molt, abrasion, or combined strategy), we used Pagel's (1994) discrete variable method to test whether the evolution of two categorical variables is correlated. This method is based on Markov chain models, and uses likelihood ratio tests to compare the fit of two alternative models: one assuming independent evolution of the two variables (e.g. habitat and abrasion), and another assuming that the rate of change in one variable depends on the state of the other variable (Maddison & Maddison, 2006). Statistical significance was estimated by running Monte Carlo tests using simulated data, with p-values based on 5000 simulation replicates. As this method cannot handle variables with more than two categories, we converted testis size into a dichotomous variable by assigning 0 to species with smaller than expected (negative) residual testis size and 1 to species with greater than expected (positive) residual testis size. Breeding onset was converted to 0 when < 13 (the median interval, i.e. the first third of May) and to 1 when ≥ 13 . Variables with three categories (mating system and diet) were dichotomized in two different ways, by merging the middle category with either the first or the last category.

Second, we used the extent of pre-breeding molt as a continuous dependent variable in Phylogenetic Generalized Least Squares (PGLS) models (Pagel, 1997,

1999). This approach controls for the non-independence among species by incorporating a matrix of the covariances among species based on their phylogenetic relationships (Martins & Hansen, 1997, Pagel, 1997, 1999), and also estimates the importance of phylogenetic corrections in the analyses (Freckleton, Harvey & Pagel, 2002). In all analyses we set the degree of phylogenetic dependence (λ) to the most appropriate degree evaluated for each model by likelihood ratio statistics. Note however that our conclusions remained unchanged when we repeated the analyses by setting λ to 0, which means species-level analyses with no phylogenetic control, and to 1, which is principally equivalent to the method of independent contrasts (Felsenstein, 1985, Martins & Hansen, 1997). Mating system, flocking behavior, habitat and diet entered the models as fixed factors, while testis size, breeding onset and migration distance were included as covariates.

To investigate the relative importance of predictor variables in explaining the occurrence and extent of color-change strategies, we applied two kinds of multivariate analyses. First, for each dependent variable we built full models including all possible predictors that were tested in bivariate analyses, then we obtained the final models using stepwise backward elimination of non-significant effects, removing the predictor with the largest p-value in each step (Grafen & Hails, 2002). Second, we also evaluated our results using a different analytical approach, the information-theoretic model-comparison (Burnham & Anderson, 2002). Here the initial models for each dependent variable included only those predictors that had a significant effect in the previous bivariate analyses or, in the case of the combined strategy, those selected by the multivariate analyses of either pre-breeding molt or abrasion. Note that including all predictors was not possible because the number of candidate models would have been too large, even exceeding the sample size. We then compared all possible submodels using the second-order Akaike's information criterion corrected for small sample size (AIC_c). We evaluated the candidate models by their relative Akaike weights (ω_i) and the predictors by the sums of their Akaike weights across all models that contain the given predictor (Σ). In this approach, inference is based not on a single final model but on an entire set of plausible models, thereby it can estimate the importance of predictors with greater robustness and precision.

For the extent of pre-breeding molt, we used PGLS models for the multivari-

ate analyses. Since the PGLS approach cannot handle binary variables as dependents, for abrasion and combined strategy we performed the multivariate analyses using generalized linear models with binomial error and logit link function (Dallgaard, 2002) without controlling for phylogeny. We expect that the results of the latter analyses are not seriously biased by phylogenetic relatedness of the species, because the estimated value of λ was relatively small in most PGLS models (not significantly different from zero in all multivariate analyses and in 74% of bivariate models; see Table 6.2 and Appendix 6.A), indicating a low overall degree of phylogenetic dependence in our data. Note that we obtained similar results for the combined strategy when we repeated the multimodel-comparison controlling for phylogeny in PGLS models with the extent of pre-breeding molt as dependent variable, and including abrasion into each candidate model as fixed factor (results not shown).

We compiled a composite tree to represent phylogenetic relationships among species, using recent molecular data. We set branch lengths proportional to the number of nodes, i.e. gradual branch lengths, according to Nee's method (Maddison & Maddison, 2006). Pagel's analyses were conducted using the Mesquite software (Maddison & Maddison, 2006). For all other analyses we used the R statistical computing environment (R Development Core Team, 2003) with additional unpublished functions by R. Freckleton (University of Sheffield) for the PGLS procedure. Sample sizes differ across tests because data are incomplete for some species. All statistical tests are two-tailed with a 95% confidence level. Since the phylogenetic methods applied here do not allow the graphical presentation of phylogenetically corrected data, we present figures based on raw species data.

Results

Pre-breeding molt

Pre-breeding molt was more common in polygynous than in monogamous species (Table 6.1). Neither the occurrence nor the extent of pre-breeding molt was related to testis size, habitat or flocking behavior (Table 6.1-6.2). Pre-breeding molt

occurred more frequently in migratory than in resident species (Table 6.1), and species that migrate longer distances showed more extensive pre-breeding molts (Table 6.2). Species with more extensive pre-breeding molts had later breeding onset (Fig. 6.1, Table 6.2) and more insectivorous diet (Fig. 6.2 A, Table 6.2). The effect of breeding onset on molt extent remained significant when we controlled for breeding latitude and migration distance (breeding onset: $F_{1,122} = 26.35$, $p < 0.001$; breeding latitude: $F_{1,122} = 0.07$, $p = 0.794$; migration: $F_{1,122} = 8.71$, $p = 0.004$). Winter latitude was significantly related both to the extent of pre-breeding molt ($F_{1,129} = 22.74$, $p < 0.001$, $\lambda = 0.11$) and to winter diet ($F_{2,95} = 24.23$, $p < 0.001$, $\lambda = 0.01$). The interaction of diet and winter latitude had a significant effect on the extent of pre-breeding molt ($F_{3,87} = 7.98$, $p < 0.001$, $\lambda < 0.001$): towards more southern latitudes, granivorous species molt more while species with mixed diets molt less extensively (Fig. 6.2 B). After controlling for migration distance, the extent of pre-breeding molt was still significantly related to both breeding onset (migration: $F_{1,120} = 8.14$, $p = 0.005$; breeding onset: $F_{1,120} = 26.42$, $p < 0.001$) and to the interaction of diet and winter latitude (migration: $F_{1,83} = 23.62$, $p < 0.001$; diet*latitude: $F_{3,83} = 3.42$, $p = 0.021$). In stepwise model-selection, the final model contained breeding onset ($F_{1,79} = 11.58$, $p = 0.001$), the interaction of diet and winter latitude ($F_{3,79} = 8.12$, $p < 0.001$), and mating system ($F_{2,79} = 4.76$, $p = 0.011$). The best model in the AIC_c -based model-comparison was identical to the final model of the stepwise procedure (Table 6.3). Based on multimodel inference, breeding onset ($\Sigma = 0.83$), diet*latitude ($\Sigma = 0.83$) and mating system ($\Sigma = 0.81$) appeared similarly important in explaining the extent of pre-breeding molt, while migration distance had smaller impact ($\Sigma = 0.58$).

Table 6.1: Bivariate relationships of the occurrence of pre-breeding molt, feather abrasion, and their combined strategy with ecological and life-history variables, in Pagel's maximum likelihood estimations controlled for phylogeny. *P*-values are based on 5000 simulations. Mating system and winter diet were split into dichotomous dummy variables.

	Pre-breeding molt			Feather abrasion			Combined strat- egy		
	χ^2	<i>P</i>	<i>N</i>	χ^2	<i>P</i>	<i>N</i>	χ^2	<i>P</i>	<i>N</i>
Mating system ¹	11.62	0.022	129	4.48	0.421	131	12.26	0.004	119
Mating system ²	9.36	0.033	129	7.96	0.030	131	10.74	0.003	119
Testis size	1.66	0.681	106	1.88	0.584	105	1.56	0.570	96
Habitat	0.19	0.089	123	8.06	0.026	129	3.70	0.194	115
Flocking behavior	3.80	0.616	127	13.38	0.012	132	3.26	0.507	118
Migratory status	17.56	<0.001	134	7.68	0.101	140	4.32	0.273	124
Breeding onset	17.94	0.001	127				6.06	0.177	117
Diet ³	5.39	0.058	89				1.66	0.273	85
Diet ⁴	6.57	0.182	89				1.50	0.591	85

¹monogamy vs. weak or strong polygyny

²monogamy or weak polygyny vs. strong polygyny

³granivory vs. mixed diet or insectivory

⁴granivory or mixed diet vs. insectivory

Table 6.2: *Bivariate relationships of the extent of pre-breeding molt with ecological and life-history variables, in PGLS models. The degree of phylogenetic dependence (λ) was set to the most appropriate value in each model, evaluated by likelihood ratio statistics.*

	λ	F (df)	P
Mating system	0.21	1.67 (2,128)	0.193
Testis size	0.26	0.86 (1,105)	0.357
Habitat	0.11	0.78 (1,122)	0.378
Flocking behavior	0.15	0.41 (1,125)	0.524
Migration distance	<0.001	28.26 (1,129)	<0.001
Breeding onset	0.07	20.78 (1,126)	<0.001
Diet	<0.001	6.11 (2,88)	0.003

Feather abrasion

Color change by feather abrasion was associated with strongly polygynous mating systems (Table 6.1), flocking behavior (Fig. 6.3 A, Table 6.1) and open habitats (Fig. 6.3 B, Table 6.1), while it was unrelated to testis size and migratory status (Table 6.1). In stepwise model-selection, the final model contained flocking behavior only ($\chi^2_1 = 11.75$, $p = 0.001$, $n = 132$). The result of the AIC_c -based model-comparison was fully consistent with the latter result: the best model contained flocking behavior only, and the first 3 best models included flocking behavior consistently (Table 6.4). Habitat ($\Sigma = 0.47$) was more important in explaining the occurrence of abrasion than was mating system ($\Sigma = 0.29$), and both had smaller impact than flocking behavior ($\Sigma = 0.79$).

Table 6.3: Comparison of multivariate PGLS models for the extent of pre-breeding molt. AIC_c values, number of estimated parameters (k), AIC_c differences between the best model and each candidate model (Δ_i), and Akaike weights (ω_i) are given for each candidate model ($n = 82$ species). Models with $\Delta_i < 2$ are considered to have substantial support; ω_i is a relative estimate of the probability that a given model is actually the best model in the model set.

predictors	k	AIC_c	Δ_i	ω_i
breeding onset, diet*latitude, mating system	7	317.39	0.00	0.33
breeding onset, diet*latitude, mating system, migration distance	8	317.66	0.27	0.29
breeding onset, diet*latitude	5	320.30	2.92	0.08
diet*latitude, mating system, migration distance	7	320.38	2.99	0.07
breeding onset, mating system, migration distance	5	320.99	3.61	0.06
mating system, migration distance	4	321.21	3.83	0.05
breeding onset, diet*latitude, migration distance	6	321.76	4.37	0.04
breeding onset, migration distance	3	321.89	4.51	0.04
migration distance	2	322.56	5.18	0.03
diet*latitude, migration distance	5	324.36	6.97	0.01
diet*latitude, mating system	6	325.67	8.29	0.01
diet*latitude	4	327.51	10.12	<0.01
breeding onset	2	328.53	11.14	<0.01
breeding onset, mating system	4	330.23	12.85	<0.01
mating system	3	338.34	20.95	<0.01

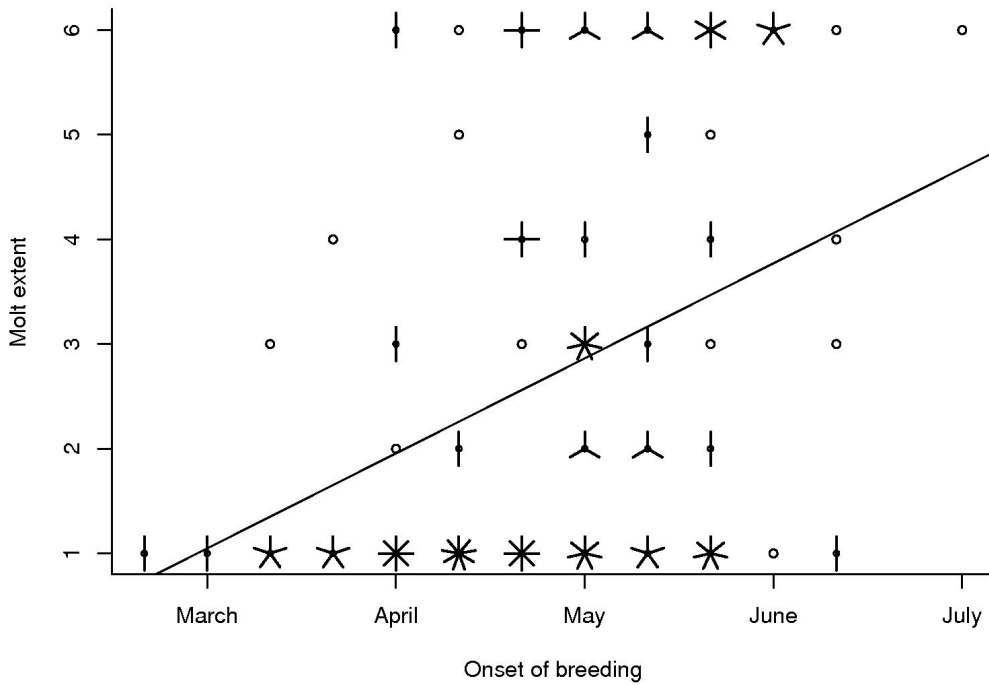


Fig. 6.1: *Species breeding later have a more extensive pre-breeding molt. The number of radii indicates the number of overlapping data points (species).*

Table 6.4: *Comparison of multivariate generalized linear models for the occurrence of feather abrasion ($n = 116$ species). See Table 6.3 for further explanation.*

predictors	k	AIC_c	Δ_i	ω_i
flocking behavior	2	156.62	0.00	0.35
flocking behavior, habitat	3	157.56	0.94	0.22
flocking behavior, mating system	4	158.29	1.67	0.15
habitat	2	158.48	1.86	0.14
flocking behavior, mating system, habitat	5	159.89	3.27	0.07
mating system, habitat	4	160.63	4.01	0.05
mating system	3	162.22	5.60	0.02

The combined strategy

The combined occurrence of pre-breeding molt and abrasion was more common in more polygynous species (Fig. 6.4, Table 6.1), while it was unrelated to all other predictors (Table 6.1). These results were qualitatively unchanged when we excluded species with no color-change strategy from the analyses (results not shown). In stepwise model-selection, the final model contained mating system only ($\chi^2_2 = 9.85$, $p = 0.007$, $n = 120$). The result of the AIC_c -based model-comparison was again fully consistent with the stepwise approach: the best model contained mating system only, and the first 4 best models all included mating system consistently (Table 6.5). The sums of Akaike weights also supported that mating system was by far the most important predictor ($\Sigma = 0.94$) of the combined color-change strategy, followed by the relatively small impacts flocking behavior ($\Sigma = 0.30$) and breeding onset ($\Sigma = 0.25$), while diet*latitude was of minor importance ($\Sigma = 0.03$).

Bivariate analyses of the predictor variables revealed several interrelations among the predictors (Appendix 6.A). However, the variance inflation factor was < 2 in all multivariate models above, indicating that multicollinearity was not a problem in our analyses.

Table 6.5: Comparison of multivariate generalized linear models for the combined occurrence of pre-breeding molt and feather abrasion ($n = 72$ species). See Table 6.3 for further explanation.

predictors	k	AIC_c	Δ_i	ω_i
mating system	3	75.81	0.00	0.50
mating system, flocking behavior	4	77.73	1.92	0.19
breeding onset, mating system	4	78.06	2.24	0.16
breeding onset, mating system, flocking behavior	5	80.04	4.23	0.06
flocking behavior	2	81.59	5.78	0.03
diet*latitude, mating system	6	82.71	6.90	0.02
breeding onset	2	82.86	7.04	0.01
breeding onset, flocking behavior	3	83.77	7.95	0.01
diet*latitude, mating system, flocking behavior	7	84.55	8.73	0.01
breeding onset, diet*latitude, mating system	7	85.17	9.35	0.00
breeding onset, diet*latitude, mating system, flocking behavior	8	87.08	11.27	0.00
diet*latitude, flocking behavior	5	87.15	11.34	0.00
diet*latitude	4	87.17	11.36	0.00
breeding onset, diet*latitude	5	89.45	13.64	0.00
breeding onset, diet*latitude, flocking behavior	6	89.53	13.72	0.00

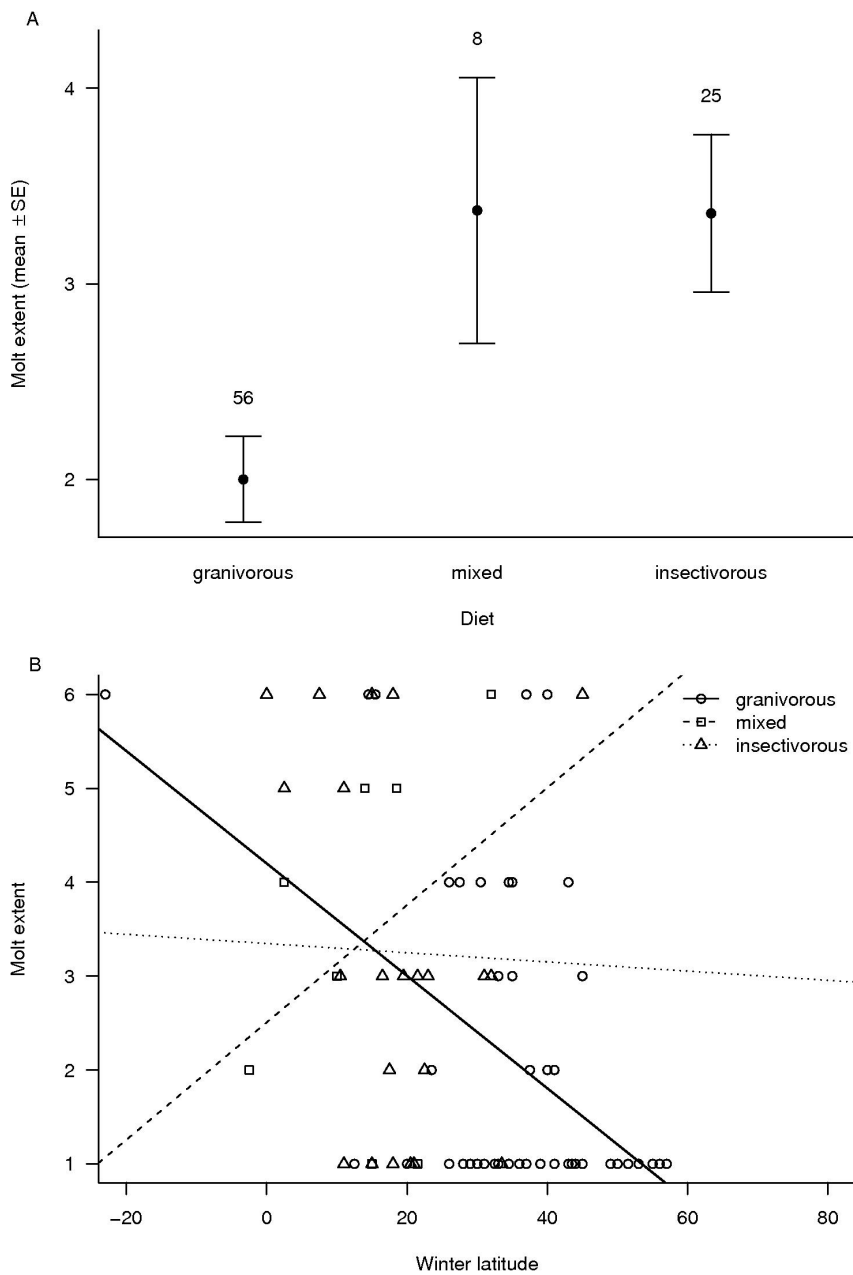


Fig. 6.2: Pre-breeding molt is more extensive in species with more insectivorous diets (A) and increases with the latitude of wintering grounds, while granivorous species molt less extensively towards greater (i.e. more northern) latitudes (B). Numbers above the whiskers denote the corresponding sample sizes.

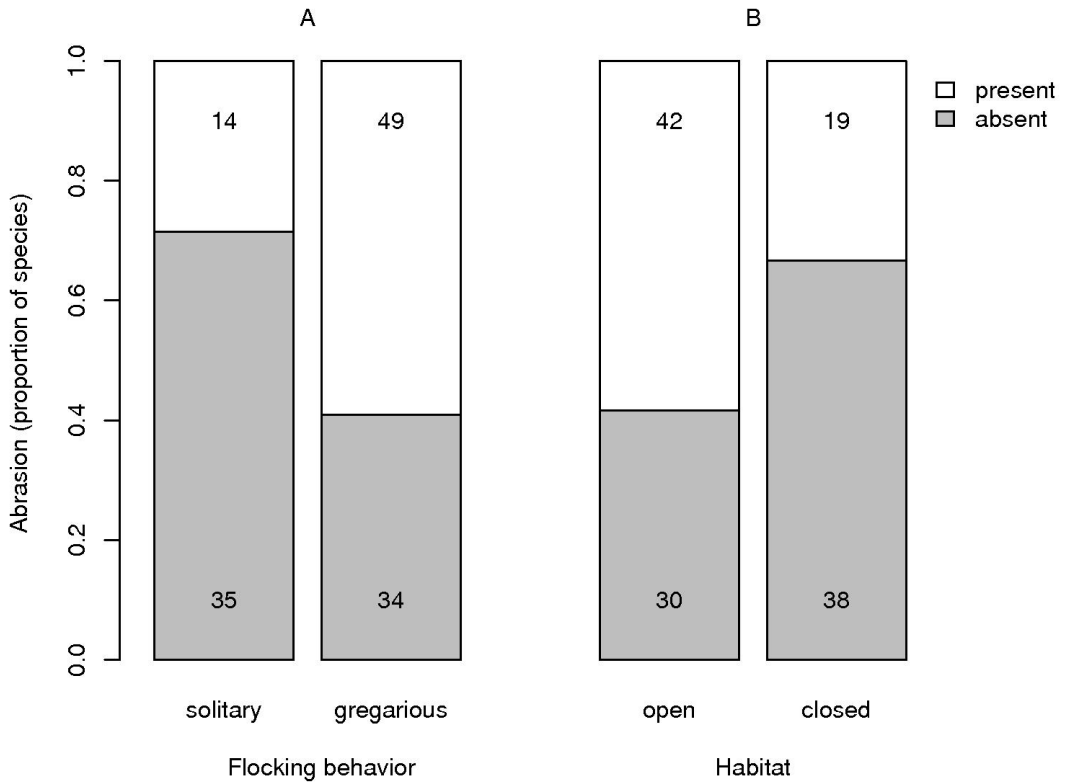


Fig. 6.3: *Feather abrasion is more common in species with winter flocking behavior (A) and open wintering habitats (B). Numbers on the bars denote sample sizes.*

Discussion

In this study we aimed to explore the environmental and life history covariates of the interspecific variation in the two main strategies of seasonal dichromatism. We obtained three key results. First, both the occurrence and the extent of pre-breeding molt was most strongly related to the onset of breeding and winter diet, that is, the factors that may constrain feather replacement due to time and energy costs. Second, color change by abrading feather tips was best predicted by non-breeding flocking behavior, indicating the role of selection for social signaling in determining the need and type of seasonal color change. Finally, the combined occurrence of pre-breeding molt and abrasion was more common in more

polygynous species, suggesting that species under strong sexual selection may use multiple strategies to acquire colorful breeding plumages. These results show that a complex set of selective forces and constraints acting in different life-cycle periods are necessary to explain the observed patterns of seasonal dichromatism among passerine birds such as finches and sparrows.

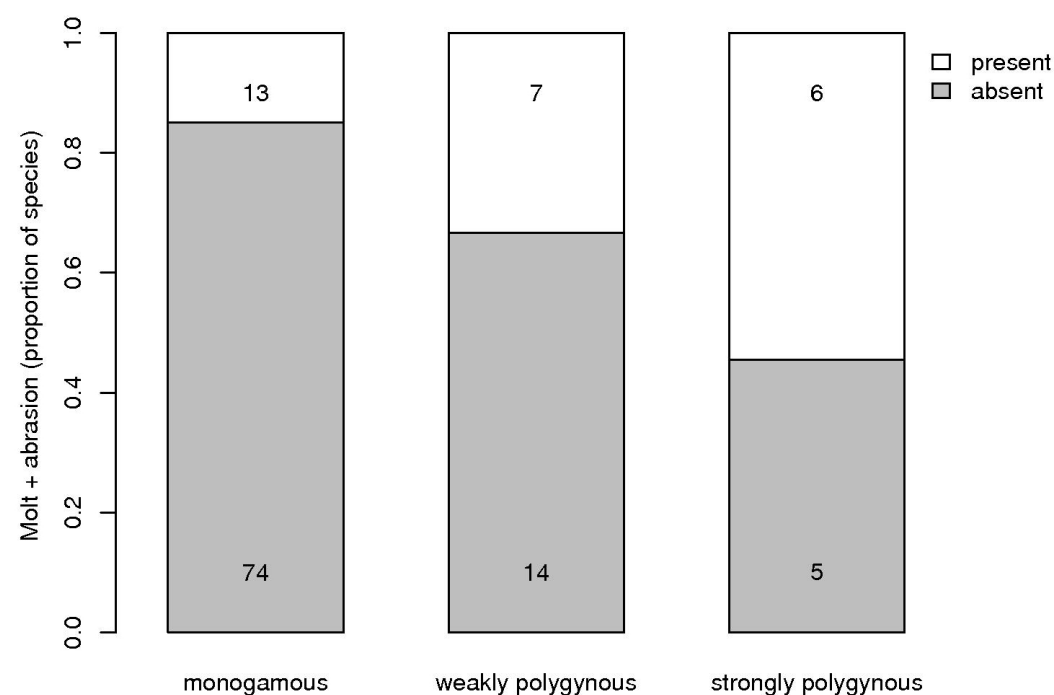


Fig. 6.4: *The combined color-change strategy (i.e. both pre-breeding molt and feather abrasion) is more common in species with more polygynous social mating system. Numbers on the bars denote sample sizes.*

Our results strongly support that the costs of molt may significantly constrain the evolution of pre-breeding molt. In line with the suggestions and findings of previous studies (Hamilton & Barth, 1962, Rohwer & Butcher, 1988, Froehlich *et al.*, 2004), we found that both the occurrence and the extent of pre-breeding molt is related to migration distance. The role of migration in shaping various molt strategies has been suggested by theoretical models and previous phyloge-

netic comparative studies alike (e.g. Holmgren & Hedenström, 1995, Svensson & Hedenström, 1999, Barta *et al.*, 2008), and this relationship is explained as an effect of natural selection that results in optimal timing of costly life-history events such as breeding, migration and molt. Froehlich *et al.* (2004) proposed that the relation between migration and pre-breeding molt may reflect time constraints on resident species that may be selected to begin breeding as early as possible, and hence no time left to molt once more before breeding. Our results are consistent with this hypothesis, demonstrating that species with later breeding onset molt more extensively in spring. Furthermore, we found that winter diet was a similarly important determinant of spring molt, suggesting that the nutritional demands of feather replacement may also be a significant constraint for the evolution of pre-breeding molt. The impact of different diet types varied with wintering latitude, implying that molt is most constrained in granivorous northern winterers and omnivorous tropical winterers. This finding is different from the results of Froehlich *et al.* (2004) who found that pre-breeding molt was unrelated to diet in temperate winterers, while it was constrained in insectivorous Neotropical winterers by the scarce abundance of insects during molt. However, their dataset was limited to species with complete (not partial) pre-breeding molts and included very few insectivorous species among temperate winterers. Based on a dataset with 67 tropical and 83 temperate winterers, our results indicate that diet has an impact on the evolution of pre-breeding molt even after accounting for the constraints of breeding onset and migration, challenging the previous assumption that partial pre-breeding molts are unlikely to have significant energetic costs (Froehlich *et al.*, 2004). Finally, our study indicates that high levels of polygyny also select for pre-breeding molt. Thus, in addition to the nutritional and time constraints, the sexual-selection advantage conferred by freshly molted breeding plumages also appear important in shaping the interspecific variation of pre-breeding molt.

Seasonal color change by the abrasion of feather tips is not a complete alternative to pre-breeding molt, as the interspecific variation in the occurrence of abrasion appears to have its determinants unrelated to pre-breeding molt. Most importantly, abrasion is more common in flocking species than in those living solitarily in the non-breeding season. Additionally, abrasion is more frequent in

open than in closed habitats. Although the latter effect was less strongly supported than the effect of flocking behavior, the second best model for abrasion contained both habitat and flocking behavior (Table 6.5). These two lines of evidence suggest that predation risk in open wintering grounds may select for a less conspicuous non-breeding plumage, but in a way that some ornaments hidden by cryptic feather tips may still be expressed in flocking species. Such „coverable badges” or „remnants of breeding coloration” may serve as status signals in winter flocks of birds, as has been shown for a number of finch and sparrow species (Hansen & Rohwer, 1986, Senar, 1999), or may facilitate early pairing (McGraw, 2004). Furthermore, birds may be able to control the degree of abrasion of their feathers by preening, thereby adjusting the expression of their color badges to the signaling needs presented by their social environment (Møller & Erritzøe, 1992, Veiga, 1996, González *et al.*, 2001). Since habitat type is related to many ecological characteristics of the species, including almost all other predictors used in our study (Appendix 6.A), it is admittedly a rather weak proxy for predation pressure on adult birds. Therefore we call for great caution when interpreting our findings on habitat type. Until more direct measures of predation pressure become available for the non-breeding seasons, our results suggest that the importance of winter predation in determining seasonal color change is medium (for feather abrasion) to low (for pre-breeding molt). This finding is in line with the recent conclusion of Møller *et al.* (2006) that the risk of predation may be a consequence rather than the determinant of sexually selected displays in songbirds. Finally, although sexual selection in polygynous species favored seasonal color change by abrasion according to our results, the occurrence of abrasion appeared more strongly influenced by selection for optimal winter coloration, i.e. for social signaling and camouflage.

Since feather abrasion as a strategy of seasonal dichromatism had been virtually unstudied by comparative approaches, our study is the first one to investigate this phenomenon in a phylogenetic context. However, there is still much to explore in this field. The apparent lack of costs associated with abrasion begs the question why not all birds achieve seasonal color change by abrasion instead of the demanding process of molt. One explanation may be that the full exposure of ornamented plumage might be difficult in less abrasive habitats (Froehlich *et*

al., 2004). Our finding that abrasion is less common in species occupying closed habitats might support this idea if feather wear is better facilitated in open habitats by airborne particles, contact with substrates, or solar radiation (Miller, 1961, Burt, 1986). To our knowledge, these possibilities are completely unexplored.

Finally, we have also found that a number of species employ both pre-breeding molt and abrasion to change their appearance seasonally. For instance, both lazuli bunting (*Passerina amoena*) and Lapland bunting (*Calcarius lapponicus*) males change from a rather dull non-breeding plumage to a spectacular breeding aspect mostly by abrading buffy feather tips, but before breeding they also renew some of their head and chin feathers by molt. Our results show that this combined strategy is strongly associated with polygynous mating system, implying that species under intensive sexual selection exhibit both more extensive pre-breeding molts and more frequent abrasion. Polygynous species may be strongly selected to express highly ornamented breeding plumage, thus they may benefit from combining molt and abrasion if this enables a more extensive or more reliable color change. For example, because of the costs of molting, a bird with partial pre-breeding molt may increase the area of colorful plumage by additionally abrading some feathers that cannot be molted. Alternatively, if abrasion is not complete, e.g. if the habitat is less abrasive or the birds cannot preen certain plumage areas (e.g. on the head) to enhance abrasion, then it may pay males to molt some feathers before breeding to ensure the expression of breeding colors. In polygynous species, the sexual-selection advantage of such multiple efforts for seasonal color change seems to override the impact of both the costs of molting and the selective forces acting on winter plumage color.

To summarize, we have provided phylogenetic comparative evidence that in a diverse clade of finches and sparrows the two strategies of seasonal dichromatism evolve in response to partially different selection pressures as surrogated by various life-history traits. We found that both nutritional and time constraints are important determinants of pre-breeding molt, which may still be selected for in strongly polygynous species. Abrasion of dull feather tips, a previously neglected component of seasonal color change, may optimize the degree of ornamentation for the different life-cycle periods, as both camouflage and social signaling seem to favor limited expression of color badges during winter, while intensive sex-

ual selection in polygynous species may promote full exposure of breeding coloration.

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Appendix 6.A

Bivariate relationships between the variables used as predictors for the occurrence and/or extent of pre-breeding molt and feather abrasion. For pairs of two categorical variables, Pagel's maximum likelihood estimations are given, with p-values based on 1000 simulations. For all other cases, PGLS models are reported.

	testis size	flocking be- havior	habitat	migration distance	breeding on- set	diet ²
mating system ¹	$F_{2,115} = 8.11$ $\lambda = 0.30$ $p < 0.001$	$\chi^2 = 3.36$ $n = 133$ $p = 0.558$	$\chi^2 = 11.18$ $n = 130$ $p = 0.004$	$F_{2,136} = 1.67$ $\lambda = 0.07$ $p = 0.193$	$F_{2,134} = 0.63$ $\lambda < 0.001$ $p = 0.534$	$\chi^2 = 4.10$ $n = 95$ $p < 0.001$
testis size		$F_{1,110} = 2.72$ $\lambda = 0.23$ $p = 0.271$	$F_{1,108} = 14.87$ $\lambda = 0.19$ $p < 0.001$	$F_{1,112} = 0.46$ $\lambda = 0.26$ $p = 0.501$	$F_{1,111} < 0.001$ $\lambda = 0.27$ $p = 0.983$	$F_{2,78} = 1.35$ $\lambda = 0.05$ $p = 0.265$
flocking behav- ior			$\chi^2 = 21.04$ $n = 129$ $p < 0.001$	$F_{1,135} = 7.12$ $\lambda = 0.10$ $p = 0.009$	$F_{1,133} = 1.37$ $\lambda < 0.001$ $p = 0.243$	$\chi^2 = 27.96$ $n = 93$ $p < 0.001$
habitat				$F_{1,131} = 9.42$ $\lambda < 0.001$ $p = 0.002$	$F_{1,129} = 3.33$ $\lambda < 0.001$ $p = 0.070$	$\chi^2 = 25.92$ $n = 89$ $p = 0.008$
migration distance					$F_{1,136} = 41.27$ $\lambda < 0.001$ $p < 0.001$	$F_{2,95} = 8.67$ $\lambda = 0.11$ $p < 0.001$
breeding onset						$F_{2,93} = 1.28$ $p < 0.001$ $p = 0.282$

¹ monogamy vs. weak or strong polygyny

² granivory vs. mixed diet or insectivory