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REVIEW

Marilyn Ramenofsky · John C. Wingfield

Behavioral and physiological conflicts in migrants: the transition between migration and breeding

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Abstract Progression of the vernal migratory life history stage to breeding presents a number of apparent behavioral and physiological conflicts. Features that characterize the migratory stage include: high mobility, sociality, repetitive cycles of feeding (hyperphagia and fattening) and migratory flight. Breeding comprises: sedentary, territorial and reproductive behaviors, an initial decline in hyperphagia and reduction of fuel stores. Because morphology, physiology and behavior change, the transition between stages cannot be instantaneous. In many species development of the reproductive system actually occurs during migration, but in others gonadal development may not commence until later. This variation in degree of overlap of migration and reproductive functions is not well understood, but may be related to migratory distance and length of the breeding season, which tends to be shorter at higher latitudes and altitudes. In these habitats, migrants may arrive at their breeding sites to find unpredictable conditions that cannot support breeding. At this juncture, migrants may retreat to refugia and prolong maintenance of facultative migratory functions, termed arrival biology, until conditions improve sufficiently to initiate breeding. In this review, we focus on the Pacific races of the white-crowned sparrow, *Zonototrichia leucophyrs*, in which the entire spectrum of migratory strategies are represented from resident to long distance migrants and about which much is known. This species presents a unique view of the appearance and variations in arrival biology. Focusing on the juncture between migration and breeding, we discuss the diversity of responses of congeners to a spectrum of environmental conditions that favor survival and reproductive success.

Keywords Arrival biology · Breeding · Endocrinology · Finite state machine theory · Migration

Introduction

When considering the complex annual cycle of a migratory species, vernal migration is followed immediately by breeding. But this overview belies the complexity of these events and the finely tuned relationship of environmental conditions with the progression of life history stages throughout spring. Predictable environmental cues, such as increasing day length, serve to regulate the progression of life history stages, either as a driver or as a *zeitgeber* for endogenous annual rhythms of morphological, physiological and behavioral changes (Farner and Gwinner 1980; Gwinner 1986, 1996). However, local predictive cues and perturbations of the environment, such as weather, temperature, food supplies, etc., maintain the organism in close alliance with both current and long term conditions (Wingfield et al. 1999; Wingfield and Ramenofsky 1999). Here, we delve into the progression of the life history stages that start on the wintering (non-breeding) grounds and culminate with the onset of breeding activities at distant locations, and then discuss the environmental and endocrine control of this transition. Much has been written on the environmental control and endocrinology of breeding and migration in birds (e.g., Gwinner 1986, 1996; Berthold 1996; Wingfield and Silverin 2002), but the interfaces and overlap of these two major events are less well known. We take a finite state machine approach (Jacobs and Wingfield 2000) using the concept of life history stages, their characteristic sub-stages, and degree of overlap (Wingfield and Jacobs 1999) as a framework for a complex period in the life cycle.

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M. Ramenofsky (✉) · J. C. Wingfield
Department of Biology, University of Washington,
Box 351800, Seattle, WA 98195, USA
E-mail: mramenof@u.washington.edu
Tel.: +1-206-6168658
Fax: +1-206-5433041

Finite state machine theory as applied to the migration breeding transition: general concept

Migration and breeding life history stages are conspicuous components of the life cycle of a migratory species that includes other, equally important, stages that occur in a set temporal sequence usually on an annual schedule (Wingfield and Jacobs 1999; Jacobs and Wingfield 2000; Ramenofsky et al. 2003). Each stage has a development phase leading to mature capability when the characteristic sub-stages can be expressed marking onset of the life history stage (Jacobs and Wingfield 2000). The conclusion of this stage is indicated by the termination phase that overlaps, to varying degrees, the development phase of the next life history stage. State of an individual is a combination of life history stages and sub-stages expressed at any point in the life cycle. Because phenotypes have a set number of stages each with a fixed number of sub-stages, there is a finite number of states that can be expressed throughout the life cycle, hence the term, finite state machine (Jacobs and Wingfield 2000). Given ecological and temporal constraints, it is possible that some species may overlap portions of two life history stages, i.e., mature capability of one stage and developmental portion of the subsequent stage. These have been termed "super states"; they are energetically expensive and tend to be short in duration (Wingfield and Jacobs 1999). However, while it is energetically and physically feasible to overlap mature capability of two life history stages, the expression (at mature capability) of both stages is not. For example, it would not be possible for birds to be territorial with a nest and eggs while still migrating. Nonetheless, the potential for overlap of the developmental phase of one life history stage with mature capability of another provides flexibility to more finely tune adjustments to variable environmental conditions (Wingfield and Jacobs 1999; Wingfield 2005).

Life history stage of vernal migration

Vernal migration, as discussed here, is the movement of a population from a wintering ground to a breeding area. Mostly, this is a migration to higher latitude and/or altitude, but in some cases a longitudinal movement is involved. Piersma (1987) classified avian migration patterns roughly into those species that cross large barriers such as the Sahara Desert, mountain ranges, or large tracts of ocean in one flight, with major "stopover" sites where birds recover and refuel. This was recently redefined as "long-bout migrants" referring to the distance covered in each leg of the journey (Landys et al. 2004). Other species migrate overland with frequent, perhaps daily, short flights interspersed with brief refueling periods en route and are labeled "short-bout migrants" (Landys et al. 2004; see also Piersma 1987). In the northern hemisphere, the overland "short-bout" strategy is probably the prevalent form of migration although it has received less research attention. Here, we will focus on *Zonotrichia* species in which initiation of the vernal phase of migration is influenced by the increase in photoperiod of spring (Farner et al. 1957; Farner 1964; Schwabl and Farner 1989; Wingfield et al. 1990; Ramenofsky et al. 1999). Lengthening days from the winter solstice induce the hypothalamic-pituitary-gonad axis to secrete relatively low (compared to the breeding season) levels of the androgens (testosterone and 5α-dihydrotestosterone) that act to organize specific appetite centers in the hypothalamus and associated neural pathways (Mattocks 1976; Schwabl and Farner 1989; Wingfield et al. 1990; Kuenzel et al. 1999). Once day length reaches a critical level of 12 h of light ($>12L$) per day, activation of these centers occurs probably through such brain peptides as neuropeptide Y to induce hyperphagia, followed by fattening and increase in body weight (Richardson et al. 1995; Boswell et al. 1998). Erythropoeisis, production of red blood cells, increases hematocrit to enhance oxygen carrying capacity of the blood, and biochemical changes within the flight muscle occur to elevate the aerobic capacity of muscle for endurance flight, plus increased thermogenic capacity and low thermal tolerance (Dawson et al. 1983; Marsh 1981; Lundgren and Kiessling 1988; Wingfield et al. 1990; Morton 1994; Swanson 1995). Liver, adipose and muscle tissues increase in size with enhanced capacity for storing and delivering fuels (Fry et al. 1972; Ramenofsky 1990; Jenni-Eiermann and Jenni 1992; Driedzic et al. 1993; Ramenofsky et al. 1999; Jenni-Eiermann et al. 2001; Guglielmo et al. 2002; McWilliams et al. 2004). Collectively, these events can be regarded as the development phase of vernal migration that results in mature capability (Zugdisposition) so that actual migratory flight can begin at an appropriate time. Migratory behavior and physiology include alternating patterns of anabolic and catabolic functions. The anabolic arm (sub-stages) of the cycle includes feeding, fattening, organ hypertrophy and atrophy, enzymes systems promoting fuel transfer and deposition, preparation for take-off, and elevations of glucocorticoid secretion (Landys-Ciannelli et al. 2002). This is followed by catabolic conditions (sub-stages) of take-off, oriented and navigational flight, and enzymatic and hormonal regulation of fuel delivery from stock depots to muscle and central nervous system, culminating in landing, post flight metabolic adjustments, and organ restitution (Piersma 1998; Bauchinger 2002). This may repeat numerous times depending upon species, routes covered and migration strategy (stop over biology)(Fig. 1).

Once the breeding grounds are reached, the feeding/flight cycles cease and arrival behavior and physiology ensue, the nature of which is contingent upon local phenological conditions and species. This phase, probably marking the beginning of the termination phase of vernal migration, has been called "arrival biology" (Wingfield et al. 2004) and in many species breeding at high latitudes and altitudes may involve spatial opportunism and

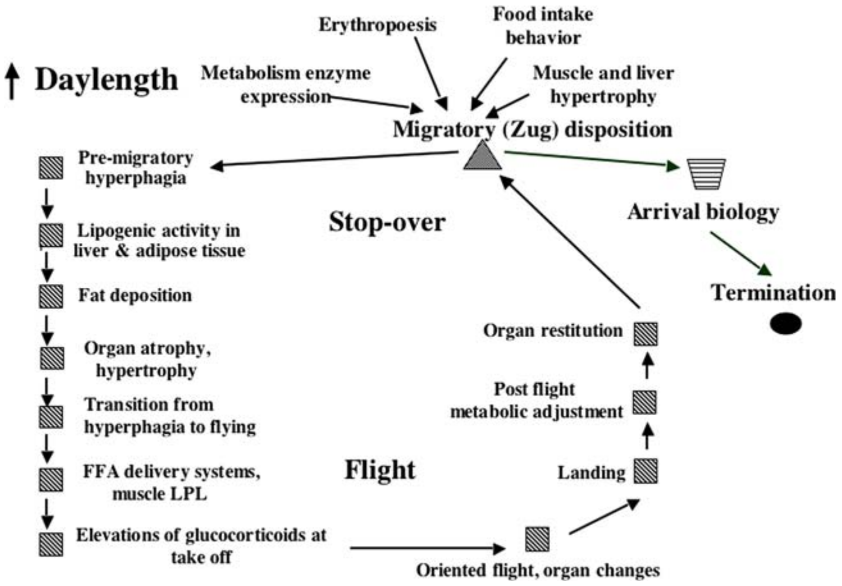

Fig. 1 Diagram of migration life history sub-stages. The environmental signal of increased daylength induces the developmental phase of migration culminating in migratory or zugdisposition (*triangle*). Expression of diverse physiological and behavioral components (sub-stages) of the mature capability phase (*rectangle*) may occur once or repeat in numerous cycles. Upon arrival on or near the breeding grounds, birds retain mobility, fuel storage, and thermogenic capacity if conditions are not conducive for breeding, as they shuttle between breeding sites and refugia (arrival biology) (*quadrilateral*). When conditions on breeding grounds ameliorate, the migratory life history stage is terminated (*circle*)

facultative altitudinal migration (Hahn and Morton 1995, Hahn et al. 2004). These concepts readdress ideas presented earlier (Helms 1963; Gauthreaux 1980; Terrill and Able 1988) concerning adaptations of physiology and behavior of migrants confronting severe conditions at either the breeding or wintering sites that include prevalent storms, decreased availability of food and heightened demands for energy. In terms of arrival biology, birds may remain on breeding territories or return to a mobile state in which they seek out sheltered locations and/or continue to wander. Hyperphagia maintains enhanced fuel stores to support mobile activity and provides protection against potential severe food limitation (snow cover) while birds remain closely associated in flocks. Species show great variation in the types of behavior displayed in these latter sub-stages and more field research is needed. Once conditions on breeding grounds ameliorate or a suitable site is located, the vernal migratory life history stage is terminated, flocks disband, hyperhagia wanes, fat stores decline, as birds become territorial and commence breeding.

Life history stage of breeding

The majority of avian, indeed all vertebrate, species breed periodically, usually on a seasonal basis, with complete development of the reproductive system leading to mature capability, followed by regression of the reproductive system to an immature state. As for vernal migration, the increase in day length in spring activates the hypothalamic-pituitary-gonad axis to initiate production and secretion of reproductive hormones, including hypothalamic neuropeptides such as the gonadotropin releasing hormones, pituitary gonadotropins [luteinizing hormone (LH) and follicle stimulating hormone (FSH)] that initiate growth, development of the endocrine and gametogenic gonad, secondary sexual features, accessory sex organs, and reproductive behavior. Together, these comprise the developmental phase (Wingfield and Farner 1980). At this point, mature capability is achieved and actual onset of breeding may follow immediately or may be delayed until a territory is established, a pair bond formed and appropriate conditions allow. Once breeding begins, a new suite of sub-stages is expressed, including nest building, ovulation and oviposition, incubation and feeding of young. These sub-stages can occur in complex sub-cycles, especially in multiple brooded species (Wingfield and Jacobs 1999). At the end of the breeding season, birds become refractory to long days and the reproduction life history stage is terminated (Nicholls et al. 1988; Dawson 2001)(Fig. 2).

Overlap of vernal migration and breeding life history stages

With the vernal migration and breeding life history stages defined, it is now possible to discuss ways in which the two could overlap. We know that, in some species, migration is completed before gonadal recrudescence begins, although these tend to be short distance migrants (examples and refs, Fig. 3). Yet others show

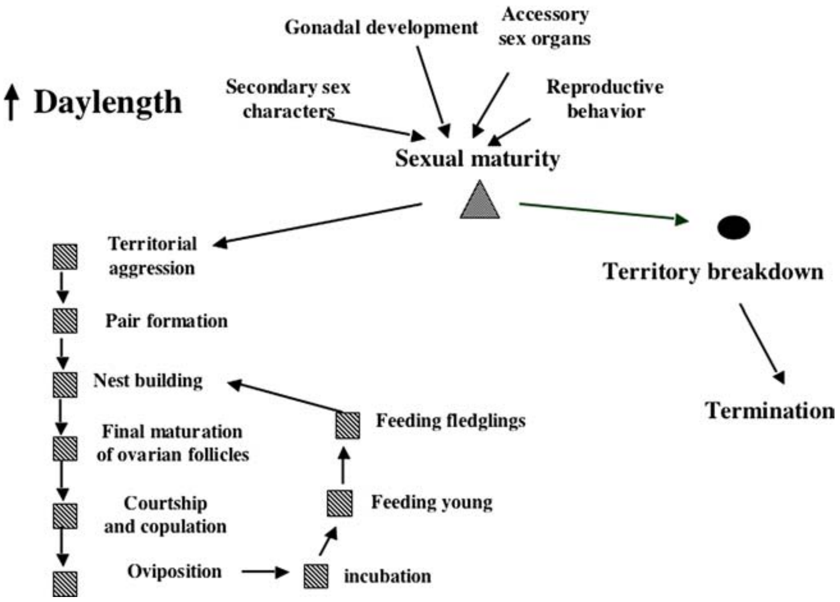

Fig. 2 Diagram of breeding life history sub-stages. Increase in daylength induces the developmental phase of breeding that culminates in sexual maturity (*triangle*). Expression of diverse physiological and behavioral components (sub-stages) of the mature capability phase (*rectangle*) proceeds sequentially and may have repeating subsets for multiple brooded species. Breeding subsides with the onset of refractoriness, moult, territory breakdown and termination (*circle*)

varying degrees of gonadal development during migration, indicating that the development phase of breeding can overlap entirely with mature capability of migration, and the termination phase of migration may overlap with mature capability of the breeding stage (examples and refs, Fig. 4). Clearly, it is not possible to overlap onset of migration with onset of breeding because birds are oviparous and must be temporarily sedentary to build a nest, incubate eggs, etc. Nonetheless, completion of the developmental phase of breeding and mature capability (but before onset of laying) will allow the mobility required for at least local migrations. Thus, the developmental phases for both males and females of many species must start during the migratory life history stage in order to be prepared to initiate breeding soon after arrival. This is particularly important in locations where the window of opportunity to breed is limited, such as at high latitude and altitude. When mature capability of breeding is expressed, the migratory life history stage must be terminated, as adults establish and maintain breeding territories, cease the mobile lifestyle, attract mates, copulate and raise young to independence (Fig. 4). In some cases, such as songbirds arriving on the arctic tundra, there may be prolonged overlap of the final stages of migration and mature capability of breeding. In these instances, birds arrive with mature, or close to mature, gonads, but may still retain an ability to migrate or remain mobile depending upon local weather that can be highly variable. In some years, arriving birds are met with complete and deep snow cover, while in

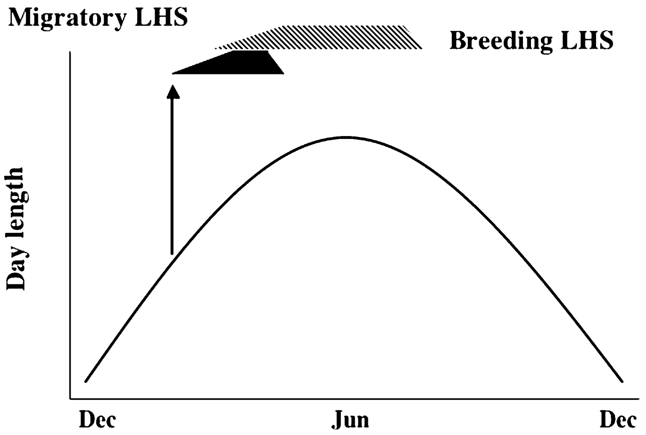

Fig. 3 Diagram of annual photoperiod and indication of the onset of migration life history stage (*arrow*) divided into the phases of development (*left-pointing black triangle*), mature capability (*black rectangle*) and termination (*black right triangle*), and the onset of breeding life history stage divided into the sub-stages described in Fig. 5, in *Zonotrichia l. pugetensis*, a short distance migrant. Data drawn from Blanchard (1942), Lewis (1975) and Wingfield and Farner (1978a)

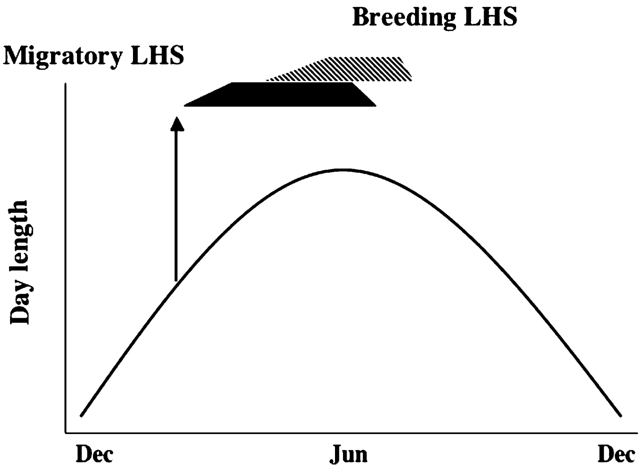

Fig. 4 Diagram of annual photoperiod and indication of the onset and progressions of migration and breeding life history stages in *Zonotrichia l. gambelii*, a long distance migrant. Figure descriptions presented in Fig. 3. Data drawn from Wingfield and Farner (1978a, b) and Hahn et al. (1995)

others the tundra may be snow-free. There is no way for birds to predict what conditions will be on arrival and they must retain the ability to move and be spatially opportunistic (Hahn et al. 1995, 2004; Wingfield and Hunt 2002; Wingfield et al. 2004). They use microhabitats to withstand inclement weather until conditions are conducive for onset of breeding. This facultative strategy that requires continued enhanced fuel stores, mobility, and readiness to initiate breeding falls under the heading of arrival biology (Wingfield and Hunt 2002; Wingfield et al. 2004) (Fig. 1).

Diverse migration strategies of the white-crowned sparrow, *Zonotrichia leucophrys*, a short-bout migrant

To better understand the transition between migration and breeding, it is helpful to draw upon a species for which much is known of its ecology, behavior, physiology of both migration and breeding and, in which the entire spectrum of migratory tendencies are represented. The north temperate races of the white-crowned sparrow, *Zonotrichia leucophrys*, provide such an example. Wagner (1930) recognized two groupings among birds in relation to their mobile tendencies: strongly migratory (highly mobile), whose breeding and wintering grounds were far apart, and resident species, who spend their entire life within a narrow range of their breeding locality. These groupings may be considered the extremes on a continuum of tendencies to migrate and time breeding. Gradations or transitional groups reside in between these extremes, exhibiting moderate distances traveled between wintering and breeding sites. The races of white-crowned sparrow, *Z. l. gambelii, leucophrys, oriantha, pugetensis*, and *nuttalli* exhibit each of these conditions to varying degrees (Blanchard 1942; Cortopassi and Mewaldt 1965; Mewaldt et al. 1968; Bent 1968). *Z. l. gambelii*, *leucophrys* and *oriantha* are strongly migratory. G*ambelii* breeds from the Canadian–US Border into the arctic tundra and taiga habitats of Alaska and Canada and overwinters from the continental US into northern Mexico (Blanchard and Erickson 1949; Morton 1976; Wingfield and Farner 1980). On average, the one-way distance covered by *Z. l. gambelii* is approximately 4,000 km (Mewaldt et al. 1964; Morton 2002). *Z. l. leucophrys*, the nominate race, appears similar in distances covered to that of *gambelii*. Birds winters in the southern tier of the USA as far west as the Rocky Mountains and into Mexico. Birds breed across the north Canadian tundra overlapping with *gambelii* west of Hudson's Bay. Far less is known of this race and it will not be considered further. *Z. l. oriantha* breeds at higher elevations of the Sierra Nevada, Southern Cascades, and Rocky Mountain ranges extending from southwestern USA into southern Canada. Birds overwinter in northern Baja California, and northern Mexico covering approximately 1,500 km migratory distances (Morton 2002). *Pugetensis* is considered a transitional migration stage that breeds from north central California to southwestern British Columbia and overwinters along the Pacific Coast of California to the Oregon border. Not all populations migrate, but among those that do, records indicate a maximum distance covered of 650 km (Blanchard 1941; Banks 1964; Farner and Lewis 1973; Morton 2002). *Z. l. nuttalli* resides at the non-migratory end of the spectrum. It is considered a resident race as it breeds and overwinters in locations along the Pacific Coast of California from Santa Barbara in the south to Humboldt County in the north (Blanchard and Erickson 1949; Mewaldt and King 1977).

Zonotrichia l. nuttalli, a resident species

Adult birds are permanently paired on territory (38°N) throughout the post-breeding season while juveniles remain in flocks. With the increase in vernal photoperiod, *nuttalli* initiate the developmental phase of the breeding life history stage, commencing in late December with gonadal recrudescence as determined by histological observations of the testes. These data indicate preliminary changes in the endocrine testis, the interstitial cells, that are responsible for production and secretion of testosterone (Blanchard 1941). Increases in testicular volume owing to enlargement of the seminiferous tubules was noted by mid to late January. During this period, juveniles also disperse to a limited extent (distances less than a kilometer) and establish territories all within the geographical home range. For both adults and juveniles, the full expression of breeding behavior and physiology appear in late January, followed by termination in mid July (Blanchard 1942; J.C. Wingfield, in preparation). No migratory life history stage is apparent as would be expected of a resident species. However, a limited number of juveniles and adults held in captivity expressed nocturnal locomotory activity from February to May with specific but non-uniform orientation (King and Farner 1963; Mewaldt et al. 1964, 1968; Smith et al. 1969). As suggested earlier (Smith et al. 1969), this activity was associated with migratory restlessness and presumably represented a vestigal remnant of the migratory history among the *Zonotrichia*, but verification of this point is needed. It is possible that this behavior is linked more with breeding, either dispersal or nocturnal activity independent of migration. Nocturnal activity including feeding, preening and singing have been reported in other normally diurnally active species during breeding, including *Luscinica megarhynchus, L. svecia, Saxicola rubetra* (Dorka 1966) and *Zonotrichia albicollis* (Helms 1963). Field observations indicate that *nuttalli* sing and are nocturnally active during breeding (Smith et al. 1969; J.C. Wingfield et al. unpublished). At present, it is unclear whether nocturnal locomotor activity observed in captive *nuttalli* is associated with breeding, dispersal or migration, and deserves further investigation. Lack of a prenuptial moult and fat deposition following photostimulation

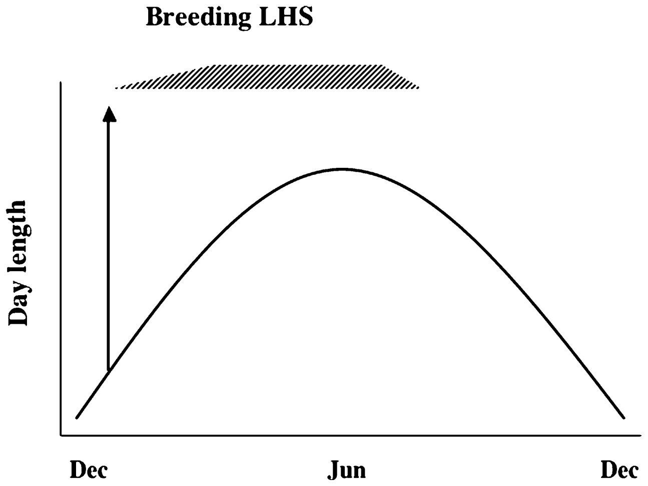

Fig. 5 Diagram of annual photoperiod and indication of the onset of breeding life history stage (*arrow*) divided into the phases of development (*left-pointing triangle*), mature capability (*rectangle*) and termination (*right-pointing triangle*) in *Zonotrichia l nuttalli*, a resident species, drawn from Mewaldt et al. (1964) and J.C. Wingfield et al. (unpublished)

offer support for absence of a migratory life history stage for this race. Thus, *nuttalli* provides a valuable comparison of a resident race within *Zonotrichia* to help elucidate the transition to breeding without the influence and/or interference of a migratory stage (Fig. 5).

Zonotrichia l pugetensis, a short distance migrant

The vernal increase in photoperiod triggers prenuptial moult, hyperphagia, moderate fattening and oriented nocturnal locomotor activity, termed migratory restlessness or *Zugunruhe*, in *pugetensis*, indicating development of the migratory life history stage (King and Farner 1963; Farner and Lewis 1973). Histological examination of the testes from free-living birds show that activity of the endocrine testis, the interstitial cells, occurs from mid to late January to departure in mid March, but with great variability across individuals (Blanchard 1941; Farner and Lewis 1973). Endocrine support for the testicular recrudescence is found with elevations of plasma LH, testosterone and 5α-dihydrotestosterone in males as well as LH, androgen and estrogen in females, sampled on the wintering grounds in February, over those collected at the conclusion of breeding during post nuptial moult and autumnal migration (Wingfield and Farner 1978a). Birds held in captivity during vernal migration display migratory restlessness that is orientated in the northerly direction (Mewaldt et al. 1964), providing support for the migratory routes north taken by free-living birds from their overwintering grounds. Expression of breeding activities on arrival vary in relation to location of breeding grounds. More southerly populations (southern Oregon) arrive gradually over a period of 2 weeks or more and do not establish territories immediately. Range of gonad size and gametogenic activity of testis are highly variable with some males arriving with testes in the early stages of spermatogenesis (Blanchard 1941). At more northerly sites, e.g., Washington State (47°N), birds arrive synchronously, territories are established immediately, with gametogenic activity of the testis well, but not fully, developed (Blanchard 1941; Farner and Lewis 1973; Wingfield and Farner 1978a). At this time, plasma LH and testosterone are maximal (Wingfield and Farner 1978a). Upon arrival, plasma levels of LH and estradiol in females are elevated over the winter samples, rising in association with growth of ovarian follicles and yolk deposition. These data indicate overlap of mature migratory and development stages of breeding in *pugetensis*, but the extent of this overlap is variable and may be contingent upon latitude and ecology of the breeding grounds (Fig. 3).

Zonotrichia l oriantha, a medium distance migrant

The mountain white-crowned sparrow has been most extensively studied on the breeding grounds of the central Sierra Nevada Mountains of California at Tioga Pass (elevation 3,030 m) (37.5°N) (Morton and Allan 1990; Morton 1994; Hahn and Morton 1995; Morton 2002; Hahn et al. 2004). Most consistently, adult males (2 years and older) arrive before other age and sex classes in early May (Morton 2002). These males have fat scores and body masses that suggest birds are still migratory and hyperphagic. This condition dissipates rapidly as males and females that arrive shortly thereafter are lean with low body masses. Upon arrival, even with heavy snow cover, males commence territorial establishment, mate attraction and defense suggesting a rapid transition from migration to breeding accompanied by elevated levels of plasma testosterone. This behavior is supported by the slow but steady growth and development of the gonads that started on the wintering grounds with the vernal increase in photoperiod (King et al. 1966; Morton 2002). Changes in the gonad include enlargement of the endocrine testis, size and volume of seminiferous tubules and tunica albuginea. Testicular growth continues for another month after arrival on the breeding grounds. Females arrive on territory with follicular growth that continues to a peak at the time of nest building within a month of arrival.

Weather in the alpine zone can be highly unpredictable at any time, but particularly in spring (Morton 2002; Richardson 2003; Hahn et al. 2004). From the time of arrival until onset of nesting, birds may abandon their territories if weather conditions deteriorate to the point where food availability is severely reduced, while energetic demands increase owing to heightened thermogenic requirements. At such times, birds quickly (within an hour) move to lower elevations (1,000 m) and benign conditions. When the weather improves, birds return to their breeding territories at elevation; the round trip constitutes a facultative altitudinal migration (Hahn et al. 2004). The proximate cues for these behavioral adjustments include both external and internal factors, many of which are not completely understood at present, but clearly involve the hypothalamic-pituitary-adrenal axis and the stress response, as measured by plasma corticosterone (Breuner and Hahn 2003). In addition to the behavioral and endocrine interactions, other factors affect a bird's response to degrading weather conditions including body condition, foraging abilities, energetic demands and physical features of the habitat (Breuner and Hahn 2003; Hahn et al. 2004).

Zonotrichia l gambelii, a long distance migrant

As seen in the other migratory *Zonotrichia*, the vernal increase in photoperiod results in prenuptial moult, onset of hyperphagia, extensive fattening, and migratory restlessness (Farner and Lewis 1973; Lewis 1975; Mattocks 1976; Schwabl and Farner 1989; Wingfield et al. 1990; Ramenofsky et al. 2003). Histological examination of the testis of birds on wintering grounds (Davis and Santa Barbara, California) indicate preliminary changes in the interstitial cells were first apparent from January to the end of February (Blanchard and Erickson 1949). Endocrine support for these early changes in the testis are found with elevations of plasma LH and androgen (testosterone and 5α-dihydrotestosterone) in males as well as levels of LH, androgen and estrogen in females, sampled on wintering grounds in February, over post breeding levels of post nuptial moult and autumnal migration (Wingfield and Farner 1978b). Early stages of spermatogenesis were detected by the presence of primary spermatocytes found in late March prior to departure in April and early May (Blanchard 1942; Farner and Lewis 1973). Males collected from populations at northern sites in Canada and Alaska nearing the end of the migratory trip had testes with maximal volume and sperm that were either nearly or fully mature (spermatozoa) (Blanchard and Erickson 1949; DeWolfe et al. 1973). These data are supported further by elevations of LH and testosterone, sampled during spring migration, that peak on arrival on the breeding grounds in the vicinity of Fairbanks, Alaska (64°C) (Wingfield and Farner 1978b) and Toolik Lake on the North Slope of Alaska (68°N) (Meddle et al. 2002). Plasma androgen in females also rose in April and peaked at the time of arrival on the breeding grounds in Alaska (Wingfield and Farner 1978b). At this time, the ovarian follicles were enlarged as estrogen levels were first apparent. Progression of ovarian development diverges from the testes, as the final and most prominent stages of maturation, including vitellogenesis (yolk synthesis) and deposition into the follicle, occur on the breeding grounds. Increased levels of estrogen are concomitant with these final stages, leading to ovulation, copulation, and oviposition shortly after arrival (Wingfield and Farner 1978b).

At higher latitudes and altitudes, the climatic conditions are more severe and prolonged, and birds can arrive before winter has relinquished its hold on the landscape, with extensive snow cover and high winds making foraging difficult or impossible. For example, at Mountain Village Alaska (62.1°N), *gambelii* breed above the treeline (Oakeson 1954). At this location, breeding sites are often snow covered at the time of arrival and birds may either remain in the sheltered valleys or continue traveling until improved conditions are located (Blanchard 1942; Oakeson 1954). Orientation of these movements are not known, but it is likely that birds no longer orient strictly north/northwest but move in more broad directions. Further north, the tundra white-crowned sparrow (a population of *gambelii*) breed on the north slope of the Brook's Range (68°N) in Alaska. The extent of this massif makes it impossible for birds arriving from the south to predict the climatic conditions on the breeding grounds north of the range and out on the tundra plane (Wingfield and Hunt 2002; Wingfield et al. 2004).

Observations of birds arriving in spring indicate that they first reside in areas where food and shelter are available south of the Brooks Range. At this juncture, birds remain in the migratory stage, hyperphagic with extensive stores of fat, in flocks, and highly mobile. Daily, birds fly over the passes into north facing valleys to the breeding sites. If conditions are severe, they will return repeatedly to assess climatic conditions. Once conditions on the breeding grounds improve, birds will remain on the site, become territorial and commence breeding, and terminate the migratory stage (Wingfield and Hunt 2002; Wingfield et al. 2004).

Transitions

In spring, a major hurdle facing early arriving migrants at high latitudes and altitudes is the increasingly poor climatic conditions both en route and at their destination (Elkins 1983). If birds arrive too early or experience intolerable conditions associated with unpredictable storms and unsettled atmospheric conditions, they can suffer increased mortality (Whitmore and Whitmore 1977; Gessaman and Worthen 1982). Countering this are the strong selective advantages for individuals, particularly males, to arrive as early as possible to establish a territory, attract a mate and produce an early clutch (Lack 1968; Perrins 1970; Wingfield 1983). In light of this trade-off, the transition from migration to breeding life history stages (arrival biology) varies by locality and from year to year depending upon local conditions (Gauthreaux 1980). Adaptations of the migratory stage, including hyperphagia, fattening, high mobility, increased thermogenic capacity of flight muscle to tolerate low ambient temperatures, aid the ability of migrants to withstand energetically demanding conditions both during and at the conclusion of the stage (Dawson et al. 1983; Morton 1994; Swanson 1995). Thus, arrival biology provides behavioral and physiological options for migrants to cope with unpredictable climatic conditions on or near the breeding grounds.

Endocrine aspects of arrival biology

Accompanying the vernal activation of the hypothalamic-pituitary-gonad axis with associated elevations of plasma testosterone, male *Z. l. gambelii* show an increase in baseline plasma levels of corticosterone, and stress-induced (by capture, handling and restraint) levels late in migration, peaking on arrival on the north slope of Alaska (Wingfield and Hunt 2002). There is a parallel increase in corticosterone binding globulin (CBG) that appears to "protect" individuals from these high levels of corticosterone, particularly the free or unbound corticosterone that is thought to be available to enter cells and have biological effects (Breuner et al. 2003; Wingfield et al. 2004). The CBG exerts a buffering effect, by protecting target tissues from increased levels of corticosterone, and thus may allow males to resist severe conditions on arrival, at least temporarily. If conditions worsen or remain inclement for too long, then CBG levels in plasma can decline within 24 h, resulting in a marked increase in free corticosterone (Lynn et al. 2003). The free corticosterone impinging upon target tissues would then trigger rapid departure from the area and delay onset of breeding even further (e.g., Wingfield et al. 1998, 2004). Thus, CBG may be a major regulatory protein in the arrival biology of the migrant birds in the Arctic, and possibly at other stringent sites such as high altitude (Breuner et al. 2003). Much more information of this type is needed before we can fully assess the endocrinology of arrival biology of migrants.

Captive studies

Under free-living conditions, expression of the mature capability of the migratory and breeding stages are distinct and sequential. Once on the breeding grounds under optimal conditions, the migratory stage is terminated giving way to territoriality and breeding, etc. In captivity, many species fail to show this pattern. Onset of the migratory stage commences with exposure to the natural increase in daylength and proceeds on a time scale commensurate with free-living counterparts (Farner 1955; Weise 1956, 1963; Helms 1963; Lewis 1975; Gwinner and Czeschlik 1978). However, termination is delayed as migratory restlessness and fattening persist beyond the migratory period of free-living counterparts, and only terminates when birds are refractory and undergoing postnuptial moult without expressing mature stages of breeding (Eyster 1954; Merkel 1956; Weise 1956, 1963; Lewis 1975; Gwinner and Czeschlik 1978; Wingfield and Farner 1980; Schwabl and Farner 1989). This pattern has been observed in both short and long distance migrants including *Zonotorichia l. pugetensis* and *Z. l. gambelii*, (Eyster 1954; Mewaldt et al. 1964; Lewis 1975), *Z. l. albicollis* (Helms 1963; Weise 1963), *Junco hyemalis*, *Melospiza georgiana, Passerella iliaca*, *Hylocichla guttata* (Weise 1963), *Sylvia borin*, *S. curruca, S. atricapilla, Phoenicurus phoenicurus, Fringilla montifringilla*, *Pylloscopus collybita*, and *P. trochilus* (Gwinner and Czeschlik 1978), *Fringilla coelebs* (Shumakov 1976), *Paserina cyanea* (Emlen 1967), and *S. communis* (Wagner 1930). By contrast, studies of captive partial migrants in spring indicate a clear separation of migratory and breeding stages in European blackbird, *Turdus merula* (Schwabl 1981) and European robin, *Erithacus rubecula* (Merkel 1956, 1961). Furthermore, timing of the onset and termination of autumn migratory restlessness appears to coincide with activity of free-living birds for *Sylvia* and *Phylloscopus* species (Gwinner and Czeschlik 1978) and *Z. l. gambelii* (Ramenofsky et al. 2003) (see Terrill 1990 for review). Various hypotheses have been proposed to explain the extension of the vernal migratory stage, in terms of endocrine and neuroendocrine systems, owing to the lack of opportunity to breed in captivity, as well as the absence of visual cues representative of the breeding grounds (Gwinner and Czeschlik 1978; Schwabl and Farner 1989). Tests of either hypothesis have proven negative; yet, the potential for examining endogenous and external factors involved in the overlap of migratory and breeding stages remains open.

One approach to this enigma may reside in the alteration of intensity and pattern of the locomotor activity, representative of migratory restlessness, in captive migrants throughout the course of the vernal stage. At the outset, intensity of activity is high and onset occurs early in the dark or nocturnal phase. Helms (1963) defined this as the motivational component that is regulated largely by the interaction of photoperiod and endogenous annual rhythms. In this phase, birds express strict orientation directed toward the breeding areas, persisting throughout the period of migration of free-living counterparts. Later, the intensity of activity wanes and nightly onset of activity is delayed until closer to dawn (Helms 1963; Ramenofsky et al. 2003). Helms (1963) labeled this as the adaptational component, more recently defined as the facultative stage for fall migrants (Terrill and Able 1988; Terrill 1990) and captive *Z. l. gambelii* during the vernal stage (Ramenofsky et al. 2003). Activity during this stage is influenced to a greater extent by environmental factors (Helms 1963; Terrill and Able 1988) and we suggest that this phase represents the behavior and physiology of the arrival biology of migrants moving into breeding sites at high altitude and latitude. Under stringent conditions, birds become spatial opportunists moving between refugia and breeding territories. They maintain fuel stores, mobility, thermogenic capacity and possibly increased elevated corticosterone and CBG while searching and/or waiting for optimal habitats to open up. Uniform orientation measured in captive birds during facultative stage dissipates in *Z. l. gambelii* (Mewaldt et al. 1964), *Fringilla coelebs* (Shumakov 1976) and *Passerina cyanea* (Emlen 1967;

Emlen et al. 1976), suggesting that movements are less directed toward a specific site, as birds travel in more generalized directions, and probably occurring during daylight hours. Thus, we consider the facultative stage observed in captive migrants as a representation of the arrival biology of long distance migrants breeding in tenuous habitats at high altitude and latitude, and provide an experimental model for testing these ideas. If conditions on the breeding grounds are similar to those in the wintering areas, as for short distance or partial migrants, there may be little need for a facultative stage providing sufficient time to terminate migration and initiate breeding.

Conclusions

Whereas a great deal is known of the environmental control and endocrinology of the migration and breeding life history stages in birds, the transition and overlap of these two major events remain largely unexplored. We apply the finite stage machine theory to dissect the sub-stages of migration and breeding in relation to the Pacific races of *Zonotrichia leucophrys*, which exhibit the entire spectrum of migratory tendencies from resident to long distance migrants. At the resident end, birds residing permanently on territory proceed directly into breeding, from a post breeding or wintering life history stage, with increasing day length. As the distance between wintering and breeding grounds lengthens among the short distance migrants, the degree of overlap of the migratory stage and developmental phase of breeding increases. At greater distances, the window of opportunity for breeding decreases while environmental conditions at high altitude and latitude become increasingly unpredictable. Overlap of the final stages of migration and mature capability of breeding is far greater among this class of migrants, to allow for flexibility to withstand harsh conditions yet be prepared to initiate breeding as soon as conditions ameliorate. Thus, the transition between migration and breeding represents a facultative state, named arrival biology, that aligns the migrant with local conditions and thus increases chances of survival and subsequent reproductive success.

Zusammenfassung

Ethologische und physiologische Konflikte bei Zugvögeln: der Übergang zwischen Zug und Brut

Der Übergang des Frühjahrszuges in das Brutgeschäft ist mit einer Reihe von ethologischen und physiologischen Konflikten verbunden. Eigenschaften, die die Zugphase charakterisieren, sind hohe Mobilität, Gemeinschaftsverhalten, sich wiederholende Zyklen von Nahrungsaufnahme (Hyperphagie und Fettdeposition) and der Flug an sich. Das Brutgeschäft dagegen beinhaltet Ortsstetigkeit, Territorial- und Fortpflanzungsverhalten, und eine anfängliche Reduktion der Hyperphagie und der Körperreserven. Da sich Morphologie, Physiologie und Verhalten ändern, kann dieser Übergang kein sprunghafter sein. Bei vielen Arten beginnt die Entwicklung des Fortpflanzungssystems bereits während des Zuges, bei anderen dagegen erst nachher. Diese Variation in der Überlappung von Eigenschaften des Zug- und Fortpflanzungsverhaltens sind bisher kaum verstanden. Sie können jedoch in engem Bezug zur Zugweglänge und der zeitlichen Ausdehnung der Brutperiode, die in höheren geografischen Breiten und größerer Meereshöhe kürzer ist. In diesen Brutgebieten können die Zugvögel nach ihrer Ankunft noch ungünstige Bedingungen vorfinden, die einer Brut nicht förderlich sind. Unter solchen Bedingungen mögen sich Zugvögel in Refugien zurückziehen and ihre fakultativen Zugeigenschaften (als Ankunftsbiologie bezeichnet) länger aufrechterhalten, bis wieder bessere Bedingungen für einen Start des Brutgeschäftes herrschen. In dieser Übersicht behandeln wir besonders Unterarten der Dachsammer (*Zonototrichia leucophyrs*), bei der sich das gesamte Spektrum von Zugstrategien findet, von Standvögeln bis zu Langstreckenziehern, und die recht gut bekannt sind. Diese Art erlaubt einen einzigartigen Blick in das Vorkommen und die Variation der Ankunftsbiologie. In unserer Diskussion konzentrieren wir uns auf den Übergang von Zug und Brut und wir diskutieren die Vielfalt der Reaktionen von artgleichen Vögeln ebenso wie das Spektrum der Umweltbedingungen, die die Überlebensrate und den Fortpflanzungserfolg begünstigen.

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