ENDOGENOUS CIRCANNUAL RHYTHMICITY IN BODY MASS, MOLT, AND PLUMAGE OF GREAT KNOTS (*CALIDRIS TENUIROSTRIS*)

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ABSTRACT.—Four Great Knots (*Calidris tenuirostris*) were kept for six years in a constant-temperature indoor aviary. For two of those six years, they were kept under photoperiodic conditions that mimicked natural changes in daylength for wild birds, followed by four years under a constant photoperiod (light:dark cycle 12:12 h). Under cyclical "natural" photoperiods, three of the four birds maintained cycles of body mass and contour and flight-feather molt somewhat comparable to that of free-living birds, though the multiple mass peaks characteristic of northward migration were replaced by a single period of high body mass; the mass peaks for southward migration appeared to be absent. Contour-feather molts between nonbreeding and breeding plumages were delayed, and the period of wing molt was longer than in free-living birds. Under constant photoperiods, clear circannual phenotype cycles were maintained. The length of the period with elevated body mass tripled but was partly compensated by a shortening of the duration of wing molt (which never coincided with high body masses). Nevertheless, total cycle lengths were >13 months. Perhaps most interestingly, under constant photoperiod, there was evidence that two components of what is normally considered an integrated phenotypic event, the prebasic molts of contour and wing feathers, were desynchronized. This suggests that the underlying organizational structure of traits is modular to some extent. Such modularity would increase the flexibility and versatility of the cyclic phenotype in evolutionary contexts. *Received 20 september 2006, accepted 30 March 2007.*

Key words: *Calidris tenuirostris*, circannual rhythms, Great Knot, modularity, phenotype, photoperiod, seasonality, shorebirds.

Ritmo del Ciclo Anual Endógeno del Peso Corporal, Muda y Plumaje en *Calidris tenuirostris*

RESUMEN.—Cuatro individuos de la especie *Calidris tenuirostris* fueron mantenidos en un aviario de interior bajo condiciones de temperatura constante por seis años. Durante dos de los seis años, estas aves fueron mantenidas bajo condiciones de fotoperíodo que imitaban los cambios en la duración del día a los que están sujetas las aves en su ambiente natural. Durante los cuatro años siguientes, las aves fueron mantenidas bajo condiciones de fotoperíodo constante (ciclo de luz:oscuridad 12:12 h). Bajo ciclos de fotoperíodo "natural", tres de las cuatro aves mantuvieron sus ciclos de peso corporal y muda de plumas de contorno y vuelo de manera más o menos comparable a los ciclos observados en aves en libertad, a pesar de que los múltiples picos en el peso corporal que caracterizan la migración hacia el norte fueron reemplazados por un periodo único de peso corporal alto. Los puntos máximos de peso presentes durante la migración hacia el sur parecieron estar ausentes. Las mudas entre los plumajes reproductivos y no reproductivos de las plumas de contorno estuvieron retrasadas, y el período de muda de las plumas del ala fue más largo que el de las aves en libertad. Bajo condiciones de fotoperíodo constante, los ciclos anuales se mantuvieron claramente. La extensión del período con peso corporal elevado se triplicó, pero ésta fue compensada parcialmente por una reducción en la duración del período de muda de las plumas del ala (el cual nunca coincidió con los períodos de alto peso corporal). Sin embargo, la duración total de los ciclos fue de >13 meses. Quizás lo más interesante es que, bajo condiciones de fotoperíodo constante, hubo evidencia de que dos componentes de lo que se considera normalmente como un evento fenotípico integrado, las mudas prebásicas de las plumas de contorno y las alas, ocurrieron de forma no sincrónica. Esto sugiere que hasta un cierto grado la estructura organizacional subyacente de los caracteres es modular. Esta característica modular podría aumentar la flexibilidad y versatilidad del fenotipo cíclico en un contexto evolutivo.

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THERE IS FIRM experimental evidence for endogenous circannual clocks in birds (Gwinner 1986). These "clocks" orchestrate many different annual phenotypic cycles, including plumage and body-mass changes and gonadal development. However, Gwinner (1986) presented experimental evidence showing this for only a single group of birds, the songbirds (order Passeriformes). In constant environments, passerines tended to have circannual cycles of less than a year. Two more recent studies have reported the presence of endogenous circannual cycles in Red Knots (*Calidris canutus*), a shorebird species belonging to the order Charadriiformes, and both studies found that free-running circannual cycles of Red Knots lasted >12 months (Cadée et al. 1996, Piersma 2002b). Combined with field data, such studies of captive birds may provide insight into how animals use internal and environmental signals to orchestrate complex sequences of changing behavior, physiology, and morphology.

Here we present data on circannual rhythmicity in several phenotypic traits (body mass, plumage states, and the processes of feather replacements, i.e., molts) in the Great Knot (*C. tenuirostris*), a sandpiper closely related to the Red Knot. Great Knots migrate between breeding areas in eastern Russia and tropical nonbreeding grounds in northern Australia and have several major mass peaks in the course of a year (at least two during northward migration, and possibly also during southward migration). They show distinctive seasonal plumage changes, with colorful alternate and supplemental plumages during the migration and breeding periods and dull gray-brown basic plumage during the rest of the year (Battley et al. 2004, 2006). Wing molt occurs on the nonbreeding grounds, as do most of the prealternate and presupplemental molts of the contour feathers; prebasic molt of contour feathers starts on southward migration and continues on the nonbreeding grounds.

Four Great Knots were studied in captivity for seven years, initially under seasonally changing photoperiods that mimicked the daylength changes encountered in the wild, and later under constant photoperiodic condition (light:dark = 12:12 h). We measured changes in several seasonally phenotypic traits that we refer to as separate "phenotype cycles." These changes can be thought of as phenotypic aspects of annual sequences of "life-cycle stages" (Jacobs and Wingfield 2000, Wingfield 2005). We explored whether these cycles were similar during simulated natural photoperiods to those in free-living Great Knots and whether the cycles were maintained when, under constant conditions, we removed photoperiodic information on the progression of the seasons. The finding of a change in the phase relationship, under constant photoperiodic conditions, between the onset of wing molt and that of prebasic molt leads us to discuss the degree to which the overall phenotypic organization of birds is modular rather than fully integrated (West-Eberhard 2003).

METHODS

Birds were captured by cannon-net on 21 March 1998 on the nonbreeding grounds, the northern beaches of Roebuck Bay, northwest Australia (18°00′S, 122°22′E), about a week before the first migratory departures were observed that year (27 March). These four focal individuals belonged to a group of eight birds transported live to the Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands. During the five-day period of transport from Australia to The Netherlands by commercial airlines (from Broome, via Perth and Singapore to Amsterdam), birds were force-fed a limited amount of food (kitten-food pellets and Trouvit trout-food pellets) and given fresh water *ad libitum*. The aim was to keep the birds healthy (the combination of heat and captivity caused some birds to temporarily suffer capture myopathy; Rogers et al. 2004) and to ensure that they did not lose too much mass before studies started (Battley et al. 2001a, b). After arrival at NIOZ, they were fasted down to an estimated "arrival mass" for a study on metabolism and body composition during and after a period of enforced weight loss that mimicked the period of fasting during a long-distance migratory flight (see Battley et al. 2001a). Of the eight birds, three were sacrificed for body-composition analyses when they had reached predicted arrival mass (Battley et al. 2000, 2001b); one died during the transition period between fasting and feeding on food pellets.

Birds were sexed using small blood samples and a molecular assay verified for Red Knots by Baker et al. (1999). All four birds were males. Body size, mass, and molt were typical for Great Knots in Roebuck Bay at that time of year (Battley et al. 2004).

During the three weeks of metabolic studies, birds were kept at 17–21°C under a 12:12 h light–dark cycle. Once they had started to eat trout-food pellets, they were shifted to a permanent room where the photoperiodic cycles were adjusted to approximate the light conditions that wild birds would experience when undergoing migrations between the breeding and nonbreeding grounds. After three weeks with the photoperiod found in the Yellow Sea region of China (light:dark 19.5:4.5 h), on 20 May the light conditions were changed to mimic the birds' sub-Arctic alpine–tundra breeding grounds at ~65°N (light:dark 22:2 h). This was followed on 20 July by another period with the light regime of the Yellow Sea (19.5:4.5 h). From early September to mid-April, birds were kept under the photoperiod changes of Broome (varying between 12:12 h in April and early September to 13:11 h in mid-December), and then we again gave them the 19.5:4.5 h of the Yellow Sea until 20 May. This schedule of changing "natural" photoperiodic conditions was repeated for another 20 months. From 4 October 2000 to the beginning of September 2004, the birds were maintained under constant photoperiods of 12:12 h (see Fig. 1).

All this time, the birds lived together in an indoor aviary that measured 1.9 × 3.9 m, with a height of 2.4 m. Air temperature was maintained at ~15°C. Birds were fed protein-rich trout-food pellets, the single staple food on which captive Red Knots have been maintained for many years (e.g., Piersma et al. 1996). Once a week, usually on Tuesdays, the birds were captured, weighed, scored for body and primary-feather molt, and checked for any physical abnormalities while their aviary was cleaned. Body mass (weighed on an electronic balance) was recorded to the nearest gram. The extent of "breeding" plumage was scored on a seven-point scale: 1 = basic plumage, 2 = a trace of "breeding" plumage present, 3 = 25% breeding plumage, 4 = 50% breeding plumage, 5 = 75% breeding plumage, 6 = only a trace of basic plumage remaining, and 7 = full breeding plumage. "Breeding" plumage may have included both alternate and supplemental plumages, because it was not known at the time that Great Knots have a supplemental plumage similar to alternate plumage but with more extensive rufous markings in the upper parts (Battley et al. 2006). Primary-feather molt (hereafter "wing molt") was scored with the traditional Ashmole system (Ginn and Melville 1983): 1 = primary lost or in pin, 2 = primary
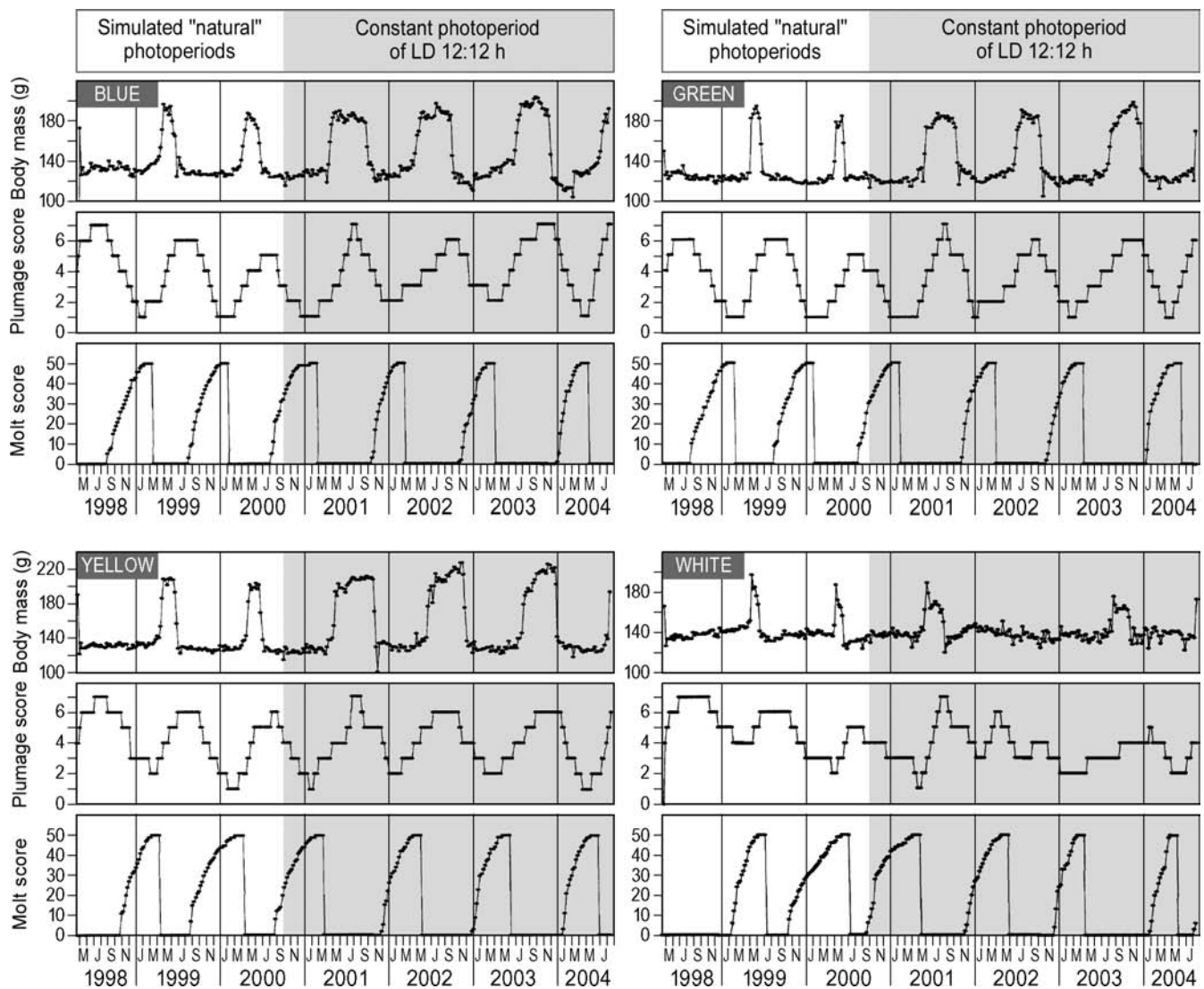
Fig. 1. Seasonal changes in body mass (top panels) and plumage (middle panels) and progress of wing molt (bottom panels) in four Great Knots during six years in captivity. From capture in early 1998 to early October 2000, the birds experienced their "normal" photoperiodic cycle (see text), but from that point on, they were kept under a constant photoperiod (light:dark 12:12 h).

25% grown, 3 = 50% grown, 4 = 75% grown, and 5 = fully grown. The total "molt score" was the sum of the scores for individual primaries. Once all 10 primaries had reached a score of 5 (total molt score = 50), molt score was reset to 0 (all primaries old) at the change to the new calendar year if molt was complete by then or, if not, as soon as possible in the new calendar year.

To analyze the length of the phenotype cycles, we scored the timing of occurrence of eight "phenotypic events" each year. Two of these are related to body-mass changes: (1) the end of the rapid body-mass increase and (2) the end of the subsequent body-mass decrease. Four events are related to plumage changes: (3) the end of prebasic molt (when breeding-plumage scores had reached 1), (4) the start and (5) the end of prealternate–presupplemental molt (when breeding-plumage scores had stopped increasing), and (6) the start of the prebasic molt (when breeding-plumage

scores started to decrease). The final two are related to wing molt: (7) start and (8) end of primary molt. The length of the cycle was defined as the time (weeks) between phenotypic events in one year and the following.

Results

General observations.—Over the six years of the study, all four Great Knots maintained fairly clear body-mass, plumage, and wing-molt cycles (Fig. 1). Cycles were similar and synchronized in three of the four birds (Blue, Green, and Yellow) but were more irregular and seemingly suppressed in White, a bird that had a nervous disposition and an aberrant, slightly upcurved, bill. All birds showed single mass peaks that overlapped in time with the molts from basic to alternate–supplemental plumage and
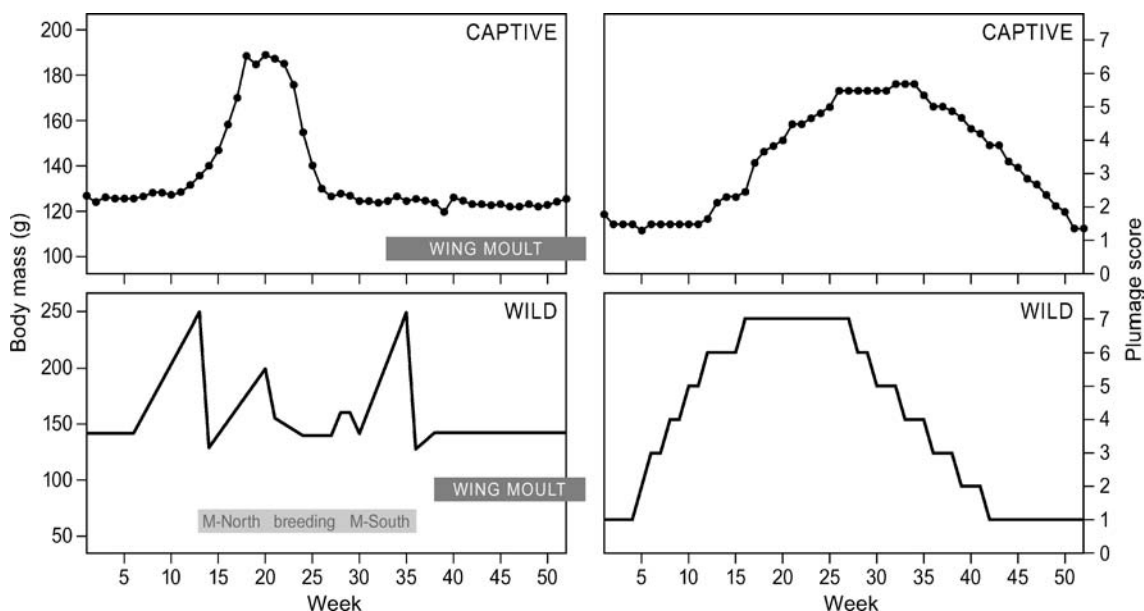
FIG. 2. Molt and body-mass cycles of captive and wild Great Knots. Upper two plots show mean body masses and plumage scores (measured weekly) for three captive birds (Blue, Green, and Yellow) over two years (1999–2000) under simulated natural daylight changes. The lower plots show indicative patterns of body mass, molt, and plumage expected for wild birds. Values assumed are 8 weeks of fueling from 142 to 250 g in Australia; 7 weeks of refueling from 127 to 200 g in the Yellow Sea (departure mass is surmised but assumes a 3,400-km flight to the breeding grounds); refueling from 140 to 160 g as birds leave the breeding grounds; refueling from 140 to 250 g as birds return from Asia to Australia; and 17 weeks of wing molt after arrival in Australia. Note that data for weeks 14–36 are largely assumed on the basis of the timing of migration and reproduction. Sources: Higgins and Davies (1996), Tomkovich (1997), and Battley et al. (2000, 2006). Bars show the timing of major events in the annual cycle (M-North and M-South refer to migration periods).

preceded the annual wing molts. Under constant photoperiods, all birds, including White, showed strikingly longer body-mass peaks compared with the first two years (Fig. 1); this will be analyzed further below.

Compared with cycles of wild adult Great Knots (Fig. 2), captive birds under simulated natural photoperiods (the first two years of the study) differed in three main ways: (1) there was one body-mass increase rather than several, (2) the mass increase and the seasonal plumage changes started later than in wild birds, and (3) the duration of wing molt was longer.

Length of circannual phenotype cycles.—Under simulated natural photoperiods, the length of most phenotype cycles was close to 52 weeks, a year (Table 1). Over all four birds, the average of all phenotype cycles was 51.5 weeks. Under constant photoperiodic conditions, average phenotype cycles increased to 57.4 weeks (or ~13.5 months) (Table 2). Responses were variable among traits, but the largest increases in cycle length were at the start and end of prebasic molt and at the start of wing molt. The six-week increase in circannual cycle length under constant photoperiods indicates an endogenous free-running rhythm of 13–14 months.

Body-mass and wing-molt characteristics.—In addition to an increase in cycle lengths, there were clear differences between the cycle characteristics under changing and constant photoperiods (Fig. 1). For the three individuals showing regular cycles, wing molt took an average of six weeks less under constant (12:12 h) than under variable photoperiodic conditions (Table 3). By contrast,

the duration of the peak ("the plateau") in body mass lasted 12 weeks (three months) longer under constant photoperiods. Peak body mass was somewhat higher under constant photoperiods and showed a tendency to increase with time (from an average of 189 g in the second peak to 206 g in the fifth; Table 3). Maximum daily rates of body-mass increase and decrease were both in the range of 3–7 g day^{-1}, with rates of increase being higher under "natural" photoperiods than under constant photoperiods, and rates of decrease lower (Table 3).

Synchronization between different phenotype cycles.—The variations between the lengths of the different phenotype cycles under constant photoperiods (Table 2) indicate that these cycles are not fully synchronized when free-running. We examined this further by plotting the times of different phenotypic events against each other (Fig. 3). The first example (Fig. 3A) shows that the rapid body-mass increase was always complete 3–30 weeks after the start of prealternate molt. During "natural" photoperiods, the interval was a little shorter than during constant photoperiods, but the data points for different individuals and years are parallel to the $x = y$ line and indicate a phase shift rather than desynchronization. Figure 3B shows that wing molts usually started shortly after the end of the rapid mass decrease but that this start was a little later under "natural" photoperiods (by about two weeks) than under constant photoperiods (by one week or less), which again suggests a phase shift. Under "natural" photoperiods, prebasic molt of contour feathers started one to six weeks after the beginning of

Table 1. Length (weeks) of different phenotypic cycles of four Great Knots during two years of normal, seasonally structured, photoperiodic conditions (see text and Fig. 1 for details).

Phenotypic trait	Marker	Cycle length 1999–2000				
		Blue	Green	Yellow	White	Average
Body mass	Rapid mass increase complete	52	52	53	52	52.3
	End of rapid mass decrease	53	51	53	52	52.3
Plumage	End of prebasic molt	48	49	48	63	52.0
	Start of prealternate molt	55	52	50	62	54.8
	End of prealternate molt	53	52	52	54	52.8
	Start of prebasic molt	49	47	48	45	47.3
Wing molt	Start	51	52	52	35	47.5
	End	55	57	50	52	53.5
Overall average						51.5

Table 2. Mean lengths across years (weeks) of the different phenotypic cycles of four Great Knots during three years of constant photoperiodic conditions (light:dark 12:12 h).

Phenotypic trait	Marker	Cycle length (2001)–2002–2003–(2004)				
		Blue	Green	Yellow	White[a]	average
Body mass	Rapid mass increase complete	60	57	58	53	57.0
	End of rapid mass decrease	61	61	61	56	59.8
Plumage	End of prebasic molt	63	58	58		59.7
	Start of prealternate molt	57	54	60		57.0
	End of prealternate molt	53	54	55		54.0
	Start of prebasic molt	57	58	59		58.0
Wing molt	Start	59	60	60	55	58.5
	End	57	57	56	49	54.8
Overall average						57.4

[a]For White, cycle length for body mass was based on the cycles in 2001 and 2003, with total length divided by two, and the interval in the years 2003–2004. Cycle length in plumage scores could not be reliably assessed.

wing molt (Fig. 3C), but several weeks earlier under constant photoperiods. Under the latter conditions, the temporal advance of body molt became smaller with successive cycles in all three individuals (indicated in Fig. 3 by the later starting times that result from the cycles longer than one year). This suggests that the molt of contour and wing feathers, which are usually considered a fundamental single prebasic molting event, are uncoupled to some degree.

Discussion

Annual-cycle characteristics in captivity compared with those in the wild.—The summary plot of the annual cycles of captive and wild Great Knots (Fig. 2) shows that captive birds under simulated natural photoperiods retained some of the key phenotypic changes experienced by wild birds: a migration-related body-mass increase, a breeding-plumage molt, and a "postbreeding" wing molt. However, there were also major contrasts within these traits: (1) only one migratory mass increase was evident, later than in free-living birds; (2) the molts from basic into alternate–supplemental

plumages and back were delayed; and (3) the duration of the wing molt was longer.

These differences indicate that the variations in daylength with which we simulated a "normal" annual cycle of photoperiods helped synchronize the phenotype cycles (Table 1, and see below) but were not sufficient to ensure completely typical cycles of body mass and molts. The delayed single body-mass peak during the first two years of varying photoperiods indicates that some other environmental triggers are needed to initiate fueling. The secondary mass peaks representative of southward migration seemed completely absent, as they were in Red Knots studied under constant photoperiods (Cadée et al. 1996). The single body-mass peak of about four to five weeks shown by the Great Knots is much too short to include the southward migration period (July–August), so the Great Knots appeared to miss out on the southward migration stimulus. Some aspect of physically undergoing the migration and breeding may be necessary for the entire set of phenotypic cycles to occur or for the sequence of all life-cycle stages to run its course (cf. Jacobs and Wingfield 2000). One option is that the southward fueling is stimulated by complex hormonal interactions that

TABLE 3. Duration of wing molt and plateau summer body mass, peak body mass, and maximum rates of mass increase and decrease in three Great Knots during two years with "natural" photoperiods and three years with constant photoperiodic conditions (light:dark 12:12 h).

Variable	Individual	"Natural"		Constant photoperiod		
		1999	2000	2001	2002	2003
Duration of wing molt (weeks)	Blue	21	25	13	16	17
	Green	20	23	16	17	17
	Yellow	25	23	20	20	13
	average	**22.0**	**23.7**	**16.3**	**17.7**	**15.7**
Duration of plateau mass (weeks)	Blue	4	6	18	19	17
	Green	5	4	15	13	17
	Yellow	6	6	23	20	16
	average	**5.0**	**5.3**	**18.7**	**17.3**	**16.7**
Peak body mass (g)	Blue	192	183	185	192	198
	Green	194	184	186	189	197
	Yellow	206	200	208	223	222
	average	**197.3**	**189.0**	**193.0**	**201.3**	**205.7**
Body-mass increase (g day^{-1})	Blue	3.4	2.1	3.0	2.4	2.3
	Green	7.8	5.7	4.0	2.6	2.4
	Yellow	4.4	5.4	5.4	4.9	4.6
	average	**5.20**	**4.40**	**4.13**	**3.30**	**3.10**
Body-mass decrease (g day^{-1})	Blue	−5.4	−2.6	−3.3	−4.2	−5.1
	Green	−4.0	−5.1	−5.0	−5.3	−4.6
	Yellow	−5.0	−4.4	−5.7	−5.3	−6.5
	average	**−4.80**	**−4.03**	**−4.67**	**−4.93**	**−5.40**

depend on the physical activity of migration, the act of breeding, or both. Another is that an external navigational cue signals whether such refueling is necessary. For Thrush Nightingales (*Luscinia luscinia*) migrating south from Sweden for the first time, birds that were exposed to a magnetic field that simulated environmental conditions before a major ecological barrier (the Sahara) put on more mass than birds not given this magnetic information (Fransson et al. 2001). It is possible that similar cues along the migration route are needed for migrants such as Great Knots to initiate refueling for a southward migration. Whatever the mechanism, the lack of refueling can be considered an adaptive response to times when a migration is not embarked upon or is not completed (e.g., Driscoll and Ueta 2002)—there is no benefit to fueling needlessly.

Additional stimuli, and perhaps the induction of hormone-driven feedback loops by seasonally appropriate behaviors, may also be necessary for the proper synchronization of the different phenotype cycles. For example, whereas in free-living Great Knots (and most other coastal shorebird species) wing molt starts when the molt from alternate to basic plumage is well underway (Fig. 2; D. I. Rogers et al. pers. comm.), the captive birds, when exposed to constant photoperiods, commenced wing molt many weeks before they even started losing their breeding plumage (Fig. 3C).

When putting on mass (Fig. 1), captive Great Knots under both natural and constant photoperiods achieved much higher daily-mass-increase rates than birds in the wild are believed to manage: 3–5 g day^{-1} in captivity (Table 3) compared with an estimated 1.1 g day^{-1} for free-living Great Knots in northwest Australia (this value is scaled up from an empirical value for Red Knots; Piersma et al. 2005). Because the captive birds generally peaked at ~200 g (Table 3) and wild birds usually reach departure masses of 250 g (Fig. 2), overall fueling periods are much longer in the wild birds than they were in the captive birds.

Under simulated natural photoperiodic conditions, the completion of wing molt took 22–24 weeks (Table 3), which is longer than in the field, where birds take approximately 17–18 weeks to molt (C. D. T. Minton and D. I. Rogers pers. comm.). This long wing molt is surprising because in captivity there should be no nutritional, energetic, or safety constraints on the rate of flight-feather growth (Boere 1976, Grubb 1989). Under constant photoperiods, the 16– to 18-week duration of wing molt was slightly shorter than in the field. Although this confirms that there are probably no nutritional constraints on molt in the captive Great Knots, the slower molt under simulated natural photoperiodic conditions remains unexplained. The captive birds may have been able to afford to molt more slowly to maximize feather quality; Serra (2001) provided evidence that slowly molted flight feathers are more resistant to wear and tear.

Functionality of the strict phase relationship between body-mass loss and start of wing molt.—As shown in Figure 3B, wing molt always started after mass was lost at the end of the plateau phase. This makes sense, because heavy Great Knots with
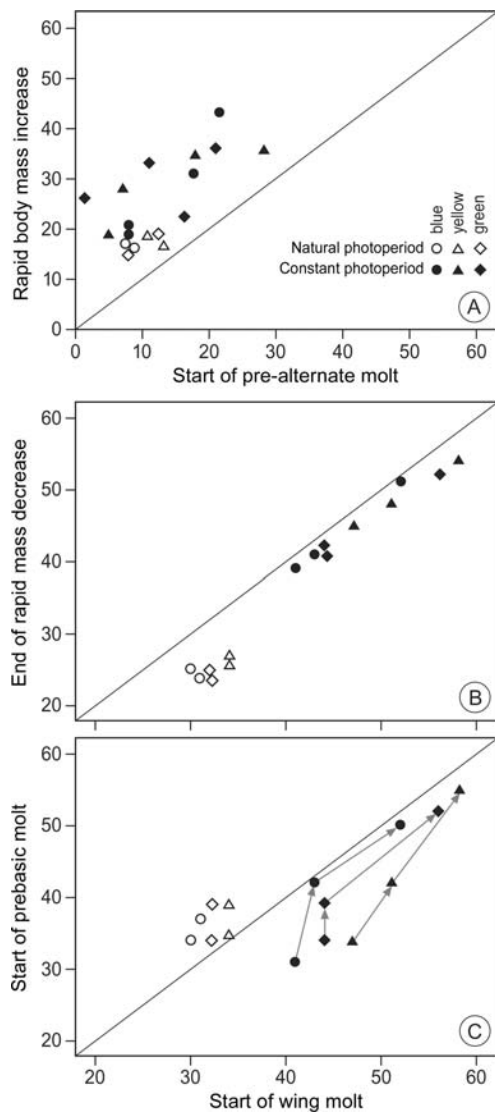
Fig. 3. Examples of the degree of synchronization between different phenotypic events in Great Knots and the effect of a change from simulated seasonal photoperiodic conditions (open symbols) to constant light:dark (12:12 h) photoperiodic conditions (closed symbols). Data from the individuals Blue, Green, and Yellow were used for six circannual cycles starting in 1999 (see Fig. 1). Axes represent weeks of the year, with 1 representing the first week of January, and 52 the last week of December. In a few cases, phenotype cycles extended into the following calendar year, which explains values between 52 and 60. To aid the eye, lines parallel to $x = y$ establish occasions where cycle lengths do not differ from a year (52 weeks). In C, data points from successive cycles of the three different individuals are connected.

gaps in the wing would be significantly penalized by reduced maneuverability and much-increased danger of predation (e.g., Lind 2001). Selection pressures may be such that there is a deep-seated organizational fail-safe mechanism to prevent shorebirds from initiating wing molt before mass loss is complete (D. I. Rogers pers. comm.).

Are circannual cycles longer than a year typical for shorebirds?—Clear evidence for circannual cycles longer than a year has been shown by a Red Knot that was kept as a pet in The Netherlands (Piersma 2002b). Even after 20 years in captivity, this bird maintained strong body mass and plumage cycles of ≤18 months. Cadée et al. (1996) also suggested the presence of endogenous circannual cycles of a year or more for Red Knots. Great Knots, only the second Charadriiform species examined, also show clear internally driven circannual phenotype cycles with lengths of 13–14 months. In all passerines studied, including transequatorial migrants (summary in Gwinner 1986), endogenous circannual cycles are shorter, rather than longer, than a year.

One of the striking differences between the phenotype cycles of Great Knots under simulated natural photoperiods and constant light:dark 12:12 h conditions is the length of time that high body mass is maintained. Great Knots experiencing natural light changes kept a high body mass for ~5 weeks, whereas under constant photoperiods, they maintained high body masses for 15–23 weeks (an average of ~17 weeks) (Fig. 1, Table 3). The three-month extension of the body-mass plateau (also found in Red Knots; Cadée et al. 1996, Piersma 2002b) is two months more than the extra month that makes up the free-running annual cycle of 13–14 months. Free-running Great Knots "catch up" by compressing the duration of wing molt (Table 3), compressing the interval between the end of the body-mass plateau and the start of wing molt (Fig. 3B), and increasingly synchronizing the start of the wing and contour-feather molts (Fig. 3C; the individual data points get closer to the $x = y$ line over time). If the birds had not sped up their wing molt, the cycle length would have increased to 15 months and resulted in highly abraded primaries. In terms of missing cues, the lack of a change in daylength direction in midsummer may cause birds to remain heavy and, perhaps, ready for migration. It may be some while before the circannual clock system becomes effective and induces the change into the next life-cycle stage.

In contrast to cycles in Red Knots (Cadée et al. 1996) and some passerines (Gwinner 1986), Great Knot phenotype cycles did not decrease in magnitude over time (Fig. 1 and Table 3). By contrast, peak body masses increased over time. The exception is provided by the bird "White," who skipped one cycle of increased body mass and concurrently showed modified and reduced body molt (Fig. 1) but maintained strong circannual cyclicity in wing molt. Does this reflect that wing molt is an evolutionarily "deep" character (i.e., found in all flying birds), whereas body-mass changes and seasonal plumage changes are more recently derived characteristics?

Modularity of the phenotype cycles.—Although the constancy of the order and timing of phenotypic cycles in the wild suggests that different phenotypic traits are tightly linked to one another, the relative timing of some of these in Great Knots changed over the course of four circannual cycles under constant photoperiods. Even within what is considered part of a single prebasic molting event, the relative timing of wing molt and contour-feather molt changed over the course of the study (Fig. 3C). Synchrony of prebasic wing and contour-feather molts underlies much of the thinking on plumage homologies (Humphrey and Parkes 1959, Howell et al. 2003). This very concept of fully integrated plumage change as a phenomenon demanding an evolutionary explanation is not supported by the present findings.

Changing phase relationships, if confirmed more widely, also have considerable repercussions for how we view the integration of events in the annual cycle. There is evidence for disassociable phenotype cycles in other birds (Gwinner 1986), which suggests that the overall phenotypic make-up of birds is modular (West-Eberhard 2003). Such modularity may increase the flexibility and versatility of the phenotypic parts in evolutionary contexts. At the same time, the existence of modularity implies that the life-cycle stages proposed by Wingfield and others (e.g., Jacobs and Wingfield 2000; Piersma 2002a, 2004; Wingfield 2005; but see Gwinner 1986) may not be as tightly integrated and fixed as perhaps envisioned.

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