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Correlation between timing of juvenile moult and onset of migration in the blackcap, *Sylvia atricapilla*

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In small bird species, energy-demanding life cycle stages such as moult and migration are generally separated in time. The extent of separation can vary considerably within and between species, but the causes of this variation are largely unknown. We studied the phase relation between postjuvenile moult and autumn migration by experimentally manipulating the timing of these events in the blackcap. In a split-brood experiment, we hand-reared 30 blackcaps and kept them under either natural daylengths or a time-shifted photoperiod that altered the timing and intensity of moult. We determined the onset and termination of moult and the onset of nocturnal migratory restlessness. In both groups, onset of migratory activity was correlated with termination of moult. The extent of moult–migration overlap was unaffected by the photoperiod manipulation, suggesting resilience of this correlation against environmental perturbation. Strong family effects explained a large proportion of phenotypic variation. The correlation between the timing of postjuvenile moult and migration is, therefore, likely to result from genetic covariation. We predict that selection for delayed termination of moult will result in more overlap between moult and migration. Because of this correlated selection response, adaptive changes in the timing of migration could be retarded, and independent adaptive evolution of moult and migration schedules could be constrained.

Feathers wear out and birds have to replace them regularly to maintain plumage function. This process of moult requires substantial amounts of energy and nutrients for feather synthesis and may bear additional costs in terms of reduced flight ability and insulation capacity of plumage (Jenni & Winkler 1994). In small avian species with high mass-specific metabolic rates, moult is usually separated from other energy-demanding life cycle stages such as breeding and migration (Jenni & Winkler 1994; Kjellén 1994). In most passerines, there is little overlap between postjuvenile moult and autumn migration, yet the extent of temporal separation may vary considerably within and between species (Jenni & Winkler 1994). Although adaptive explanations for the variation in the overlap between moult and migration have been widely discussed in terms of time and energy constraints, it is practically unknown at which level this variation is to be found (e.g. within or between individuals or populations), and to what extent it can respond to selection.

Rapid, ongoing climatic changes have caused phenological changes in plants and insects (Walther et al. 2002; Root et al. 2003). As a consequence, the timing of breeding and migration of many birds is expected and has been shown to change considerably (Berthold 1991, 1998). To be able to predict whether the timing of moult and migration can independently respond to selection, we need to investigate the patterns of phenotypic and genetic variation in these traits, and genetic covariation between them. Variability of the phase relation between moult and migration is a prerequisite for the independent adaptive response of these life cycle events. Low levels of phenotypic and genetic variation and unfavourable genetic correlations could constrain adaptive evolution of the avian calendar (Pulido 2000; Pulido et al. 2001a; Coppack & Both 2002).

Moult and migration are expensive activities, so we expect trade-offs and separation in time between these life history stages (e.g. Holmgren & Hedenström 1995). As a consequence, delayed moult should lead to a later initiation of migration. However, in species under strong time constraints, such as long-distance migrants or birds breeding at high latitudes, the costs of leaving the breeding area too late could exceed the costs of an overlap between moult and migration. In these species, we would

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therefore expect to find less separation, or even an overlap, between moult and migration. Adaptive changes in the scheduling and intensity of moult (Berthold 1996; Helm & Gwinner 1999, 2001; Hall & Fransson 2000) could facilitate such an overlap between moult and migration.

We investigated the temporal link between postjuvenile moult and autumn migratory activity under laboratory conditions in a short-distance passerine migrant, the blackcap. Moult and migration cycles in songbirds have been shown to be the result of endogenous physiological rhythms that are strongly modified by daylength (Berthold 1996; Gwinner 1996; Dawson 2002). This sensitivity to photoperiod allows experimental manipulation of the timing of these events (e.g. Hall & Fransson 2000; Coppack et al. 2001). Using a split-brood experimental design, whereby full siblings from each family were separated and assigned to either a treatment group (i.e. birds exposed to an altered photoperiod regime) or a control group, we separated genetic and environmental sources of variation in the overlap between moult and migration.

METHODS

Study Animals, Rearing and Housing Conditions

We used 30 blackcaps that had hatched between 14 and 18 May 1998 near Radolfzell, Germany (47°46′N, 9°E). Birds were taken from six nests at 5–7 days and transferred to the laboratory, where we housed them in a climate-controlled room at a constant temperature of 27°C and 75–80% relative humidity. Nestmates were kept in groups of two to three individuals on sterilized nest material in open wooden boxes (18×11 cm and 11 cm high). Nestlings were fed by hand every 45 min from 0600 to 2030 hours. They were provided with bee larvae or ant pupae supplemented with a calcium mixture and occasionally with vitamins (Berthold 1981).

At an age of 12 days, each nestling group was transferred to a wooden cage (20×47 cm and 30 cm high), which enabled the birds to get used to independent feeding and drinking. These cages had two fixed perches, a food bowl and two drinking vessels. From day 23 onwards, birds were hand-fed once every 90 min. At 28 days, hand feeding was reduced to five times per day.

Once individuals attained full independence at an age of about 33 days, they were kept in two climatic chambers (15 cages per chamber) in which temperature was held constant at 20 ± 1.5°C and a relative humidity of 75–80%. Birds were kept individually in aluminium cages (45×23 cm and 38 cm high) equipped with two drinking vessels, one feeder and two movable perches. Food and vitamin-supplemented water were given ad libitum; food was changed every morning and water was changed at least three times per week. From independence until release, birds were fed a mixture developed particularly for feeding blackcaps, which consisted of hard-boiled egg, crumbled rusk, dried sour milk, mealworms and calcium (Berthold et al. 1990).

Manipulation of Photoperiod

After attaining independence, all birds were assigned to one of two experimental treatments so that each family was represented by at least two individuals in each group. The first group ($N = 15$) was kept under daylengths similar to those experienced in the wild. The second group ($N = 15$) was exposed to a time-shifted light–dark regime simulating 6-weeks-earlier hatching (see figure in Coppack et al. 2001). This photoperiod prolonged juvenile moult by more than a month. Furthermore, time-shifted birds initiated autumn migratory activity later (Coppack et al. 2001).

Measurement of Moult and Migratory Behaviour

We monitored the progress of postjuvenile moult by daily inspecting 21 body feather tracts and the wing coverts (six tracts; Berthold et al. 1970). In the blackcap, juvenile moult is partial and does not involve flight feathers (Jenni & Winkler 1994). Moult intensity was scored on a scale of 0 to 5, depending on the number of moulting feather tracts (adapted from Berthold et al. 1991; 1 = moult in up to five feather tracts, 2 = moult in 6–10, 3 = 11–15, 4 = 16–20, 5 = more than 20). We defined onset of moult as the date at which the first moulted feather was detected, and termination of moult as the date at which no growing feather was visible.

For each bird, the onset of migration was defined as the first night on which it was active during at least five 30-min intervals (Pulido et al. 2001a). For two birds, one male from the control group and one female from the treatment group, we could not determine onset of migratory activity accurately by this criterion. For this reason, their data were excluded from analyses of onset of migratory activity and moult–migration overlap.

We defined two variables as measures of temporal separation between termination of moult and onset of migration, interval (time lag) between moult completion and onset of migration, and moult intensity at the onset of migratory activity.

Statistical Analysis

All variables except the onset of moult were normally distributed (Shapiro-Wilk's test: $P > 0.05$). Because deviations from normality in onset of moult were marginal, we used two-tailed parametric tests for testing statistical hypotheses throughout. Data for males ($N = 12$) and females ($N = 18$) were pooled because there were no between-sex differences in any of the variables. Furthermore, between-family differences in hatching date were minimal (≤4 days) and affected neither the timing of moult and migration nor moult–migration overlap. Actual hatching date was thus disregarded in all analyses presented.

We estimated causal variance components using the restricted maximum likelihood (REML) approach implemented in the VARCOMP procedure of SAS (SAS Institute

1990). Heritabilities were calculated as twice the between-family variance component. Heritability estimates derived from resemblances between full siblings are usually considered unreliable because they include a large proportion of common-environment and dominance variance (Roff 1997). However, under controlled environmental conditions, common-environment and dominance effects on resemblances in the timing of migration may be negligible, as indicated by the good correspondence between heritability estimates derived from full-sibling covariances and those derived by other, more accurate, methods (Berthold & Pulido 1994; Pulido et al. 2001a; Pulido & Berthold 2003).

We obtained a crude approximation of the additive genetic correlation from the phenotypic correlation of family means. This estimate approaches genetic correlations if family sizes are large, heritabilities are close to one and environmental variation is minimal (Lynch & Walsh 1998). Although sample sizes in our study were small and heritabilities of the timing of moult and migration were lower than one, we believe that this correlation is close to the actual genetic correlation for two reasons. First, phenotypic correlation may be a good indicator of genetic correlation (Roff 1997). Second, for migratory traits, there is a close correspondence between family-mean correlations and genetic correlations derived from full-sibling pairs (Pulido 2000; Pulido & Berthold 2003; see also Garland 1988 for the reliability of this method).

Ethical Note

The blackcap is one of the most common bird species breeding in southwestern Germany, and is not endangered either locally or globally. A legal permit for collecting blackcap nestlings in the wild and conducting experiments, including the present study, was granted to P. Berthold by the Regierungspräsidium Freiburg.

In the spring after the experiments, all birds were released into the same area where they had been collected. Before release, birds were transferred from cages to aviaries to regain full flight ability. Hand-reared blackcaps reintroduced to the wild by this method have had a high probability of both survival and successful reproduction (Berthold & Bairlein 1984). Our experimental condition simulated a difference in hatching date, so we expected the effects of the shift in photoperiod to correspond to the effects of natural variation in hatching date. Variation in natural hatching dates influences postjuvenile moult and the initiation of autumn migration, but there is no effect on subsequent life cycle stages (e.g. winter moult, spring migration or gonadal development; e.g. Widmer 1999; Pulido 2000). Thus, we do not expect an effect of the photoperiodic manipulation after release.

RESULTS

In both groups, the onset of migratory activity was significantly correlated with the termination but not with the onset of moult (Table 1). The phase relation between termination of moult and onset of migration did not change (Fig. 1). Under both natural and time-shifted photoperiods, blackcaps initiated migratory activity about 9 days before they completed moult (control: $\overline{X} \pm \mathrm{SE} = -8.79 \pm 1.96$ days; photo-shifted: -9.07 ± 2.65 days; *t* test: $t_{26} = 0.09$, NS). Moult intensity at the onset of migratory activity was low (mean ± SE moult score, control: 2.02 ± 0.46; photo-shifted: 2.33 ± 0.41) and did not differ between experimental treatments ($t_{26} = 0.50$, NS).

The two measures of overlap between moult and migration, i.e. time lag between moult and migration and moult intensity at migration onset were highly correlated with each other, and to a lesser extent with the termination of moult. Variation in moult–migration overlap, however, was related to neither the onset of moult nor the onset of migratory activity (Table 1).

A General Linear Model (GLM, type III) revealed that family was a significant factor predicting the extent of overlap between moult and migration (time lag: $F_{5,16} = 6.24$, $P < 0.01$; moult intensity at migration onset: $F_{5,16} = 6.34$, $P < 0.01$). However, neither the photoperiod treatment (time lag: $F_{1,16} = 0.66$, NS; moult intensity at migration onset: $F_{1,16} = 1.90$, NS) nor the family-by-treatment interaction had a significant effect on moult–migration overlap (time lag: $F_{5,16} = 0.36$, NS; moult intensity at migration onset: $F_{5,16} = 0.22$, NS).

The strong family effect on the overlap between moult and migration was supported by the analysis of variance components. Heritability estimates suggested that practically all variation in time lag and intensity of moult at migration onset was caused by differences in family means (Table 2; Fig. 2). The heritability of the timing of moult completion was also statistically significant.

Table 1. Correlations between phenological variables of moult and migration

	Moult onset	Moult termination	Migration onset	Time lag	Moult intensity at migration onset
Moult onset	●	0.176	0.151	−0.037	0.138
Moult termination	−0.288	●	0.653*	−0.457†	0.556*
Migration onset	−0.306	0.688**	●	0.375	−0.193
Time lag	0.091	−0.691**	0.049	●	−0.907**
Moult intensity at migration onset	−0.138	0.555*	−0.034	−0.798**	●

Numbers above the diagonal give Pearson correlation coefficients for blackcaps kept under natural photoperiod ($N = 14$), those below the diagonal correlations for photo-shifted birds ($N = 14$).
†$P < 0.1$; *$P < 0.05$; **$P < 0.001$.

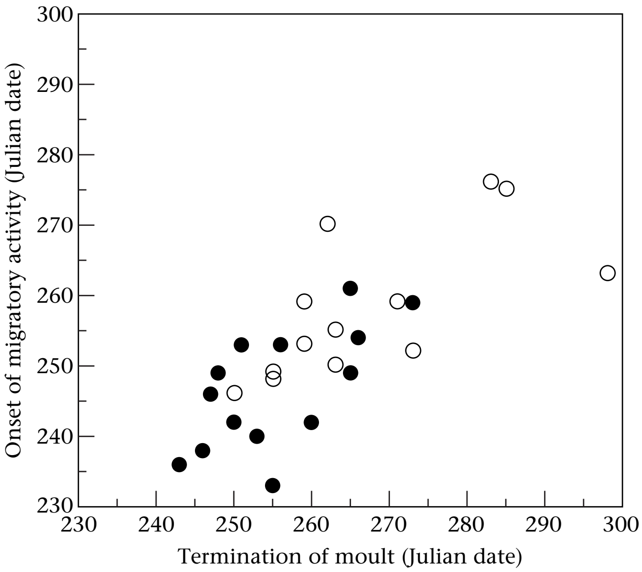

Figure 1. Correlation between termination of postjuvenile moult and onset of autumn migratory activity in individual blackcaps kept under the natural photoperiod (●) and under a shifted photoperiod (○).

Heritability estimates for moult and migration onset were moderate to low and not significantly different from zero (Table 2). Family means of moult onset and migration onset were not significantly correlated with any other phenological variable (Table 2).

DISCUSSION

Moult–migration Overlap and Environmental Sensitivity

We found in individual birds a strong correlation between the termination of moult and the onset of migratory activity. Most blackcaps initiated autumn migration before they had completed postjuvenile moult. Moult and migration, however, generally overlapped during only a short interval, when moult was almost completed and moult intensity was low. This moult–migration overlap is in accord with field data showing that, in the blackcap, moult intensity peaks before migration starts and that a high percentage of individuals migrate when moult intensity is low (Berthold et al. 1991).

The strong correlation between the timing of moult and migration found in southern German blackcaps was insensitive to changes in the timing of moult and migration induced by a time-shifted photoperiod mimicking 6-weeks-earlier hatching (Coppack et al. 2001). Despite this resilience to environmental manipulation, variation in the overlap between moult and migration was considerable. Most of this variation was explained by between-family differences in the timing of moult completion. Large family effects on the overlap between moult and migration, and a high correlation between family means provide evidence for a genetic covariation between these traits. Thus, individuals from families with ‘genes for’ late termination of moult had a strong overlap between moult and migration regardless of whether they had hatched early or late in the season. This finding suggests that environmentally induced variation in the timing of moult and migration will only marginally, if at all, change the genetic predisposition for a weak or strong overlap between moult and migration.

Does this hypothesis hold for all hatching dates and photoperiods? Our experiment simulated photoperiods experienced by blackcaps hatching very early in the season, when most individuals had just arrived on their breeding grounds. Coppack et al. (2001) found that under these conditions, the response of the onset of migration to differences in hatching date did not differ from the mean response in the population, that is, of birds hatching later in the season. We are thus confident that our finding of insensitivity of moult–migration overlap to variation in the photoperiod holds for most of the range of current hatching dates, a result confirmed by data on Irish stonechats, *Saxicola torquata* (Helm 2002). However, it is likely that birds hatching very late in the season, which are under time stress, do show a stronger overlap between moult and migration. Individuals that hatch late in the season save time by shortening their juvenile development. This is achieved by initiating moult at an earlier age, increasing moult intensity, an extended overlap between different stages of juvenile plumage development or reducing the extent of moult (Jenni & Winkler 1994; Berthold 1996; Bojarinova et al. 1999, 2002; Noskov et al. 1999; Dawson et al. 2000; Hall & Fransson 2000). Mukhin

Table 2. Correlations between family means and heritabilities (h^2) for moult and migration phenology

	Moult onset	Moult termination	Migration onset	Time lag	Moult intensity at migration onset
h^2	0.466†	0.843*	0.150	1.201**	1.318**
Moult onset	●	0.263	0.346	−0.004	0.202
Moult termination	−0.155	●	0.073	−0.785†	0.871*
Migration onset	−0.062	0.708	●	0.560	−0.402
Time lag	0.164	−0.782†	−0.113	●	−0.973**
Moult intensity at migration onset	0.059	0.754†	0.131	−0.944**	●

Numbers above the diagonal give Pearson correlation coefficients for blackcaps kept under the natural photoperiod ($N=6$), those below the diagonal correlations for photo-shifted birds ($N=6$).
†$P < 0.1$; *$P < 0.05$; **$P < 0.001$.

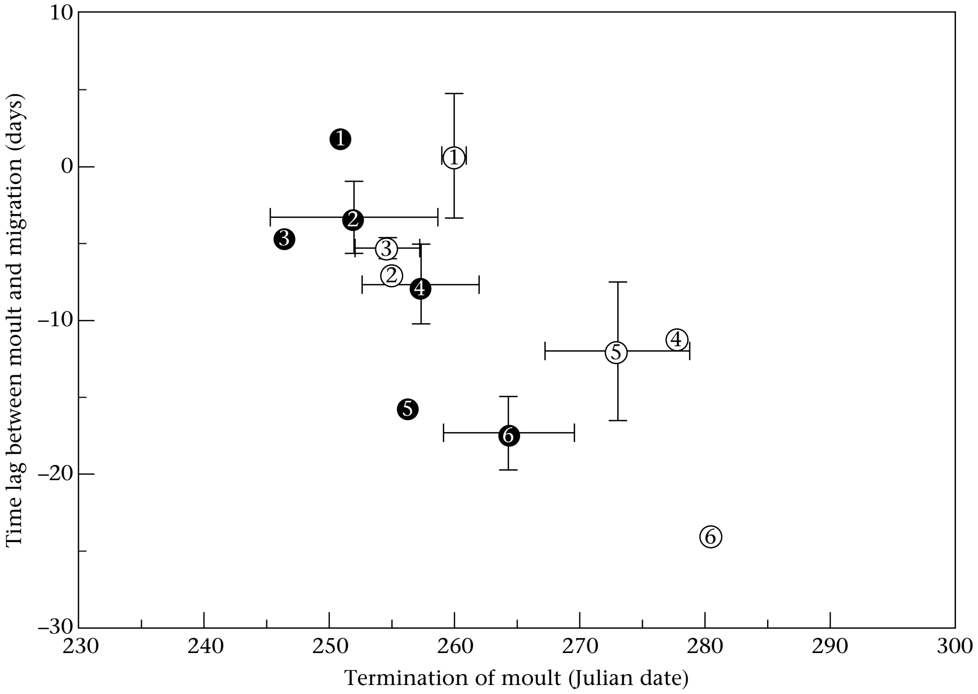

Figure 2. Correlation between termination of moult and extent of temporal separation between moult and migration. Points give family means for blackcaps kept under a natural photoperiod (●), and under a shifted photoperiod regime (○). Numbers within circles identify different families. Error bars give 1 SE (given only if family sizes >2).

(2002) provided evidence for a stronger overlap between moult and migration in late-hatched birds in an experimental study on reed warblers, *Acrocephalus scirpaceus*. Similarly, early experimental studies in blackcaps showed that in birds hatching at the end of the breeding season, i.e. early August, the overlap between moult and migration was about a week longer than in individuals hatching in mid-May (Figure 9 in Berthold 1988). Although these results are suggestive, they cannot address whether the increase in moult–migration overlap in late-hatched birds is attributable to between-family variation, as found in this study, or a consequence of individual responses (i.e. phenotypic plasticity). Split-brood experimental designs, such as the one we used, in which time stress is induced by simulating late hatching (e.g. Lindström et al. 1994; Dawson et al. 2000; Hall & Fransson 2000) could help to separate the causes of this variation.

Control of Moult–migration Overlap

We previously showed that blackcaps do not migrate at a fixed date, but that for every 2 days that they hatch earlier, they advance migration onset by about 1 day (Coppack et al. 2001; Pulido et al. 2001b). This 'partial compensation' of differences in hatching date is linked to changes in the duration of juvenile moult (Berthold 1996). In the present study, we found that the timing of migration cannot be adjusted by changing the temporal separation of moult and migration. Furthermore, our results indicate that migration onset in the blackcap is not determined by a fixed moult stage, because we found large between-family variation in moult intensity at migration onset, that is, each family was at a different moult stage when initiating migration.

The consistency of moult–migration overlap between full siblings that differed considerably in onset, termination and duration of moult, suggests that moult–migration overlap is constrained by physiological trade-offs. These trade-offs would operate regardless of whether both moult and migration directly respond to changes in daylength, or whether daylength only triggers the onset or termination of moult, and migration timing is indirectly modified through its physiological link with moult.

Because families that terminate moult late also moult longer, we would expect, assuming equal extent of moult, a lower intensity of moult in families with a large overlap between moult and migration. This prediction, however, was not supported by our results. Blackcaps with a late termination of moult (and hence a long moult duration) had a higher intensity of moult at migration onset. This result indicates that families with a pronounced moult–migration overlap may not have a 'co-adapted' moult pattern, as found, for instance, in long-distance migrants, which reduce moult intensity towards the end of moult (Berthold 1996).

Evolutionary Change of Moult and Migration Schedules

Current climatic changes are expected to change avian life cycles (e.g. Berthold 1998; Walther et al. 2002). One of the most important changes predicted for short-distance migratory birds is prolonged time spent on the breeding grounds, that is, selection for earlier arrival and later departure from the breeding grounds (e.g. Berthold 1998; Pulido & Berthold 1998; Coppack & Both 2002; Jenni & Kéry 2003). Individual birds, however, may not be able to respond adaptively to these changing environmental conditions. In southern German blackcaps, reaction norms of the timing of migration in response to hatching date will cause earlier migration with earlier breeding (Coppack et al. 2001). However, selection in this population is expected to favour late migration as a consequence of increasing temperatures and improved food availability on the breeding grounds in autumn. Existing reaction norms in the southern German blackcap population thus seem to constrain the independent adaptation of the timing of breeding and migration in response to climate change (Coppack et al. 2001).

How could the time spent on the breeding grounds be prolonged? In principle, the onset of migration could be delayed by increasing the interval between hatching and the onset of moult by expanding the duration of moult, that is, by ending moult later, or by a longer separation between moult and migration. The significant heritabilities of the onset and termination of moult, and of moult–migration overlap that we found indicate that these traits could respond rapidly to selection. However, the high family-mean correlations between moult completion and moult–migration overlap that we found suggest that timing of moult and of migration may not evolve independently. That is, selection favouring a late termination of moult would result in a greater overlap between moult and migration, which may impede an adaptive delay of the onset of migration. Similarly, selection for a longer temporal separation of moult and migration would not lead to later migration, because the termination of moult would be delayed as a correlated selection response. Therefore, it is unlikely that rapid genetic changes in the timing of migration can be achieved by changes in the termination of moult or in moult–migration overlap. Changes in the mean onset of migratory activity in response to artificial selection for later migration, as found in an artificial selection experiment in blackcaps from this population (Pulido et al. 2001a), are probably the result of changes in the age at moult onset. The presence of moderate-to-high levels of genetic variation in this trait (Table 1; see also Widmer 1999; Helm & Gwinner 1999, 2001) is in accord with this hypothesis.

Conclusions

Our results suggest that genetic correlations between moult and migration may constrain the independent, adaptive evolution of the timing of moult and of migration. We do not know whether this constraint is common in passerine birds. However, recent studies of Irish stonechats (Helm 2002) and two central European garden warbler, *Sylvia borin*, populations (F. Pulido & M. Widmer, unpublished data) suggest that there is variation in the control of moult–migration overlap and its correlation with the timing of moult both within and between species. Studies of moult–migration overlap in other species and the investigation of its causes will help to identify adaptive patterns of trait variation associated with different life histories, such as in short- versus long-distance migrants (Svensson & Hedenström 1999). We also need a deeper understanding of the mechanisms controlling the temporal organization of breeding, moult and migration, as well as the flexibility in the timing of these events, to be able to predict the extent to which birds will be constrained in the adaptive evolution of life cycles. This information could then be used to set limits on the transition of states in annual routine models (e.g. McNamara et al. 1998) for making reliable medium-term predictions of how the complete annual cycle will respond to environmental change.

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