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Invited reply

Reconsidering the role of precipitation and food availability in relation to the effect of photoperiod on spring departure of a migratory bird

Ramenofsky [1] asserts that our paper [2] discounts the role of photoperiod in organizing the spring departure programme of American redstarts (*Setophaga ruticilla*) from their non-breeding grounds in Jamaica. We disagree with this opinion and argue here that our research design and discussion of our findings attribute an important role to photoperiod in stimulating the transition from the tropical non-breeding period to the spring migration phase of the annual cycle. We found that reductions in rainfall and food availability over the study predicted a 3–5 day delay in departure on spring migration. Only redstarts followed for 2–6 years were included in the dataset, so our analysis and conclusions were based on longitudinal change in departure of individual birds. We interpreted these results as consistent with the hypothesis that environmental conditions during the non-breeding period can modify the stimulus to migrate that is initially triggered by photoperiod.

Ramenofsky [1] frames her commentary by citing a statement made in the Abstract of our paper—that our results challenge the idea that photoperiod alone regulates the onset of migration—arguing that few authors, if any, have made such a claim. In fact, several influential papers investigating how temperate zone climatic warming alters the phenology of bird migration have suggested that some species fail to advance their arrival at breeding areas because spring departure schedules are fixed by responses to photoperiod [3–5]. The data most often cited in support of this idea come from laboratory experiments which concluded that irregular fluctuations in tropical environmental conditions are not likely to influence circannual rhythms, such as the spring timing of departure [6–8]. Thus, rather than being a statement few authors, if any, have made, the idea that spring departure is determined by photoperiod has become an important paradigm, particularly in research on the consequences of climate change.

That this notion has taken root in the literature is understandable not only based on evidence from laboratory experiments, but also because of the lack of empirical data on the factors that shape the onset of spring migration from the tropics. There is little doubt that the seasonal photoperiod change in Jamaica is sufficient to provide the initial predictive cue for spring migration. But what role does photoperiod play in guiding actual departure? Ramenofsky [1] argues that departure timing has little to do with photoperiod *per se*; instead, photoperiod change stimulates birds to enter the developmental phase of migration, and local weather conditions determine the actual timing of departure. She presents these ideas as though they apply to all birds, yet the research cited to support her claims focused primarily on photoperiod regulation of breeding, song and moult in non-migratory species [9]. The only migratory species considered was the white-crowned sparrow (*Zonotrichia leucophrys*), and these studies examined the role of photoperiod in terminating spring migration or initiating autumn migration [10–12]. There is no *a priori* evidence that these findings apply to long-distance migratory birds making the transition from the stationary winter period in the tropics to the spring migratory phase. Ramenofsky [1] herself states that photoinduction would stimulate behavioural and physiological changes in preparation for spring migration, but *probably* would not affect departure times, a qualification that accurately reflects the absence of data from the tropical non-breeding period. A major motivation of our study was to address this knowledge gap and assess the degree to which annual variation in environmental conditions and food resources can modify the photoperiod stimulus to migrate.

In formulating our null hypothesis, we considered all factors believed to be important for determining redstart spring departure dates. Previous research showed that departure timing varied between habitats, with birds in mangrove forest leaving earlier that those in dry scrub habitat [13–15]. Although this pattern held irrespective of sex, in some years males departed earlier than females within each habitat [14,16]. Our null hypothesis therefore contained effects for habitat, sex and their two-way interaction. To evaluate whether birds changed their departure timing among years in relation to rainfall, we fit a model with rainfall and food availability, plus all terms in the null model. After accounting for variation owing to bird demography, we reasoned invariant departure schedules in relation to annual differences in rainfall and food would suggest that fixed responses to photoperiod prevented individuals from changing the timing of migration. Given the strong evidence that photoperiod initiates migratory behaviour [6,8], our null hypothesis that the same individuals would depart at the same time each year if the photoperiod response dominated the spring departure programme is sound deductive science, not an approach built on faulty assumptions as Ramenofsky [1] contends.

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Our finding that the same individual redstarts delay their departure time as the amount of rainfall declines did not lead to a rejection of our null hypothesis, and at no point in the paper do we argue that photoperiod was unimportant. Instead, we state that our data are consistent with the hypothesis that strong variation in rain and food resources can modify the photoperiod stimulus to migrate, something that, to our knowledge, had not been demonstrated previously in the field. Such information represents a forward step in our understanding of how changing climate acts throughout the annual cycle of migratory birds, especially because of recent evidence that a 3.5-day delay in the arrival of male redstarts at breeding grounds is correlated with an 11 per cent reduction in the probability of successfully fledging offspring [17].

In nearly every paragraph of our discussion, we elaborate on the role photoperiod might have played in orchestrating the spring departure patterns we observed, a treatment we believe does not equate to discounting its importance. In particular, we suggest that one way to interpret the intraclass correlation coefficient (ICC) of 0.38 that we report is as the degree of individual repeatability of departure date owing to photoperiod response. Our findings suggest the need for paired laboratory and field experiments to directly quantify the role that photoperiod and other factors in the environment play in regulating the timing of departure on spring migration from the tropics.

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