This is the authors' version of: Watts et al. 2022. Environmental cue integration and phenology in a changing world. *Integrative and Comparative Biology*. https://doi.org/10.1093/icb/icac032

Environmental cue integration and phenology in a changing world

Heather E. Watts[1,2], Ashley R. Robart[3], Thomas P. Hahn[4], Richard Gomulkiewicz[1]

[1]School of Biological Sciences, Washington State University
[2]Center for Reproductive Biology, Washington State University
[3]Department of Biology, Southern Oregon University
[4]Department of Neurobiology, Physiology and Behavior, University of California, Davis

Corresponding author:
Heather E. Watts
School of Biological Sciences
Washington State University
P.O. Box 644236
Pullman, WA 99164-4236
(office) 509-335-5591
heather.watts@wsu.edu

Running title: Cue integration and phenology

Keywords: annual cycle, climate change, environmental cues, phenology, photoperiod, seasonality

Abstract

Many organisms use environmental cues to time events in their annual cycle, such as reproduction and migration, with the appropriate timing of such events impacting survival and reproduction. As the climate changes, evolved mechanisms of cue use may facilitate or limit the capacity of organisms to adjust phenology accordingly, and organisms often integrate multiple cues to fine-tune the timing of annual events. Yet our understanding of how suites of cues are integrated to generate observed patterns of seasonal timing remains nascent. We present an overarching framework to describe variation in the process of cue integration in the context of seasonal timing. This framework incorporates both cue dependency and cue interaction. We then summarize how existing empirical findings across a range of vertebrate species and life cycle events fit into this framework. Finally, we use a theoretical model to explore how variation in modes of cue integration may impact the ability of organisms to adjust phenology adaptively in the face of climate change. Such a theoretical approach can facilitate exploration of complex scenarios that present challenges to study *in vivo* but capture important complexity of the natural world.

This is the authors' version of: Watts et al. 2022. Environmental cue integration and phenology in a changing world. *Integrative and Comparative Biology*. https://doi.org/10.1093/icb/icac032

Introduction

The ability of organisms to time events in the annual cycle (e.g., reproduction, migration, hibernation) such that they coincide with suitable environmental conditions can be critical to fitness (Post and Forchhammer 2008; Thomas et al. 2001). Consequently, many animals have evolved to use proximate environmental cues (e.g., photoperiod, food availability, temperature) to appropriately time these events (Bradshaw and Holzapfel 2007; Wingfield 2008). Yet climate change poses a serious challenge to the maintenance of appropriate timing of life cycle events. Of particular concern is the potential for climate change to alter the correlation between proximate environmental cues and suitable environmental conditions. Such cue-environment mismatch can occur under climate change if the phenology of important resources (e.g., food) changes relative to the timing of proximate cues (Visser 2008). For instance, many animals use changes in photoperiod as an important cue to time annual events (Bradshaw and Holzapfel 2007). However, photoperiod cycles will remain unaltered in all locales with ongoing climate change, regardless of other phenological changes. Climate change may also lead to cue-environment mismatches by inducing range shifts, if such shifts bring organisms into areas where the relative timing of proximate cues and environmental conditions are different than in the environment in which they evolved (Coppack and Pulido 2004; Huffeldt 2020). To understand the potential for such cue-environment mismatches and to predict their impact, an understanding of cue use in the timing of annual events is essential.

We now have a wealth of knowledge about how particular proximate cues can influence the timing of life cycle events, including reproduction, migration, and hibernation. Photoperiod is arguably the best studied proximate cue (Bradshaw and Holzapfel 2007; Bronson 1989; Dawson et al. 2001), but our understanding of the roles of others, such as temperature, food availability, and social cues, is growing (Caro et al. 2013; Chmura et al. 2020; Helm et al. 2013; Williams et al. 2014). Moreover, although these cues have often been studied independently, there is a long-standing recognition that animals typically use multiple cues to fine-tune the timing of events (Ball 1993; Bronson 1989; Wingfield 1983; Wingfield et al. 1992). Nonetheless, our understanding of how cues are integrated to time annual events remains nascent.

There is a pressing need to better understand cue integration if we wish to understand and predict changing phenology and the consequences of climate change (Chmura et al. 2019; Edwards and Yang 2020; Visser et al. 2010). Here, we present a new framework for describing variation in cue integration for the timing of life events and then summarize how existing findings across a range of life events fit into this framework. We then develop and apply a theoretical model to examine how different modes of cue integration may facilitate or limit the capacity of organisms to adjust phenology in the face of changes in cue-environment relationships. This modeling approach affords an opportunity to explore questions that can be challenging to address *in vivo* (e.g., requiring experiments that are time- and animal-intensive). Overall, the focus of our approach is on organismal-level processes; however, it could be applied or expanded to address questions at other levels of organization, including neural or molecular mechanisms (e.g., Stevenson and Ball 2011).

Cue integration framework and examples

Our cue integration framework describes variation in the modes by which cues can be integrated by considering both cue dependency and cue interaction (Figure 1). Previous models of cue integration have typically focused on what we call cue dependency, describing two alternatives: serial (also called hierarchical) or parallel (Ball 1993; Chmura et al. 2020; Hahn et al. 2015; Perfito et al. 2008). When cue dependency is ***serial***, the presence of one cue is a prerequisite for response to another cue. When cue dependency is ***parallel***, any one of a suite of alternate cues can generate a similar response on its own, independent of the other cue(s), and each cue can therefore substitute for the others. For instance, if a threshold photoperiod must be reached before an animal will respond to additional cues, this would be a case of serial cue dependency. Our framework builds on previous conceptual work on cue dependency to add another important, but overlooked in this context, dimension of cue integration – the interaction among cues. Here, we draw from the field of sensory ecology (Partan and Marler 1999) to identify three different modes of cue interaction (or lack thereof), which can occur in conjunction with serial or parallel cue dependency. Cue interactions can be ***redundant***, ***enhancing***, or ***differential***. In the case of a redundant interaction, each cue elicits the same response alone or in combination. In contrast, in an enhancing interaction, cue combinations generate greater responses than any cue alone. Finally, a differential interaction occurs when the cues elicit different behavioral or physiological responses involved in the life-cycle transition. The outcomes of different combinations of cue dependency and interaction are illustrated in Figure 1. By considering both cue dependency and cue interactions, this framework allows important nuances of cue integration to be examined in greater detail than was possible with previous models that have focused only on a single dimension (cue dependency; Ball 1993; Chmura et al. 2020; Hahn et al. 2015; Perfito et al. 2008), or on the relative reliance on long-term versus short-term predictive cues (Stevenson and Ball 2011; Wingfield et al. 1992). Below, we draw from the literature to illustrate examples of different modes of cue integration across a range of life history events. In examining the literature, we have focused on studies that use full factorial designs of cue combinations, as these are necessary to distinguish among modes of cue integration.

Parallel and enhancing cue integration has been observed in the timing of reproduction, hibernation, and migration. For instance, in deer mice (*Peromyscus maniculatus*), both long photoperiods and abundant food are stimulatory cues for the onset of reproductive development, with each cue showing a positive effect on its own but the combination of the two cues together yielding the strongest effect (Nelson et al. 1997). These cues – photoperiod and food availability – are also integrated in a parallel and enhancing manner to time termination of reproduction in California voles (*Microtus californicus*, Nelson et al. 1983). Parallel and enhancing integration is also seen in the integration of photoperiod and temperature cues to time hibernation in Arctic ground squirrels (*Urocitellus parryii*, Drescher 1967) and reproductive development in female green anoles (*Anolis carolinensis*; Licht 1973). Finally, red crossbills (*Loxia curvirostra*) integrate food availability and social cues in this manner in the context of a facultative migratory response (Cornelius et al. 2010).

Serial and enhancing cue integration has been documented primarily in the context of reproductive timing. This type of integration has been found to occur in small mammals, particularly rodents, with appropriate photoperiod cues being necessary for further enhancing effects of food availability (*Peromyscus californicus*, Steinman et al. 2012), social cues (*Phodopus sungorus*, Paul et al. 2009; *Peromyscus leucopus*, Pyter et al. 2005), or temperature (*Peromyscus maniculatus*, Desjardins and Lopez 1983; *Microtus ochrogaster*, Kriegsfeld et al. 2000). Similarly, it occurs in small mammals with the integration of food cues with other non-photic cues (*Peromyscus maniculatus*, Demas and Nelson 1998; *Suncus murinus*, Wayne et al. 1991). It has also been documented to occur in the integration of temperature and photoperiod cues in the context of reproductive timing of fishes and reptiles (*Menidia beryllina*, Huber and Bengtson 1999; male *Anolis carolinensis*, Licht 1971; *Stenotherus odoratus*, Mendonça and

Licht 1986; *Heteropneustes fossilis*, Sundararaj and Vasal 1976). Finally, serial and enhancing cue integration also occurs in the integration of photoperiod and a social cue, male song, by female white-crowned sparrows (*Zonotrichia leucophrys*) – male song was only stimulatory when photoperiod was sufficiently long (Morton et al. 1985).

Differential cue integration is illustrated primarily by work in birds. In male white-crowned sparrows, Moore (1983) has described a parallel differential response to the integration of a long day photoperiod cue and the presence of a sexually receptive female in the transition to a breeding state – the photoperiod cue stimulated gonadal development and the receptive female stimulated the expression of sexual behavior. Moreover, neither cue was necessary for a response to the other, indicating parallel cue dependency. That is, males on short day photoperiods still expressed sexual behavior when paired with a sexually receptive female. Yet, both cues in combination were necessary for the expression of traits associated with a mature breeding state. Differential cue integration has also been noted in female birds, whereby a photoperiod cue will stimulate initial maturation of the ovaries, but additional cues from males are necessary to stimulate progression to yolk deposition (Perfito et al. 2015; Watts et al. 2016; Wingfield et al. 1997).

Although we have illustrated the cue integration framework focusing primarily on the integration of two cues, it can also be applied to interactions among multiple cues. For instance, in male red crossbills, Hahn and colleagues (Hahn 1995; Hahn et al. 1995) found that photoperiod alone, or food and social (i.e., access to females) cues in combination, can stimulate gonadal development during the transition to a breeding stage. Thus, we can describe photoperiod as being parallel and redundant with the combination of food and social cues, though either food or social cues alone appear to be insufficient to reach full reproductive capabilities. Further, when we consider the integration of food and social cues in this example, these cues could be described as serial and enhancing. The example of food and social cues here highlights that when cues are serial and enhancing, it can be the case that an initial cue generates some response which is further enhanced by a subsequent cue, or alternatively, as appears to be the case in crossbills, it can be that it is only when both cues are present that a response is generated. The latter situation has also been observed in Siberian hamsters (*Phodopus sungorus*) where the combination of an intermediate photoperiod, such as would occur in the late summer or autumn, and reduced food availability can stimulate termination of breeding, though either cue alone has minimal effect (Paul et al. 2009).

Potential consequences of variation in cue integration under climate change

Considering the evidence for variation in modes of cue integration, it is worthwhile to consider the potential consequences of differences in cue integration. As a first step towards examining the potential consequences of different modes of cue integration under climate change, we have developed a theoretical model. This theoretical model combines information about cue integration and the optimal timing of a seasonal life history event to examine the effects on fitness under different cue-environment associations (the code used to implement the model is available as described in the Data Availability Statement). For simplicity, we focus here on comparing two types of cue integration: parallel and enhancing integration and serial and enhancing integration. Although the number of cues that could conceivably be combined to determine a particular response is potentially quite large, we will consider the simplest case of just two cues, which we denote by c_1 and c_2. For example, c_1 might represent photoperiod and c_2 might be a measure of temperature. Our model assumes that an animal uses these two cues to determine the timing at which a life cycle event or transition occurs. For illustration, we imagine that a female uses these two cues to determine its day of breeding (e.g., initiation of egg laying), but our model could be applied to other events. If we denote this day by b, then in mathematical terms, the day of breeding is determined by $b = f(c_1, c_2)$, where f is a *cue integration function*. We represent each mode of cue integration as an integration function form. The first form is *parallel and enhancing*: $b = z_1c_1 + z_2c_2$, where z_1 and z_2 are coefficients that describe the animals' "sensitivities" to the two cues. The second form of cue integration we consider is *serial and enhancing.* In this form, breeding date is influenced by the second cue only if the first cue reaches a threshold value, C_1, so that $b = z_1c_1$ if $c_1 < C_1$ and $b = z_1 c_1 + z_2 c_2$ if $c_1 \geq C_1$. Thus, when the first cue value exceeds C_1, the function assumes the same form as parallel and enhancing.

To examine potential consequences of these different forms of cue integration, we assume that the organism's fitness depends on its breeding date b and that there is an optimal breeding date during the season, denoted by θ, at which a female's fecundity F would be maximized; fecundity at earlier and later breeding dates declines with the magnitude of deviation from this optimum. A relatively simple mathematical function that describes this intermediate optimum scenario is the Gaussian function

$$F = \hat{F}e^{-s\frac{(b-\theta)^2}{2}}$$

where $s > 0$ and $\hat{F}$ is the maximum fecundity a female achieves when breeding on the optimal date, $b = \theta$. The parameter s, a measure of the magnitude of selection, describes how quickly fecundity declines from the maximum for females that breed on non-optimal dates, $b \neq \theta$; the squared term in the exponent indicates that the extent of decline is the same for breeding dates the same distance before and after θ. Environmental conditions could affect any or all of $\hat{F}$, s, and θ. We will consider only effects on the optimal breeding date θ in this article to illustrate our main points as simply as possible and leave examination of effects of the other parameters to future study. Moreover, we note that other functions could be used to describe the relationship between breeding day and fecundity, and for example, declines in fitness before and after θ need not be symmetrical as our model assumes.

We assume that the optimal breeding date in this original environment is statistically associated with the two cues, specifically, that it is described by the linear regression equation

$$\theta = \beta_1 c_1 + \beta_2 c_2$$

where β_1 and β_2 are partial regression coefficients. Thus, the partial regression coefficient, β, for a given cue reflects the reliability of that cue as an indicator of optimal timing. In an organism with parallel and enhancing cue integration, that is, $b = z_1 c_1 + z_2 c_2$, for all cue values, multivariate quantitative genetic theory (Lande 1979) tells us that with sufficient genetic variation, selection in a stable environment will favor the evolution of mean sensitivities that match the regression coefficients; that is, the mean of sensitivity z_1 would evolve to the value β_1 and the mean of sensitivity z_2 would evolve to β_2, because those values would optimize the fecundity function (F). For parallel and enhancing integration then, females with sensitivities $z_1 = \beta_1$ and $z_2 = \beta_2$ would always choose the optimal breeding date and, thus, obtain maximal fecundity $\hat{F}$, across all cue combinations (Figure 2A). By comparison, females that rely on serial and enhancing cue integration would breed on non-optimal dates under many cue conditions when the first cue value is below the threshold C_1 (even if $z_1 = \beta_1$ and $z_2 = \beta_2$) and thus would realize less than optimal fecundity in these conditions (Figure 2B). We should note that our model only considers the fitness consequences of timing in terms of expected fecundity in the current breeding season. It may be, for example, that serial and enhancing integration has evolved in a number of species because it confers advantages in terms of future survival and fecundity that are not considered in the present model.

To consider the potential consequences of climate change, we next imagine that the environment changes in such a way that the regression relation between the two cues and the optimal breeding date is changed to

$$\theta = \beta_1^* c_1 + \beta_1^* c_2$$

where β_1^* and β_2^* describe the new associations between the optimal breeding date and cues $c_1$and c_2, respectively. In this novel environmental scenario, we set β_1^* and β_2^* so c_1 now has a weak relationship to optimal breeding date and c_2 has a strong relationship. As the animals' cue sensitivities (z_1 and z_2) do not change, this case sets up greater potential for cue-environment mismatch. In this scenario, we see fecundities reduced across both forms of cue integration for many cue conditions (Figure 3). Even females using parallel and enhancing cue integration that was optimal in the previous environment (i.e., $z_1 = \beta_1$ and $z_2 = \beta_2$) will frequently select breeding dates *b* that are suboptimal in the novel environment (Figure 3A). Moreover, when we compare fecundity between serial and parallel modes of integration in the first environment (i.e., $z_1 = \beta_1$ and $z_2 = \beta_2$) and in our novel environment, we see that serial integration leads to a greater reduction in fecundity compared to parallel integration over a range of cue values (Figure 4). However, there are conditions under which serial integration will perform better than parallel (Figure 4).

In comparing performance of the two modes of cue integration across environmental scenarios, two aspects of our findings are particularly noteworthy. First, it can be seen that differences in fecundity between serial and parallel integration arise when the first cue is below the C_1 threshold (Figure 4). This could be representative of the type of situation that animals might encounter if optimal timing of an event were to advance such that it was occurring earlier than a photoperiod threshold needed to stimulate appropriate physiological and behavioral changes. Second, our examination of the literature suggests that serial and enhancing cue integration is frequently used in the context of reproductive timing, with a photoperiod cue being necessary for responsiveness to a second cue. This suggest that these species may be particularly vulnerable to negative effects of cue-environment mismatch such as what we have modeled here. More generally, by modeling relatively simple scenarios, our results suggest that mechanisms of cue integration can be an important determinant of the extent to which animals may be able to adjust timing to match novel environmental conditions.

Conclusions and future directions

It is generally understood that animals typically integrate multiple environmental cues to time events in their annual cycles. However, we still have much to learn about how this cue integration occurs. Here, we have presented a framework to describe variation in modes of cue integration that considers both the cue dependency and interactions between the cues. Drawing from the vertebrate literature, we find empirical evidence for variation in the modes of cue integration within this framework. Finally, using a theoretical approach, we find evidence that differences in modes of cue integration may impact the abilities of animals to shift timing in response to climate change. We suggest that future work using both empirical and theoretical approaches will be important if we wish to understand how climate change will impact phenology.

Empirical studies to test modes of cue integration across more species, life cycle events, and environmental cues are needed to develop a comprehensive understanding of cue integration. Studies that yield data for comparative analyses will be particularly useful for elucidating the circumstances under which different cue integration mechanisms evolve and discerning general 'rules'. For instance, constancy/contingency models of environmental predictability (Stevenson and Ball 2011; Wingfield et al. 1992) could be used in comparative analyses to evaluate whether particular patterns of environmental predictability are associated with different modes of cue integration. Studies that allow for comparisons between sexes will also be particularly valuable. Although we know that the sexes often differ in their use of a given environmental cue (Ball and Ketterson 2008; Chmura et al. 2020; Tolla and Stevenson 2020), the extent of sex differences in cue integration has received relatively little attention (but see Licht 1971; 1973). We suggest that considering these differences and their potential consequences will be an important area for future work.

In combination with empirical work, theoretical approaches will be an important tool for predicting how different patterns of cue use and cue integration are likely to impact phenological responses to climate change. Here, we start with a relatively simple model that considers two environmental cues and two modes of cue integration. This approach could well be expanded to incorporate more cues and modes of cue integration, as well as to consider a range of life cycle events and even full annual cycles. Theoretical approaches could facilitate exploration of these more complex scenarios that present considerable logistical challenges to empiricists, but that likely capture important complexity of the natural world.

Funding

This work was supported by the National Science Foundation [grant numbers IOS-1755245, IOS-1756976 to HEW].

Data availability statement

No new data were generated or analysed in support of this research. The code used for the model is available in the Washington State University institutional repository, Research Exchange, at https://doi.org/10.7273/000003369.

Acknowledgements

We thank three anonymous reviewers for comments that improved the manuscript.

References

Ball GF. 1993. The neural integration of environmental information by seasonally breeding birds. American Zoologist 33:185-199.

Ball GF, Ketterson ED. 2008. Sex differences in the response to environmental cues regulating seasonal reproduction in birds. Philosophical Transactions of the Royal Society B: Biological Sciences 363:231-246.

Bradshaw WE, Holzapfel CM. 2007. Evolution of animal photoperiodism. Annual Review of Ecology, Evolution, and Systematics 38:1-25.

Bronson FH. 1989. Mammalian Reproductive Biology. Chicago: University of Chicago Press.

Caro SP, Schaper SV, Hut RA, Ball GF, Visser ME. 2013. The case of the missing mechanism: How does temperature influence seasonal timing in endotherms? PLoS Biology 11:e1001517.

Chmura HE, Kharouba HM, Ashander J, Ehlman SM, Rivest EB, Yang LH. 2019. The mechanisms of phenology: the patterns and processes of phenological shifts. Ecological Monographs 89:e01337.

Chmura HE, Wingfield JC, Hahn TP. 2020. Non-photic environmental cues and avian reproduction in an era of global change. Journal of Avian Biology 51: e02243.

Coppack T, Pulido F. 2004. Photoperiodic response and the adaptability of avian life cycles to environmental change. Advances in Ecological Research 35:131-150.

Cornelius JM, Breuner CW, Hahn TP. 2010. Under a neighbour's influence: public information affects stress hormones and behaviour of a songbird. Proceedings of the Royal Society B: Biological Sciences 277:2399-2404.

Dawson A, King VM, Bentley GE, Ball GF. 2001. Photoperiodic control of seasonality in birds. Journal of Biological Rhythms 16:365-380.

Demas GE, Nelson RJ. 1998. Photoperiod, Ambient Temperature, and Food Availability Interact to Affect Reproductive and Immune Function in Adult Male Deer Mice (*Peromyscus maniculatus*). Journal of Biological Rhythms 13:253-262.

Desjardins C, Lopez MJ. 1983. Environmental Cues Evoke Differential Responses in Pituitary-Testicular Function in Deer Mice*. Endocrinology 112:1398-1406.

Drescher JW. 1967. Environmental Influences on Initiation and Maintenance of Hibernation in the Arctic Ground Squirrel, *Citellus Undulatus*. Ecology 48:962-966.

Edwards CB, Yang LH. 2020. Evolved Phenological Cueing Strategies Show Variable Responses to Climate Change. The American Naturalist 197:E1-E16.

Hahn TP. 1995. Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the red crossbill, *Loxia curvirostra* (Aves: Carduelinae). Journal of Experimental Zoology 272:213-226.

Hahn TP, Brazeal KR, Schultz EM, Chmura HE, Cornelius JM, Watts HE, MacDougall-Shackleton SA. 2015. Annual Schedules. In: Scanes CG, editor. Sturkie's Avian Physiology (Sixth Edition). San Diego: Academic Press. p. 847-867.

Hahn TP, Wingfield JC, Mullen R. 1995. Endocrine bases of spatial and temporal opportunism in Arctic-breeding birds. American Zoologist 35:259-273.

Helm B, Ben-Shlomo R, Sheriff MJ, Hut RA, Foster R, Barnes BM, Dominoni D. 2013. Annual rhythms that underlie phenology: biological time-keeping meets environmental change. Proceedings of the Royal Society B: Biological Sciences 280:20130016.

Huber M, Bengtson DA. 1999. Effects of photoperiod and temperature on the regulation of the onset of maturation in the estuarine fish *Menidia beryllina* (Cope) (Atherinidae). Journal of Experimental Marine Biology and Ecology 240:285-302.

Huffeldt NP. 2020. Photic Barriers to Poleward Range-shifts. Trends in Ecology & Evolution 35:652-655.

Kriegsfeld LJ, Ranalli NJ, Bober MA, Nelson RJ. 2000. Photoperiod and Temperature Interact to Affect the GnRH Neuronal System of Male Prairie Voles (*Microtus ochrogaster*). Journal of Biological Rhythms 15:306-316.

Lande R. 1979. Quantitative Genetic Analysis of Multivariate Evolution, Applied to Brain: Body Size Allometry. Evolution 33:402-416.

Licht P. 1971. Regulation of the Annual Testis Cycle by Photoperiod and Temperature in the Lizard *Anolis Carolinensis*. Ecology 52:240-252.

Licht P. 1973. Influence of Temperature and Photoperiod on the Annual Ovarian Cycle in the Lizard *Anolis carolinensis*. Copeia 1973:465-472.

Mendonça MT, Licht P. 1986. Photothermal effects on the testicular cycle in the musk turtle, *Sternotherus odoratus*. Journal of Experimental Zoology 239:117-130.

Moore MC. 1983. Effect of female sexual displays on the endocrine physiology and behaviour of male White-crowned sparrows, *Zonotrichia leucophrys*. Journal of Zoology 199:137-148.

Morton ML, Pereyra ME, Baptista LF. 1985. Photoperiodically induced ovarian growth in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*) and its augmentation by song. Comparative Biochemistry and Physiology Part A: Physiology 80:93-97.

Nelson RJ, Dark J, Zucker I. 1983. Influence of photoperiod, nutrition and water availability on reproduction of male California voles (*Microtus californicus*). Reproduction 69:473-477.

Nelson RJ, Marinovic AC, Moffatt CA, Kriegsfeld LJ, Kim S. 1997. The Effects of Photoperiod and Food Intake on Reproductive Development in Male Deer Mice (*Peromyscus maniculatus*). Physiology & Behavior 62:945-950.

Partan S, Marler P. 1999. Communication Goes Multimodal. Science 283:1272-1273.

Paul MJ, Galang J, Schwartz WJ, Prendergast BJ. 2009. Intermediate-duration day lengths unmask reproductive responses to nonphotic environmental cues. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 296:R1613-R1619.

Perfito N, Guardado D, Williams TD, Bentley GE. 2015. Social Cues Regulate Reciprocal Switching of Hypothalamic Dio2/Dio3 and the Transition Into Final Follicle Maturation in European Starlings (*Sturnus vulgaris*). Endocrinology 156:694-706.

Perfito N, Kwong JMY, Bentley GE, Hau M. 2008. Cue hierarchies and testicular development: Is food a more potent stimulus than day length in an opportunistic breeder (*Taeniopygia g. guttata*)? . Hormones and Behavior 53:567-572.

Post E, Forchhammer MC. 2008. Climate change reduces reproductive succes of an Arctic herbivore through trophic mismatch. Philosophical Transcations of the Royal Society of London, B 363:2369-2375.

Pyter LM, Neigh GN, Nelson RJ. 2005. Social environment modulates photoperiodic immune and reproductive responses in adult male white-footed mice (*Peromyscus leucopus*). American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 288:R891-R896.

Steinman MQ, Knight JA, Trainor BC. 2012. Effects of photoperiod and food restriction on the reproductive physiology of female California mice. General and Comparative Endocrinology 176:391-399.

Stevenson TJ, Ball GF. 2011. Information theory and the neuropeptidergic regulation of seasonal reproduction in mammals and birds. Proceedings of the Royal Society B: Biological Sciences 278:2477-2485.

Sundararaj BI, Vasal S. 1976. Photoperiod and Temperature Control in the Regulation of Reproduction in the Female Catfish *Heteropneustes fossilis*. Journal of the Fisheries Research Board of Canada 33:959-973.

Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598-2600.

Tolla E, Stevenson TJ. 2020. Sex Differences and the Neuroendocrine Regulation of Seasonal Reproduction by Supplementary Environmental Cues. Integrative and Comparative Biology 60:1506-1516.

Visser ME. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275:649-659.

Visser ME, Caro SP, van Oers K, Schaper SV, Helm B. 2010. Phenology, seasonal timing and circannual rhythms: towards a unified framework. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3113-3127.

Watts HE, Edley B, Hahn TP. 2016. A potential mate influences reproductive development in female, but not male, pine siskins. Hormones and Behavior 80:39-46.

Wayne NL, Wade GN, Rissman EF. 1991. Effects of food restriction and social cues on sexual maturation and growth in male musk shrews (*Suncus murinus*). Reproduction 91:385-392.

Williams CT, Barnes BM, Kenagy GJ, Buck CL. 2014. Phenology of hibernation and reproduction in ground squirrels: integration of environmental cues with endogenous programming. Journal of Zoology 292:112-124.

Wingfield JC. 1983. Environmental and endocrine control of avian reproduction: An ecological approach. In: Mikami SI, Homma K, Wada M, editors. Avian Endocrinology: Environmental and ecological perspectives. Berlin: Japan Scientific Society Press, Springer-Verlag. p. 265-288.

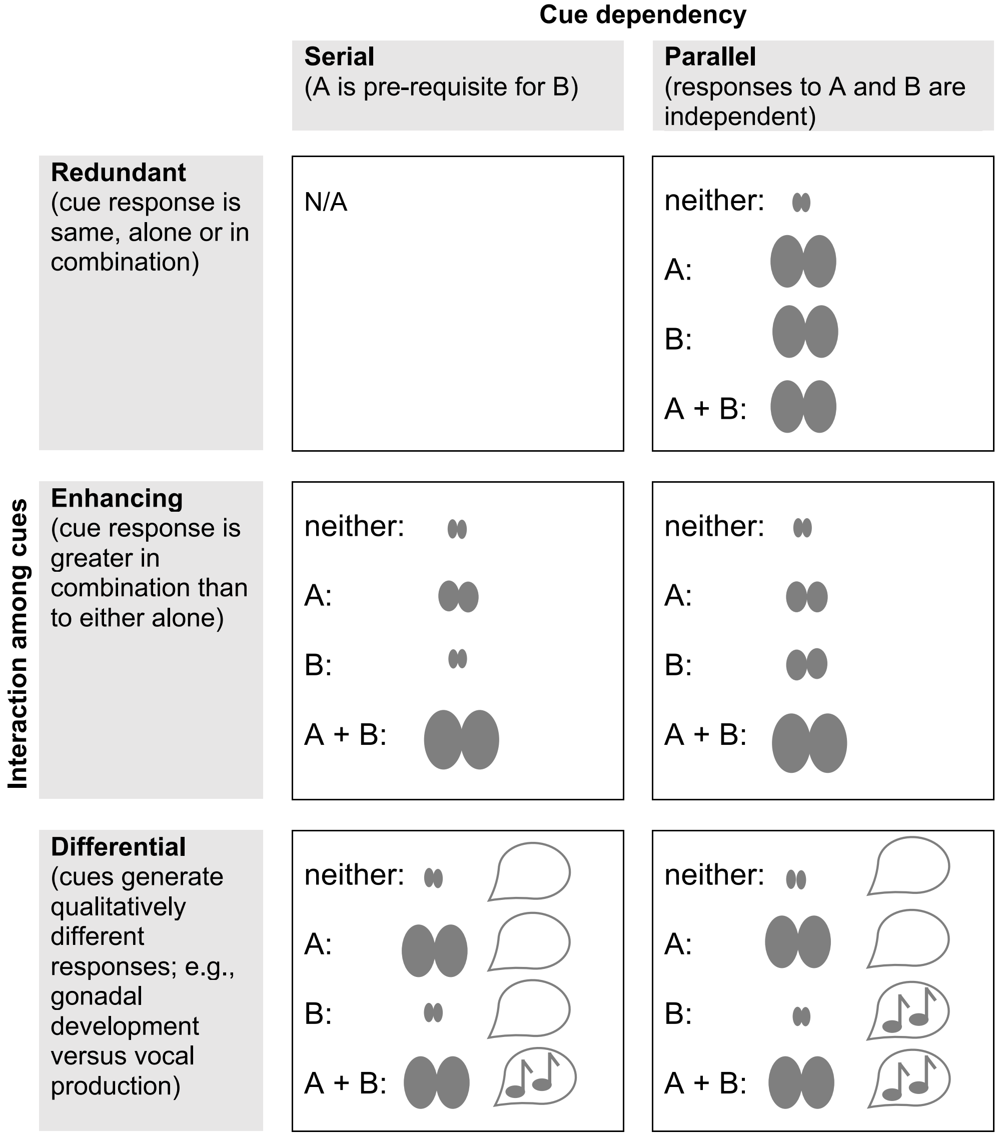
Wingfield JC. 2008. Organization of vertebrate annual cycles: implications for control mechanisms. Philosophical Transactions of the Royal Society B: Biological Sciences 363:425-441.

Wingfield JC, Hahn TP, Levin R, Honey P. 1992. Environmental predictability and control of gonadal cycles in birds. Journal of Experimental Zoology 261:214-231.

Wingfield JC, Hahn TP, Wada M, Schoech SJ. 1997. Effects of day length and temperature on gonadal development, body mass, and fat depots in white-crowned sparrows, *Zonotrichia leucophrys pugetensis*. General and Comparative Endocrinology 107:44-62.

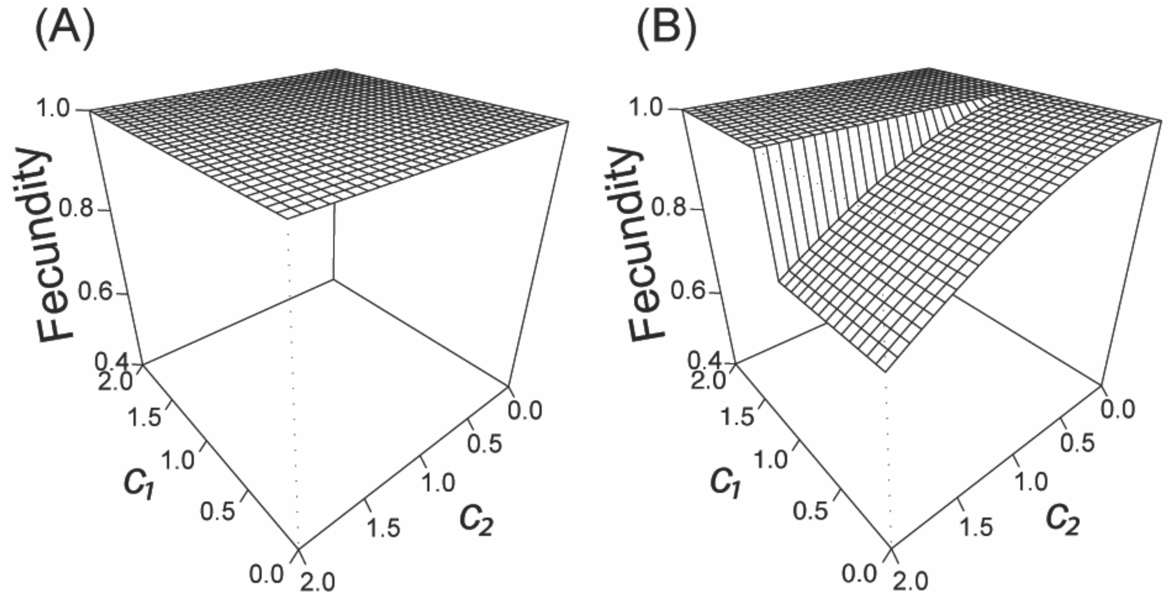
Figures

Figure 1. Conceptual overview of different modes of cue integration. Responses to two cues, A and B, alone and in combination are illustrated using the examples of gonadal (testicular) recrudescence (larger testes indicate greater advancement to breeding state) and vocal production (e.g., courtship vocalization shown as present/absent). Note that only differential cue interactions will result in two responses, so vocal production is only a potential response in those cases.


Cue dependency
Serial
(A is pre-requisite for B)
Parallel
(responses to A and B are independent)
Interaction among cues
Redundant
(cue response is same, alone or in combination)
N/A
neither:
A:
B:
A + B:
Enhancing
(cue response is greater in combination than to either alone)
neither:
A:
B:
A + B:
neither:
A:
B:
A + B:
Differential
(cues generate qualitatively different responses; e.g., gonadal development versus vocal production)
neither:
A:
B:
A + B:
neither:
A:
B:
A + B:

446

Figure 2. Fecundity realized based on breeding date using (a) parallel and enhancing cue integration, and (b) serial and enhancing cue integration for two environmental cues (c_1 and c_2) and cue sensitivities (z_1 and z_2) that matched partial regression coefficients (β_1 and β_2) that describe the relationship between the cues and optimal breeding date (i.e., cue-environment match). Results are shown for model parameters: $z_1 = z_2 = \beta_1 = \beta_2 = 0.5$, $C_1 = 1$, $s = 0.5$ and are qualitatively representative of a range of values that we ran to reflect the described scenario. For serial cue integration (b), the change in fecundity at $c_1 = 1$ reflects the change in influence of c_2 on breeding date.



This is the authors' version of: Watts et al. 2022. Environmental cue integration and phenology in a changing world. *Integrative and Comparative Biology*. https://doi.org/10.1093/icb/icac032

Figure 3. Fecundity realized based on breeding date using (a) parallel and enhancing cue integration, and (b) serial and enhancing cue integration for two environmental cues (c_1 and c_2) and cue sensitivities (z_1 and z_2) under a novel relationship between environmental cues and optimal breeding date (described by partial regression coefficients β_1^* and β_2^*; cue-environment mismatch). In this case, c_1 now has a weak association with optimal breeding date ($\beta_1^* = 0.1$) and c_2 has a strong association ($\beta_2^* = 0.9$). Other model parameters remained the same as for Figure 2 ($z_1 = z_2 = 0.5$, $C_1 = 1$, $s = 0.5$). Results for the parameter values shown here are qualitatively representative of a range of values that we ran to reflect the described scenario. For serial cue integration (b), the change in fecundity at $c_1 = 1$ reflects the change in influence of c_2 on breeding date.

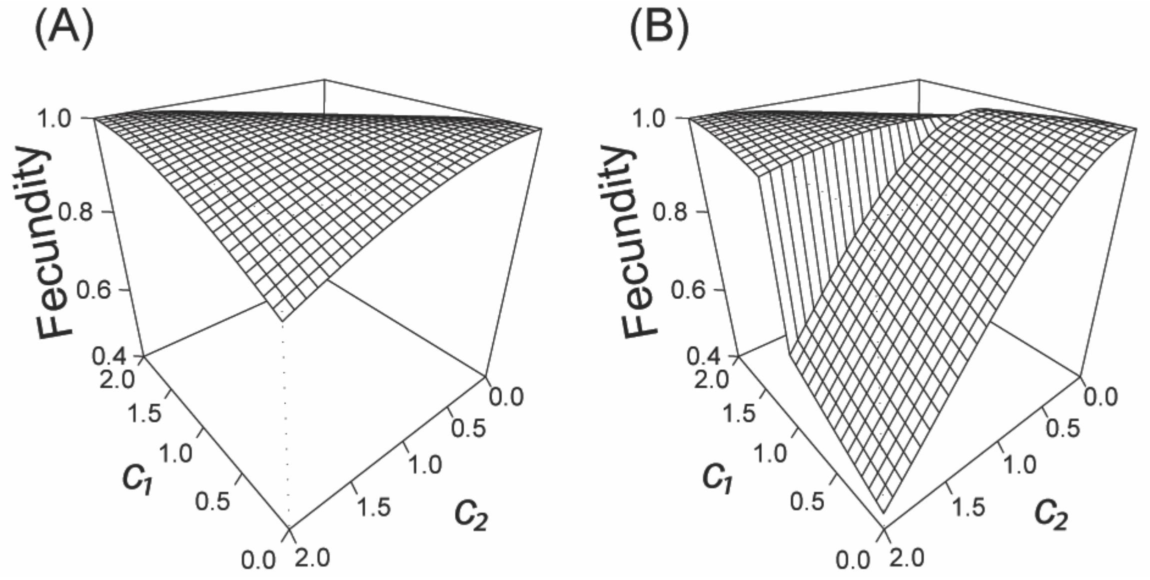


Figure 4. Difference in fecundity between serial and parallel enhancing cue integration (F_{serial} – F_{parallel}) under original (a) and novel (b) relationships between two environmental cues (c_1 and c_2) and optimal breeding date. Negative values indicate that parallel integration yields higher fecundity. Inset shows the same plot as (b) but rotated around z-axis so that positive values for difference in fecundity are visible. Fecundity values used to calculate difference are shown in Figures 2 and 3. Note that the difference in fecundity changes at $c_1 = 1$ due to the change in influence of c_2 on breeding date under serial cue integration.