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Mechanisms for adaptive cohort splitting

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ABSTRACT

Understanding the role of adaptive plasticity under random environmental variation is a central challenge of contemporary life history analysis. An important class of plastic responses is "cohort splitting" (Sunderland et al., 1976), in which groups of organisms beginning development at nearly the same time follow discrete developmental pathways or tracks differing in duration. We identify published studies on the topic and focus on three mechanisms predominant in those studies; we refer to the mechanisms as *initiation asynchrony*, in which differences in start-up timing can cause a split; *mid-point cueing*, a bifurcation at some seasonal time and intermediate developmental stage; and *diversified tracking*, in which individuals are assigned to developmental tracks probabilistically at the outset of development. We use optimization models to evaluate production of cohort splits by these mechanisms. We show that initiation asynchrony is generally a possible explanation but is highly sensitive to environmental conditions. Initiation asynchrony may result either from random variation in development or environment, with subsequent adaptive choices of life-cycle pathway—or from adjustments in developmental onset via diversified bet hedging. Mid-point cueing requires sufficiently high random variation in developmental rates. The adaptive response for Mid-point cueing results from matching the fitness-maximizing pathway to the stage of development at the bifurcation point. Diversified tracking can result from diversified bet hedging, but in this case, high random variation between pathways in reproductive success is essential for diversified tracking to prove adaptive. When diversified tracking results instead from frequency dependence of survival or reproductive success, this mechanism is potentially independent of environmental variation, but frequency dependence is challenging to demonstrate. Additional empirical analyses, especially experimental and comparative approaches, are high priorities for future work.

1. Introduction

Cohort splitting is a bifurcation in life-cycle timing arising when individuals from a cohort (born at essentially the same time) follow alternative developmental pathways differing in duration. Though it is possible that cohort splits may be genetically determined, in the absence of convincing evidence for this (see below) we address cohort splitting as a discrete form of life-history plasticity and focus on its adaptive properties. A wide variety of organisms exhibit cohort splitting, including both animals and plants (e.g. facultative biennials, which reproduce in a single episode but vary in duration of their life cycles (Baskin and Baskin, 1979a,b; Gross, 1981; Lacey, 1986), and the many plant species with seed banks, implying highly variable timing of developmental onset within cohorts (Baskin and Baskin, 2001)). Cohort splitting has appeared in the literature across a variety of animal taxa (see Table 1) in every decade since the term was first introduced into the ecological literature by Sunderland et al. (1976). The term "cohort splitting" seems to have been applied exclusively to animals, despite the many obvious plant examples, and we therefore emphasize animal examples here. Nevertheless, the phenomenon is clearly far more extensive than its explicit mention in the literature would indicate.

Cohort splitting in one example, the dragonfly *Epitheca cynosura*, is illustrated in Fig. 1A (based on a similar figure in Johnson, 1986). Larval development slows down on the slow track as the split becomes apparent, while fast-track larvae develop rapidly to the first winter, emerging in the spring. Slow-track larvae have a similar burst of rapid development the following fall, with emergence in the subsequent spring. These data suggest the difficulty of determining the exact seasonal timing of the split onset, though in this particular study tracking development of individuals indicated separation into separate tracks in mid-summer, somewhat before the clear seasonal separation between the two sub-cohorts (Johnson, 1986).

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Table 1
Examples of cohort splitting across species categorized by three general mechanisms: initiation asynchrony (IA), when differences in start-up timing cause a split, mid-point cueing (MC), when a split occurs at some seasonal point and intermediate developmental stage, and diversified tracking (DT), when individuals are assigned to developmental tracks probabilistically at the outset of development.[a]

Species/taxon	Mechanisms		
	Proposed	Notes/other	References
Beetles			
Curculio elephas	BH/DT	Variable lipid resources	Menu and Debouzie (1993), Menu et al. (2000) and Menu and Desouhant (2002)
Dendroctonus rufipennis	BH/DT		Hansen and Bentz (2003)
Caddisflies			
Protonemura meyeri	MC		Pretty et al. (2005)
Craneflies			
Tipula sacra	MC, BH/DT	Temporal instability	Pritchard, 1976 (1980)
Tipula montana	MC	Temperature fluctuation	Todd (1996)
Damselflies			
Coenagrion hastulatum	MC, O	Interference competition, spatial variation	Norling (1984b) and Johansson and Norling (1994)
Coenagrion resolutum	MC		Baker and Clifford (1981)
Coenagrion mercuriale	BH/DT	(Genetic polymorphism)	Watts and Thompson (2012)
Ischnura elegans	DT	(Genetic polymorphism)	Parr (1970) and Thompson (1977)
Lestes sponsa	MC		Johansson et al. (2001)
Dragonflies			
Asiagomphus pryeri	MC		Aoki (1999)
Epitheca cynosura	IA, MC, O	Interference, cannibalism	Johnson (1986), Martin et al. (1991) and Johnson et al. (1995)
Cordulegaster boltonii	MC		Ferreras-Romero and Corbet (1999)
Leucorrhinia dubia	MC	Photoperiod	Norling (1984c)
Dobsonflies			
Protothermes spp.	MC	Seasonal prey size decline	Hayashi (1994)
Moths			
Coleophora alciicoletta	MC	Photoperiod	Butterfield et al. (1999)
Zygaena hippocrepidis	MC	Temperature	Wipking (1990)
Spiders			
Pardosa agrestis	BH		Kiss and Samu (2005)
Stoneflies			
Protonemura intricata	MC	Photoperiod	Kozáčeková et al. (2009)
Pteronarcys tateri	DT	(Genetic polymorphism)	Schultheis et al. (2002)
Pteronarcys californica	IA	Extended larval recruitment	Townsend and Pritchard (1998) and Schultheis et al. (2008)
Agnetina capitata	IA	Extended larval recruitment	Moreira and Peckarsky (1994)
Nemurella pictetii	O	Intraspecific competition	Lieske and Zwick (2008) and Nesterovitch and Zwick (2003)
Webworms			
Hyphantria cunea	MC, DT	Phenotypic plasticity (Genetic polymorphism)	Gomi (1996)
Isopods (Woodlice)			
Ligia oceanica	IA	Early broods vs. late broods	Willows (1987a,b)
Porcellio scaber	MC		Zimmer and Kautz (1997)
Phyloscia muscorum	MC, BH/DT		Sunderland et al. (1976)
Trichiniscus pusillus	MC		Phillipson (1983)
Tylos europaeus	MC	Male–male competition	Gonçalves et al. (2005)
Millipedes			
Polydesmus angustus	MC, BH/DT	Temperature, food quality	David et al. (1993) and David et al. (1999)
	BH/IA	(Maternal effects)	David (2009) and David and Geoffroy (2011)
Shrimp			
Pandalid shrimp	MC		Charnov (1989)
Sea urchins			
Paracentrotus lividus	O	Interference competition	Grosjean et al. (1996)
Salmon			
Salmo salar	MC	Interference competition, changes in appetite, developmental switch	Thorpe (1977) and Metcalfe et al. (1988)
Perch			
Perca flavescens	O	Interference competition, Spatial variation	Post et al. (1997)
Perca fluvatilis	IA	Initial perch size	Huss et al. (2007, 2010)
Bluefish			
Pomatomus saltatrix	MC	Water temperature	Callihan et al. (2008)

[a] Where an author has proposed bet hedging (BH) as an explanation, we show BH/IA or BH/DT when one or the other mechanism seems to apply best, but simply BH when either DT or IA may fit. Other mechanisms are indicated as O (=other); those in parentheses under notes/other were proposed, but no supporting experimental evidence was found. For additional examples of cohort splitting, see Danks (1992, Table 4).

The extensive literature of plasticity contains many examples of flexible life-cycle patterns (Scheiner, 1993; Gotthard and Nylin, 1995; West-Eberhard, 2003), including discrete features like polyphenism (Grime, 1979; Nylin and Gotthard, 1998). But cohort splitting, with its mixture of discrete alternative trajectories over seasonal time, raises important new questions about how selection might favor the mix of life-cycle timing that have not yet been addressed in the plasticity literature. The shift in perspective from the continuous reaction norms predominant in the plasticity literature to discrete alternative pathways requires a different perspective.

To establish a conceptual framework for addressing cohort splitting, we consider discrete alternatives available to individuals in a species with plasticity of life-cycle duration. A cohort beginning development at a particular seasonal time is generally constrained to mature in some restricted seasonal window, and for simplicity