






SYMPOSIUM INTRODUCTION

Birth and the Pathway to Adulthood: Integration across Development, Environment, and Evolution

Christopher J. Mayerl ^{*,1}, Terry R. Dial ^{†,2}, Mark C. Mainwaring [‡], Ashley M. Heers[§] and Rebecca Z. German[¶]

*Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA; †Department of Biology and Ecology Center, Utah State University, Moab, UT 84532, USA; ‡Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA; §Department of Biological Sciences, California State University, Los Angeles, CA 90032, USA; ¶Northeast Ohio Medical University, Rootstown, OH 44272, USA

From the symposium “Pathways to adulthood: environmental, developmental, and evolutionary influences on the ontogeny of form and function” and “Biology at birth: the role of infancy in providing the foundation for lifetime success” presented at the annual meeting of the Society for Integrative and Comparative Biology annual meeting January 3–7, 2023, virtual January 16–March 31, 2023.

¹E-mail: christopher.mayerl@nau.edu

²E-mail: terry.dial@usu.edu

Introduction

Birth, and the period shortly thereafter, is a perilous time for any organism. Following parturition or hatching, individuals face many challenges, including environmental stressors (e.g., temperature or humidity), competition, and/or predation, all of which can impact selection (Lindstrom 1999; Metcalfe and Monaghan 2001; Gluckman and Hanson 2004). Furthermore, major anatomical, behavioral, and physiologic changes occur throughout the ontogenetic period. As such, the conditions an organism experiences throughout the ontogenetic period have implications for their survival, success, and ultimately, their fitness (Lindstrom 1999; Lee et al. 2003; Nord and Nilsson 2016; Nord and Giroud 2020). An understanding of developmental strategy, neonatal condition, and environmental challenges, as well as the physiology of newly born/hatched individuals experiencing those conditions, is critical for evaluating how adult organisms function and survive. However, these topics are often studied in isolation, both across different systems, and at a single point in time.

Two sibling symposia “Biology at birth: the role of infancy in providing the foundation for lifetime suc-

cess” and “Pathways to adulthood: environmental, developmental, and evolutionary influences on the ontogeny of form and function” address these concerns from different but complementary perspectives. The first, “Biology at birth,” highlights the importance of understanding infancy from an integrated perspective, and how infancy can shape an individual’s future. The goal of this symposium is to bring together researchers across various life science disciplines for conversation, collaboration, and interaction across boundaries as a way of promoting novel and innovative research at this specific moment of development. Herein, we examine infancy through multiple physiologic and comparative perspectives, under three general topic headings: (1) how the pre- and perinatal environments shape infant phenotype (e.g., maternal effects); (2) infant physiology and development; and (3) the lifetime impacts of infant experiences on phenotype and performance, especially when development is disrupted. Authors in this symposium span multiple physiologic systems (including neurological, cardiovascular, musculoskeletal, digestive, endocrine) and multiple model species (humans, pigs, sheep, rodents).

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The second symposium, “Pathways to adulthood,” seeks to bring attention to the importance of understanding how factors experienced during ontogeny shape adult organismal biology. The central premise of this symposium is that, in order to fully understand how organisms work, we must also understand the vast array of effects that influence the acquisition of form, function, performance, and behavior. Rather than focus solely on ontogeny, here defined as postnatal development, this symposium highlights how ontogeny unfolds under varying environmental conditions and how different life history strategies impact adult form and function. Although the incorporation of life history variation in a symposium on organismal form and function appears disconnected, contributors present convincing evidence that the morphological pathway to adulthood is shaped by the pace and age sequence of events leading to maturity. The overall intention herein is to refocus attention on developing organisms and how they work, in an effort to better understand (1) how organisms function as juveniles and adults and (2) how ontogeny unfolds to produce a wide array of phenotypes upon which selection acts.

The papers from these two symposia represent a broad integrative perspective on development, starting at birth/hatching and extending into adulthood. Here, we introduce several general themes uniting the two symposia and the specific papers covering a range of taxa, systems, and perspectives of evolution and performance: (1) Physiology and Performance during development; (2) Lifelong consequences of conditions experienced during early life; and (3) Life history strategies. Our goal herein and going forward is to galvanize interactions and cross-fertilizations across disciplines. We hope that in doing so, we will promote new and integrative work on both the underlying normal physiology and the specific pathophysiology that characterize development.

Physiology and performance during development

Most research regarding organismal function, evolution, and ecology tends to focus on adult animals (Dial et al. 2015). However, neonates are not small adults—few lineages grow isometrically (i.e., Fiorello and German 1997; Maie et al. 2013), and young interact with the physical world differently than adults (Schmidt-Nielson 1984). These factors are especially critical to consider because in order to become a reproductive adult, an individual must survive neonatal and juvenile stages, which typically have the highest rates of predation (Case 1978; Promislow and Harvey 1990; Adams et al. 1995). Here, we highlight research on sev-

eral aspects of organismal function, across a range of lineages, highlighting the ontogeny of physiology and performance. Together, these emphasize the need to consider multiple systems and multiple organismal levels when evaluating function in a developing organism.

Understanding the ontogenetic limits of performance is perhaps most well studied in regards to the musculoskeletal system, particularly with respect to locomotor function (e.g., Carrier 1996). In this issue, we highlight the ontogeny of locomotor performance across a range of vertebrate taxa, including whales, birds, pigs, crocodylians, and amphibians, from a variety of perspectives. There is extensive variation in the musculoskeletal system at the tissue level. For example, bones typically become more resistant to fracture through ontogeny (Carrier 1983), and muscles vary in fiber type and mitochondrial density in many species (Noren et al. 2015; Periasamy et al. 2017). Furthermore, the musculoskeletal system is highly plastic, and varies due to factors including locomotor mode, usage, and environment (Haapasalo et al. 1996; Du and Standen 2017). One lineage that goes through a fairly extreme shift in environment are frogs, which often metamorphose from aquatic juveniles to terrestrial adults. Kinsey et al. (this volume) investigated how the material properties of the femur changes through ontogeny in a species of frog that goes through metamorphosis (*Lithobates catesbianus*), compared to one that remains aquatic throughout its life (*Xenopus laevis*). These authors found that the species exhibited different changes in bone mineral density and material properties through ontogeny, highlighting the impact of both development and the environment on maturation of the skeletal system. Another lineage that experiences high demands in locomotor performance at a young age are cetaceans, which must be able to immediately sustain locomotion under hypoxic conditions to remain with their mothers. Noren et al. (this volume) highlight how this occurs across cetaceans by reviewing the postnatal maturation in both mitochondrial density, muscle fiber type, and locomotor performance. They demonstrate that in cetaceans, the primary changes in locomotor muscles occur through increases in mitochondrial density and myoglobin content, with little change in muscle fiber type.

In addition to variation at the level of the tissue, there is also a high degree of variation in overall locomotor performance through ontogeny (Carrier 1996). In this volume, Aerts et al. and Young et al. both investigate how locomotor function varies within a precocial mammal, the pig (*Sus scrofa*). Aerts and colleagues highlight how intrauterine undernutrition impacts gait dynamics in low birth weight individuals, and show that when development is normal, variation in gait pat-

terns is primarily related to size, rather than neuromotor control. However, when intrauterine development is experimentally varied, and infants are born prematurely, Young *et al.* (this volume) demonstrate that there are severe locomotor consequences, and that a normally precocial mammal can function similarly to an altricial species. The authors suggest that rather than being a function of size, these changes likely relate to neurological immaturity. Thus, we can see differential impacts of development on performance depending on whether an individual is born at term, where size dictates performance, or if an individual's prenatal development is disrupted, resulting in neuromotor impairments to performance. This work highlights the importance of considering both prenatal and postnatal development in discussions on performance. In addition, Heers (this volume) highlights how juveniles with developing locomotor structures can achieve surprisingly high levels of locomotor performance through compensatory mechanisms that vary by group. For example, ground birds employ their wings early in development and compensate for the rudimentary nature of their wings through anatomical, kinematic, and behavioral mechanisms. In contrast, waterfowl have delayed wing development and compensate by having high leg investment and performance (Dial and Carrier 2012). Such changes in locomotor function or performance are not restricted to endothermic parasagittal vertebrates. Iijima *et al.* () highlight how locomotor kinetics, kinematics, and morphology vary across three orders of magnitude in American alligators, a sprawling ectothermic vertebrate. They demonstrate that unlike mammals, which typically adjust locomotor function in proportion to the Froude number (Alexander 1976, 1984), alligators prioritize reducing mechanical work during stance at the expense of higher costs for swing as they increase in size. Additionally, limb posture, ground reaction forces, and limb mass also vary through alligator ontogeny (Iijima *et al.*, this volume), highlighting the need to expand our investigations of locomotor ontogeny and evaluate how function differs in lineages with different histories and postures.

Finally, this work highlights that there is an extensive gap in knowledge of the physiology and performance of neonates. Although the authors in this issue highlight that there is still work to be done in the ontogeny of the locomotor system, our gaps in knowledge extend to several other aspects of organismal function. For example, Steer *et al.* (this volume) highlight variation in anatomy, physiology, and function of the mammalian feeding apparatus during the transition from suckling to drinking. They demonstrate that neuromotor control and the movements of the tongue are drastically different during suckling and drinking in the infant pig, and that

these changes are not necessarily intuitive. Investigating how neuromotor control varies in concert with variation in other systems, such as the endocrine system—which has extreme ontogenetic variation (Crespi and Denver 2005; Wada 2008)—is relatively unexplored. Additionally, Matthews *et al.* (this volume) highlight the need to link the mechanistic studies above with microevolutionary processes. They highlight three potential avenues for exploring these links, through structural equation modeling, robotics, and multimodal data acquisition. The use and development of these tools, and others like them, will facilitate integrative and comparative biologists to ask deeper, broader, and more nuanced questions about the links between ontogeny, selection, and fitness.

Lifelong consequences of conditions experienced during early life

The conditions that individuals experience during early life can impact their performance during adulthood and thus have lifelong consequences (Lindstrom 1999; Metcalfe and Monaghan 2001). Such effects have been documented to occur in flora and fauna inhabiting terrestrial and aquatic ecosystems globally and encompass all taxa. Several factors interact to cause variation in the conditions experienced by individuals through ontogeny. For example, climatic environmental conditions can have broad impacts on adult metabolism, survival, behavior, and fitness (Nord and Nilsson 2016; Marshall *et al.* 2017; Ancona *et al.* 2018; Azpillaga *et al.* 2018; Leblanc *et al.* 2019; Stawski and Geiser 2020). Furthermore, the social environmental conditions also can impact adult phenotype and performance (Albon *et al.* 1987; Ozanne and Hales 2004; Ruploh *et al.* 2013; Hopwood *et al.* 2014; O'Hagan *et al.* 2015; Riley *et al.* 2017; Noguera and Velando 2020), as well as factors such as the genetic similarity of parents, predation, resource limitation, and parasitism (Royle *et al.* 1999, 2005; Remes 2006; Coslovsky and Richner 2011; Huchard *et al.* 2016; Pigeon and Pelletier 2018; Jarrett *et al.* 2018; Arct *et al.* 2019). These factors all interact during early life, can have impacts into adulthood, and can even be passed on to offspring via transgenerational effects, thereby influencing the fitness of successive generations (Jones and Friedman 1982).

Establishing links between early life conditions and subsequent performance during adulthood is logistically challenging because of the resources required to track individuals throughout their lives. Consequently, many studies focus on how conditions experienced in early life influence performance during ontogeny rather than adulthood and in this volume, studies examine, for example, how temperature influences offspring perfor-

mance in birds (Tabb and Nord, this volume) and fish (Berio et al., this volume). Other studies examine the impact of early life conditions on lactation and suckling in mammals (Josefson et al., this volume; Steer et al., this volume), locomotor development (Aerts et al., this volume; Young et al., this volume), and the ontogeny of the microbiome (Murphy et al., this volume). Nonetheless, the application of sophisticated analytical techniques has helped provide overarching conclusions that are impossible using single-species studies. In this issue, Albecker et al. (this volume) conducted a meta-analysis to examine if developmental plasticity in response to varying larval environments in anuran amphibians produced changes in metamorphic phenotypes and found that the larval environments partly explained metamorphic phenotypes. In addition, the use of increasingly small tracking devices has enabled scientists to follow creatures as small as ants and bumblebees (Maggiore et al. 2019; Burns et al. 2021). In this issue, Rittschof and Denny (this volume) review how early life conditions shape the adult phenotypes and fitness of bees and show that early life conditions influence traits such as adult body size, which subsequently influence fitness at the individual level and possibly even at the population level.

Parental, and in particular maternal, effects on infants are significant factors in evolution, operating through developmental plasticity (Uller 2008). Within mammals, lactation and maternal feeding of infants is a mechanism with the potential for profound effects (Josefson et al., this volume; Steer et al., this volume; Pittet and Hinde, this volume). Josefson et al. (this volume) document the impact of stress on lactation performance, and thus neonate and infant success. Chronic stress decreased both quantity of milk, in lower yields, and quality of milk, in terms of lipid and energy concentrations in lactating females, but did not impact protein and lactose components. Interestingly, this stress did not change expression of milk synthesis genes in mammary glands. These results, taken together, are significant for our understanding of the mechanisms by which milk composition changes in response to the maternal environment.

Another important, but understudied, source of parental influence and input to infant biology is the maternal microbiome. For parent–infant dyads, vertical transmission of microbiota can produce variation that impacts ultimate offspring survival and success. Murphy et al. (this volume) systematically review the literature to assess how often vertical transmission occurs and whether evidence of maternal transmission affecting offspring phenotype exists. They found that many studies examining vertical transmission of microbiomes failed to collect whole microbiome samples

from both maternal and offspring sources, compromising their utility. The suggestions for future studies (to include a *functional* diversity of microbes, host factors, microbe–microbe interactions, and environmental factors) will make such studies more valuable for understanding relationships between microbiomes and evolution.

Empirical research examining links between adversity experienced during early life and performance during adulthood have focused overwhelmingly on the trade-off between growth and reproductive success (Metcalf and Monaghan 2001). The “grow now, pay later” concept proposes that juveniles employ rapid growth to compete effectively with siblings (Royle et al. 1999) or escape adverse conditions experienced in the nest, but then pay for that initial investment later in their lives by having, for example, shorter lifespans, fewer reproductive opportunities, and thus lower levels of lifetime reproductive success (Richner et al. 1989; Lindström 1999; Metcalfe and Monaghan 2001; Fisher et al. 2006; ; Krause and Naguib 2011; Mainwaring and Hartley 2012; Vetter et al. 2016; Spagopoulou et al. 2020). Gay et al. (this volume) show that captive Mongolian gerbils (*Meriones unguiculatus*) that hatched prematurely and were thus not fully developed at birth had significant impairments to learning at later stages of growth when compared to offspring not born prematurely.

Expanding on this idea, Pittet and Hinde (this volume) examined trade-offs between investment in the self-maintenance of mothers and investment in offspring in captive rhesus macaques (*Macaca mulatta*). In this species, mothers give birth to first-born offspring before they reach full maturity, and first-born offspring suffer in relation to later-born offspring because mothers are still investing significantly in growing themselves such that first-born offspring receive 16% less milk than later-born offspring. In agreement with the “grow now, pay later” concept, first-borns accelerated growth during infancy, but had slowed growth during juvenility and lower body mass throughout adulthood compared to later-born offspring. Although first-born and later-born offspring began to reproduce at similar ages, first-born offspring had lower body masses during adulthood, which persisted throughout their lives (Pittet and Hinde, this volume).

Mainwaring et al. (this volume) review those instances in which individuals suffering adversity during early life either outperform conspecifics that enjoy better upbringings or at least make the best of a bad situation (Luevano et al. 2022). For example, Mainwaring et al. (2012) used mate choice trials to show that late hatched males within asynchronously hatched zebra finch (*Taeniopygia guttata*) broods were more attractive

to females than early hatched males. Similarly, wild rhesus macaques that experienced hurricanes during early life bred at a younger age than dominant conspecifics that never experienced hurricanes, and thus exhibited a higher reproductive output during their prime reproductive years, indicating that subordinate individuals born during hurricane years overcame such early life adversity (Luevano et al. 2022).

In terms of surviving to adulthood, subordinate individuals employ “sneaky” tactics, such as adaptively timing foraging behaviors to avoid dominants and thus maximizing their chances of surviving to the next breeding season (Mainwaring et al., this volume). During adulthood, subordinate individuals rely on tactics such as adaptive dispersal behaviors and competing for partners at optimal times to acquire copulations whenever possible. In cooperatively breeding species, for example, dominant individuals sire offspring that are helped by subordinate helpers, and subordinate individuals are strongly constrained from siring offspring themselves by the dominant individuals. Although subordinates accrue indirect fitness benefits through raising related offspring, Young et al. (2007) showed that extra-territorial forays by subordinate male meerkats (*Suricata suricatta*) resulted in copulations and that 70% of their offspring were sired in this way. Such extra-group forays result in subordinate individuals siring 20–25% of all young in the population (Young et al. 2007). Consequently, there are instances where subordinate individuals employ “sneaky” tactics that allow them to outperform, or at least compete with, dominant conspecifics during adulthood (Mainwaring et al., this volume).

In short, there is widespread evidence that conditions experienced in early life influence performance during adulthood. The same principles apply to humans and there is an increasing focus on how conditions experienced during childhood influence the health of humans in later life (Lummaa and Clutton-Brock 2002; Merry 2004). Illustratively, Lynch et al. (2020) used records of Finnish women during the second World War to show that young girls serving in a paramilitary organization subsequently waited less time to reproduce, had shorter inter-birth intervals, and had more children than their non-serving peers or sisters. Other studies have shown that the tradeoff of early and frequent reproduction is the production of smaller offspring (Reznick 1983). However, it is well established that when humans have a small size at birth and during infancy, and then undergo a period of accelerated weight gain before the age of 10 years old (compensatory growth), they are susceptible to health issues such as coronary heart disease, type two diabetes, and hypertension in humans (Shanley and Kirkwood 2000; Barker et al. 2002; Singhal

et al. 2003; Bateson et al. 2004). Along similar lines, Cole and Adolph (this volume) show that behavioral flexibility allows human infants to cope with an ever-changing body as they navigate an ever-changing world, whilst Hubbard et al. (this volume) show that preterm birth occurs in 10% of all live births and creates a variety of challenges to neonatal life, which then go on to persist well into adulthood.

Life history strategies

Life histories, or the age schedule of events throughout the lifespan of an organism, have a rich theoretical and experimental history and are foundational to evolutionary theory. The age schedule of morphological maturation is widely varied throughout vertebrates (e.g., altricial vs. precocial development; Stark and Ricklefs 1998), but the vast majority of investigations into locomotor biomechanics, neuromuscular function, and adaptive morphology concern that of the adult. Despite this, a growing body of work is focusing attention on developing forms; not only shifting attention to early ontogenetic stages, but also to the impact of variation in life history strategy on form and function in early life. This latter focuses on how variation in life histories impacts the function of newly born or hatched organisms is wildly exciting and no doubt a rich and expansive direction for future investigation.

Perhaps not surprisingly, the environment induces a tremendous degree of variation on the pace of life histories. Albecker et al. (this volume), in a meta-analysis on developmental plasticity among anurans, present convincing evidence of environmental stressors influencing developmental timing and organismal size, across a broad phylogeny. High temperatures and drought lead to shorter larval periods and thus smaller individuals at metamorphosis, whereas limited food and/or high density of conspecifics lengthen the larval period (Albecker et al., this volume). Response to the environment alters the life history strategy—faster or slower—and such plastic effects show that life history strategy is not set in stone, particularly among organisms with discrete life stages.

Among those studies on early life stage form and function, most focus on organisms that produce precocial young. Precocial strategies are those where the selective pressure of survival is placed more squarely on the individual juvenile than the caring parent, and thus we observe relatively advanced or mature locomotor morphology, biomechanics, and neuromuscular control (Carrier 1996). Altricial young are born or hatch at a relatively small and immature state compared to a precocial counterpart (Roff 1992; Stearns 1992; Stark and Ricklefs 1998), and several studies from this volume

show postural and locomotor deficits among altricial individuals (Young et al., this volume) and delayed onset of performance in altricial locomotor systems among developing birds (Heers, this volume). New, fascinating work contrasting precocial development with altricial acquisition of form and function is revealing tradeoffs in: avian limb investment (Heers, this volume), piglet gait kinematics (Aerts et al., this volume), investment in armor plating (Hoover et al., this volume), and neuromuscular control (Young et al., this volume) as well as insights into the development of human walking dynamics (Cole and Adolph, this volume). Studies are revealing that altriciality, although defined by relatively immature and helpless young, is not as limiting as previously thought. Indeed, kinematic data on piglet gait reveal no obvious tradeoff to being born smaller and less mature (Aerts, this volume). Furthermore, the musculoskeletal growth that occurs among altricial juveniles can vastly outpace that of their precocial counterparts, leading to novel morphologies that otherwise would not have been possible under a precocial strategy (Heers, this volume; Matthews et al., this volume; Dial and Carrier 2012; Dial et al. 2012).

In contrast, precocial strategies produce young with relatively advanced or mature locomotor morphology (Carrier 1983; Garland 1985). This relatively mature morphology compensates for the small size and naivete of early life stages and contributes to adult-level performance of escape behaviors (Carrier 1996). Selection is likely quite strong on the escape performance of these vulnerable life stages, and thus favors investment into relatively robust limb musculoskeletal systems, which scale with negative allometry (Carrier 1983). Such compensatory anatomy, functioning maturely in the juvenile life stages, is canalized into the adult stage of precocial species (Carrier 1996). It is only among altricial organisms—where the adult stage is responsible for protecting helpless, developing young—that we observe positive allometry in the locomotor anatomy through ontogeny (Dial and Carrier 2012; Dial et al. 2012, 2016). Positive allometry indicates that the trait of interest is more extreme in the larger adult, implying that it has departed morphologically and possibly entered novel morphospace at the adult level. In this way, it is likely that the life history strategy of a species influences the extent to which locomotor morphology is canalized (precocial) or left relatively unconstrained (altricial) into adulthood.

Compared to locomotor anatomy, we generally observe less canalization of the craniofacial morphology underlying feeding anatomy. This is largely explained by the selective pressures driving positive allometry of craniofacial morphology. The dearth in supply of larger but more energetically nutritious food in the environ-

ment suggests that the advantages of positive allometry outweigh the advantages of compensating for juvenile handicaps. Studies show that one fundamental element to the feeding performance of juvenile organisms is the underlying maturation of the musculoskeletal system at birth/hatching. Among the live-bearing Trinidadian guppies (*Poecilia reticulata*) that are born in populations adapted to highly competitive feeding regimes (low predation environments), offspring are not only larger (by ~20%) but are much more mature (~80%) in craniofacial musculoskeletal traits (Dial et al. 2017a). This early maturation in offspring born to high competition environments is likely responsible for the observed competitive advantage and subsequent higher survival rate of these offspring (Bashey 2008). The mature morphology of high competition offspring appears to be the heterochronic result of hypermorphosis or prolonged development, as opposed to an accelerated rate or early onset of morphological maturation (Dial et al. 2017b). But, the extent to which this heterochronic shift in the timing of birth affects the adult morphology remains unknown and is illustrative of the kind of work required going forward.

Matthews et al. (this volume) present a case study on experimental manipulation of gene expression that directly targets a heterochronic shift in morphological maturation. By upregulating Wnt expression in larval zebrafish, the study examines the morphological and performance effects of feeding with an experimentally induced neotenic form. This heterochronic shift accomplishes two objectives: first, it locks in a neotenic morphology, which allows for examination of an arguably more altricial craniofacial apparatus, and second, induces a morphology consistent with repeated examples of adaptation to benthic feeding (i.e., more downturned mouth). Furthermore, the study attempts to link genetic change to morphological and performance outcomes using path analysis. The authors make a case for the continued pursuit of Arnold's 1983 challenge to link many levels of biological variation (genes → phenotype → performance → fitness) in order to better understand the evolution of complex systems (Matthews et al. this volume; Arnold 1983).

Concluding remarks

Here, in these two symposia on the effects of birth and early life influences on performance, contributors present current and leading data on the environmental, genetic, epigenetic, and life history conditions shaping organismal form and function. Contributors show that the adult phenotype is a collection of early life influences that shape the terminal phenotype, and only by teasing apart these various influences (current climatic condi-

tions, evolutionary selective regimes, epigenetic influences, locomotor, or feeding demands) can we truly appreciate the form and function of the organisms that we seek to understand.

Author contributions

All authors contributed to the conceptualization, execution, drafting, and review of the manuscript.

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Conflict of interest

The authors declare no conflicts of interest.

Data Availability

No new data were generated or analyzed in support of this symposium introduction.

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