Received: 13 October 2022 | Accepted: 27 April 2023

DOI: 10.1111/ede.12440

RESEARCH ARTICLE

WILEY

Agency in Reproduction

Laura Nuño de la Rosa

Department of Logic and Theoretical Philosophy, Complutense University of Madrid, Madrid, Spain

Correspondence
Laura Nuño de la Rosa
Email: lauranun@ucm.es

Funding information
Ministerio de Ciencia e Innovación, Grant/Award Number: PID2021-127184NB-I00

Abstract

While niche construction theory and developmental approaches to evolution have brought to the front the active role of organisms as ecological and developmental agents, respectively, the role of agents in reproduction has been widely neglected by organismal perspectives of evolution. This paper addresses this problem by proposing an agential view of reproduction and shows that such a perspective has implications for the explanation of the origin of modes of reproduction, the evolvability of reproductive modes, and the coevolution between reproduction and social behavior. After introducing the two prevalent views of agency in evolutionary biology, namely those of organismal agency and selective agency, I contrast these two perspectives as applied to the evolution of animal reproduction. Taking eutherian pregnancy as a case study, I wonder whether organismal approaches to agency forged in the frame of niche construction and developmental plasticity theories can account for the goal-directed activities involved in reproductive processes. I conclude that the agential role of organisms in reproduction is irreducible to developmental and ecological agency, and that reproductive goals need to be included into our definitions of organismal agency. I then explore the evolutionary consequences of endorsing an agential approach to reproduction, showing how such an approach might illuminate our understanding of the evolutionary origination and developmental evolvability of reproductive modes. Finally, I analyze recent studies on the coevolution between viviparity and social behavior in vertebrates to suggest that an agential notion of reproduction can provide unforeseen links between developmental and ecological agency.

KEYWORDS
agency, evo-devo, reproduction

1 | INTRODUCTION

In the past two decades, the received view of organisms as passive objects of evolution has been challenged on two major grounds. Niche construction theory has disputed the conceptualization of organisms as passive objects of selective pressures, while development-oriented biologists have challenged the view of organisms as epiphenomena of genetic programs, stressing their self-constructing capacities, as well as their ability to plastically adapt to environmental circumstances. Both lines of criticism have brought to the front the active role of organisms in

evolution as ecological and developmental agents, respectively (Walsh, 2015). In this context, agents are defined as a special kind of goal-directed systems, goals being understood as "stable end-states actively attained and maintained by the system despite perturbations" (Walsh & Rupik, this issue). This organismal view of agency contrasts with the mainstream view of agency in evolutionary biology. Inspired by rational choice theory in economics, the selectionist approach to agency conceives of biological entities as agents evolved to maximize fitness (Okasha, 2018). In its mainstream shape, this mode of agential thinking applies not to organisms but to genes. From the gene's eye perspective, evolution is heuristically described as a competition between alternative genes (or alleles), which behave *as if* they were goal-directed agents (Ågren, 2021). Evolutionary genes are depicted as "strategic genes" aiming to maximize fitness "in an evolutionary game played with other strategic genes" (Haig, 2012, p. 470). For the purposes of clarity, I will name these two approaches to agency *organismal agency* and *selective agency*, respectively.

Organismal agency and selective agency have paid very unequal attention to reproduction. Agential thinking is deep-rooted in life history theory, where maximizing the number of offspring is identified as the goal explaining the different reproductive strategies of evolutionary agents (in most accounts, genes) for achieving such a goal (Okasha, 2018, p. 10). Therefore, the agential perspective of evolution endorsed by advocates of gene selectionism counts on a coherent account of reproduction. Just like behavioral or physiological traits, reproductive traits are explained as strategies of genes for maximizing fitness. In contrast, organismal approaches to evolution have widely neglected the role of agency in reproduction. In this theoretical framework, agency is minimally defined as the capacity of a biological system to "act on its own behalf" and the goal of reproduction is excluded from definitions of agency. Two recent quotations from this literature might help to illustrate this omission:

> [T]he capacity of living systems to participate in their own development, maintenance, and function by regulating their own structures and activities in response to the conditions they encounter. (Sultan et al., 2022, p. 1)

> Organisms are agents; they are naturally purposive systems. They are self-building, self-synthesizing, self-regulating systems. They are robust adaptive systems that respond to their conditions in ways that secure their own persistence and well-functioning. They do this by altering their structures, their activities, and their circumstances in ways that promote the attainment of their goals. (Walsh, 2023, p. 356)

A germane, philosophical approach to agential perspectives of evolution, also runs into difficulties in integrating reproduction. The so-called organizational approach, rooting back (at least) to Maturana and Varela's theory of autopoiesis, regards living systems as "integrated and active systems that must continuously interact with their environment to self-generate and maintain their own dissipative organization" (Barandiaran et al., 2009, p. 375), and defines biological functions as causal relations contributing to the maintenance of these systems (Moreno & Mossio, 2015). Since reproductive activities, such as gamete production, egg retention, or embryo provisioning, do not seem to contribute to self-maintenance, but rather to the generation and maintenance of other selves, they can hardly be considered as individual functions, and are, therefore, excluded from the very nature of organismal agency (Mossio et al., 2009). In a nutshell, organismal accounts of agency resolve the Darwinian concern by the goal of survival, but seem to be unable to provide a naturalized account of the goal-directed activities addressed to reproduction.

In this paper, I argue that, if one aims at providing a true alternative organismal framework of agency to that of selective agency, we need an organismal, agential account of reproduction. As a case study, I discuss recent empirical and philosophical work on the evolution of vertebrate viviparity, particularly in mammals. After discussing the mainstream view of genes as agents of reproduction, I argue that the agential role of organisms in reproduction is irreducible to developmental and ecological agency. Instead, accounting for the developmental evolution of reproduction requires us to include reproductive goals into our definitions of agency. Second, I explore the evolutionary consequences of endorsing an agential approach to reproduction with regard to novelty and evolvability. Finally, I argue that an agential notion of reproduction might provide unforeseen links between developmental and ecological agency. To substantiate this claim, I look at recent studies on the evolutionary developmental relationship between viviparity and social behavior in vertebrates.

2 | GENES AS CONFLICTING AGENTS OF REPRODUCTION

Reproductive patterns, or the different ways in which animals reproduce, are generally characterized according to three parameters, namely the mode of fertilization

(external or internal), the locus of embryonic development (viviparity or oviparity), and the mode of offspring provisioning (e.g. yolk feeding or mother feeding) (Furness et al., 2015). In the neo-Darwinian tradition, reproductive patterns are explained in the framework of life history theory. Life history theory seeks to understand how evolution shapes organismal traits throughout their life cycles, including "size at birth, growth rate, age and size at maturity, age-specific reproductive investment, number and size of offspring, age-specific survival, and lifespan" to enhance their reproductive success (Flatt & Heyland, 2011, p. ix). The classical approach to life histories is optimization theory (summarized in Stearns, 1992; Roff, 1993), where reproductive patterns are seen as "reproductive strategies" to maximize fitness. Therefore, reproductive modes have associated advantages and disadvantages that explain their evolutionary origination and affect their evolution. For instance, viviparity is hypothesized to evolve when the associated benefits (e.g., increased offspring quality or survival) outweigh the costs (e.g., reduced locomotor performance) (Furness et al., 2015), and not when this situation does not hold. Thus, viviparity might have never originated in birds because there is no need for it to evolve. Birds would have achieved most of the advantages provided by egg retention by other means, such as endothermy, egg incubation, nest construction, parental care, albumen provision, or calcareous eggshells (Blackburn & Evans, 1986).

Once reproductive modes evolved, life history theory predicts that their evolutionary modification is also affected by the advantages and disadvantages associated with each mode. Importantly, costs and benefits affect parents and offspring in different, and often conflictual, ways. So-called conflict theory regards reproductive modes as setting "arenas" for sexual, parent-offspring, and sibling conflict (Furness et al., 2015, p. 11). These "arenas for conflict" are defined as "shared traits" between the different agents participating in reproduction. Consequently, reproductive traits become "adaptations reflecting a history of antagonistic selection" (p. 5). A classic example of a shared character is offspring size (Furness et al., 2015). For instance, in turtles, where nutrient supply is under full maternal control, egg size corresponds to the optimal size from the mother's perspective. Since mothers are interested in sharing their resources among the maximum number of offspring, egg size is expected to be smaller than the optimal size from the embryo's perspective (Janzen & Warner, 2009). By contrast, viviparous embryos (specially matrotrophic species) can partly modulate the maternal transfer of nutrients. As a consequence, offspring size is expected to be a compromise solution between parental and offspring's interests (Crespi & Semeniuk, 2004).

Life history theory not only predicts the evolution of reproductive modes, but also the coevolution between reproductive modes and other life strategies, such as secondary sexual traits or mating systems (Furness et al., 2015). For instance, some studies have shown that there is an evolutionary relationship between reproductive modes and secondary sexual characteristics. In poeciliid fishes, the evolution of viviparity precedes the evolutionary loss of secondary sexual traits, suggesting that there has been a shift from precopulatory mechanisms to postfertilisation embryo selection mechanisms (Reznick et al., 2021). Concerning mating systems, it has been suggested that the strategy of polyandry, or mating with multiple mates, in primate females, has been selected to compensate for genetic incompatibility associated with implantation (Zeh & Zeh, 2001).

In most accounts of conflict theory, the goal of maximizing fitness through reproductive strategies is not predicated on individual organisms, but on genes. As applied to reproduction, the view of evolution as a game among strategic genes is exemplified in the conflict theory of pregnancy advanced by David Haig (1993, 1996). Conflict theory sees pregnancy as a genetic conflict over the allocation of maternal resources: fetal genes are described as aiming at increasing the transfer of nutrients from the mother, and maternal genes as seeking for limiting this transfer so that energetic resources are shared among future offspring. Evolutionary studies of genomic imprinting, or parent-of-origin gene expression, in the placenta, exemplify this gene eye's perspective of reproduction. Thus, "it is predicted that the genes that increase nutrient demand from the mother will be paternally expressed and the genes that restrict embryo growth will be maternally expressed" (Saldívar-Lemus & Macías Garcia, 2022, p. 68; see also Renfree et al., 2013). Imprinted genes bring to the arena of conflict not only the genes of mothers and embryos, but also the fathers' genes, adding sexual conflict as a new type of conflict driving the evolution of pregnancy (Haig, 1996).

Conflict theory does not entail that the evolution of pregnancy is only driven by the conflicting interests of genes. Instead, advocates of conflict theory acknowledge the existence of multiple aligned interests between all the genetic agents involved in this reproductive strategy. The emphasis on conflict versus cooperation rather seems to emphasize that *some* reproductive phenomena, such as imprinting, cannot be explained as adaptations of individual organisms, but can only be understood if genes are admitted as the true agents of evolution. Genetic conflict in pregnancy thus adds as a further

evidence to cases of intragenomic conflict such as sperm killing, meiotic drive, cytoplasmatic male sterility, or sex ratio distortions, advocated by defenders of the gene's eye viewpoint (see Okasha, 2018, ch. 2).

As I will argue in the following section, evo-devo studies of mammalian viviparity call for shifting the attribution of agency from the gene to the organism level. From this perspective, organismal agency is not the locus where the evolutionary interests of genes and individual organisms overlap, agency being a unit in which all parts share the goal of maximizing fitness (as argued by Okasha, 2018). In organismal agency, goals defined at an organismal level, or even at a supraorganismal level, are not selected effects, and organismal traits are not strategic means to achieve such effects. Instead, I will argue that an organismal view of reproductive agency provides distinct explanations of evolution, where individual organisms as well as supraorganismal agencies resulting from the developmental entanglement between parents and offspring, actively regulate their own reproduction in a goal-directed way that, in turn, enables and biases evolution. Gene-centered and organism-centered views of evolution do not need to be in opposition. They might just deal with different aspects of reproduction, as advocates from both camps have defended (see, e.g., Haig, 2012; Walsh & Rupik, this issue, as representatives of these two positions). Although I do favor a pluralist perspective, this is not the place to discuss this long-standing controversy. Instead, I will focus on how an organismal view of agency provides a perspective of reproduction that cannot be offered by the selectionist view of genes as evolutionary agents.

3 | REPRODUCTIVE MODES AS AGENTIAL ADAPTATIONS

In the last decades, various lines of criticism have challenged the gene-centered view of evolution in different directions, where the need to reconsider the role of reproduction recurrently comes to the fore. Developmental systems theory has emphasized the collaboration of multiple developmental resources into the reconstruction of life cycles in each generation (Oyama, 2000). James Griesemer (2000, 2005) has opposed the neo-Darwinian reduction of reproduction to gene replication, and argued for including material overlap across generations into our understanding of evolution. Pleas for an extended view of inheritance aim to understand how different inheritance systems participate in the intergenerational reconstruction of phenotypic traits (Jablonka & Lamb, 2005). And recently, developmental approaches to evolution have started to study modes of reproduction, not as evolutionary strategies for maximizing fitness, but as material processes involving complex relations among organismal entities (Nuño de la Rosa et al., 2021).

All these lines of criticism agree in shifting explanation from the gene to the organism level, attributing to organisms an active role in the intergenerational reproduction of form, from the self-regulation of development in the face of environmental signals, to the building of reliable environments. From this perspective, reproductive modes arguably play two simultaneous roles in evolution. On the one hand, parental bodies not only scaffold the reliable development of offspring, but also bias the production of variation, influencing evolvability. On the other hand, reproductive modes, as well as their associated generative capacities, themselves evolve. How can an agential perspective help in conceptualizing these two roles of reproduction in evolution? One possibility is to consider reproduction as an agential adaptation in the terms already explored by organismal perspectives of evolution. To adapt to the external environment, organisms as agents can either build a more tolerable microenvironment (niche construction), or they can adjust their bodies and behavior to their environmental conditions (phenotypic plasticity) (Laland et al., 2019). Both activities clearly appear in reproduction, insofar as organisms alter their bodies and behaviors in response to new environmental circumstances related to reproduction, be they external (e.g., competition for mates) or internal (e.g., reaching the fertile stage, implanting to a uterus, etc.). In the case of eutherian reproduction, both embryos and pregnant females actively coparticipate in reproduction by modifying their bodies and behaviors, as well as their respective environments. However, in applying agential notions of plasticity and niche construction to pregnancy, we readily encounter difficulties concerning the nature, the bearer(s), and the goals of pregnancy: What is agency in pregnancy? Are developmental and ecological notions of agency sufficient to account for reproduction? Who is the agent in pregnancy? Although agency is generally seen "as a property of the individual organism" (Laland et al., 2019, p. 132), the referent of individuality itself is debated in the case of pregnancy (Kingma, 2020; Nuño de la Rosa et al., 2021): Is it both the embryo and the mother? Is it some sort of shared or collective agency, or rather a higher-level agent including these two systems? And what are the goals of pregnancy? To adapt? To develop? To reproduce? All of them?

These are not independent questions, and different answers might be given in different theoretical, disciplinary contexts, such as those of developmental and

evolutionary biology. As a consequence, different agents and different goals might be identified in a single reproductive process depending on our epistemic purposes. In the remainder of this section, I will first discuss how our understanding of pregnancy can benefit from the agential perspectives of developmental plasticity and niche construction. Second, I will interrogate the limits of the developmental and ecological notions of agency to account for the evolution of pregnancy, and more generally for the evolution of animal reproduction.

3.1 | Pregnancy, developmental niche construction and developmental plasticity

Although niche construction theory has traditionally focused on the active role of organisms in shaping their external, ecological environment, in the last few years several authors have emphasized the need to include the active role of organisms in their developmental environment. In the context of this debate, the concept of "developmental niche" has received different interpretations. Some consider it as an instance of a selective niche (Flynn et al., 2013), while others see it as a fully new process, namely "a multi-dimensional space of environmentally induced and developmentally regulated, heritable resources that scaffold development" (Stotz, 2017, p. 2). As will be argued throughout this section, an agential perspective of eutherian reproduction better aligns with the latest interpretation, and further allows us to individuate the agential systems that drive phenotypic evolution through the regulation of reproduction.

Minimally, pregnancy nicely fits into examples of niches created by organisms to control development against variable environments, just like a nest or a burrow. In this line, Bernd Rosslenbroich (2014) has argued that eutherian reproduction is a key event in the evolution of internalization. In rendering the environment easier to control, internalization brings down the costs of homeostasis, and increases the reliability of development. In turn, the idea of scaffolding emphasizes the role of pregnant females in enabling offspring development (Nuño de la Rosa et al., 2021), although authors differ in what they mean by "enabling." Some conceptualize maternal scaffolding in rather passive terms, by reducing pregnancy to nutrient provisioning (e.g., Minelli, 2006). In contrast, agential perspectives of developmental niche construction tend to emphasize the reciprocal nature of the organism–environment interaction (Nadolski & Moczek, 2023; Schwab et al., 2017). In this framework, the notions of developmental niche and developmental plasticity meet, allowing us to distinguish "external niche construction" whereby organisms modify their external environmental conditions, from "experiential niche construction" whereby organisms modify themselves in ways that improve the experienced environment (Sultan, 2015). In container models pervading biomedical views of pregnancy (Kingma, 2019), pregnant females are conceived of as carriers of their offspring, attributing organismal agency to embryos only. However, eutherian pregnancy is a clear case of reciprocal external and experiential niche construction. Both the mother and the embryo simultaneously modify, their own and each other's development, physiology, and behavior in response to new environmental conditions, generating an "affordance landscape"[1] that seems to favor their own goals (Nadolski & Moczek, 2023). On the embryo side, the uterine environment resulting from maternal–embryonal interactions enables the embryo's pursuit of its own development. On the female side, pregnant females respond to implantation in a way that promotes their own, as well as their embryo(s)' survival. While evolutionary research on pregnancy has classically focused on the evolution of embryonic structures, particularly on the placenta, recent studies have unraveled the active evolutionary role of female structures (see Nuño de la Rosa et al., 2021). This includes new female cell types engaged in regulating the interaction with the embryo, such as the decidual cell (Wagner et al., 2014), major modifications of the inflammatory reaction to implantation (Stadtmauer & Wagner, 2020), and integral modifications of the female skeletal, circulatory, and immunological systems. In turn, reciprocal causation can be seen as a feedback loop between two interacting entities, or more radically, as a relationship of "ontological co-constitution" where the organism and its environment form a single system (Baedke et al., 2021). While the container view of pregnancy has traditionally assumed a unidirectional or a very weak form of causal reciprocity between mothers and embryos, recent philosophical discussions on the ontological status of pregnancy have called for an alternative individuation that considers mother and embryo(s) as entangled in a single individual system (Kingma, 2019; Nuño de la Rosa et al., 2021).

An agential perspective focused on the organismal nature of pregnancy seems to be necessary to account for the developmental and physiological changes involved, and their evolution. Referring only to "the genes of pregnancy," decontextualized from the organismal context in which reproduction takes place, is insufficient for accounting for the origination and evolution of pregnancy. Instead, one needs to refer to the whole female organismal context, as well as to the active participation of females and embryos in the pursuit of their goals.

In this regard, developmental and ecological agency can account for many of the goal-directed activities involved in reproductive processes. However, these two approaches to agency met serious difficulties in accounting for reproduction unless the goal of offspring production is admitted as an explanatory component of agential accounts of reproduction. The reason is that neither the goal of self-development, nor that of self-maintenance, seem to sufficiently account for the adaptive plasticity and the niche construction activities deployed to achieve the goals of pregnancy.

3.2 | The goals of pregnancy

Various tentative arguments for not including reproductive goals in the definition of organismal agency have been explored in the philosophical literature. One possibility is to challenge the distinction between development and reproduction itself, considering that they are, indeed, one single process, and are, therefore, addressed to the same goals. This seems to be the strategy followed by developmental systems theorists (e.g., Robert, 2004): self-generation is indeed self-reproduction, and organisms participate in many ways (including developmental plasticity and niche construction) in building the internal and external environment in which this process takes place. As applied to animal reproduction, parents and offspring might be regarded from this perspective as agents pursuing the goal of self-development/self-reproduction in a coupled manner. The issue with this solution is that it seems unlikely that we can conceptualize the processes and activities of reproducers as self-reconstructive unless one shifts the bearer of these processes and activities to the life cycle. This is the strategy followed by some: organismal individuals are artificial divisions of the life cycle, and development and reproduction are different stages of a single process (see references in Nuño de la Rosa, 2010). While deciding on when reproduction starts and ends is not a trivial question, I believe that denying the reality of birth and death of individual agents renders incomprehensible most biological research. We need a criterion to individuate organismal agents and their goal-directed activities, including those involved in reproduction.

A different solution explored by DiFrisco and Mossio (2020) is to preserve the goal of self-maintenance in the definition of organismal identity and distinguish development from reproduction by virtue of additional systemic criteria. In the organizational tradition, the diachronic identity of organisms is associated with the preservation of their "organizational closure." Organizational closure is defined as a mutual dependence between the components and activities of a biological system that causally instantiates the self-maintenance of such a system. However, the continuity between organizational systems, minimally defined, is preserved between parents and offspring, and cannot distinguish between these two systems. DiFrisco and Mossio (2020, p. 178) suggest a numerical solution to this puzzle: "organizational continuity is sufficient for diachronic identity unless there is a change in the local number of organized systems that are organizationally continuous with one another, either via an event of multiplication (fission) or reduction (fusion)." Thus, in the case of pregnancy, mothers and embryos constitute a single organism during pregnancy, but organismal identity multiplies at birth.

Fission and fusion, however, are criteria that allow the individuation of organisms, but do not account for *why* fission and fusion themselves occur and evolve. As pointed out in the introduction, from the organizational perspective, reproductive activities are not functional, insofar as they do not necessarily contribute to the self-maintenance of individual organisms. What is then the reason for those developmental, physiological, and behavioral processes leading to the fission or fusion of organizational systems? How can reproductive goals be a source of normativity in living agents? Having these questions in mind, advocates of the organizational approach suggested a different, tentative solution to the "objection" of reproduction: reproductive functions might be functional if they contribute to the self-maintainance of higher-level individuals, be they historical individuals (lineages) or ecological individuals (Mossio et al., 2009, pp. 834–835). The main issue with this solution is that it is hard to imagine how organizational closure would work in this case. How the maintenance of an ecological community or that of a lineage is supposed to feedback into the production of reproductive activities? While this might be the case for some reproductive phenomena, such as population density-dependent reproduction, most reproductive activities (e.g., implantation or nutrition regulation) do not seem to be functionally dependent on supraorganismal levels.

In a previous work on the evolutionary status of pregnancy, we argued for a different perspective: the kind of maternal–offspring interactions that occur in pregnancy can only be explained if pregnant females are conceived of as integrated individuals entangled in the goal of reproduction (Nuño de la Rosa et al., 2021). From an agential perspective, reproductive goals, therefore, individuate a new level of biological organization, namely that of reproductive agents. From this perspective, it can be hypothesized that reproductive goals result

from the encounter of the developmental goals of agents at different stages of their life cycles and, therefore, at different levels of organization. This does not mean that, since agency emerges at the level of the whole reproductive system, the individual goals of mothers and embryos, and therefore, their respective individual agencies, disappear during pregnancy. Just like in other cases of collective agency, goals at different levels of organization can coexist and even conflict, and different explanatory projects can be interested in identifying these different goals at these various levels (for an analogous argument on the individuality of pregnancy, see DiFrisco & Mossio, 2020; Nuño de la Rosa et al., 2021). Moreover, this view of reproductive agency opens the possibility of considering other agents involved in reproduction as members of this collective agency. Microbes play a major role in mammalian reproduction (Chiu & Gilbert, 2015), but it remains an open question whether their contribution to the development and birth of mammals is a trade-off of the pursuit of their own self-maintenance and reproduction, or whether they rather qualify as members of a single reproductive system.

In this section, I have mainly discussed vertebrate viviparity, and more specifically, eutherian pregnancy. Some of the issues raised by this reproductive mode, such as the emergence of a sustained collective reproductive agency from implantation to birth, seem to be specific to pregnancy. Reproductive agency might fully overlap with developmental agency as in asexual reproduction, or last for a much shorter period in other viviparous species such as marsupials. Nonetheless, I believe my general argument still holds for other modes of reproduction: the goals of reproduction need to be attributed to agents defined at organismal levels of organization, and seem to be irreducible to the goals of self-generation and self-maintenance. In the following section, I will argue that adopting an agential approach to reproduction has major implications for explaining the evolutionary origination of reproductive modes, as well as their causal role in evolvability.

4 | REPRODUCTIVE AGENCY AND EVOLUTION

A major research agenda in evo-devo where agency is claimed to play a key role is that of *evolutionary innovation*. While population genetics deals with the spread of extant variants and is blind to the origin of new complex traits, evo-devo attempts to explain how novelties originated in evolution (Müller & Newman, 2005). This contrast between the explanatory agendas of population genetics and evo-devo applies to selectionist and evo-devo approaches to pregnancy. On the one hand, adaptive approaches have focused on the evolutionary modification, rather than on the origination, of pregnancy. For instance, evolutionary research of genomic imprinting in placentation does not answer the question of how and why eutherian pregnancy itself originated. On the other hand, adaptive explanations of reproductive novelties do not distinguish the specificities of these innovations. While from the point of view of the evolutionary interests of genes, different forms of viviparity are conceived as the same "solution" resulting from outweighing costs and benefits for parents and offspring (Furness et al., 2015), a developmental perspective of reproduction requires distinguishing between different kinds of integration between zygotes and parents (see Lodé, 2012), and therefore between different agents involved. Thus, the innovations tangled in the origination of this reproductive mode call for considering pregnancy as a major transition in reproductive individuality (Nuño de la Rosa et al., 2021). The origination of pregnancy entailed the historical individuation of a new transient, developmental stage, specifically integrated with the physiology and life cycle of eutherian females. From an agential perspective, this evolutionary transition did not only entail the origination of new characters, such as the placenta or the decidual cell, but a new level of collective agency in which both female and embryonic structures became entangled in the goal of producing offspring.

In individuating *What* kind of agents have originated in evolution, the agential perspective sets the stage for making distinctive *How* and *Why* questions on the evolution of reproduction (see Uller, 2023, on how agential concepts provide distinctive evolutionary explanations). As indicated above, agential explanations invoke more detailed, proximate accounts of the origination and evolution of reproductive modes where goal-directed activities of organisms are included in the explanation. In the remainder of this section, I argue that agential perspectives further allow us to answer ultimate questions concerning the distinct evolvabilities associated with reproductive modes. Together with variation, reproduction is one of the two principal components of natural selection. Modes of reproduction "[influence] the amount of variation and vice versa; the two together permit natural selection to operate, and selection in turn modifies the mechanisms of reproduction and variation" (Bonner, 2019). Although the role of reproduction in evolvability has been mainly explored in relation to sexual reproduction as a mechanism for increasing variation, the material ways that organisms reproduce have also important consequences for the evolution of variation. The various ways in which

organisms have been claimed to have an agential role in their own reproduction that, in turn, affect their lineage evolvability, can be classified into three broad categories.

First, reproductive modes have evolved to ensure the *robustness of offspring development* (Griesemer, 2014; Rosslenbroich, 2014). Eggshells in oviparous species and maternal environments in live-bearing animals, ensure the protection of embryos from environmental perturbations, and therefore participate in the reliable production of phenotypes. In egg-laying species, the control of development is, to a great extent, a self-control, although parental care of eggs plays an important role in some lineages. In placental mammals, the extra-embryonic membranes of the amniote egg evolved from being tissues for protection, to become tissues for maternal–embryonic interaction (Griffith & Wagner, 2017), and mothers turned into core agents in regulating the environmental conditions for embryo development. The maternal regulation of the embryo's accessibility to environmental variables, such as predators, temperature, or nutrition, not only ensures the reliable reproduction of offspring but likely affects plasticity and evolvability in many ways.

Second, reproductive agents are *generators of new variational possibilities*. Viviparity seems to be correlated to diversification in several clades, including fishes (Helmstetter et al., 2016) and reptiles (Pincheira-Donoso et al., 2013; Pyron & Burbrink, 2014). How this correlation depends on the internal properties of this reproductive mode as opposed to new environmental opportunities enabled by viviparity is still unclear. Among mammals, recent evidence suggests that pregnancy has endowed eutherians with a capacity for phenotypic experimentation. The degree of modularity in the mammalian skull varies among taxa (Porto et al., 2009) and probably had important consequences for the evolvability of these lineages, "with stronger integration associated with a smaller capacity to respond in the same direction of selection, and with weaker integration associated to responses more aligned to selection" (Marroig et al., 2009, p. 147). In contrast to marsupials, whose early birth and feeding by lactation constrain the evolution of head and limbs, eutherians might have more freedom to explore the morphospace during their uterine development (Lillegraven, 1975). An agential perspective directs our attention from new genes involved in placentation to the developmental capabilities (released from biomechanical goals) entailed by pregnancy. Again, this evolutionary ability is not reducible to either the embryo or the mother, but rather to the reproductive system resulting from the interaction between the two systems.

Finally, reproductive agents can be regarded as *generators of new levels and kinds of selection*, emphasizing the role of organisms as active regulators of variation. Variation in reproductive success partly depends on behavioral strategies such as mating strategies, but also on reproductive modes. In vertebrate evolution, two major innovations brought more control to females in the selection of variation. Internal fertilization allows females to select on their mates, opening a new kind of biotic interaction with a high effect on viability, namely that of gamete selection (Kekäläinen & Evans, 2018). The evolution of mammalian viviparity created a new further selective level, namely oocyte selection in implantation, based on screening of genetic compatibility (Kekäläinen, 2021). Although the mechanisms for female choice at this level are still unclear, a good deal of it is known to be dependent on immunological compatibility.

If embryos and mothers are seen as parts of an integrated reproductive system, maternal selection might be interpreted as a case of internal selection (Schwenk & Wagner, 2001). Fertilization and implantation result from the transient functional integration of two subsystems, namely maternal and paternal gametes, in the case of gamete selection, and mothers and oocytes, in that of oocyte selection. Maternal agents actively select their offspring on the basis of their ability to be integrated into their life cycles during the period of gestation. Just as other cases of internal selection, gamete and oocyte selection are widely independent of the external environment, traveling with mothers across very different environmental contexts.

5 | LINKING DEVELOPMENTAL AND BEHAVIORAL AGENCY THROUGH REPRODUCTION

The study of development and behavior, as well as of their evolution, have been traditionally unconnected (Bertossa, 2011). This disconnection is reflected as well in the literature on agency, where development and behavior are treated as different ways to adapt to the environment. While life history theory counts on a good explanation of the relationship between reproductive modes and related behaviors, such as mating strategies (see Section 2), there is no alternative conceptualization in animal biology of these relationships from an organismal, agential perspective. Nonetheless, in the last few years, some attempts to apply evo-devo to the whole functional phenotype have opened promising insights into the relationship between development and behavior (Bertossa, 2011; Toth & Robinson, 2007). In this last

section, I argue that reproductive agency is key in explaining this relationship, and therefore that between developmental and behavioral agency, a longstanding concern in the philosophical literature on agency (see, e.g., Moreno & Mossio, 2015, ch. 5).

Evolutionary developmental relationships between reproduction and behavior seem to be widespread in the animal kingdom. Molecular pathways controlling feeding behavior and reproduction in solitary insects suggest that they are part of the same genetic toolkit underlying the evolution of the division of labor among workers in honeybee colonies (Toth & Robinson, 2007). In vertebrates, several lines of evidence suggest an analogous relationship between viviparity and social behavior. In squamate reptiles, the multiple independent evolution of live birth precedes that of social complexity (Halliwell et al., 2017). This phylogenetic correlation between viviparity and social complexity might result from correlated selection, but might also be caused by a developmental association. The intergenerational relationship between development and behavior is well-known in placental mammals. In therians (which include both placental mammals and marsupials), the fetal hypothalamus and the placenta develop in interaction with the hypothalamic structures of the mother (Keverne, 2015). This means that the placenta and the maternal hypothalamus have coevolved to ensure the development of the fetus and the reproduction of the mother, linking various reproductive traits and functions regulated by the maternal hypothalamus in interaction with placental hormones, such as maternal feeding, parturition, milk letdown, maternal care, and the suspension of fertility and sexual behavior (Keverne, 2014). Since the effects of maternal care on the social behavior of offspring are well-known, particularly in rodents (see Sachser et al., 2020), the evolution of pregnancy likely had a major impact on that of social behavior in mammals.

All this recent empirical evidence on the evolutionary relationship between development and behavior links developmental and behavioral agency in a way whose consequences remain to be explored. From this perspective, these two dimensions of agency are not only analogously related. They are materially connected through the shared goal of reproduction. A deeper mechanistic understanding of these connections will make clear in which specific ways reproductive modes bias the evolution and development of behavioral agency. The integration of developmental mechanisms into the life history framework (Flatt & Heyland, 2011) promises to be a powerful ally in this enterprise. Under this perspective, the coevolution of maternal-offspring interactions during intrauterine development and postnatal maternal care, might not be only dependent on selective trade-offs related to competitive resource allocation, but rather on the shared developmental mechanisms regulating these interactions.

Co-option of developmental mechanisms regulating unrelated characters is tantamount to evolution, and it might be argued that the aforementioned examples only instantiate this widespread evolutionary mechanism for building characters. However, an agential approach to the relationship between development and behavior in the context of different reproductive modes seems to indicate that they are more than chancy associations. The reason why some genetic toolkits are reused for behavioral purposes might not be random but be causally linked by the functional goals they serve to. In particular, developmental pathways evolved for regulating the interaction of organisms of the same species at different stages of their life cycles (e.g., those operating in placentation) seem to be more likely to be reused for other relational purposes (e.g., those involved in lactation or social behavior).

6 | CONCLUSION

In this paper, I have claimed that evo-devo studies of reproductive modes, as illustrated by recent work on the evolution of vertebrate viviparity, call for an organismal, agential perspective of reproduction. In analyzing the role of the organismal agents involved in offspring production, I have argued that developmental and ecological notions of agency are necessary, but not sufficient, to provide a full account of reproduction. An agential notion of reproduction that includes the goal of having offspring is needed in a theory of agency that can be tested, in explanatory and predictive power, against the view of genes as strategic agents of evolution. While further theoretical work on the concept of "reproductive goals" is much needed, such a notion allows us to better capture the innovations involved in the origination of reproductive modes, as well as their distinct evolvabilities. Reproductive agents have a major role in ensuring the robustness of offspring development and generating new levels and kinds of selection, as well as new variational possibilities in evolution. Finally, I have reflected upon the possibility that an agential notion of reproduction might provide unforeseen links between developmental and behavioral agency. While this insight is still embryonic, exploring such a connection promises to advance our understanding of the material coevolution between development and behavior from an agential perspective.

ACKNOWLEDGMENTS

This work received financial support from the Spanish Ministry of Science and Innovation (project # PID2021-127184NB-I00). I am extremely grateful for the feedback provided by Gunter Wagner and an anonymous referee of this journal. Earlier drafts of this manuscript were discussed with audiences at the KLI Workshop "Agency in Living Systems" (June 2022), the Venice Summer School on "The character concept" (August 2022), a BioKoinos seminar at the Complutense University of Madrid (October 2022), and a PhilBio seminar at the IHPST (December 2022).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Laura Nuño de la Rosa http://orcid.org/0000-0003-0513-0077

ENDNOTE

[1] The notion of affordance has an important role in current theories of agency, insofar as it defines the environment as a set of opportunities for action determined by the purposive biological system itself (Walsh, 2015).

REFERENCES

Ågren, J. (2021). *The gene's-eye view of evolution*. Oxford University Press.

Baedke, J., Fábregas-Tejeda, A., & Prieto, G. I. (2021). Unknotting reciprocal causation between organism and environment. *Biology & Philosophy*, *36*(5), 48. https://doi.org/10.1007/S10539-021-09815-0

Barandiaran, X. E., Di Paolo, E., & Rohde, M. (2009). Defining agency: Individuality, normativity, asymmetry, and spatio-temporality in action. *Adaptive Behavior*, *17*(5), 367–386. https://doi.org/10.1177/1059712309343819

Bertossa, R. C. (2011). Morphology and behaviour: Functional links in development and evolution. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *366*(1574), 2056–2068. https://doi.org/10.1098/rstb.2011.0035

Blackburn, D. G., & Evans, H. E. (1986). Why are there no viviparous birds? *The American Naturalist*, *128*(2), 165–190. https://doi.org/10.1086/284552

Bonner, J. T. (2019). Reproduction. *Encyclopedia britannica*. Accessed May 17, 2023. https://www.britannica.com/science/reproduction-biology

Chiu, L., & Gilbert, S. F. (2015). The birth of the holobiont: Multi-species birthing through mutual scaffolding and niche construction. *Biosemiotics*, *8*(2), 191–210. https://doi.org/10.1007/S12304-015-9232-5

Crespi, B., & Semeniuk, C. (2004). Parent-offspring conflict in the evolution of vertebrate reproductive mode. *The American Naturalist*, *163*(5), 635–653. https://doi.org/10.1086/382734

DiFrisco, J., & Mossio, M. (2020). Diachronic identity in complex life cycles. In A. S. Meincke, & J. Dupré (Eds.), *Biological identity* (pp. 177–199). Routledge.

Flatt, T., & Heyland, A. (2011). *Mechanisms of life history evolution: The genetics and physiology of life history traits and trade-offs*. Oxford University Press.

Flynn, E. G., Laland, K. N., Kendal, R. L., & Kendal, J. R. (2013). Target article with commentaries: Developmental niche construction. *Developmental Science*, *16*(2), 296–313. https://doi.org/10.1111/DESC.12030

Furness, A. I., Morrison, K. R., Orr, T. J., Arendt, J. D., & Reznick, D. N. (2015). Reproductive mode and the shifting arenas of evolutionary conflict. *Annals of the New York Academy of Sciences*, *1360*(1), 75–100. https://doi.org/10.1111/NYAS.12835

Griesemer, J. R. (2014). Reproduction and scaffolded developmental processes: An integrated evolutionary perspective. *Towards a Theory of Development* (pp. 183–202). Oxford University Press. https://doi.org/10.1093/ACPROF:OSO/9780199671427.003.0012

Griesemer, J. R. (2005). The informational gene and the substantial body: On the generalization of evolutionary theory by abstraction. In M. R. Jones, & N. Cartwright (Eds.), *Idealization XII: Correcting the model* (Vol. 68, pp. 59–115). Brill.

Griesemer, J. R. (2000). Reproduction and the reduction of genetics. In P. J. Beurton, R. Falk, & H.-J. Rheinberger (Eds.), *The concept of the gene in development and evolution: Historical and epistemological perspectives* (pp. 240–285). Cambridge University Press.

Griffith, O. W., & Wagner, G. P. (2017). The placenta as a model for understanding the origin and evolution of vertebrate organs. *Nature Ecology & Evolution*, *1*(4), 1–10. https://doi.org/10.1038/s41559-017-0072

Haig, D. (1993). Genetic conflicts in human pregnancy. *The Quarterly Review of Biology*, *68*(4), 495–532. https://doi.org/10.1086/418300

Haig, D. (1996). Altercation of generations: Genetic conflicts of pregnancy. *American Journal of Reproductive Immunology*, *35*(3), 226–232. https://doi.org/10.1111/J.1600-0897.1996.TB00035.X

Haig, D. (2012). The strategic gene. *Biology & Philosophy*, *27*(4), 461–479. https://doi.org/10.1007/S10539-012-9315-5

Halliwell, B., Uller, T., Holland, B. R., & While, G. M. (2017). Live bearing promotes the evolution of sociality in reptiles. *Nature Communications*, *8*(1), 2030. https://doi.org/10.1038/s41467-017-02220-w

Helmstetter, A. J., Papadopulos, A. S. T., Igea, J., Van Dooren, T. J. M., Leroi, A. M., & Savolainen, V. (2016). Viviparity stimulates diversification in an order of fish. *Nature Communications*, *7*(1), 11271. https://doi.org/10.1038/ncomms11271

Jablonka, E., & Lamb, M. J. (2005). *Evolution in four dimensions: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. MIT Press.

Janzen, F. J., & Warner, D. A. (2009). Parent–offspring conflict and selection on egg size in turtles. *Journal of Evolutionary Biology*, *22*(11), 2222–2230. https://doi.org/10.1111/J.1420-9101.2009.01838.X

Kekäläinen, J. (2021). Genetic incompatibility of the reproductive partners: An evolutionary perspective on infertility. *Human Reproduction*, *36*(12), 3028–3035. https://doi.org/10.1093/HUMREP/DEAB221

Kekäläinen, J., & Evans, J. P. (2018). Gamete-mediated mate choice: Towards a more inclusive view of sexual selection. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1883), 1–10. https://doi.org/10.1098/RSPB.2018.0836

Keverne, E. B. (2014). Significance of epigenetics for understanding brain development, brain evolution and behaviour. *Neuroscience*, *264*, 207–217. https://doi.org/10.1016/J.NEUROSCIENCE.2012.11.030

Keverne, E. B. (2015). Genomic imprinting, action, and interaction of maternal and fetal genomes. *Proceedings of the National Academy of Sciences*, *112*(22), 6834–6840. https://doi.org/10.1073/PNAS.1411253111

Kingma, E. (2019). Were you a part of your mother? *Mind*, *128*(511), 609–646.

Kingma, E. (2020). Biological individuality, pregnancy, and (Mammalian) reproduction. *Philosophy of Science*, *87*(5), 1037–1048. https://doi.org/10.1086/710612

Laland, K. N., Odling-Smee, J., & Feldman, M. W. J. (2019). Understanding niche construction as an evolutionary process. In T. Uller, & K. N. Laland (Eds.), *Evolutionary causation: Biological and philosophical reflections* (pp. 127–152). M.I.T. Press.

Lillegraven, J. A. (1975). Biological considerations of the marsupial-placental dichotomy. *Evolution*, *29*(4), 707–722.

Lodé, T. (2012). Oviparity or viviparity? That is the question. *Reproductive Biology*, *12*(3), 259–264. https://doi.org/10.1016/j.repbio.2012.09.001

Marroig, G., Shirai, L. T., Porto, A., de Oliveira, F. B., & De Conto, V. (2009). The evolution of modularity in the mammalian skull II: Evolutionary consequences. *Evolutionary Biology*, *36*(1), 136–148. https://doi.org/10.1007/s11692-009-9051-1

Minelli, A. (2016). Scaffolded biology. *Theory in Biosciences*, *135*(3), 163–173.

Moreno, A., & Mossio, M. (2015). *Biological autonomy* (Vol. 12). Springer. https://doi.org/10.1007/978-94-017-9837-2

Mossio, M., Saborido, C., & Moreno, A. (2009). An organizational account of biological functions. *The British Journal for the Philosophy of Science*, *60*(4), 813–841.

Müller, G. B., & Newman, S. A. (2005). The innovation triad: An EvoDevo agenda. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, *304*, 487–503.

Nadolski, E. M., & Moczek, A. P. (2023). Promises and limits of an agency perspective in evolutionary developmental biology. *Evolution & Development*, 1–21. https://doi.org/10.1111/EDE.12432

Nuño de la Rosa, L. (2010). Becoming organisms: The organisation of development and the development of organisation. *History and Philosophy of the Life Sciences*, *32*(2–3), 289–315.

Nuño de la Rosa, L., Pavličev, M., & Etxeberria, A. (2021). Pregnant females as historical individuals: An insight from the philosophy of evo-devo. *Frontiers in Psychology*, *11*, 572106. https://doi.org/10.3389/fpsyg.2020.572106

Okasha, S. (2018). *Agents and goals in evolution*. Oxford University Press.

Oyama, S. (2000). *The ontogeny of information: Developmental systems and evolution* (2nd ed.). Duke University Press.

Pincheira-Donoso, D., Tregenza, T., Witt, M. J., & Hodgson, D. J. (2013). The evolution of viviparity opens opportunities for lizard radiation but drives it into a climatic cul-de-sac. *Global Ecology and Biogeography*, *22*(7), 857–867. https://doi.org/10.1111/GEB.12052

Porto, A., de Oliveira, F. B., Shirai, L. T., De Conto, V., & Marroig, G. (2009). The evolution of modularity in the mammalian skull I: Morphological integration patterns and magnitudes. *Evolutionary Biology*, *36*(1), 118–135. https://doi.org/10.1007/s11692-008-9038-3

Pyron, R. A., & Burbrink, F. T. (2014). Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology Letters*, *17*(1), 13–21. https://doi.org/10.1111/ELE.12168

Renfree, M. B., Suzuki, S., & Kaneko-Ishino, T. (2013). The origin and evolution of genomic imprinting and viviparity in mammals. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *368*(1609), 20120151. https://doi.org/10.1098/RSTB.2012.0151

Reznick, D. N., Travis, J., Pollux, B. J. A., & Furness, A. I. (2021). Reproductive mode and conflict shape the evolution of male attributes and rate of speciation in the fish family poeciliidae. *Frontiers in Ecology and Evolution*, *9*, 295. https://doi.org/10.3389/FEVO.2021.639751/BIBTEX

Robert, J. S. (2004). *Embryology, epigenesis, and evolution*. Cambridge University Press.

Roff, D. (1993). *Evolution of life histories: Theory and analysis*. Routledge.

Rosslenbroich, B. (2014). The concept of biological autonomy. *History, Philosophy and Theory of the Life Sciences*, *5*, 19–40. https://doi.org/10.1007/978-3-319-04141-4_3

Sachser, N., Zimmermann, T. D., Hennessy, M. B., & Kaiser, S. (2020). Sensitive phases in the development of rodent social behavior. *Current Opinion in Behavioral Sciences*, *36*, 63–70. https://doi.org/10.1016/J.COBEHA.2020.07.014

Saldívar-Lemus, Y., & Macías Garcia, C. (2022). Conflict and the evolution of viviparity in vertebrates. *Behavioral Ecology and Sociobiology*, *76*(5), 68. https://doi.org/10.1007/S00265-022-03171-Z

Schwab, D. B., Casasa, S., & Moczek, A. P. (2017). Evidence of developmental niche construction in dung beetles: Effects on growth, scaling and reproductive success. *Ecology Letters*, *20*(11), 1353–1363. https://doi.org/10.1111/ELE.12830

Schwenk, K., & Wagner, G. P. (2001). Function and the evolution of phenotypic stability: Connecting pattern to process. *American Zoologist*, *41*(3), 552–563.

Stadtmauer, D. J., & Wagner, G. P. (2020). Cooperative inflammation: The recruitment of inflammatory signaling in marsupial and eutherian pregnancy. *Journal of Reproductive Immunology*, *137*, 102626. https://doi.org/10.1016/J.JRI.2019.102626

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Stotz, K. (2017). Why developmental niche construction is not selective niche construction: And why it matters. *Interface Focus*, *7*(5), 20160157. https://doi.org/10.1098/RSFS.2016.0157

Sultan, S. (2015). *Organism and environment: Ecological development, niche construction, and adaptation*. Oxford University Press.

Sultan, S. E., Moczek, A. P., & Walsh, D. (2022). Bridging the explanatory gaps: What can we learn from a biological agency perspective? *BioEssays*, *44*(1), 2100185. https://doi.org/10.1002/bies.202100185

Toth, A. L., & Robinson, G. E. (2007). Evo-devo and the evolution of social behavior. *Trends in Genetics*, *23*(7), 334–341. https://doi.org/10.1016/J.TIG.2007.05.001

Uller, T. (2023). Agency, goal-orientation and evolutionary explanations. In P. Corning, S. A. Kauffman, D. Noble, J. A. Shapiro, R. I. Vane-Wright, & A. Pross (Eds.), *Evolution 'on purpose': teleonomy in living systems*. Vienna series in theoretical biology. MIT Press.

Wade, M. J. (2022). Maternal-offspring interactions: Reciprocally coevolving social environments. *Journal of Heredity*, *113*(1), 54–60. https://doi.org/10.1093/jhered/esab044

Wagner, G. P., Kin, K., Muglia, L., & Pavlicev, M. (2014). Evolution of mammalian pregnancy and the origin of the decidual stromal cell. *The International Journal of Developmental Biology*, *58*(4), 117–126. https://doi.org/10.1387/ijdb.130335gw

Walsh, D. M. (2015). *Organisms, agency, and evolution*. Cambridge University Press.

Walsh, D. M. (2023). Evolutionary foundationalism and the myth of the chemical given. In P. A. Corning, S. A. Kauffman, D. Noble, J. A. Shapiro, R. I. Vane-Wright, & A. Pross (Eds.), *Evolution 'on purpose': Teleonomy in living systems*. KLI Vienna, studies in theoretical biology series. MIT Press.

Walsh, D. M., & Rupik, G. (this issue). The agential perspective: Countermapping the modern synthesis. *Evolution & Development*.

Zeh, J. A., & Zeh, D. W. (2001). Reproductive mode and the genetic benefits of polyandry. *Animal Behaviour*, *61*(6), 1051–1063. https://doi.org/10.1006/ANBE.2000.1705

How to cite this article: Nuño de la Rosa, L. (2023). Agency in Reproduction. *Evolution & Development*, *25*, 418–429. https://doi.org/10.1111/ede.12440