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REVIEW

Causes and Consequences of Phenotypic Plasticity

Harbingers of change: Towards a mechanistic understanding of anticipatory plasticity in animal systems

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Abstract

1. Phenotypic plasticity is a strategy by which animals alter behaviour, morphology and/or physiology in response to cues of current conditions to cope with environmental heterogeneity.
2. If environmental change is impending and cues reliably predict future conditions, animals can also respond in anticipation of these changes (i.e. anticipatory plasticity) if they possess the mechanistic architecture necessary to do so. This phenomenon has been documented across the tree of life, but how animals integrate cues of future conditions and mount anticipatory responses remains largely ambiguous.
3. Here, we synthesize theoretical principles from sensory biology and animal communication with recent advances in physiological ecology to identify candidate physiological mechanisms underpinning anticipatory plasticity in animal systems.
4. We discuss how socio-ecological rhythms, cue perception and interactions between the epigenome, neuroendocrine system and gut microbiota can contribute to the maintenance and evolution of anticipatory plasticity, including anticipatory reproduction.
5. We shed light on the proximate and ultimate mechanisms that facilitate the evolution and maintenance of anticipatory plasticity in the face of environmental heterogeneity, contributing to a broader understanding of how animals may respond to rapid global change as environmental cues become unreliable and conditions unpredictable.

KEYWORDS
anticipation, environmental cues, evolution, phenotypic plasticity, physiological ecology

1 | INTRODUCTION

Heterogeneous environments are widespread in nature, and compared with theoretically uniform environments, impose higher fitness costs for animals that inhabit them (Levins, 1968). In the absence of reliable information about changing environmental conditions, animals can minimize costs through a number of strategies (Dantzer, 2023). For instance, they can produce a single, canalized phenotype (e.g. the remarkably consistent production of the *Drosophila* compound eye, Tsachaki & Sprecher, 2012; Waddington, 2014). Bet-hedging is another strategy to cope with heterogeneity when reliable information is unavailable (Kvalnes et al., 2018; Simons, 2011). By producing

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a mix of phenotypes through random phenotypic variation, bet-hedging can maximize geometric mean fitness over the long term as fitness optima oscillate, ensuring that at least some phenotypes will match environmental demands (Tufto, 2015). Bet-hedging may also 'pre-adapt' populations to contemporary and rapid environmental change, which is expected to be largely unpredictable (Crowley et al., 2016; van Baaren et al., 2024).

But when reliable information about environmental conditions *is* available, phenotypic plasticity—in which a single genotype can produce multiple different phenotypes in response to environmental information—is expected to evolve (Scheiner, 1993; West-Eberhard, 2003). Plasticity in response to cues of current environmental conditions, which we term responsive plasticity, is widespread in nature and can be adaptive. For instance, in response to changes in rainfall, birds flexibly shift breeding behaviour and timing (Nussey et al., 2005); in response to drought, plants alter leaf morphology to reduce water loss (Gratani, 2014); in response to photoperiodic shifts, insects adjust rates of development and growth (De Block & Stoks, 2003). Adaptive responsive plasticity can facilitate population persistence even if it constrains genetic responses to selection by shielding genotypes from environmental variation (Huey et al., 2003; Muñoz & Losos, 2018; Price et al., 2003).

In a special case of phenotypic plasticity, animals can respond to predictive cues, or 'harbingers', of future—rather than current—conditions (i.e. 'cued' or anticipatory plasticity, Dantzer, 2023; West-Eberhard, 2003). Anticipatory plasticity is characterized by an elongated temporal lag between when animals receive a cue and when the environmental conditions indexed by that cue will occur, and thus when fitness benefits can be reaped (Mariette, 2020). This lag can span an animal's singular lifetime (within-generational anticipatory plasticity) or bridge parent-offspring environments (anticipatory parental effects, Marshall & Uller, 2007). Environmental heterogeneity strongly favours the evolution of anticipatory plasticity (Jablonka et al., 1995; Lachmann & Jablonka, 1996), particularly under two conditions. First, cues of the future environment must be reliable and available to organisms (Bonamour et al., 2019; Levins, 1968; Reed et al., 2010; Scheiner, 1993). Unreliable cues can hamper the evolution of anticipatory responses given that the lag between cue perception and future conditions introduces error risk in both cue reliability and perception (Gavrilets & Scheiner, 1993; Moran, 1992; Reed et al., 2010). Second, animals must possess the physiological architecture necessary to sense and integrate these predictive cues (Kronholm, 2022), which can be complex and transmitted through ecological features distinct from those they index (Levins, 1968).

As rapid change continues to shape and reshape ecosystems, identifying the predictive architecture through which animals respond to environmental instability becomes crucial (Donelan et al., 2020). This urgency, coupled with a greater biological reality that can be gleaned by distinguishing anticipatory plasticity from other types of plasticity (Table 1), necessitates a deeper understanding of proximate and ultimate drivers of this phenomenon. Here, we present a mechanistic framework for disentangling the causes and consequences of anticipatory plasticity. We provide widespread evidence for anticipatory plasticity across animal systems, and discuss the social, ecological and molecular 'gears' that can maintain anticipatory plasticity in a population and potentiate its evolution over other alternative strategies. In doing so, we guide future studies

TABLE 1 Natural selection is continually shaping organismal responses to both current and future environmental conditions (Williams, 1966).

Type of plasticity	Responsive	Anticipatory	Transgenerational
Alternative terms	*Activational or direct plasticity* (West-Eberhard, 2003); *passive plasticity* (Whitman & Agrawal, 2009); *contextual plasticity* (Stamps & Groothuis, 2010).	*Cued plasticity* (West-Eberhard, 2003); *active plasticity* (Whitman & Agrawal, 2009); *anticipatory parental effects* (Marshall & Uller, 2007); Developmental plasticity	
Definition	Plasticity whereby phenotypic change occurs in response to cues of current conditions	Plasticity whereby phenotypic change occurs in response to cues of future conditions; includes adaptive parental effects when embryos are present at the time of parental cue detection (Burton & Metcalfe, 2014)	Plasticity whereby cues detected in one generation alter the phenotypes of future generations; effects span multiple generations
Timing of cue relative to conditions	Immediate	Lag, within an individual's lifetime or across a single generation (parent-offspring)	Lag, across multiple generations (e.g. one generation removed from the parental environment to offspring)
Adaptive?	Sometimes	Always/often	Sometimes

Note: Although anticipatory plasticity is necessarily associated with an increase in population mean fitness, responsive and transgenerational plasticity do not have to be adaptive (i.e. favoured and/or maintained by natural selection, Whitman & Agrawal, 2009). Natural selection may thus favour a transition to anticipatory plasticity from responsive plasticity when predictive cues are available and reliable, elongating the temporal lag between cue detection and the future selective environment. Similarly, selection may favour a narrowing of transgenerational phenotypic responses that span multiple generations down to single- or within-generation anticipatory plasticity if environments become unstable enough that predictive cues lose long-term fidelity.

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towards integrating conceptual and theoretical frameworks on phenotypic plasticity with modern physiological and ‘omics tools to interrogate the bounds of anticipatory phenotypic plasticity in light of environmental change.

2 | ECOLOGICAL RHYTHMS OF ANTICIPATION

Rhythmic environmental changes generate a landscape of predictability for animals in which future conditions are perpetually imminent and animals are always some inevitable distance from those conditions. Unlike random events with no intrinsic cyclicity (e.g. asteroid impacts), ecological rhythms allow animals to fine-tune their physiology based on prior experience or predictive information (Berrigan & Scheiner, 2004), similar to Bayesian updating (Valone, 2006). The duration of these rhythms (short/long) and their regularity (regular/episodic) can vary as a function of environmental grain (Levins, 1968), which may in turn favour different types of anticipatory plasticity.

2.1 | Seasonal environments

In seasonal environments, annual fluctuations in vegetation growth, animal behaviour and biodiversity are largely predictable. The corresponding animal responses that drive phenological shifts inherent to seasonal environments are thus inherently anticipatory in nature (Réale et al., 2003). Migratory birds flee to warmer regions as winter approaches (Kölzsch et al., 2015), and Atlantic salmon (*Salmo salar*) shift foraging behaviours ahead of seasonal changes in energetic demand (Bull et al., 1996). Hibernating mammals exhibit remarkable metabolic flexibility in response to seasonal cues of impending nutritional scarcity (Heldmaier et al., 2004). In Arctic ground squirrels (*Urocitellus parryii*), the onset of hibernation and timing of emergence involve an array of anticipatory metabolic changes before resources become scarce (Sheriff et al., 2012). Insects slow development and metabolic activity during dormancy or diapause (Kostál, 2006), which has evolved multiple times across different taxa (Tauber & Tauber, 1981) and life-history stages (Denlinger, 1986). Animals can also maximize fitness ahead of hostile seasonal changes through anticipatory morphological shifts in traits like coloration and reproductive structures. Arctic foxes (*Vulpes lagopus*) and snowshoe hares (*Lepus americanus*) undergo seasonal moulting of their brown coats, growing white fur ahead of winter to enhance predator escape (Hersteinsson & Hersteinsson, 1989; Merilaita & Lind, 2005; Nagorsen, 1983). Many salmon undergo reproductive morphological changes in gonad size, regulated by shifts in sex steroid production, prior to swimming upstream to spawn (Truscott et al., 1986). Ultimately, by increasing predictability, the cyclical and short-term nature of seasonal changes can potentiate fine-tuned organismal detection of predictive environmental information (Tolla & Stevenson, 2020).

2.2 | Resource pulse environments

Resource pulse events are infrequent, short-lived and dramatic increases in a particular resource for consumers. Similar to seasonal changes, resource pulses also have an inherent temporal rhythm. However, unlike seasonal changes, pulses occur episodically and intermittently rather than regularly over time (Yang et al., 2008). Resource pulses can be distinguished from seasonality through a consumer-centric approach focused on (1) their irregularity, brevity and intensity relative to consumers, and (2) the extent to which they cause perturbations to consumer ecosystems (Yang et al., 2008). By this definition, many large-scale ecological events can be considered resource pulses, including the terrestrial productivity triggered by El Niño-Southern Oscillation (ENSO) rainfalls (Thomsen et al., 2018), coral reef spawning events (McCormick, 2003), and the 13- and 17-year emergence of periodical cicadas (Williams & Simon, 1995), each of which ephemerally increases food availability for relevant consumers.

In terrestrial ecosystems, mast seeding is a common type of resource pulse where trees and shrubs produce large quantities of seed in some years but little to no seed in others (Kelly & Sork, 2002; Nowlin et al., 2008). The evolutionary functions of mast seeding are debated. Masting may ‘swamp and starve’ seed predators, facilitating seed escape (Fletcher et al., 2010; Zwolak et al., 2022). It may increase pollinator efficiency (Moreira et al., 2014), and/or reflect anticipatory increases in tree reproduction in years when seed survival is favoured (Pearse et al., 2016). Unlike unpredictable resource pulses (e.g. ENSO rainfalls, Yang et al., 2008), masting appears predictable to many consumer populations (Boutin et al., 2006; Tissier et al., 2020; Vekhnik, 2019). This predictability may favour the evolution of anticipatory plasticity as a consumer counter-strategy by which animals can optimally time phenotypic responses to maximize fitness in the face of extreme variability in food (Boutin et al., 2006). However, the strength of selection for anticipatory plasticity may hinge in part on pulsed resource stability. Some pulses are highly destructible, like the sudden aggregation or emergence of insects (Yang, 2004), while others can be stored for future use, like seed (Marcello et al., 2008). Stable resources that remain accessible or can be stored may extend the selective phenotypic response period, allowing for lower precision and greater flexibility in anticipatory responses. By contrast, unstable resources may favour fine-tuning of anticipatory responses to increase precision. The strength of selection for anticipatory plasticity may therefore increase with the perishability of the resource, such that consumers aim to maximize their use of a time-sensitive pulse while simultaneously minimizing the likelihood of failure to detect the cue or respond incorrectly (Figure 1). This framework can be applied more generally to anticipatory plasticity in response to non-pulsed resources (e.g. monopolizability of mates or territories).

2.3 | Social rhythms

Social environments are presumed to be largely unstable, but regular temporal and spatial fluctuations in social partners, mates

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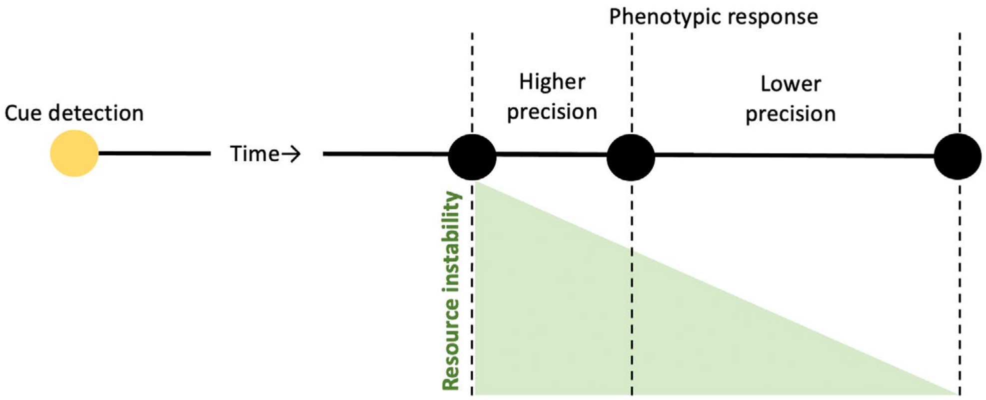

FIGURE 1 Anticipatory plasticity as a function of pulsed resource stability. Stable or easily monopolized pulsed resources may extend the selective period in which an anticipatory response is favoured, relaxing selection for precise detection of predictive cues. Perishable resources may favour the evolution of highly precise anticipatory responses because they shorten the selective period in which fitness benefits of anticipatory plasticity can be reaped.

and competitors can index changes in future mating opportunities, resource accessibility and reproductive risk. In insects, anticipation of resource-linked increases in density triggers anticipatory changes in sperm production, motility and maturation that maximize male reproductive success when male–male competition is high (Gage, 1997). Following seasonal increases in female mortality and in anticipation of high male–male competition, soapberry bug (*Jadera haematoloma*) populations become male-biased (Carroll & Salamon, 1995). Female North American red squirrels (*Tamiasciurus hudsonicus*) respond to anticipated increases in conspecific competition associated with resource pulses by accelerating juvenile postnatal growth (Dantzer et al., 2013). In some taxa, the dispersal of males into solitary life stages or extra-group coalitions leads to the inevitable introduction of novel males into established social groups (Lukas & Huchard, 2014). This stratification of mating opportunities can increase infanticide risk, favouring regulatory mechanisms that promote reproductive disinvestment in anticipation of future offspring loss (Roberts et al., 2012).

3 | SENSORY BIOLOGY OF PREDICTIVE CUES

Broadly, phenotypic plasticity involves the transfer and receipt of information between sender and receiver, and can thus be conceptualized through the lens of animal communication. Although 'cues' and 'signals' have been used interchangeably in studies of phenotypic plasticity, they are distinct phenomena. A cue describes ecological information that an animal uses to make a decision, and can facilitate 'eavesdropping' of information unintended for the receiver's perception (Bernal et al., 2007). By contrast, a signal is defined by its ability to elicit a response from the receiver intended by the sender and has evolved through natural selection (Bradbury & Vehrencamp, 1998). Cues can transition into signals if they gain precision through ritualization (Tinbergen, 1952), and signals can double as cues when optimization of receiver detection makes signals more conspicuous to unintended targets (Roberts et al., 2007). Because we almost universally lack data on how evolution has shaped the ecological information that induces anticipatory plasticity, we use the term predictive cue to describe a feature of the environment through which an organism can infer future conditions.

3.1 | Cue reliability is a principal driver of anticipatory plasticity

For anticipatory plasticity to evolve, predictive cues must have high reliability, particularly in 'noisy' environments (Box 1). They must foreshadow not only future environmental conditions but the future selective environment, ensuring selection can act on the phenotypic response (Moran, 1992; Reed et al., 2010). Unreliable cues increase the likelihood of a mismatch between phenotype and environment (Ashander et al., 2016; Reed et al., 2010), and thus the likelihood of a transition from anticipatory plasticity to bet-hedging (Botero et al., 2015; Donelson et al., 2018; Tufto, 2015). Furthermore, because uncertainty is inevitable in changing environments, predictive cue reliability may depend on the lag length between cue perception and future conditions. Indeed, this lag is hypothesized to be a major constraint in the evolution of phenotypic plasticity writ large (DeWitt, 1998). Reliability may decrease with an increase in lag (e.g. time between detection of a mast cue and the mast event itself; time between generations in species with elongated gestation) because environmental stochasticity can render otherwise reliable cues unreliable and mortality risk can leave the fitness benefits of anticipatory plasticity unrealized. Changes in the internal somatic state of an organism during this period (e.g. due to infection or injury) may impair or hinder an anticipatory response. With increasing lag length, cues may become less reliable, weakening selection for the evolution of anticipatory plasticity.

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BOX 1 Insights from signal detection theory

Heterogeneous environments are inherently noisy: animals can receive multiple cues indexing multiple different current and future conditions. Moreover, cue modalities used by animals can vary across taxa, life-history stages and ecologies. These complexities generate the potential for unclear transfer of information, creating a 'cocktail party problem' in which animals need to discern relevant (e.g. fitness-related) cues from irrelevant background noise (McDermott, 2009). The temporal lag inherent to anticipatory plasticity further increases the probability of detection error. Principles of signal detection theory (SDT) can provide a framework for understanding the strategies that animals use to respond to relevant cues in noisy environments and navigate the risk of error innate to anticipatory plasticity (Getty, 1996; MacMillan, 2002). With its roots in engineering and later adoption by psychology and neuroscience, SDT offers a powerful lens through which evolutionary biologists can interrogate how animals communicate with their broader environments to anticipate future conditions. Indeed, associations between ecological cues and organismal responses are typically weak because of constraints related to both signal reliability (how well a cue indexes its condition) and receiver bias (how well organisms respond to those cues, Getty, 1996). Yet, weak associations may not negate anticipatory plasticity for two reasons:

1. In a given environment, an animal can respond to information in 1 of 4 ways: (1) by correctly detecting a cue and responding to it ('hit'), (2) by incorrectly detecting a cue ('false alarm'), (3) by failing to respond to a cue when present ('miss') or (4) by responding correctly in its absence ('correct rejection'). In 1994, R. Haven Wiley applied this framework to animal communication to understand how animals balance unequal costs of errors (false alarms and misses). Wiley hypothesized that organisms minimize error costs by biasing responses: when false alarms cost more than missed detections, under-responsiveness to cues prevents costly gullibility; when misses cost more than false alarms, over-responsiveness to cues prevents costly negligence (Wiley, 1994). Apparently non-adaptive anticipatory responses may obscure such broader strategies, particularly when deception (e.g. by a prey item) and general uncertainty (e.g. under episodic or irregular ecological rhythms) are expected (Ghalambor et al., 2007; Petrullo et al., 2023).
2. Applications of SDT to state-dependent optimality theory suggest that the optimal response for an animal in its current environment can differ from the optimal response over longer time-scales, such as within the extended temporal lag inherent to anticipatory plasticity (McNamara & Trimmer, 2019; Trimmer, Ehlman, McNamara, et al., 2017). Because animals often need to make simultaneous, sequential phenotypic decisions, costs and payoffs will be modified by the risk accrued by any single response (McNamara & Trimmer, 2019). Thus, the lag between cue perception and future conditions introduces substantial risk. Anticipatory responses to predictive cues are perhaps better viewed as a series of phenotypic 'stepping stones' towards future conditions. Pressure to evolve anticipatory plasticity may therefore be modified by the series of decisions needed to reach the future selective environment (McNamara & Trimmer, 2019; Trimmer, Ehlman, & Sih, 2017).

Rather than representing a single phenotypic response, anticipatory plasticity may therefore comprise multiple temporally distinct phenotypic responses made sequentially as fitness optima fluctuate with respect to geometric mean fitness and lifetime trade-offs.

3.2 | Cue modalities

Predictive visual cues like increasing or decreasing day lengths can foreshadow changes in the biotic and/or abiotic environment, inducing anticipatory plasticity. Zooplankton use abiotic cues of photoperiod to induce diapause in anticipation of the future increase in predation risk associated with seasonal change (Slusarczyk, 1995). Biotic visual cues, common triggers for responsive plasticity, can also provide information about future conditions. The turrets of mud produced by cicada nymphs on the soil surface can alert mice to an upcoming emergence, facilitating adaptive shifts in foraging behaviour and reproduction (Marcello et al., 2008). Visual exposure to specific food items during development can refine adult dietary preferences based on expected future food availability in cuttlefish (Darmaillacq et al., 2008), and predator ground shadows elicit movement responses in anticipation of falling prey in chickens (Wilson & Lindstrom, 2011). Changes in the appearance of buds and other reproductive structures may cue an upcoming resource pulse for consumers of masting species of trees (Boutin et al., 2006), while visual cues of fire may indicate an upcoming resource boom for consumers of fire-stimulated flowering plants (Beck et al., 2024).

Chemical cues can also induce anticipatory responses: in response to anticipated increases in sperm competition cued by rival odours, bank voles (*Myodes glareolus*) develop larger seminal vesicles (Lemaître et al., 2011). Many anticipatory cyclical behaviours, such as those of spawning fishes, are regulated by chemical cues of environmental quality (Buchinger et al., 2015). In palaemonid shrimps (*Palaemon argentinus*) conspecific chemical cues induce anticipatory hatching and the production of larger larvae (Ituarte et al., 2019). Kairomones, unintentional chemical cues in which only the eavesdropping organism benefits, can trigger anticipatory behaviours that facilitate predation or escape (Brown Jr et al., 1970; Ruther et al., 2002). Amino acids found in mucus and other excretions (e.g. urine) are common kairomones: the development of anti-predator

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morphology is induced in *Daphnia* in response to kairomones present in predatory fish mucus (Brönmark & Hansson, 2012).

In resource pulse ecosystems, mast seeding may shed light on the cue modalities that consumers use to predict upcoming food booms. Mast seeding is typically highly synchronous at local, but not continental, scales (LaMontagne et al., 2020; Pearse et al., 2016). Trees in close proximity may synchronize reproduction by responding to the same localized weather cues (Rees et al., 2002), or through volatile organic compounds (VOCs) that serve as a central pathway of conspecific communication in plants (Holopainen, 2004). VOCs can both cue and signal impending conditions (Hagiwara & Shiojiri, 2020; Kon et al., 2005; Ninkovic et al., 2021; Pearse et al., 2016), for instance by inducing defence system priming in anticipation of future predation attempts (Morrell & Kessler, 2014). Although eavesdropping is most often associated with visual and acoustic cues (e.g. predators eavesdropping on prey mating calls, Lehmann & Heller, 1998), mast seeding synchronized by VOCs may inadvertently transmit chemical information about future food availability to seed consumers.

Finally, acoustic cues related to the movement of water, wind and ice can foreshadow upcoming seasonal change, while biotic cues like conspecific vocalizations can foreshadow the future social environment (Rosenthal & Ryan, 2000). Juvenile field crickets (*Teleogryllus oceanicus*) adaptively adjust maturation rates in response to mating calls in the rearing environment that index the density and quality of competitors and mates in the adult environment (DiRienzo et al., 2012; Kasumovic et al., 2011). Male crickets reared alongside abundant long-range calls of other males invest more in reproductive tissues and attain better adult condition compared with males reared in silent environments (Bailey et al., 2010). In mammals and birds, territorial vocalizations can serve as a deterrent and reinforce territorial boundaries while also serving as cues of both current and future population density (Dantzer et al., 2013; Siracusa et al., 2017).

3.3 | Catalyst cues

Anticipatory plasticity may be maintained in part by the Pareto principle or '80–20 rule' whereby 80% of the response of a population to a predictive cue is instigated, or catalysed, by 20% of the individuals in that population. This is analogous to leadership or keystone individuals in animal societies where a 'leader' exerts power over the daily activities of others (e.g. movement and time budgets, Marshall et al., 2012; Owen-Smith et al., 2010). Ultimately, a small number of individuals (~20%) wield tremendous influence over how the other ~80% of individuals spend their time. Anticipatory plasticity exhibited by a small number of individuals (leaders) may elicit the same plastic response in other individuals (followers). As a form of 'social power', leaders could possess coveted access to reliable cues of the future environment (e.g. as a result of social status, life history, age) and exhibit adaptive plasticity to those cues, while others follow. Such heterogeneous cue integration within a population may also be driven by negative-frequency dependence. Information 'producers' can maintain the mechanistic architecture to sense predictive cues and exhibit anticipatory plasticity, while information 'scroungers' rely on social feedback loops to induce anticipatory phenotypic change (Laland, 2004).

3.4 | Co-opted cues

Cues that induce anticipatory plasticity may be transmitted through the ecological factors they reflect, but they do not have to be (Levins, 1968). Indeed, heterogeneous environments often exhibit strong covariance across multiple ecological dimensions. This may result in cue co-opting, whereby a cue related to one ecological feature provides predictive information about a different feature. For instance, in eastern chipmunks, the abundance of red maple cues future abundance of a different, more fitness-relevant food item (beech seed, Tissier et al., 2020). The use of predictive co-opted cues may offer greater flexibility for receivers, for example, by facilitating detection of one cue component during a particular life-history stage but a different component at a different stage.

3.5 | Multimodal and mosaic cues

Environmental information can comprise multiple distinct sensory parts (i.e. a multimodal cue) transduced across multiple modalities, forming a mosaic cue whose reliability hinges on the sum of its parts. Mosaic cues may boost organismal fitness by fine-tuning processes of predictive cue detection and response, particularly in highly variable environments (Dore et al., 2018). *Drosophila* use redundant auditory, olfactory and tactile cues of the competitive environment to adaptively adjust reproductive behaviour (Bretman et al., 2011; Maguire et al., 2015). Larval cane toads rely on a combination of abiotic (light) and biotic (conspecific chemicals) cues to stimulate aggregation (Raven et al., 2017), and scatter-hoarding rodents like chipmunks, grey squirrels and deer mice combine olfactory, visual and memory cues to locate buried food (Ramirez & Steury, 2024; Wall, 2000).

Because mosaic cues provide highly detailed information about environmental conditions, they may boost reliability when the temporal lag between cue detection and future conditions is long. If one sensory modality is altered but the others stay the same, animals may retain the capacity to decipher relevant information. Indeed, carnivorous bats can circumvent obstructed acoustic cues by shifting to visual cues when hunting (Gomes et al., 2016). Cue-switching can also occur within the same sensory modality, like when fiddler crabs (*Uca vomeris*) switch from visual cues of predator speed to visual cues of predator retinal size during predation attempts (Hemmi & Pfeil, 2010). Predictive mosaic cues may offer animals 'escape routes' towards adaptive responses when information is obstructed, and/or may also reduce the likelihood of phenotypic mismatches or errors. However, mosaic cues may be more susceptible to disruption if each component is necessary to transmit relevant information.

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4 | EPIGENETIC, HORMONAL AND MICROBIAL MODULATORS OF ANTICIPATORY PLASTICITY

Anticipatory plasticity is an inherently flexible phenomenon likely to be driven by similarly flexible physiological machinery. Here, we discuss independent effects and synergies among three systems that may contribute to the mechanistic architecture underpinning anticipatory plasticity. Each rapidly responds to environmental input and governs the expression of plastic phenotypes through a series of complex cellular and molecular pathways (Figure 2).

4.1 | Epigenetic change

The epigenome likely plays a major role in regulating anticipatory plasticity, as epigenetic change (chemical modification of histones, DNA and RNA) can accelerate adaptive evolution at its earliest stages without changes to underlying gene sequences (Kronholm & Collins, 2016; Turner, 2009). Many of the environmental fluctuations that induce anticipatory plasticity have target and non-target effects on the epigenome (McCaw et al., 2020; Ruuskanen, 2024). These effects may explain why epigenetic mechanisms of anticipatory plasticity can evolve even when there is adequate standing genetic variation in the direction of fitness optima (Kronholm, 2022).

Epigenetic inheritance, for instance, appears to act as a principal driver of parental adjustments of offspring phenotype in response to predictive cues of future conditions (Guerrero-Bosagna et al., 2018; Kronholm, 2022). In *Drosophila* and *C. elegans*, small RNAs are produced in response to nutritional stress, which, when inherited by offspring, alter offspring genetic expression to facilitate adaptive phenotype–environment matching (Duempelmann et al., 2020; Rechavi et al., 2014). Small RNAs present in seminal fluid may elicit anticipatory responses in females (Curley et al., 2011; Mashoodh et al., 2023), and can also be vertically transmitted, suggesting epigenetic mediation of anticipatory parental effects even in the absence of parental care (Eaton et al., 2015). These pathways of inheritance open the door for environmentally-induced epigenetic change in parents to adaptively alter the developmental trajectories of offspring (Wang et al., 2017), facilitating epigenetic-environmental matching across a single generation (Marshall & Uller, 2007).

Less work has investigated epigenetic contributions to within-generation anticipatory plasticity, which likely relies less on inherited epigenetic changes and instead on more proximate epigenetic changes like chromatin modification and methylation (Horsthemke, 2022). Indeed, many anticipatory responses common in seasonal environments

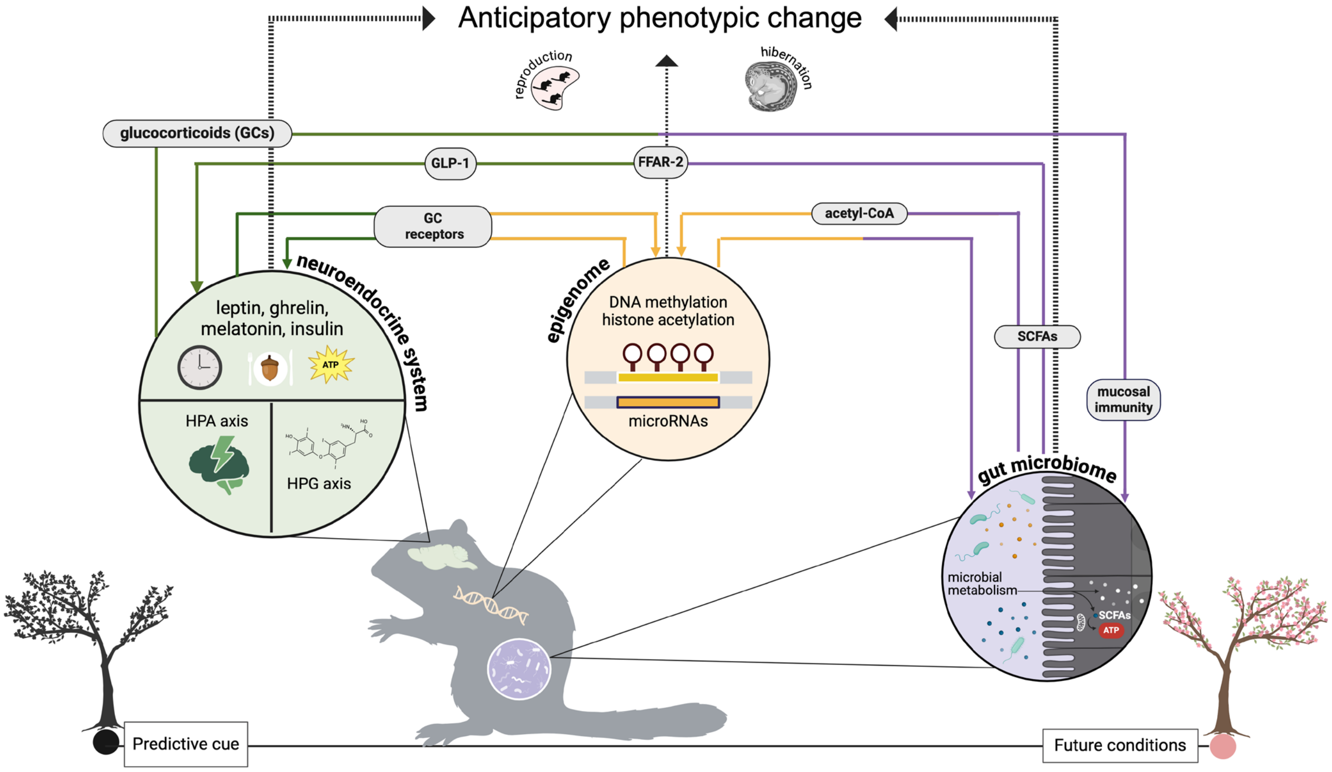

FIGURE 2 Mediation of anticipatory plasticity by the neuroendocrine system, epigenome and gut microbiota, their putative molecular mechanisms, and their synergies. Interactions among these systems can occur via the gut–brain axis, and through interplay among substrates like short-chain fatty acids (SCFAs), stress- and appetite-related hormones and their receptors, and genetic regulatory proteins like histones. Through independent and collective effects of these physiological systems and their connections, animals may sense and integrate predictive cues to coordinate anticipatory phenotypic change.

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(e.g. migration and hibernation) are encoded by epigenetic regulation of circannual rhythms (Helm & Lincoln, 2017), and many candidate gene pathways driving seasonal phenotypes are governed by DNA methylation (Alvarado et al., 2014). Shifts in methylation accompany anticipatory physiological changes to stress-related hormones in laboratory rodents (Thomassin et al., 2001), with support in wild animals: eastern chipmunks (*Tamias striatus*) adaptively increase reproductive output ahead of a pulse in beech seed production with a concomitant increase in DNA methylation (Leung et al., 2020; Tissier et al., 2020). In non-resource pulse years, methylation rates are low and reproduction is minimal or absent entirely, suggesting that epigenetic change may support anticipatory reproduction (Leung et al., 2020).

4.2 | Hormonal cascades

Among vertebrates, the neuroendocrine system can integrate cues of environmental conditions to coordinate downstream phenotypic responses (Dantzer, 2023; Martin et al., 2011). In particular, the hypothalamic–pituitary–adrenal (HPA) axis, a cascade of hormonal feedbacks that begins with the integration of environmental information by the brain and culminates in the production of glucocorticoid hormones (GCs), is central to the physiological stress response and metabolic regulation (Sapolsky et al., 2000). Anticipatory increases in GCs are induced in response to cues of conspecific rivals or predators (Boonstra, 2013), as well as ahead of the metabolic demands associated with reproduction and migration (Romero, 2002). Direct or indirect transfer of GCs to offspring can also mediate anticipatory parental effects (Champagne & Meaney, 2006; Hau et al., 2016; Moore & Power, 1986; Wilcoxon & Redei, 2007). For instance, maternal adjustments to offspring growth in response to cues of conspecific competition are triggered by GCs in red squirrels (Dantzer et al., 2013). Similar effects occur in sticklebacks (Giesing et al., 2011) and mice (Santarelli et al., 2014), whereby mothers facilitate offspring phenotype–environment matching via anticipatory changes in GCs. In European starlings (*Sturnus vulgaris*), experimentally elevated concentrations of yolk GCs, which may serve as a cue of poor maternal quality to offspring, enhance future flight performance in fledglings (Chin et al., 2009) and repeated predation attempts shrink clutch sizes via reduced GCs (Travers et al., 2010). Enzymes that activate and deactivate GCs (e.g. 11β-HSD I and II) are also central to anticipatory plasticity in migrating birds, especially in response to photoperiodic cues of impending seasonal change (Pradhan et al., 2019).

The preparatory changes associated with migration are also mediated by the hypothalamic–pituitary–gonadal (HPG) axis, which governs the release of gonadal androgens (oestrogens, progesterone and testosterone, Ramenofsky et al., 2012). The HPG axis can enhance future flight performance by shrinking reproductive organs (Bauchinger et al., 2007) and increasing fat stores in response to photoperiodic cues (Tonra et al., 2011). Anticipatory increases in testosterone can increase future competitive ability (Gleason et al., 2009), and HPG integration of photoperiodic and demographic factors shapes anticipatory plasticity in sex ratios in fish (Le Roy et al., 2017; Liu et al., 2017). The HPG axis also offers a potential route by which plant secondary metabolites may influence animal reproduction. Plant phytoestrogens may cue future food production by binding to oestrogen receptors in consumers, altering consumer reproductive physiology (Fidler et al., 2008; Labov, 1977).

Other hormonal cascades likely play a role in the underlying mechanistic architecture of anticipatory plasticity. For instance, pineal release of melatonin governs circadian rhythms and can mediate reproductive behaviour (Ohta & Konishi, 1992). Ghrelin and leptin—hormones related to metabolism, appetite and fat storage—may drive anticipatory metabolic adjustments ahead of changes in food availability. Experimental administration of leptin, which suppresses hunger, cues energetic supply in great tits (*Parsus major*) and modifies brood numbers (Lõhmus & Björklund, 2009); ghrelin, which stimulates appetite, regulates pre-hibernation feeding behaviour in ground squirrels (Healy et al., 2010). Production of oxytocin and vasopressin, which can be triggered by olfactory cues, may also contribute to the integration of predictive cues related to conspecific densities and predator abundance (Bielsky & Young, 2004).

4.3 | Synergy between the neuroendocrine system and the epigenome

Stress-related hormones like GCs can alter DNA methylation patterns in GC receptor genes (Adcock et al., 2004; Bartlett et al., 2019; Turecki & Meaney, 2016), recalibrating organismal stress sensitivity ahead of anticipated challenges. Despite a historic focus on perinatal or early-life stress (Szyf et al., 2005; Weaver et al., 2004), stress-inducing stimuli experienced can also alter DNA methylation during adulthood (Dirven et al., 2017; Roth, 2013). In fear conditioning and extinction studies in rodents, contextual fear learning tasks induce DNA methylation in genes associated with memory and neural plasticity (Miller & Sweatt, 2007). While the environment drives the emergence of epigenetic modifications, these changes, in turn, enable the neuroendocrine system to fine-tune hormonal responses, optimizing physiological and behavioural adaptations in response to predictive cues. For instance, epigenetic mechanisms can modify hormone synthesis essential for regulating growth, development, reproduction, energy balance and metabolism (Sibuh et al., 2023). These pathways can prime the neuroendocrine system, illuminating genetic–epigenetic–hormonal interactions that can facilitate anticipatory plasticity in dynamic environments (Horsthemke, 2022).

4.4 | Mediation of host metabolism by microbial symbionts

The past few decades have ushered in a growing appreciation for a regulatory role for the trillions of symbiotic microorganisms that inhabit different host body sites in the broader physiology, behaviour

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and fitness of their hosts. Microbial symbionts, particularly those in the gastrointestinal tract (hereafter, gut microbiota), which houses one of the densest collections of microbes on Earth, are highly sensitive to both intrinsic and extrinsic inputs. As such, gut microbiota can serve as powerful transducers of predictive cues by augmenting the range of cue modalities used to induce phenotypic change (e.g. by integrating nonphotic cues to adjust host circadian rhythms, Choi et al., 2021). Because microbiota have co-evolved alongside their hosts over evolutionary time (Lim & Bordenstein, 2020), they may serve as a mechanism of rapid adaptation by providing the functional architecture necessary to facilitate the evolution and maintenance of anticipatory plasticity (Alberdi et al., 2016).

Notably, gut microbiota can flexibly adjust host metabolism by reorganizing following host dietary change (David et al., 2014), toxin exposure (Kohl et al., 2014) and thermoregulatory demands (Khakisahneh et al., 2020; Moeller et al., 2020; Zhang et al., 2018). This flexibility can extend the range of phenotypes that can be produced in response to predictive cues by increasing crude energy available to hosts. Gut microbiota can modify host nutrient assimilation through the production of microbial metabolites like short-chain fatty acids (SCFAs, including acetate, propionate and butyrate) during fibre fermentation, which can serve as de novo energy substrates for animals (den Besten et al., 2013). These molecules can buffer animals during periods of resource scarcity (Mallott et al., 2022) and potentially facilitate investment into anticipatory phenotypic change, particularly in extreme and fluctuating environments (Zhu et al., 2024). For instance, the metabolic demands of bird migration may be compensated for by preparatory microbial enhancement of host energy harvest (Risely et al., 2018), and the increased fat deposition characteristic of hibernating animals is regulated, at least in part, by metabolic changes in the gut microbiota (Sommer et al., 2016; Xiao et al., 2019; Zhou et al., 2022). Microbial metabolism may even allow hosts to compensate for the physiological costs of anticipatory responses and ameliorate expected life-history trade-offs (e.g. by fuelling catch-up growth while minimizing oxidative damage, Dantzer et al., 2013, 2020; Petrullo, Baniel, et al., 2022).

4.5 | The gut–brain axis and microbial messengers

Gut microbiota can also mediate anticipatory shifts in host behaviour and reproduction by interfacing with the neuroendocrine system through a bidirectional ‘gut–brain axis’ for which evidence now exists beyond the laboratory in wild animals (e.g. Noguera et al., 2018; Petrullo, Ren, et al., 2022; Stothart et al., 2016). Through this axis, gut microbiota may induce anticipatory behavioural responses by altering microbial production of hormones and other molecules, driving behavioural and/or reproductive change (e.g. by increasing mating or foraging behaviour ahead of changes in food or density, Davidson et al., 2020; Schretter, 2020). GCs themselves, through their effects on immune function, can alter mucosal immunity in the gut, shifting immune targeting of microbiota to ‘feed’ or ‘fight’ particular microbiota (Ilchmann-Diounou & Menard, 2020). In turn, microbial production of signalling molecules, including neurotransmitters, such as gamma-aminobutyric acid (GABA), dopamine (DA), norepinephrine (NE), serotonin (5-HT) and histamine, as well as SCFAs (Dicks, 2022) can shape host metabolism, stress resilience and even reproduction (e.g. butyric acid regulates progesterone and oestradiol porcine granulosa cells, Lu et al., 2017).

SCFAs can also influence glucose metabolism by activating free fatty acid receptors 2 and 3 (FFAR2 and FFAR3), which stimulate the release of peptide YY (PYY) to promote satiety and enhance insulin-mediated glucose clearance, and glucagon-like peptide-1 (GLP-1), which augments insulin secretion and suppresses glucagon production. Leptin secretion can be induced by SCFAs through FFAR2, contributing to glucose homeostasis by facilitating glucose uptake in brown adipose tissue, skeletal muscles and the liver, and promoting glycogen synthesis in hepatic tissues (Acharya & Shetty, 2024). These metabolic effects highlight the integral role of SCFAs in nutrient absorption, with implications for organismal adaptation to fluctuating food. SCFAs also impact the host physiological stress response: SCFAs attenuate heightened stress reactivity in mice exposed to psychosocial challenge (van de Wouw et al., 2018). Gut microbiota also contribute methyl and acetyl groups that can be used for histone modification and methylation processes in the epigenome. These processes occur through microbial synthesis of molecules like folate (a major substrate for DNA methylation) and through SCFA-regulated production of enzymes and other molecules involved in histone acetylation (e.g. histone deacetylases and acetyl-coA, Woo & Alenghat, 2022).

Moreover, by serving as a secondary detection system following the primary integration of a predictive cue by the HPA axis, gut microbiota may amplify or emulate predictive cues of future conditions. Gut microbiota are involved in the neuroendocrine integration of olfactory cues in rodents (Bienenstock et al., 2018), and signalling molecules and hormones of microbial origin facilitate olfaction in some species (Ezenwa & Williams, 2014). Gut microbiota may also integrate dietary cues to induce downstream epigenetic modifications that underlie anticipatory phenotypic adjustments (Bhat & Kapila, 2017; Gilbert, 2005; Jaenisch & Bird, 2003). Interactions between gut microbiota and intestinal pathogens may cue anticipatory changes in reproductive investment via fecundity compensation (Schwanz, 2008), with microbial sensing of pathogens indexing future conspecific density and mortality risk. Finally, because early-life host–microbe symbioses prime later-life immune function and pathogen resistance (Knutie et al., 2017), gut microbiota may induce anticipatory modulation of the immune system in response to cues of the future pathogenic environment (Bäumler & Sperandio, 2016).

4.6 | A role for microbial transmission in anticipatory parental effects

In predictable coarse-grained environments, anticipatory parental effects can offer an alternative to polymorphisms if parents can use predictive cues of the offspring environment to adjust offspring

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development (Bell & Hellmann, 2019; Burgess & Marshall, 2014; Lind et al., 2020; Marshall & Uller, 2007). The parental microbiome is the origin source for inherited microbial communities in mammals and many other animals (Funkhouser & Bordenstein, 2013; Murphy et al., 2023). Parents may therefore calibrate their own microbiota to transmit a customized suite of microbes and adjust offspring developmental trajectories in anticipation of future conditions (Amato et al., 2024; Murphy et al., 2023). In support of this hypothesis, empirical data show that first-time non-human primate mothers transmit more milk-digesting microbiota to offspring, maximizing offspring capacity for milk nutrient assimilation in anticipation of the lactational constraints associated with primiparity (vervet monkeys, Petrullo, Baniel, et al., 2022; geladas, Baniel et al., 2022). In oviparous taxa, eggshells present a barrier to vertical transmission: Although they contain some maternal-origin microbiota, they also house environmental microbiota from the nest and broader environment. This may swamp maternal microbial signals, weakening selection for microbiome-mediated anticipatory parental effects by increasing stochasticity in microbial transmission and assembly (van Veelen et al., 2018). Finally, while deterministic transmission may facilitate transgenerational anticipatory plasticity when the offspring environment is predictable, stochastic transmission may serve as an alternative bet-hedging strategy to maximize microbial variation among offspring when the offspring environment is unpredictable (Björk et al., 2019; Bruijning et al., 2022; Donaldson-Matasci et al., 2013). Future studies aimed at identifying anticipatory plasticity could test alternative hypotheses related to deterministic (e.g. via precise transmission) and stochastic (e.g. via imprecise transmission) strategies of vertical microbial transmission as a function of cue reliability.

5 | ANTICIPATORY REPRODUCTION

The adjustment of one or more reproductive phenotypes in anticipation of future conditions (i.e. anticipatory reproduction) is a widespread phenomenon documented across an array of taxa and reproductive phenotypes (Figure 3). Importantly, it can be a major mechanism regulating population structure (Vekhnik, 2020). Anticipatory reproduction in resource pulse ecosystems can eliminate the expected lag in the consumer numerical response to an increase in prey (Boutin et al., 2006; Tissier et al., 2020), subverting predictions from classic population ecological models (Ostfeld & Keesing, 2000).

5.1 | Reproductive delay

Reproductive delays can occur between mating and fertilization (delayed fertilization), fertilization and implantation (embryonic diapause), and during embryonic development following implantation. Because similar underlying mechanisms are presumed to regulate delays at all three stages, animals often display capacity for anticipatory delays at multiple—or even all—stages (Burns, 1981). Genetic mechanisms underlying arrested reproductive delays include epigenetic changes (e.g. small RNAs, histone modifications), circadian clock shifts and signalling pathways of cell cycle arrest (Hand et al., 2016). Changes in HPG axis function, especially oestrogen, progesterone and prolactin synthesis, also play a role (Krishna & Bhatnagar, 2011). The stage at which reproductive delays can occur may reflect constraints within the underlying mechanisms of arrested development, and/or differences in the timing of cue perception.

5.1.1 | Delayed fertilization

Delayed fertilization is typically present in species with the capacity to store sperm in the female reproductive tract following copulation (Wimsatt, 1975). In bats, delayed fertilization is an anticipatory response to hibernation and seasonal change, and this strategy elicits various counter-strategies in males (Orr & Zuk, 2013; though not all bats that delay fertilization hibernate, Racey & Entwistle, 2000). In guppies, prolonged storage of sperm in females facilitates adaptive timing of female reproduction, but increases sperm competition. Males respond to cues of future competition through sperm-priming, whereby the final stages of sperm maturation are accelerated (Cardozo et al., 2020; Cattelan & Pilastro, 2018). Similarly, male bats in species with delayed fertilization typically grow larger testes than those in species without this type of delay in anticipation of future sperm competition (Orr & Zuk, 2013).

5.1.2 | Embryonic diapause

Embryonic diapause is a period of suspended development at the blastocyst stage prior to implantation (Hand et al., 2016). Following embryonic diapause, implantation can be immediate or delayed (Renfree & Fenelon, 2017). In seasonal environments, embryonic diapause allows females to pause offspring development and resume it only when the offspring environment is expected to be favourable (Sandell, 1990). For example, some weasels and badgers can reproduce at 3 months old but not give birth until the following year (Wright, 1942; Yamaguchi et al., 2006). In a more extreme example, solitary American black bears (*Ursus americanus*) can optimize reproductive fitness through repeated fertilization with different paternities (superfetation) and the diapausing of all embryos before they are resumed together ahead of optimal conditions (Himelright et al., 2014). Some animals exhibit embryonic diapause even in stable environments like the tropics (Wimsatt, 1975). In some cases, the predictive cues inducing embryonic diapause have been identified, but the underlying physiological mechanisms remain unknown. Roe deer (*Capreolus capreolus*), for instance, use photoperiod changes to pause embryonic development ahead of winter but do so without conspicuous changes in HPG axis function (Aitken, 1974).

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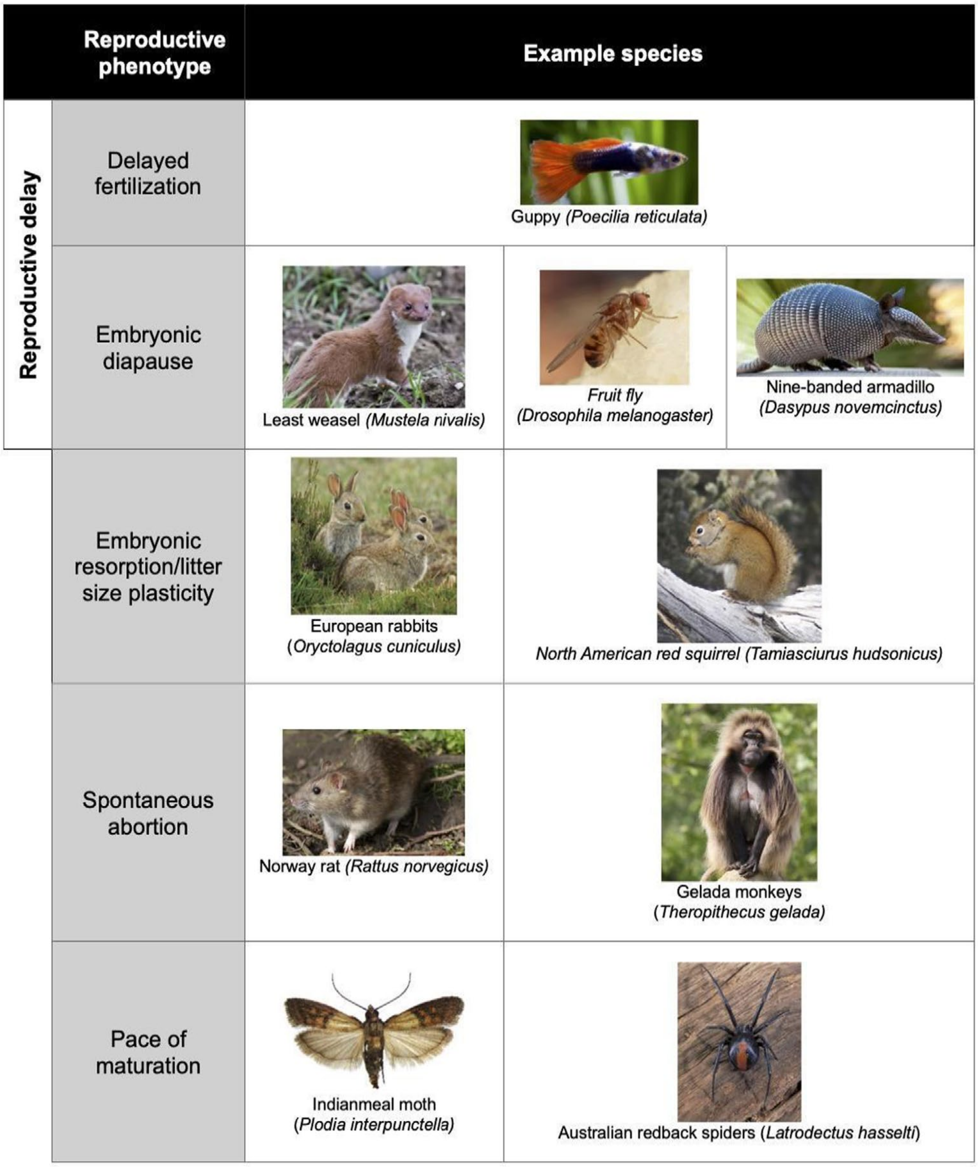

	Reproductive phenotype	Example species		
Reproductive delay	Delayed fertilization	Guppy *(Poecilia reticulata)*		
	Embryonic diapause	Least weasel *(Mustela nivalis)*	Fruit fly *(Drosophila melanogaster)*	Nine-banded armadillo *(Dasypus novemcinctus)*
	Embryonic resorption/litter size plasticity	European rabbits (*Oryctolagus cuniculus*)	North American red squirrel *(Tamiasciurus hudsonicus)*	
	Spontaneous abortion	Norway rat *(Rattus norvegicus)*	Gelada monkeys (*Theropithecus gelada*)	
	Pace of maturation	Indianmeal moth (*Plodia interpunctella*)	Australian redback spiders (*Latrodectus hasselti*)	

FIGURE 3 The remarkable breadth of anticipatory reproduction. Anticipatory reproduction spans a variety of reproductive phenotypes, enabling animals to optimize functional traits like reproductive timing and reproductive output in response to cues of future environmental change. The broad range of taxa within which these strategies have been documented—from insects to non-human primates—underscores their evolutionary significance, particularly in fluctuating and unstable environments.

5.2 | Embryonic resorption

The resorption of embryos in polytocous mammals reflects anticipatory reproduction at one of its earliest stages and can be partial (some embryos resorbed) or, less often, complete (entire litters resorbed). In European rabbits (*Oryctolagus cuniculus*), up to 60% of litters can be resorbed depending on the timing and onset of the breeding season (Brambell, 1944), and in European brown hares (*Lepus europaeus*) and swamp rabbits (*Sylvilagus aquaticus*), resorption occurs regularly (Conaway et al., 1960; Schroeder et al., 2011). Similar effects occur in house mice (*Mus musculus*), whereby females adjust sex ratios through embryonic resorption (Krackow, 1992). In montane voles (*Microtus montaus*), dietary and photoperiodic cues interact to regulate resorption rates. Resorption rates are lower and litter sizes larger in response to sprouted wheat (Pinter & Negus, 1965), which is high in fibre and contains phytohormones that can interface with the HPG axis—a primary mechanism governing litter size plasticity at all levels (Labov, 1977; Wilsterman et al., 2024). Similarly, sow litter sizes can be experimentally increased by modulating the gut microbiota with a high-fibre diet (Che et al., 2011; Veum et al., 2009). In some cases, predictive cues related to future food scarcity can trigger complete embryonic resorption. In the edible dormouse (*Glis glis*), complete resorption occurs in all females ahead of food-poor years (Vekhnik, 2019). Captivity also increases the rate of embryonic resorption, suggesting a role for the physiological stress response. American mink (*Neogale vison*) can strategically monopolize paternity

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BOX 2 Understanding anticipatory reproduction ahead of a resource pulse in mammalian consumers

A key challenge for resource pulse consumers is maximizing fitness given episodic fluctuations in food. Some animals migrate (Kitchell et al., 1999), some use scatter- or larder-hoarding (Larsen et al., 1997; Zwolak et al., 2021), and others exhibit anticipatory reproduction to optimally time offspring development to food abundance. Wild boar (*Sus scrofa*) adjust oestrus timing depending on cues of a future oak mast (Cachelou et al., 2022), and anticipatory increases in reproduction ahead of a food pulse occur in North American and Eurasian red squirrels (Boutin et al., 2006), eastern chipmunks (Tissier et al., 2020), white-footed mice (Marcello et al., 2008) and edible dormice (Fidler et al., 2008). Some seed consumers reproduce only during mast years, remaining reproductively inactive in years when this phenomenon does not occur (Fidler et al., 2008; Tissier et al., 2020). Yet, the physiological mechanisms governing pulse consumer reproductive flexibility remain elusive (Dri et al., 2022).

In the southwest Yukon, female North American red squirrels (*Tamiasciurus hudsonicus*) exhibit multi-level anticipatory reproduction ahead of a pulse in their primary food source, seed from white spruce (*Picea glauca*). In the months before a pulse, females breed earlier and more frequently, having larger and sometimes multiple litters, resulting in higher recruitment of offspring into the breeding population (Boutin et al., 2006; McAdam et al., 2019; Petrullo et al., 2023). Proximate drivers may include increased maternal access to food (White, 2007, 2013), but females do not require additional food to increase reproductive output (Boutin et al., 2013), and both experimental food supplementation and larger food hoards do not predict larger litters (Larsen et al., 1997; Petrullo et al., 2023). Dietary shifts towards other non-pulsed items could increase amino acid intake (White, 2007), but there is no evidence of diet—switching in Yukon red squirrels (Fletcher et al., 2010).

Instead, females may anticipate masts using predictive chemical cues. The consumption of immature sexual structures like buds, which emerge during the breeding season, may cue an upcoming mast (Descamps et al., 2008; Elliott, 1978). These structures contain VOCs and phytohormones that can bind along the consumer HPG axis (Berger et al., 1981; Labov, 1977; Simons & Grinwich, 1989). Buds may differ in composition and/or concentration of these molecules in mast years, such that their consumption in the months preceding a pulse induces anticipatory reproduction in a dose-dependent manner (i.e. squirrels become ‘swamped’ with chemical cues). Buds may also contain different macronutrient profiles than mature seed. Indeed, bud consumption is associated with a distinct microbial signature in the red squirrel gut microbiota, including an increase in SCFA-producing microbes (e.g. *Oscillospira*, Ren et al., 2017). These changes mirror those induced via increased fibre consumption in experimental elevations of litter sizes in pigs (Veum et al., 2009). If bud consumption varies in mast years, nutritional and/or chemical cues may trigger anticipatory reproduction by way of gut microbial reorganization, with implications beyond red squirrels. Chipmunks and boar gather most of their food from the forest floor, limiting their access to immature seeds in the canopy. They may instead sense chemical and/or nutritional cues of an impending beech mast by consuming springtime beech or oak flowers (Berger et al., 1981; Tissier et al., 2020).

through flexible embryonic resorption in the wild, but in captivity, nearly half of all embryos are consistently resorbed (Hansson, 1947). These data suggest that embryonic resorption is a major mechanism of litter size plasticity (Wilsterman et al., 2024), with implications for understanding anticipatory increases in reproductive output in consumer–resource pulse systems (Box 2).

5.3 | Spontaneous abortion

Some animals can decrease investment in offspring—or terminate it entirely—in anticipation of a hostile future environment. When males are certain that paternity is not their own, infanticide can increase male fitness by accelerating a female's return to reproductive receptivity and curtailing investment in unrelated offspring. In some species, females can use cues of novel males to induce spontaneous abortion ahead of future infanticide in what has been termed the ‘Bruce effect’ (Bruce, 1960). This effect has been documented in laboratory rodents (mice, Bruce, 1960) and Norway rats (Marashi & Rülicke, 2012), and in wild populations of marmots (Hacklander, 1999), bank voles (Eccard et al., 2017) and gelada monkeys (*Theropithecus gelada*, Roberts et al., 2012). In geladas, ~80% of gestations end in spontaneous abortion following take-over events in which an extra-group male seizes control of a social group and typically kills unrelated offspring (Beehner & Bergman, 2008). Spontaneous abortion severs maternal investment in offspring doomed to a fate of infanticide, and returns females to oestrus sooner, facilitating earlier mating with a novel male. Yet, the physiological mechanisms that underpin the Bruce effect are unknown. In rodents, males may ‘hack’ female physiology via urinary or olfactory chemical cues (e.g. male oestradiol reducing female prolactin, de Catanzaro, 2023), but females could also use chemical cues of novel males to adaptively terminate reproductive investment (Zipple et al., 2019). In non-human primates, a weaker capacity for olfactory cue use suggests a different modality (e.g. visual cues that induce an HPA-HPG axis response, Roberts et al., 2012).

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5.4 | Adjusted pace of reproductive maturation

Anticipatory acceleration or delay in reproductive maturation can be highly context-dependent. In response to cues of high conspecific density, larvae of the male Indianmeal moth (*Plodia interpunctella*) slow reproductive maturation to facilitate the production of larger testes and more sperm, enhancing future competitive ability (Gage, 1997). But when cues instead index a low-density environment, males mature faster in anticipation of greater time investment locating females (Gage, 1997). Male Australian redback spiders (*Latrodectus hasselti*) respond to chemical cues of females by accelerating maturation (at the expense of body condition) but slow maturation (to achieve better body condition) in response to rival chemical cues (Kasumovic & Andrade, 2006). Similar manipulation of rates of reproductive maturation in response to density cues has been documented in yellow dung flies (Blanckenhorn et al., 2007) and web-building spiders (Neumann & Schneider, 2016).

6 | PREDICTING THE FUTURE IN A CHANGING WORLD

At present, global climate change is generating extreme and unpredictable weather events in many parts of the world with unclear implications for animals in vulnerable regions (Thornton et al., 2014). This instability may interrupt predictive cue transmission (Kelley et al., 2018; Sih et al., 2011) and dampen cue reliability (Bonamour et al., 2019). Increased artificial light at night could alter or impede photoperiodic cues (van Geffen et al., 2014), and eutrophication caused by nutrient pollution may diminish an aquatic animal's ability to perceive relevant shifts in photoperiod (Candolin, 2009). Visual cues may be obstructed by smog and urbanization in terrestrial animals (Proppe, 2022), while air pollution inhibits the detection of olfactory and chemical cues (Lürling & Scheffer, 2007; Weiss, 2022), and anthropogenic noise interferes with an animal's ability to detect important auditory cues (Kelley et al., 2018). These interruptions could shift reliance towards co-opted, multimodal and mosaic cues, which may be more robust to climate-induced degradation of cue reliability in affected populations (Abarca, 2019; Fuxjäger et al., 2019).

For anticipatory plasticity to evolve, moderate levels of environmental change are favoured. However, if environmental conditions change too fast, plasticity may lead to phenological mismatches (Kronholm, 2022). For instance, female ground squirrels in the Arctic have begun to emerge from hibernation before males, reducing both male and female reproductive success (Chmura et al., 2023). Light and noise pollution disrupt phenological patterns of cross-species interactions (McMahon et al., 2017), and moulting—a typically adaptive anticipatory response to seasonal change—may become maladaptive if snow cover declines (Zimova et al., 2018). Agricultural and industrial chemicals containing xenoestrogens may mimic chemical cues that induce anticipatory reproduction by incorrectly foreshadowing future conditions (Ottinger et al., 2011). Ultimately, populations that rely on anticipatory plasticity to maximize fitness will need to detect and reject, or ignore, unreliable cues to evade the fitness costs associated with phenotype–environment mismatching (McNamara et al., 2011).

Nonetheless, anticipatory plasticity may remain a viable and perhaps faster adaptive strategy compared with genetic evolution (Snell-Rood et al., 2018, but see Fox et al., 2019), bolstering a need for empirical studies that identify anticipatory responses in animal systems (Box 3). Animals with anticipatory mechanistic architecture already in place may be better able to flexibly synchronize key life-history traits like growth and reproduction to variations in future resource availability (Sun et al., 2018). This could facilitate rapid adaptation to shifts in resources caused by climate change (Charmantier et al., 2008; Clement et al., 2023). Moreover, the moderate levels of gene flow caused by climate change may ultimately favour the evolution of anticipatory plasticity (Leimar & McNamara, 2015). Finally, while newly unreliable cues can weaken selection for plasticity writ large (Gavrilets & Scheiner, 1993), they may still preserve organismal fitness if they generate developmental variation among individuals that increases the likelihood of a phenotypic match to the future environment (Donaldson-Matasci et al., 2013). But a transition from anticipatory plasticity to bet-hedging, and/or towards integrative strategies combining the two, may nonetheless be inevitable in populations where cue reliability is disintegrating due to global change (Cohen, 1966; Donaldson-Matasci et al., 2013). Novel environments may render anticipatory plasticity non-adaptive as animals become phenotypically constrained in a direction away from new fitness optima (Ghalambor et al., 2007). Future studies that empirically test how cue reliability and standing genetic variation interact to predict organismal strategies will help to identify critical thresholds of transition between bet-hedging and anticipatory plasticity (Botero et al., 2015).

7 | CONCLUSIONS

Compared with other types of phenotypic plasticity, anticipatory plasticity has been historically understudied despite its potential to serve as a mechanism of organismal adaptation. Advances in our understanding of the mechanistic architecture that facilitates anticipatory plasticity will be gleaned through integrative, eco-physiological studies that combine classic physiological tools with newer 'omics approaches to perform field-based experiments in animals in their natural environments. Given the scope at which rapid change continues to affect entire ecosystems, a better understanding of how anticipatory plasticity may constrain or potentiate population-level responses to environmental instability will remain a priority for functional ecologists and organismal biologists for the foreseeable future.

AUTHOR CONTRIBUTIONS

Lauren Petrullo and Ben Dantzer conceived of the idea for the manuscript. Lauren Petrullo wrote the original draft of the manuscript.

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BOX 3 Methodological approaches to uncovering anticipatory plasticity

As strong circumstantial evidence for adaptive plasticity, anticipatory responses should index *adaptive* phenotypes, necessitating quantification of fitness outcomes (Whitman & Agrawal, 2009). Ideally, quantification would span the costs and gains associated with each phenotype expressed across each iteration of the environment in a factorial framework (DeWitt, 1998; Wiley, 2006). Under controlled laboratory conditions, or through experimental manipulations like cross-fostering, phenotypes can be intentionally mismatched to future conditions in a factorial manner and resulting fitness outcomes quantified and compared (Storm & Lima, 2010). In the absence of direct fitness measures, experimental manipulation of factors driving responsive plasticity can provide support for anticipatory plasticity through process of elimination. In papilionid butterflies (*Iphiclidies podalirius*), manipulation of food, photoperiod and temperature—immediate cues inducing responsive plasticity—failed to explain seasonally induced differences in body size, suggesting that body size variation is instead an anticipatory response to upcoming seasonal change (Esperk et al., 2013).

Comparative studies in populations of the same species may reveal otherwise hidden anticipatory responses (Cachelou et al., 2022), and comparative biological surveys can illuminate the proximate mechanisms that mediate anticipatory plasticity (Guindre-Parker, 2018; Rubenstein et al., 2016; Vitousek et al., 2019). Studies in species in which anticipatory plasticity is expected to be favoured (e.g. because it would enhance fitness) but is absent can shed light on anticipatory constraints (Sandell, 1984). Despite relying on pulses of catkins from masting trees, Siberian flying squirrels (*Pteromys volans*) do not exhibit anticipatory reproduction in advance of a mast (Selonen & Wistbacka, 2016). Failure to foreshadow upcoming mast may suggest unreliable predictive cues, and/or physiological constraints that inhibit anticipatory reproduction. In line with this hypothesis, female flying squirrels can only increase reproductive output when body condition improves. As capital breeders, they may be unable to use diet-switching or stored food to fuel anticipatory reproduction ahead of a mast (Selonen & Wistbacka, 2016).

Finally, integrative approaches capitalizing on recent 'omics advances also offer promise in revealing inconspicuous anticipatory responses. In suspected cases of anticipatory reproduction in resource pulse ecosystems, coupling non-invasive observations of feeding behaviour with faecal DNA metabarcoding and/or metagenomics to track shifts in dietary intake and composition can test diet-switching hypotheses (Ando et al., 2020; Srivathsan et al., 2016; Taberlet et al., 2007). Similar genomic approaches can capture host exposure to chemical or phytohormonal cues by the neuroendocrine system or gut microbiota (Chanclud & Lacombe, 2017; Iason, 2005), providing insight into predictive cue modalities.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to disclose.

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