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Bet-hedging in parasitoids: when optimization is not the best strategy to cope with climatic extremes

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ABSTRACT

Bet-hedging occurs when unreliable environments select for genotypes exhibiting a lower variance in fitness at the cost of a lower mean fitness for each batch of progeny. This means that at the level of the genotype, the production of mostly non-optimal phenotypes may be favored when at least some phenotypes are successful. As extreme unreliable climatic events are increasing because of climate change, it is pertinent to investigate the potential of bet-hedging strategies that allow insects to cope with climate change. Evidence for bet-hedging is scarce in most insects, including parasitoids, but the unique lifestyle and biology of parasitoids leads to the expectation that bet-hedging may occur frequently. Here, we evaluate a range of parasitoid traits for which a bet-hedging strategy could be envisioned even if bet-hedging has not been identified as such yet. Under-identification of bet-hedging in nature could have resulted from a major focus of studies on parasitoid life history evolution and foraging behavior on optimality models, predicting how mean fitness can be maximized. Most environmental factors, however, vary unpredictably. Life history and behavioral adaptations are thus expected to be affected by environmental stochasticity. In this paper, we review different aspects of parasitoid behavior, physiology, and life histories and ask the question whether parasitoid traits could have evolved under selection by environmental stochasticity.

1. Introduction

Understanding how unreliability of the environment affects organisms remains a major challenge in evolutionary biology (Simons, 2011). Getting more insight into the role played by non-reliable environments is now particularly important, because Human-Induced Rapid Environmental Changes (HIREC; Sih et al., 2011), including climate change, are becoming more extensive. For example, average temperatures are increasing and extreme events, such as frost and heat waves, are becoming more frequent (Hance et al., 2007; Easterling et al., 2000). While phenotypic and adaptive responses are favored under variable but reliable climatic conditions, responses induced by unreliable environmental conditions have remained largely understudied: risk aversion, also known as bet-hedging. Bet-hedging in response to strong, stressful environmental variation is a strategy guaranteeing at least some success across successive generations, rather than having high success for a few generations and no success at all for other generations (Hopper, 1999). Bet-hedging is, therefore, favored in the most stochastic, unreliable environments (Le Lann et al., 2021), and represents an adaptation to long-term non-reliable fluctuating selection pressures (Simons, 2011).

Bet-hedging differs from genetic adaptation, as bet-hedging could be considered "an adaptation to unpredictability or change itself", and being a property of a genotype, can occur at a rapid pace (Simons 2011). Adaptive plasticity differs from bet-hedging, as for plasticity a single genotype can generate several optimal phenotypes in different environments. Bet-hedging produces a suboptimal phenotype in an environment, but never leads to null fitness (Simons, 2011). For both plastic and evolutionary responses (Sorensen et al., 2020), studies have shown that the selection pressures generated by unreliable temperatures are stronger than those generated by variable, predictable temperatures

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(Logan and Cox, 2020; Castaneda et al., 2015). Strong selection pressures due to unreliable temperatures have been detected at the molecular level (Sorensen et al., 2020) and at the organismal level on traits such as diapause, where bet-hedging-type strategies have indeed been observed (Tougeron et al., 2019).

Environmental unreliability can affect an individual during its lifetime and/or its progeny over several generations with markedly different effects on fitness. For example, selection in stochastic environments can lead to the expression of a seemingly unfavourable trait in one generation and environment, while expression of that trait could be adaptive in an alternative environment. The capacity to withstand extreme hot and cold events due to high thermal limits is costly in a stable environment (i.e., an unfavorable phenotype), but crucial in an environment where temperatures vary unexpectedly (Sunday et al., 2019). For example, Sunday et al. (2019) demonstrated a positive relationship between thermal tolerance limits and exposure to temperature extremes. Despite the potential major consequences of unreliable environments, only very few studies consider environmental unpredictability to explain species adaptation. Indeed, during the last 50 years evolutionary theory has relied heavily on an optimality approach (Charnov, 1976). For optimality modelling, populations are mainly made up of individuals sorted by natural selection based on higher fitness. Optimality models thus focus on predicting how the arithmetic mean fitness can be maximized within a relatively constant environment over multiple generations. In contrast, bet-hedging is a strategy by which organisms can cope with unreliable environmental variability through risk spreading. For bet-hedging, fitness variance is reduced in unreliably variable environments over several generations (i.e., a higher geometric mean fitness), but at the expense of a reduction in mean fitness within a generation (i.e., a lower arithmetic mean fitness; Hopper 1999). Rather than focusing on the trade-off between arithmetic and geometric mean fitness, Yasui (2022) proposed a new definition for bet-hedging as "any strategy to increase the between-generational geometric mean fitness to avoid extinction of its controlling genotype against unpredictable environmental fluctuation".

Only very few studies have explicitly tested for bet-hedging empirically, which is why Simons (2011) proposed a classification to categorize the level of proof for the existence of a bet-hedging strategy. For category I, candidate bet-hedging can be proposed and relevant environmental variation is present. Cases in category I are generally studies with an untested hypothesis, and most studies mentioning bet-hedging fall into this category. For category II, trait expression differs between populations depending on the level of environmental predictability. For category III, phenotypic trait variability is genotype-dependent. For category IV, selection pressures acting on a trait are linked to environmental unpredictability, meaning that there is an impact on fitness. For category V and VI, the adaptive significance of a potential bet-hedging trait is directly tested. Of importance here is that the average geometric mean fitness is compared between bet-hedgers and non-bet-hedgers (Fig. 1). For category VI, there must further be direct proof that unpredictability of the environment modifies phenotypes and that the rate of adoption of alternative phenotypes is linked to the degree of environmental unpredictability. Since the publication of Simon's (2011) classification, category V and VI studies have still remained very rare.

Parasitoids are insects that develop on or in a host arthropod

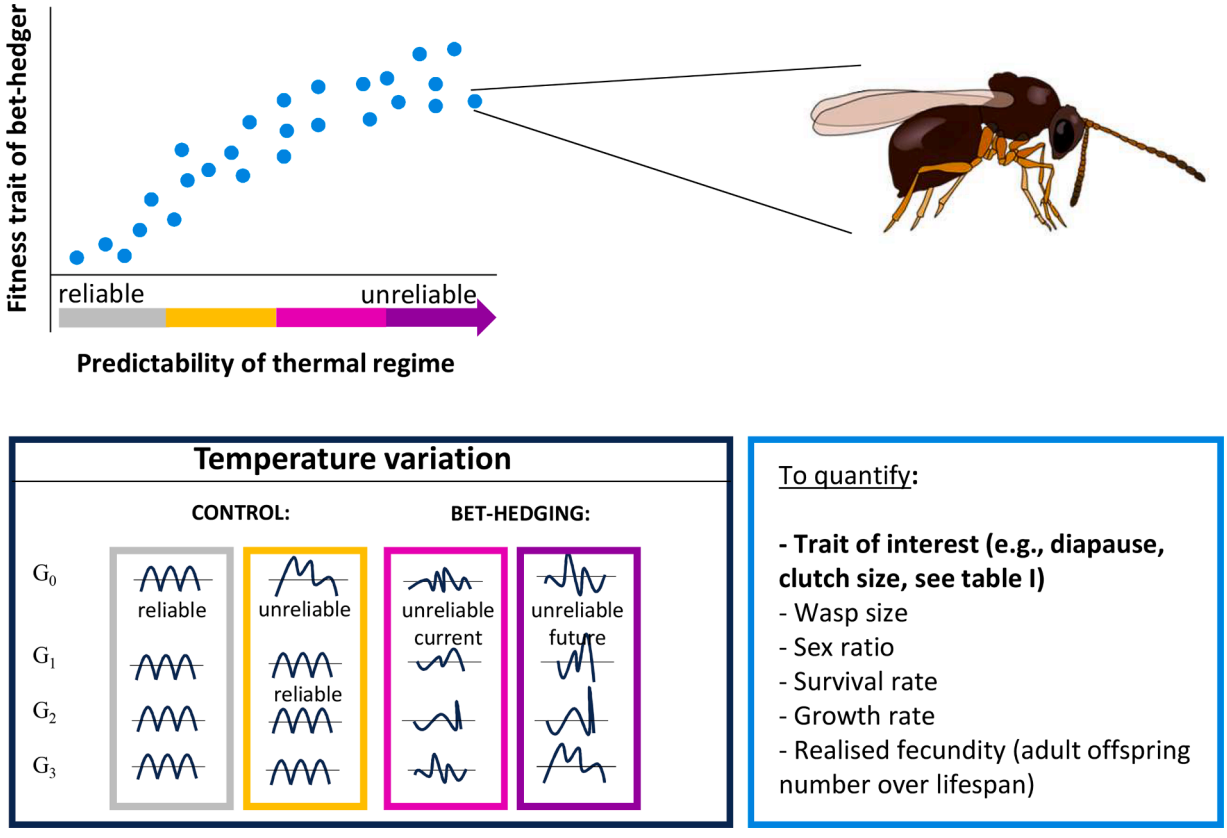

Fig. 1. Overview of an experimental design for testing bet-hedging in response to unreliable and reliable thermal variation in a parasitic wasp. Phenotypes can be quantified at each generation for all offspring, preferably using clones or inbred lines (blue box). To assess the benefit of a bet-hedging strategy over time compared to plasticity (i.e., within- or transgenerational, referred to as « Control »), one can measure the effects of an exposure to reliable thermal fluctuations at each generation G_0 to G_3 (grey box), as well as the effects of a single exposure in G_0 to unreliable temperatures followed by reliable thermal conditions (yellow box), and how this affects phenotypes of future generations. To test for bet-hedging, responses to current (pink box) and future (purple box) unreliable temperatures can be measured over subsequent generations. This set up allows for calculating geometric mean fitness over consecutive generations under four thermal regimes that should favour bet-hedging or not.

resulting in the death of the host when parasitoid development is completed (Eggleton and Gaston, 1990; Godfray, 1994). Parasitoids are most common within Hymenoptera, although parasitoids also evolved repeatedly in other insect orders, such as Diptera and Coleoptera. Parasitoids are completely dependent on a single host; hence foraging for hosts and host quality are typically directly linked to life histories and fitness. Like other animals, parasitoids face unreliable biotic and abiotic environmental conditions that can result in the expression of suboptimal phenotypes (risk spreading) that are not predicted by optimization models. We choose to focus this review on parasitoids, because there is a lot of data available for this diverse group of insects suggesting that bet-hedging may be occurring frequently in nature. Most studies on

Table 1
Overview of parasitoid traits for which we can expect to see selection for bet-hedging. A division in made between direct effects on parasitoids (i.e., as a result of increased unpredictable environmental changes) and indirect effects of increased unpredictable environmental changes on hosts with trophic consequences for parasitoids. Also included is whether bet-hedging occurs at a spatial or temporal scale (or both). We refer to relevant examples for which existing emperical data could be suggestive of bet-heding (although in all cases this remains to be explicitly tested). We use the categorization described by Simons (2011) with regard to the type of evidence for bet-hedging and the type of study used to demonstrate it.

Trait	Effect	Trait type	temporal/ spatial bet-hedging	Potential parasitoid example	Family	Type of study	Type of evidence	Reference
Direct abiotic effects								
diapause	temperature	behavioral	temporal	*Nasonia vitripennis*	Pteromalidae	comparative	III	Paolucci et al 2013
diapause	temperature	behavioral	temporal	*Aphidius ervi*	Braconidae	comparative	III	Tougeron et al., 2019
fat accumulation	temperature	physiological	spatial + temporal	*Leptopilina heterotoma*	Figitidae	within-population	III	Le Lann et al., 2014
patch exploitation: no. of patches	temperature	behavioral	spatial	*Anaphes victus*	Mymaridae	comparative	III	Boivin, 1994; Hance et al., 2007
sex allocation	temperature	behavioral	spatial + temporal	*Trichogramma euproctidis*	Trichogrammatidae	within-population	II	Moiroux et al., 2014
Indirect biotic effects on hosts or mates (i.e., location, availability, quality etc…)								
gamete production and dispersal	mate availability	life history	temporal	*Trichogramma evanescens*	Trichogrammatidae	within-population	II	Martel & Boivin, 2007
gamete production and dispersal	mate availability	life history	spatial + temporal	*Aphytis aonidae*	Aphelinidae	within-population	II	Heimpel and Rosenheim, 1998
patch exploitation: no. of patches	host availability + temperature	behavioral	spatial	*Anaphes victus*	Mymaridae	comparative	III	Boivin, 1994; Hance et al., 2007
patch exploitation: patch leaving time	host quality	behavioral	spatial	*Aphidius rhopalosiphi*	Braconidae	within-population	II	Outreman et al., 2001
patch exploitation: ovipositions per patch	host mortality (due to leaf senescens)	behavioral	spatial	*Anagrus delicates*	Mymaridae	within-population	II	Cronin & Strong, 1993
patch exploitation: patch leaving time + host acceptance	intra-specific competition between adults	behavioral	spatial	*Aphidius ervi*	Braconidae	within-population	II	Le Lann et al., 2011
superparasitism	host availability	behavioral	temporal	*Aphidius ervi*	Braconidae	within-population	I	Ortiz-Martinez et al., 2019
patch exploitation: patch leaving time + host acceptance	inter-specific competition	behavioral	spatial	*Aphidius rhopalosiphi*	Braconidae	within-population	II	Le Lann et al., 2008
parasitoid virulence: host preference	host immunity	behavioral	spatial	*Asobara tabida*	Braconidae	comparative	III	Kraaijeveld and van Alphen, 1995; Kraaijeveld and Godfray, 1999
host stage selection	host mortality (due to hypothetical herbivory)	behavioral	temporal	*Aphidius colemani*	Braconidae	within-population	I	Barrette et al., 2009
host feeding	host availability	behavioral	spatial + temporal	*Encarsia formosa*	Aphelinidae	within-population	I	Burger et al., 2004
host feeding	host availability	behavioral	spatial + temporal	*Aphytis* sp.	Aphelinidae	within-population	I	Heimpel et al., 1994
host feeding	host availability	behavioral	spatial + temporal	*Nasonia vitripennis*	Pteromalidae	within-population	I	Rivero & West, 2005
host feeding	host availability	behavioral	spatial + temporal	*Trichogramma turkestanica*	Trichogrammatidae	within-population	I	Ferracini et al., 2006
fatty acid synthesis and fat accumulation (and plasticity therein)	host quality	physiological	spatial + temporal	*Leptopilina heterotoma*	Figitidae	comparative	III	Visser et al., 2021
clutch size	host quality	life history	spatial	*Aphaereta minuta*	Braconidae	within-population	I	Vet et al., 1993
clutch size: offspring size	host availability	life history	spatial	*Copidosoma floridanum*	Encyrtidae	within-population	I	Ode 2018
trade-off reproduction/ longevity	host availability + distribution	life history	spatial	*Asobara tabida*	Braconidae	comparative	II	Ellers et al., 1998; Ellers et al., 2000

parasitoids are performed under constant laboratory conditions and quantitative data on selection in unreliable environments are scarce. Behavioural deviations from optimality have often been explained by information and/or memory constraints due to a supposed weak capacity of the parasitoid to cope with the complexity of its environment (Stephen and Krebs, 1986). In practice, measuring geometric mean fitness is exceedingly difficult to accomplish, because it requires phenotype measurements over several consecutive generations. Consequently, Hopper (1999), as well as Simons (2011), found little empirical proof for bet-hedging in insects. However, as stochastic environmental events can affect all types of life history traits and behaviors, apparently maladaptive phenotypes should be considered as an alternative each time data do not correspond to the predictions of optimization models.

In parasitoids, theoretical and optimization models predicting the impact of variable environments provide different quantitative predictions. For example, it was shown that parasitoids lay smaller clutch sizes than expected by Lack's optimal clutch size principle, which states that clutch size (in birds) corresponds to the largest number of young the parents can feed (Haccou and McNamara, 1998). In parasitoids, the use of mixed clutch size strategies instead of pure strategies leads to the allocation of more resources to precocious reproduction at the expense of a shorter lifetime (Haccou and McNamara, 1998). This implies that egg limitation (i.e., running out of eggs prior to death) should be rare (Ellers et al., 2000). Parasitoids further show partial preferences rather than following the zero-one rule. Partial preferences mean that parasitoids accept suboptimal hosts, including previously parasitized hosts or more virulent hosts that kill the developing parasitoid. By using suboptimal hosts, the risk of death for the eggs or larvae of the parasitoid increases (Lapchin, 2002) leading to sub-maximal oviposition rates in host patches instead of rate maximization (Cronin and Strong, 1993). Smaller clutch sizes and partial preferences can also result from trade-offs and constraints.

Parasitoids play a critical role in ecological communities by regulating insect populations. Considering the rate of environmental changes, there is an obvious need to better understand the evolutionary importance of environmental variability and unpredictability on parasitoid behavior, physiology, and life histories. We need both theoretical and empirical evidence to discriminate between relevant environmental factors, which remains a major challenge. Le Lann et al. (2021) already proposed methods to distinguish between plasticity and bet-hedging strategies in insects. In this review, we synthesize different aspects of parasitoid behavior (section 1), physiology (section 2), and life histories (section 3), and ask the question if current available data can be interpreted as (candidate) bet-hedging or if a trait could have evolved under selection by environmental stochasticity (see Table 1 with an overview of the trait involved, the evidence acquired according to Simons (2011), and the environmental factor considered). We aim to show that fitness variance can indeed be reduced by behavioral, physiological, or life history adaptations (and trade-offs therein) that spread risks in time and/or space. For several of the examples, we make suggestions for further empirical testing to obtain more evidence for the existence of bet-hedging in parasitoids.

2. Behavior

2.1. Diapause

Extreme climatic events can be stressful and are generally unreliable. In temperate areas, most insect species have a period of dormancy or temporarily arrested development, termed diapause, at times when environmental conditions are unfavorable, e.g., harsh winters or hot summers. Diapausing has pros and cons because unfavourable conditions can be avoided, but reproduction does not take place and diapausing is energetically costly (Hahn & Denlinger, 2011). Energetic costs can explain why in areas with mild winters the threshold to enter diapause is no longer reached in several insect species as a consequence of winter warming, which has been particularly well studied in parasitoids (Andrade et al., 2016; Tougeron et al., 2017; Tougeron et al., 2018a; Tougeron et al., 2019). Individuals that do not enter diapause during winter are exposed to cold spells that occur suddenly during "warmer on average" winters. Bet-hedging is a strategy that should be favored under such conditions with some individuals entering diapause and others remaining active during the entire winter season. Potential bet-hedging has indeed been observed between years (Tougeron et al., 2018b) and one female can produce both non-diapausing and diapausing phenotypes (Tougeron et al., 2019). For at least two parasitoid species (*Aphidius ervi* and *Nasonia vitripennis*) with overlapping ranges at the continental scale, variation in diapause rate has been demonstrated among populations (Paolucci et al., 2013; Tougeron et al., 2018b) and genotypes (Tougeron et al., 2019). In the parasitoid *Nasonia vitripennis* (Walker), studied along a gradient from the South to the North of the USA, populations entered diapause at different rates depending on photoperiod (Paolucci et al., 2013). Genetic differentiation between *N. vitripennis* populations was already demonstrated; hence experimental evolution using similar thermal regimes could be used to show the existence of bet-hedging, where bet-hedging genotypes should outcompete non-bet-hedgers in unreliable environments (Le Lann et al., 2021).

Diapause can also take several years, a behavior called prolonged diapause (Wermelinger et al., 1995). During prolonged diapause, a part of the population stays in diapause for more than one unfavorable season at the risk of losing at least one reproductive opportunity and increasing the chance of death before breeding (Ringel et al., 1998). Menu et al. (2000) and Mahdjoub and Menu (2008) showed theoretically that environmental stochasticity favored the evolution of prolonged diapause at a low frequency over simple diapause (i.e., emergence after one unfavorable season). The observation that species undergoing prolonged diapause use unreliable cues underpins this conclusion (e.g., Brockerhoff and Kenis, 1997, Ringel et al., 1998). Exposing populations with prolonged diapause to both reliable and unreliable environments and measuring the level of survival over several generations is needed to determine if prolonged diapause is a true bet-hedging strategy.

The choice of overwintering location can also be an interesting case of bet-hedging. In parasitoids, koinobionts keep the host alive until the parasitoid reaches the nymphal instar, while idiobionts paralyze or kill the host arresting its development at the time of egg laying. In koinobiont parasitoids, the overwintering site may not be a site where the host typically overwinters, due to the manipulation of the host's behaviour by the parasitoid (Alford et al. 2017). The parasitoid then forces the host to move to a more favorable site for parasitoid overwintering. In contrast, idiobiont overwintering must occur in the habitat where the host was parasitized. When overwintering site is dictated by the site of host parasitism, spatial bet-hedging may be adaptive. For example, in the North American weevil egg parasitoid *Anaphes victus* (Huber; Hymenoptera: Mymaridae), females disperse eggs over different patches more in the fall than in the spring, parasitizing fewer hosts per patch, but visiting more patches, limiting the loss of offspring. Indeed, *A. victus* larvae do not survive at temperatures below -23°C, while weevil eggs deposited on plants can withstand -35°C. Female parasitoids cannot control the sites where the weevils lay eggs. When weevil eggs are covered in snow, the temperature is less cold protecting the parasitoids, but the depth of snow cover is unreliable, depending on the amount of snowfall and winds that lead to the accumulation of more or less snow. Females that disperse clutches of multiple patches may thus have a greater number of offspring protected from the cold (Boivin, 1994; Hance et al., 2007). In the *A. victus*-weevil system, evidence for different fall and spring phenotypes was already provided (Boivin, 1994). To prove the existence of bet-hedging, one could investigate the existence of distinct seasonal phenotypes also in other populations. Another possibility is to perform a transplant experiment in the laboratory where parasitoids originating from fall or spring are exposed to spring or fall

conditions, respectively. Measuring fitness over successive generations could then provide the evidence that bet-hedging in fall populations leads to higher fitness under fall conditions, but that offspring exposed to spring conditions (control) will have lower fitness (as bet-hedging is not adaptive), and vice-versa. Another line of inquiry is to use a split-brood design with field-caught fall/spring females, exposing half of the offspring to fall conditions and the other half to spring conditions. In conclusion, few studies have been conducted on the impact of stochasticity of environmental thermal conditions. However, more and more studies highlight the importance of selection pressures related to the variability and unpredictability of the thermal environment and it is now predicted that bet-hedging strategies will increase in natural populations (Simons, 2011; Sunday et al., 2019; Tougeron et al., 2020). As diapause and patch allocation are generally easily studied in the laboratory, these traits represent prime candidates for finding proof of bet-hedging.

2.2. Patch time allocation

In parasitoids, females search for hosts that usually occur in discrete patches in the environment. Female reproductive success is maximized when foraging times (the time females spent searching for hosts) are adjusted in the various patches that females encounter. The Marginal Value Theorem (MVT), proposed by Charnov (1976), aimed to predict the optimal time allocated to each patch and showed that the best strategy for patch exploitation is to remain in a patch until the fitness gain within that patch has decreased to a marginal value, representing the mean fitness gain of all patches in the environment. When risks increase, e.g., due to predation, hyperparasitism, intra- or interspecific competition, the time female parasitoids spend in a patch (which is correlated to the number of ovipositions in that patch) is shorter than would be predicted by the MVT, leading to sub-maximal oviposition rates. Earlier patch departures could be interpreted as spatial bet-hedging. The cereal aphid parasitoid *Aphidius rhopalosiphi* De Stefani Perez (Hymenoptera: Braconidae), for example, was shown to leave patches even when there were still many unparasitized aphid hosts available (Outreman et al., 2001). Although *A. rhopalosiphi* can discriminate between parasitized and unparasitized hosts (Outreman et al., 2001), sub-optimal patch exploitation can reduce the risks of losing progeny. Aphid colonies are often attacked by predators, such as coccinellids, syrphids, and lacewing larvae, or exploited by hyperparasitoids, or superior competitors like *A. ervi* Haliday (Le Lann et al. 2011). Spreading ovipositions between different patches to decrease the risk of losing a complete clutch following predation or hyperparasitism is a valid alternative hypothesis that deserves further study. We now need to determine first whether there is phenotypic variation in this behavior (Le Lann et al., 2021).

The parasitoid *Anagrus delicates* Dozier, a mymarid parasitizing delphacid planthopper eggs (Cronin & Strong 1993), represents another example of suboptimal foraging. Due to leaf mortality, there is a high risk that host eggs perish, increasing parasitoid mortality. *Anagrus delicatus* can spread the risk of increased mortality by ovipositing fewer eggs in each patch even if more suitable hosts are available (Reeve et al. 1994). Augustin et al. (2021) showed that patch time allocation in *Anaphes listronoti* Huber (Hymenoptera: Mymaridae) decreased when temperature increased, although the patch-leaving rules were not affected. In the context of climate change, even a single extreme unreliable event with strong temperature variation can have a major impact on host mortality, increasing the variability of host richness and/or travel times between patches. It remains to be tested if unpredictability in patch richness/availability also induces sub-maximal oviposition rates.

2.3. Selection of host species

Traditionally, host foraging by parasitoids comprises different steps including habitat location, host plant/substrate location, and location of the host itself (Vinson, 1976). Parasitoids that do not specialize on the host habitat or the host species with the highest fitness return, can exploit less profitable habitats/host species for several reasons linked to unreliable conditions. In different cereal aphid parasitoid species, host selection behavior was compared between seasons (Eoche-Bosy et al., 2016). When resources were scarce (i.e., during winter), female parasitoids generally accepted all aphid hosts encountered, including non-optimal hosts, revealing an opportunistic strategy. In contrast, during the more favorable seasons (i.e., spring), parasitoids showed a more specialized behavior, preferentially selecting the most profitable host species. Host species selection depends largely on the host's energy content, but also on host encounter rate (Bolnick et al., 2003). During winter, aphids are rare compared to the higher densities observed during spring (Andrade et al., 2013), and during winter encounter probabilities are unreliable. In areas with milder winters, we expect to see a change in overwintering strategies from diapause to increased host and parasitoid activity (see section 2.1). A change in overwintering strategy will increase the unpredictability of encounters with favorable hosts, and therefore, increase the frequency of sub-optimal quality host acceptation. An increased prevalence of more generalist species during winter is also expected to increase the level of inter-specific competition.

For species that are widely distributed along geographic gradients, bet-hedging could also occur when the degree of specialization of different populations varies according to latitude. For example, in general the stability of species interactions decreases in colder areas (Cirtwill et al., 2015). Species richness is indeed lower at higher latitudes and altitudes (Hillebrand, 2004), leading to more unreliable biotic environments. The number of trophic levels is, therefore, reduced in addition to the number of species interactions (Schemske et al., 2009; van Baaren et al., 2020). In colder areas, there is also a lower level of specialization due to limited host numbers, thereby increasing competition (Andrade et al., 2013). Applying these general concepts to host-parasitoid relationships, we can expect to see over-dispersion of data, resulting from a higher-than-expected rate of parasitism in less profitable hosts or habitats. Parasitoids, however, do not always follow the typical biogeographic pattern of increasing species richness at lower latitudes (Burington et al., 2020), probably due to the intimate interaction with their hosts (Jego et al., 2023).

Generalist host resistance, where the host can mount an immune response against several parasitoid species, should be examined in the framework of response strategies in unreliable environments. By means of a theoretical model, Lapchin (2002) studied how the specificity of resistance can evolve in a parasitoid species that can parasitize two host species. In an unreliable environment, natural selection retains a generalist level of host resistance (as hosts cannot prevent a parasitoid species from attacking them) and a more specialized level of parasitoid virulence (as parasitoids may focus more specifically on a host species). Even if the parasitoid has a lower fitness on the host species on which it is less virulent, it may retain minimal success on that species if its preferred host becomes rare. In this case, there is a partial preference and partial specialization. However, the limited virulence on the less preferred host comes at the cost of losing progeny. Partial preferences have also been explained within the framework of optimal foraging (Stephens and Krebs, 1986), mainly because of imperfect knowledge, and thus in response to an internal condition of the forager. When imperfect knowledge about the relative abundance of host species is a consequence of unreliable environmental conditions, however, such partial preferences can be considered a bet-hedging strategy. The predictions of Lapchin's (2002) model are supported by data on the virulence and partial host preference of *Asobara tabida* Nees (Kraaijeveld and van Alphen, 1995; Kraaijeveld and Godfray, 1999). Partial preference and limited virulence on less preferred host species are a consequence of selection by the unpredictability of host and host habitat abundance and thus a potential bet-hedging strategy. As the level of virulence and host preference varies among populations, the *A. tabida-Drosophila* model

represents a good system to test the link between the type of strategy adopted and the level of unpredictability of the environment.

2.4. Host stage choice

The level of variability within a habitat can also influence host stage selection by parasitoids that can oviposit in different host larval instars. When the fitness gain of the aphid parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) was measured for each host instar (of the aphid *Myzus persicae* Sulzer), the second instar led to the highest fitness return and was the preferred host instar (Barrette et al., 2009). As predicted by the Optimal Diet Theory, which states that foragers should prefer prey that provides more energy per unit of time (Charnov, 1976), we would expect specialization on the second host instar when it is available (Sih and Christensen, 2001). Contrary to this prediction, when patches containing two instars were presented to *A. colemani,* females first specialized by exploiting the host instar with the highest fitness return, but then rapidly changed to a generalist diet by also exploiting the less profitable instar (Barrette et al., 2010). Switching from a specialist to a generalist strategy could be the result of bet-hedging, because females invest progeny in hosts that reduce fitness, but that can escape stochastic mortality simply because of their developmental stage. If the aphid colony is destroyed, for example by a stressful climatic event, progeny invested in later instars that emerge earlier could escape and seek shelter, while progeny invested in seemingly more rewarding early instars (with a longer development time) will perish. So far, only one study looked at the impact of direct or indirect heat waves on host instar choice in *Diadegma semiclausum* Hellén (Hymenoptera: Ichneumonidae), showing that there was no effect (Costaz et al., 2022). The link between unreliable extreme climatic events and host-instar choice remains to be tested also in other species.

2.5. Host discrimination and superparasitism

As a host offers a limited resource for developing parasitoids, the fitness return from an already parasitized host is reduced compared to that obtained from an unparasitized host. Discrimination between parasitized and unparasitized hosts can thus be adaptive, allowing females not only to steer clear of parasitized hosts, but also to determine the level of exploitation within a host patch. Parasitoids generally have the capacity to recognize previously parasitized hosts (van Alphen and Visser, 1990). Superparasitism (i.e., the use of an already parasitized host) is, however, observed too frequently compared to theoretical predictions of optimality. The higher incidence of superparasitism can be explained as a way in which parasitoids compete with conspecifics when hosts are scarce. Superparasitism can thus be adaptive, especially when two different females oviposit in the same host, as competition occurs between unrelated individuals. When a female oviposits twice in the same host (i.e. self-superparasitism), competition takes place between siblings, with only one surviving offspring in solitary parasitoids (van Dijken and Waage, 1987). Self-superparasitism can still be selected when the presence of two or more eggs inside one host increases the probability of survival of the progeny, for example when self-superparasitism decreases the host's immune response. Furthermore, self-superparasitism can be beneficial when another female attacks the same host leading to direct competition between larvae or if conspecifics more frequently reject a host parasitized several times than a host parasitized once. Self-superparasitism could thus be a bet-hedging strategy against an uncertain future risk of losing offspring by conspecific superparasitism. As extreme climatic events may lead to unexpected decreases in host availability, competition between females increases, as does the probability of self-superparasitism. Among the cereral aphid parasitoid guild, the parasitoid *A. ervi* is known to often oviposit two or more eggs in the same host (Ortiz-Martinez et al., 2019). A first step to determining if this is a bet-hedging strategy is to demonstrate that self-superparasitism occurs more frequently at the end of the season when competition between parasitoids is high (Ortiz--Martinez et al., 2019).

Gregarious parasitoids (unlike solitary parasitoids), lay several eggs in or on a single host and the size of the emerging parasitoids is generally related to the number of eggs deposited in the host. Progeny emerging from superparasitized hosts are generally smaller in size (Godfray, 1987); hence a female may anticipate future superparasitism by laying a smaller than optimal clutch (see section 4.1). Sub-optimal oviposition fits the definition of bet-hedging, because the female's fitness gain per host is reduced, but so is the fitness variance. Parasitoids do not, however, typically have information on the risk that a second female will attack the same host. When competition is unreliable, for example because of unexpected climatic events, a female should lay fewer eggs to prevent her offspring becoming too small. In gregarious parasitoids, sub-optimal oviposition can be tested first by experimentally manipulating the number of eggs within a host by letting one or several females oviposit inside the same host. Measuring the fitness of emerging individuals can then be used to evaluate under which circumstances smaller than optimal clutch sizes can be adaptive. Females could also be exposed to different levels of temperature stress to observe how direct climatic variability leads to variation in clutch sizes between females.

2.6. Host-feeding

In several parasitoid species, females must first feed on the host's hemolymph to acquire nutrients required for egg production (Godfray, 1994). In most cases where host-feeding occurs, host quality is reduced or the host is no longer suitable at all for parasitoid development (Jervis and Kidd, 1986). The female thus needs to choose to allocate energy between current (gamete production) or future reproduction (including somatic maintenance and dispersion)(Giron et al., 2002) and her choice depends qualitatively and quantitatively on the costs and benefits of host-feeding (Rivero and West, 2005). The decision to host-feed could entail a form of bet-hedging. In habitats where resource availability is predictable, the female is expected to optimize fitness, but when the environment is unreliable, some females may start host-feeding much sooner at the cost of losing oviposition opportunities. Conversely, females may delay host-feeding, accepting immediate oviposition opportunities at the risk of being unable to resupply egg reserves or to fuel maintenance.

Some described occurrences of host-feeding could provide evidence for bet-hedging. In the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae), feeding on the host *Trialeurodes vaporariorum* Westwood increases the number of matured eggs, as well as longevity, but these increases do not exceed that observed when wasps have access to honeydew for feeding (Burger et al., 2004). Host-feeding by female *E. formosa* does, however, decrease the number of hosts available for oviposition. Females could thus bet on an increased longevity at the expense of reproduction when hosts and honeydew become rare. Females that host-feed could live longer and disperse more to find other host patches compared to females that only relied on a decreasing supply of honeydew. Concurrent host-feeders, where hosts are used both for feeding and egg laying, represent another example. In a study by Rivero and West (2005) with *N. vitripennis,* the negative consequences of concurrent host-feeding were limited to female size: the longer a host was fed on, the smaller female offspring were. Concurrent host-feeding also led to smaller individuals (both sexes) in the parasitoid *Trichogramma turkestanica* Meyer (Hymenoptera, Trichogrammatidae), feeding on lepidopteran eggs. Concurrent host-feeding thus often seems a suboptimal strategy, where progeny fitness is reduced. Whether this could be adaptive over several generations remains to be tested.

3. Physiology

3.1. Fatty acid synthesis and fat accumulation

To survive unfavorable periods when resources become rare, insects and other animals have evolved strategies of energy accumulation at times when food is abundant. Energetic reserves allow insects to survive food scarcity (Hahn and Denlinger, 2007). A short-term energy supply is provided by reserves stored in the form of glycogen, whereas a long-term energy source is provided by fat or triacylglycerols stored in the insect fat body (Arrese and Soulages 2010). Storage of fat thus allows energy to be available throughout life for many different functions, including investment in eggs and maintenance (Muller et al., 2017; Ellers, 1996).

Parasitoids have been of special interest in the context of fatty acid synthesis and fat storage, because many parasitoids do not accumulate fat as adults when feeding on high-caloric diets, including sugars and other carbohydrates (Visser and Ellers, 2008; Visser et al., 2010, Visser et al., 2021; Visser, Le Lann et al., 2023). While the synthesis of low levels of fatty acids (i.e., the building blocks of triacylglycerols and other lipids) has been reported in some parasitoids (e.g., Prager et al., 2019), empirical data in more than 29 parasitoid species showed that bulk fat reserves are not being built (see Visser, Le Lann et al., 2023 for an overview). There are, however, some exceptions where species constitutively accumulate fat (e.g., generalist gelines; Visser et al., 2010; Visser et al., 2017) or where variation in fatty acid synthesis and fat accumulation have been observed between populations (Visser et al., 2018; Moiroux et al., 2010). Synthesizing fatty acids and triacylglycerols is energetically costly, and in predictable environments it may suffice and be adaptive to use fat from fat-rich hosts. Restocking lipids as a long-term reserve could be adaptive in environments that require long flight distances or when parasitoids must survive unfavourable weather conditions, making reproduction and/or feeding impossible. Fat synthesis and accumulation should be forsaken, however, in populations/species with easy access to carbohydrates. The cost of restocking lipids, compared to using carbohydrates as an immediate energy source, is probably paid for either by a reduction in fecundity or adult lifespan. Fatty acid synthesis and fat accumulation may thus be a bet-hedging strategy to survive in spatially and/or temporally unreliable environments.

Visser et al. (2021) found that the amber wasp *Leptopilina heterotoma* Thompson (Hymenoptera: Figitidae) showed plasticity of fatty acid synthesis and fat accumulation. Focusing on 5 geographically distinct populations, Visser et al. (2021) used a split-brood design to create families where part of a mother's offspring was laid in lean hosts and another part laid in fat hosts. Fatty acid synthesis generally depended on the environment: when the offspring developed in a lean host, fatty acids were synthesized and fat was accumulated, but when the offspring developed on a fat host, fatty acid synthesis and fat accumulation did not take place. A closer look at the shape of the reaction norms suggested that there is genetic variation for plasticity: within some families there is no plasticity (i.e., constitutive or absence of fatty acid synthesis irrespective of the host environment), whereas other families showed completely opposite phenotypes (no synthesis versus high synthesis in the high or low-fat host environment, respectively). *Leptopilina heterotoma* is a generalist parasitoid attacking several *Drosophila* species that can vary considerably in size and fat content both within and between species (see Figure 3 of Enriquez et al., 2022). Under natural conditions, hosts are typically rather fat-rich (Enriquez et al., 2022), but exposure to lean hosts favors plasticity (in predictable variable environments) and potentially bet-hedging (in unreliable variable environments). Considering that an increased frequency of extreme climatic events can negatively impact *Drosophila* hosts, leading to a higher (and more unreliable occurrence) of hosts with a suboptimal smaller body size and lower fat content (Klepsatel et al., 2019; McDonald et al., 2018), we could expect that plasticity as a bet-hedging strategy could be favored by selection (Haaland et al., 2021). More work with this system is now needed to understand how life histories are affected by fat accumulation strategies, and how environmental settings and changes therein select for canalization, plasticity and/or bet-hedging.

4. Life histories

4.1. Clutch size

When too many parasitoid larvae develop together in one host, the emerging adults are small with consequences for fitness, because parasitoid size is tightly linked to fitness (Visser, 1994). According to Lack's model, a female parasitoid has a higher fitness when she lays the number of eggs that maximizes her fitness gain at the clutch level (Godfray, 1994). Bet-hedging could be involved when clutch sizes smaller than predicted are observed, which is relatively frequent (Klomp and Teerink, 1967; Charnov and Skinner, 1985; Godfray, 1987), resulting in over-dispersion of the eggs. Different explanations have been offered to account for these apparently underutilized hosts. One explanation is the risk of superparasitism (see section 2.5.). Other dynamic optimization models (Godfray et al. 1991; Hardy et al. 1992) have demonstrated that it is necessary not only to consider the behavior on a host at a given time, but also to examine reproductive success during a female's life, taking into account various physiological characteristics linked to the female (age, experience, egg load, size), as well as environmental factors such as host quantity/availability. Dynamic optimization models can consider either the quantity of eggs to be laid or time as limiting factors, and predictions show that the optimal clutch size can vary during life (Iwasa et al., 1984; Mangel, 1989 Mangel and Heimpel, 1998).

Bet-hedging could be involved when the observed clutch size cannot be completely explained by optimality theories as shown by Haccou and McNamara (1998). For example, Vet et al. (1993) studied clutch size in the parasitoid *Aphaereta minuta* Nees (Hymenoptera: Braconidae). These authors did not calculate optimal clutch size according to Lack's model, but obtained empirical data showing that clutch size of the parasitoid is only partially linked to the volume of the larvae for the two studied host species (*Delia antiqua* Meigen and *Drosophila hydei* Fallen). As a result, the largest hosts that will contain the largest number of eggs are under-exploited, which could be a way to hedge bets.

In polyembryonic wasps, where multiple offspring develop from a single egg, there is no trade-off between present and future reproduction (see below), nor is there any apparent parent-offspring conflict (Ode et al., 2018). For example, up to 3400 offspring can emerge from a single egg in *Copidosoma floridanum* Ashmead (Hymenoptera: Encyrtidae). This means that the investment in any single brood is negligible (as this is effectively a single egg), and thus any differences in clutch size and offspring size resulting from the trade-off between present and future reproduction can be excluded. Both bet-hedging and the trade-off between present and future reproduction predict lower than optimal clutch sizes; hence experiments with polyembronic wasps will permit investigating solely the effect of bet-hedging (Ode et al., 2018) but this remains to be done (Crowley and Saeki, 2009; Saeki et al., 2014). As a large amount of genetically identical individuals emerge from one host, polyembryonic species allow to differentiate between genetic and environmental effects on the phenotype. Individuals (i.e., clones) emerging from the same host can then be exposed to less (control) and more stressful environmental conditions, and fitness estimated over consecutive generations.

4.2. Sex allocation

Parasitoids attacking hosts with a clumped distribution (gregarious or quasi-gregarious solitary parasitoids) often have a local mating structure, where males mate with females emerging at the same site before dispersing, leading to a female-biased sex ratio. A female foraging alone on a patch must produce the smallest number of males, enough to fertilize all her daughters (Hamilton, 1967). This is possible in

parasitoids, because after mating, sperm are stored within the female in a spermatheca, allowing the female to open the spermatheca (thus producing a 2n-chromosome female offspring) or to leave it closed (producing a male descendant with n chromosomes). The mating capacity of males has indeed evolved under Local Mate Competition (LMC), which predicts that aggregated mating leads to mating competition amongst kin. Males are expected to have been under strong selection to inseminate a number of females close to the number of females in a patch (Hamilton, 1967). Sometimes, however, insemination capacity of males appears to be higher than predicted (Nunney and Luck, 1988, Hardy and Cook, 1995; Hardy et al., 1998). Females thus invest more in males than expected in a patch. There are several potential explanations for this behavior: If there is a probability of superparasitism by conspecific females, the sex ratio of the brood is no longer under parental control of the first female, and the first female should increase the number of male offspring (Nunney and Luck, 1988). Her male offspring could then also inseminate unrelated, conspecific females. Another reason could be that larval mortality is higher for males, leading to a higher than predicted production of males (Hardy and Cook, 1995; Hardy et al., 1998). In both cases, a female reduces her fitness gain by investing more in males than might be necessary, but in doing so she decreases the variance in fitness gain by decreasing the probabilities of a large fitness loss. When exposed to an extreme heat event, *Trichogramma euproctidis* Girault (Hymenoptera: Trichogrammatidae) females produce 80% more male offspring compared to optimal temperatures, which was demonstrated to be due solely to a behavioral change (Moiroux et al., 2014). Likewise, parasitoids with a random mating population structure sometimes produce slightly female-biased sex ratios to counteract for the all-male broods produced by non-inseminated females (as mating is not necessary, leading to all-male broods; Hardy and Godfray, 1990). The immediate sex ratio may not reflect an optimal strategy, but over several generations suboptimal sex ratios could result in higher fitness. Based on the above preliminary data, *Trichogramma* species could be used to evaluate the fitness of females exposed to sublethal stressful temperatures for a few hours (i.e., a short extreme climatic event during a heat wave) to compare sex ratios of unexposed and exposed females. Progeny could be exposed to the same type of extreme event to measure the mortality and/or reduced fitness due to absence of reproduction of the progeny, and repeated over generations.

Due to the trade-off between immediate and future reproduction in parasitoids, both the number of gametes and the timing of gamete production will be influenced by variability in the temporal and spatial distribution of reproductive opportunities. Ovigeny (Jervis et al., 2001) and spermatogeny (Boivin et al., 2005) indexes were proposed to describe the temporal distribution of gamete production in parasitoids. The early production of gametes, at the cost of reduced investment in aspects related to dispersion and mate finding, is linked to early occurrence of mating opportunities. The production of these gametes in relation to the occurrence of mating opportunities could be influenced by bet-hedging because there are costs associated with gamete production in both sexes. Species that are faced with variable temporal distribution of mating opportunities could respond by showing bet-hedging in gamete production. In *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae), sperm number at emergence in standardized-size males varies between 1100 and 1900 (Damiens and Boivin, 2005). Males with a smaller number of spermatozoa could have invested in dispersion rather than sperm production. Such a hypothesis is strengthened by the observation that in the same species some males leave the emergence patch after having used all their sperm supply while others leave the patch with their full sperm complement (Martel and Boivin, 2007).

A similar mechanism could be present in female parasitoids regarding the production of oocytes. In *Aphytis aonidae* Howard (Hymenoptera: Aphelinidae), 35% of females delay egg maturation to use larval resources for energy rather than egg production (Heimpel and Rosenheim, 1998). Females whose progeny have a lower egg complement at emergence would have a lower fitness return in good habitats but when the current habitat is poor in hosts, daughters with a lower egg reserve but with more energy to invest in dispersal and host location would do better. An increase in environmental variability or host distribution will increase variation in reproductive success, favor spreading of the reproductive effort (Wilbur and Rudolf, 2006; Simons, 2007), and favor an increase in the optimal egg load (Ellers et al., 2000).

4.3. The trade-off between reproduction and longevity

Models of optimal host selection, optimal superparasitism, and patch time allocation use rate maximization as optimization criterion. Rate maximization is based on the postulate that parasitoids are time but not egg-limited. This assumption seems somewhat paradoxical, as one would expect natural selection to favor parasitoids that allocate resources between reproduction and longevity in such a way that, on average, females could live just long enough to lay all their eggs (i.e., not time nor egg limited). Field studies on the *Drosophila* parasitoids *Leptopilina clavipes* Nordlander (Driessen and Hemerik, 1992) and *A. tabida* (Hymenoptera: Braconidae) (Ellers et al., 1998) showed that about 85% of all females die with eggs in their ovarioles, and are thus time-limited. To explain the evolution of time limitation in these parasitoids, Ellers et al. (2000) modeled egg load evolution in a range of environments. These authors showed that a high variance in spatial host distribution selects for time limitation. Selection for time-limitation happens because a relatively small number of female parasitoids find the few host-rich patches, leading to higher offspring numbers than females encountering only poor patches. In other words, spatial stochasticity selects for parasitoids that live shorter at the expense of a higher egg load. In environments with high variance in host distribution, spatial bet-hedging is expected to occur to mitigate the effects of time limitation.

5. Conclusion

We have provided several examples of parasitoid systems and traits where bet-hedging could occur (Table 1), although, like in other taxa, most of the studies are limited to categories I to III of Simons (2011), meaning the very first steps towards a true empirical demonstration of bet-hedging. Parasitoids represent excellent models for testing bet-hedging (Fig. 1), because most parasitoids are faced with stringent constraints, due to their small size, short lifespan, and the need to find rare and ephemeral (host) resources. The direct link between host-finding, exploitation behaviors, and fitness gains (offspring production) has been invoked to explain several key adaptations in parasitoids. Indeed, while an improvement in prey finding efficacy brings more food to a predator, it does not necessarily result in additional progeny. In parasitoids, any adaptations that increase the probability of encountering and parasitizing a host resulting in more offspring will be selected, including bet-hedging strategies.

Another interesting characteristic of many parasitoids is their small population sizes. Population size has been proposed as an important factor making within-generation bet-hedging unlikely (Hopper, 1999; Hopper et al., 2003). For a bet-hedging strategy to be selected, the population under selection must be small. Several parasitoid species have structured populations where most mating is done between siblings during a season, decreasing the actual population size within a geographic area. This phenomenon is even stronger in thelytokous (i.e., parthenogenic) species, where no males are present, and the all-female population is practically composed of clones. While some genetic transfer occurs in these cases, the constraint of population size is somewhat relaxed, rendering the evolution of within-generation bet-hedging strategies more plausible. Such a scenario has already been proposed by Janzen (1977) for aphids. Due to their clonal nature, these populations would be ideal for testing outstanding hypotheses on bet-hedging.

Bet-hedging could account for many instances where parasitoid

behavior, physiology, and life history cannot be predicted by optimality models based on maximization of arithmetic mean fitness. We should pay more attention to bet-hedging and build models that include both spatial and temporal variability over a large number of generations. This is particularly true considering that extreme climatic events will increase unpredictability for a wide range of environmental factors. We could thus expect that selection for bet-hedging strategies will increase in the future (Fig. 1). Studies on bet-hedging could also be of importance from an applied perspective, as the increase of extreme temperature events can decrease parasitism rates, and, therefore, the efficiency of parasitoids as natural enemies in various agro-ecosystems (Wetherington et al., 2017; Yu et al., 2022; Costaz et al. 2022).

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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