**Title: Why we need ecology and evolution for a better understanding of misdirected behaviour**

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**Abstract:**

Animal behaviour emerges from the complex interaction between internal states, as well as biotic and abiotic environmental conditions. When observed behavioural responses differ from researchers' expectations, they are often described as "misdirected behaviour" and potentially maladaptive. However, several factors including genetic background and developmental conditions, sensory perception and information processing, social and ecological context, and delayed rewards may all contribute to the observed response. Moreover, mechanisms that generate apparently erroneous behaviour may also contribute to behavioural variation, learning, and innovation. Hence, to classify unexpected behavioural responses as either adaptive, maladaptive or neutral, the frequency at which the unexpected behaviour is expressed, and its fitness consequences must be investigated. Using parental care as a focus topic, we argue that seemingly misdirected behaviours are context-dependent and may, in some cases, be adaptive when investigated across longer timescales. Finally, we discuss how anthropogenic environmental change can further disrupt established cue-environment relationships, potentially increasing misdirected behaviours, and how long-term studies are important to determine if these behaviours are a transient response that populations can overcome. In summary, we highlight that a comprehensive understanding of animal behaviour requires consideration of the underlying mechanisms, ecological and social contexts, and long-term fitness consequences.

**Keywords:** adaptation, decision-making, maladaptation, mismatch, fitness consequences, parental care

**Media summary:**

Animals do not always behave in ways that seem intuitive to us. What may look like a mistake can actually make sense depending on the animal's genetic profile, past experiences, and current situation. Using parental care as an example, we highlight that seemingly erroneous behaviours can help animals to adapt, learn, or innovate. Human-driven environmental changes are creating new ecological conditions, leading to higher occurrence of behaviours that seem unexpected, that may or may not lead to negative impacts on survival and reproduction. Understanding animal behaviour therefore requires assessing the broader context of a specific behaviour and the long-term consequences.

## Introduction

Behaviour comprises activities through which organisms fulfil basic needs for survival, maintenance, and reproduction [1]. Its expression is regulated by both internal states (e.g. hunger and reproductive state), and external/environmental conditions (e.g. food and mate availability), and their interactions [2] (Fig. 1). This dynamic regulatory input can be expected to favour variable and flexible responses both within and between individuals [3,4], which makes behaviour an important component of the phenotype that allows animals to respond and cope with environmental changes, with consequences for whole-organism performance and fitness [5]. Whole-organism traits are complex, as they are composed by multiple traits such as body size and colouration. Phenotypic traits which relate to an animal's performance in ecologically relevant, physically demanding tasks are classified as performance traits [6,7]. Behaviour is a whole-organism trait whose expression emerges from the interaction of morphological, physiological, sensory, cognitive, and environmental factors, and in turn can influence whole-organism performance and fitness [8,9].

Because of the link between behavioural expression and environmental conditions (i.e. both abiotic and biotic environment) behavioural biologists raise hypotheses regarding the function of behaviour, its effect on the organism performance, and corresponding fitness consequences. However, due to the complexity associated with behavioural expression, we may find our predictions disproven by a few individuals in a population or between populations, and even species at a given timepoint (i.e. when a study is conducted). Under such scenarios, we might feel the urge to classify such unexpected responses as misdirected behaviours. But, in order to classify an unexpected behavioural response as either misdirected and/or maladaptive, we must investigate the environmental context in combination with the animal's internal state, and other traits which may have led to the expression of the unexpected behaviour. Then, for classifying such misdirected behaviours as either adaptive, maladaptive, or neutral, their fitness consequences and frequency must be investigated (Fig. 2).

How behavioural observations are interpreted is also influenced by intrinsic characteristics of the observer and the framework within which observations are made. This includes methodological conventions and available techniques, theoretical assumptions, scientific paradigms, and prevailing cultural

and ethical perspectives [10]. While we acknowledge such potential known and unknow observer biases, our article focuses on how behaviour of organisms lead researchers to interpret it as "misdirected". We highlight the importance of (i) genetic background and developmental constraints, (ii) sensory perception and integration, (iii) socio-environmental context, and (iv) delayed rewards as important factors that should be considered when assessing and interpreting behavioural responses in animals. We further discuss the potential adaptive value of misdirected behaviour, and illustrate our arguments using parental behaviours as a focal topic due to its direct effect on the animal's fitness. Finally, we discuss how and why there has been an increase in observed misdirected behaviour due to anthropogenic modifications.

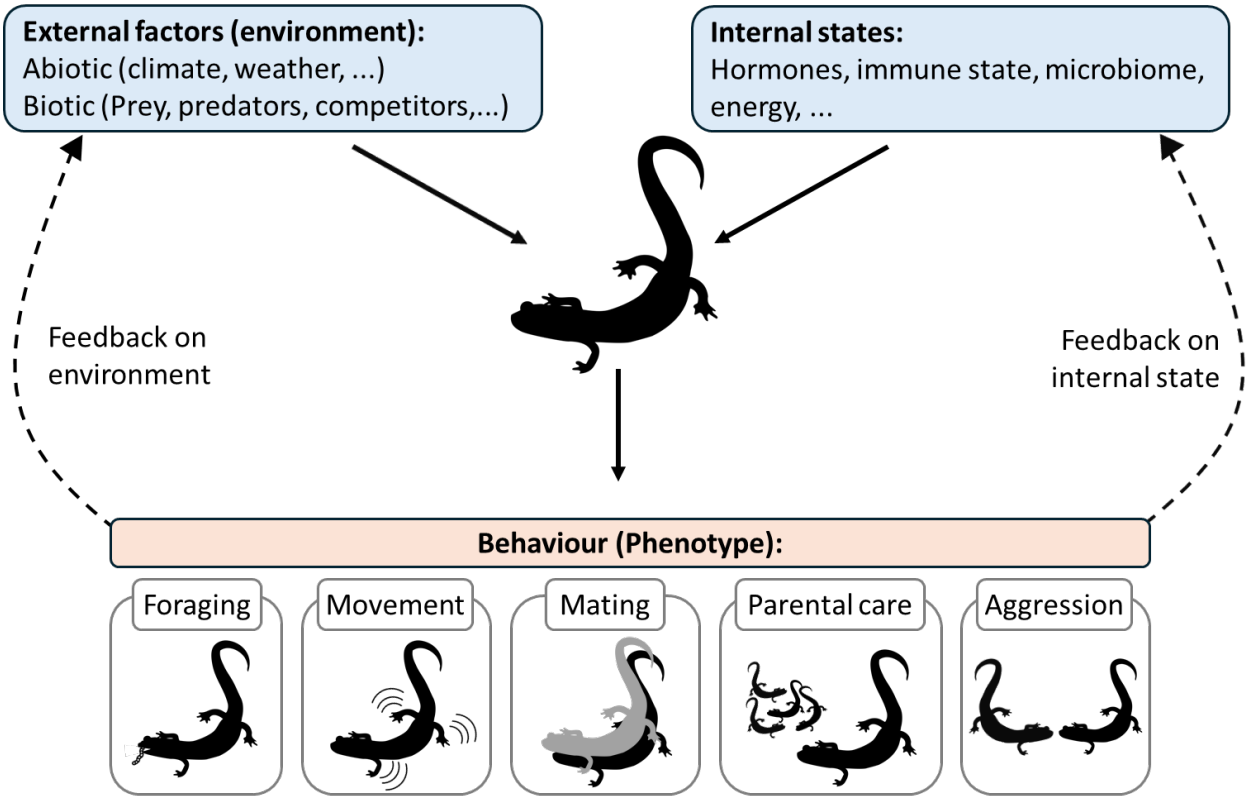
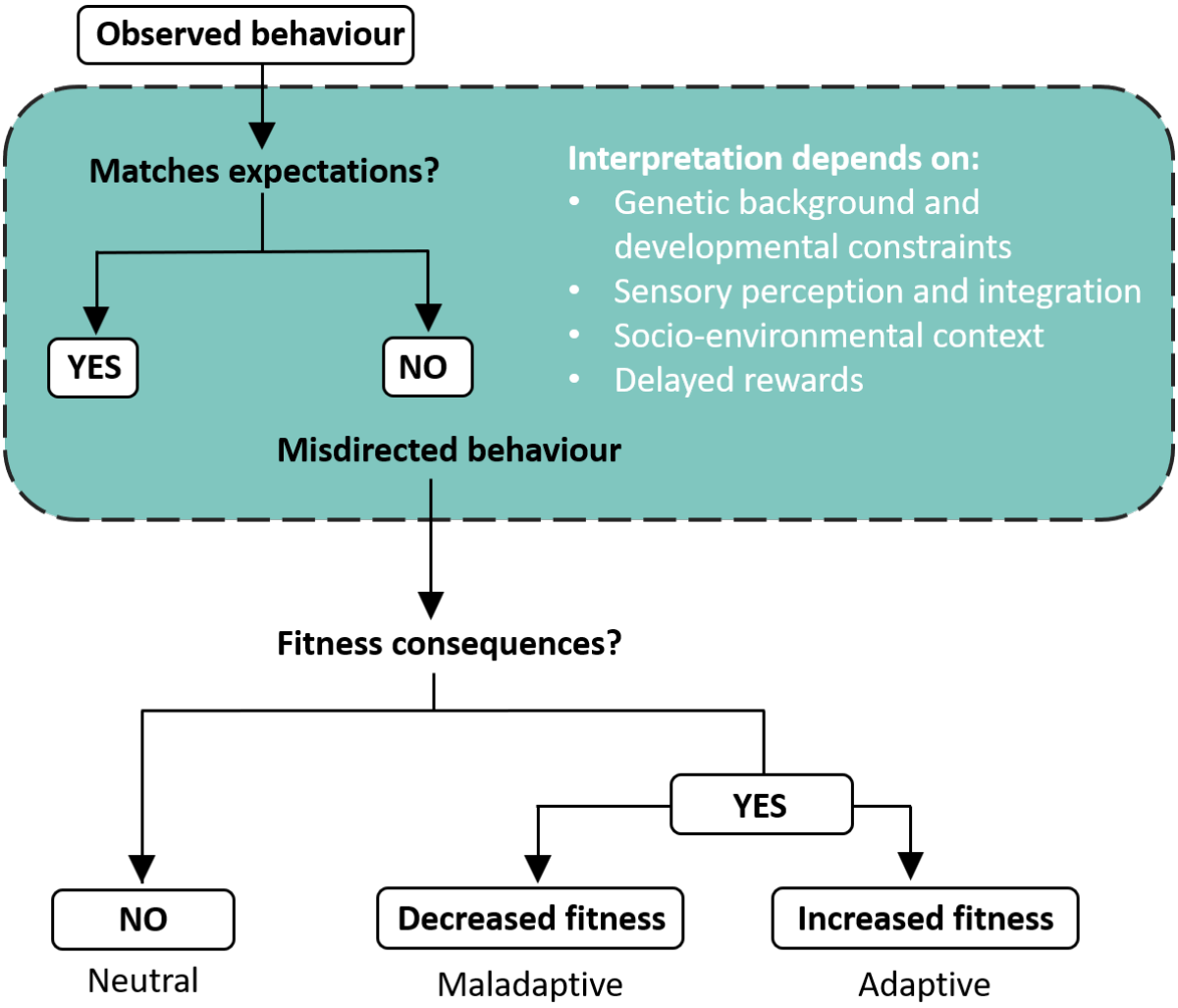



Figure 1. Diagram of the behaviour expression process, illustrating how behaviour emerges from the interaction between external/environmental conditions and internal states, resulting in flexible and variable responses within and among individuals. The salamander silhouette was designed by Andrea Novoa from Noun Project.




88

89 Figure 2. Conceptual framework for classifying behaviours. Behaviours that violate observer expectations
90 are commonly considered misdirected, but can have different fitness results (neutral, decreased
91 [maladaptive], or increased [adaptive]). The interpretation of behaviours depends always on the genetic
92 background and developmental constraints, sensory perception and integration, socio-environmental
93 context, and delayed rewards.

94

95

**Why do behavioural responses sometimes differ from our expectations?**

There are multiple, non-mutually exclusive reasons for why a behavioural response may differ from the observer's expectations, and thus, be considered misdirected:

**1) *Genetic background and developmental constraints***

Shared underlying mechanisms (e.g. genes, physiology) may cause individuals of the same species to exhibit stable behavioural types ("personalities" [11]) that differ in average levels of expression of behavioural traits. Such behavioural phenotypes can lead to different behavioural responses across individuals, even when exposed to the same conditions [12]. For example, reversal learning experiments in Rainbow trouts (O*ncorhynchus mykiss*), which were artificially selected for high- versus low-reactivity to stress, showed that high-reactive fish were more likely to adjust their behaviours, whereas low-reactive (i.e. more proactive) individuals tended to maintain their previously established "routine" [13]. Costs and benefits of such stable behavioural phenotypes have been shown to be highly context- and frequency-dependent. As such, increased fitness of one phenotype in one context might lead to decreased fitness of the same phenotype in a different context [14,15]. For example, in juvenile damselfish (*Pomacentrus amboinensis*), exposure to predation risk induces a high-risk behavioural phenotype that significantly improves survival during predator encounters. However, low-risk phenotypes outcompete high-risk phenotypes when fighting for resources in a low-risk environment [16].

Also, developmental history, such as stress or predator exposure early in life has been shown to considerably impact on adult behaviour in multiple ways, contributing to varied behavioural responses in standardized experimental settings [17,18] that might not match expected patterns. Other factors that shape animal decision-making include previously formed habits [19,20], and the presence of endowment effects [21]. The latter refers to the tendency to value resources that are already in one's possession more than resources not yet obtained [22]. For example, many species of primates are hesitant to exchange food items they have already obtained for other food items, even when the new item is preferred over the original one [21,23]. Without taking this into account, the refusal to exchange a less-preferred food reward to a generally more preferred option could lead to a seemingly suboptimal behavioural response that conflicts with the

expected outcome by the observer. In summary, if genetic and developmental constraints to behaviour are not included and considered in the experimental design and analysis, this will unambiguously lead to wrong conclusions about the decision-making process.

**2) *Sensory perception and integration***

As behaviours are often expressed in response to or mediated by external factors, animals must permanently perceive and integrate information about their biotic and abiotic environment to adjust their behaviour to the circumstances they encounter. Such information can be gathered in different sensory modalities (e.g. visual, acoustic, chemical, tactile, electrical, thermal). Information can vary across time, from predictable cycles to stochastic fluctuations or singular events. It can also vary in space, from global to local scales [24]. Particularly, information from the social environment, often in the form of communication, can be highly dynamic and more unpredictable, as it depends on the state and behaviour of other individuals and their interactions [25].

Sources for errors exist at all stages of the processing chain, from emission, transmission, detection, integration of environmental cues or signals to selecting and executing appropriate behavioural responses. Errors from these sources, and combinations thereof can cause animals to respond to cues that are irrelevant, ambiguous, unreliable, or incorrectly interpreted, potentially resulting in misdirected behaviours [24,26].

Perception itself involves filtering and categorising information as animals must distinguish between relevant and irrelevant information, such as different species, social categories and contexts, or conspecific individuals. Perception and processing of signals is often optimised via a "matched filter" [27] where sensory and processing systems are adapted to limit incoming information to only the part that is relevant under regular circumstances or expected in a given context. An example is the acoustic recognition space in the context of species recognition, that matches perception and processing of acoustic signals to the parameters of sounds produced by the own species, facilitating the recognition of conspecifics in multi-species assemblages (e.g. [28]). Broad recognition criteria may increase the probability of detecting relevant stimuli but in turn also increase the risk of false positives, and they can also facilitate non-target individuals

148 or other species to exploit the same sensory cues [29,30]. Potential routes for exploitation are for example
149 innate behavioural responses that are activated by relatively simple stimuli, without requiring the full
150 ecological context in which a behaviour normally is executed (e.g. [31]).
151
152 **3) *Socio-environmental context***
153 Behaviours that look sub-optimal at first glance may instead reflect adaptive trade-offs shaped by external
154 conditions (e.g. predation risk, social environment, as well as availability and certainty of resources), and
155 an individual's internal state (e.g. energy reserves, food motivation, rank, or mental/emotional condition).
156 Behavioural responses that are highly context-dependent may thus seem economically irrational when
157 viewed without context [32], but beneficial from an evolutionary and ecological perspective [33]. For
158 instance, perceived predation risk has been demonstrated to influence mate choice, space use, and foraging
159 preferences across many animal taxa [34,35]. If there is the risk of getting injured or even killed, a safe but
160 less preferred option might represent a better choice than a preferred but risky option [36]. Even if in
161 experimental settings no real predators are present, focal individuals might still experience the testing
162 environment as potentially "risky" and not express behavioural responses as under undisturbed, natural
163 conditions [37,38]. For example, jumping spiders (*Marpissa muscosa*) reduced movement and foraging
164 when exposed to a white background, suggesting that the degree of camouflage serves as a proxy of
165 perceived risk in this species.
166 Also, social context plays a major role in animal decision making and needs to be carefully
167 considered when interpreting behavioural responses [39]. For example, in pygmy halfbeaks (*Dermogenys*
168 *collettei*), a shoaling fish, males exhibit association preferences based on the duration of courtship behavior
169 observed, but only under specific social scenarios [40]. Another example of seemingly misdirected
170 behaviour comes from research on redirected aggression, where individuals that received aggression seem
171 to direct their future aggression towards the "wrong" target (i.e. a non-involved bystander). However,
172 redirected aggression to bystanders in fact reduces further aggression by others (including the original

aggressor) to the victim, suggesting that redirected aggression helps during conflict management (cichlid fish [41], Japanese macaques [42]).

Similarly, mating decisions that appear misdirected under certain expectations may represent the best and most feasible strategy in a given context. A recent study showed that in guppies (*Poecilia reticulata*), individuals did not consistently avoid related mates despite the costs of inbreeding [43]. Instead, mating preferences varied with sexual and social complexity, with weak tendencies towards kin association emerging only in more socially complex conditions. These findings suggest that behaviours often interpreted as failures of kin discrimination or maladaptive mating decisions may instead reflect context-dependent trade-offs shaped by social interactions, mate availability, and the costs of choosiness in natural environments. For a long time, also same-sex sexual behaviour in animals was interpreted as "error" or "aberrant behaviour" caused by discrimination errors [44,45], or social and sexual deprivation [46]. However, recent research demonstrates that same-sex sexual behaviour is prevalent in a wide range of animal taxa [47,48], as it may strengthen social bonds, build alliances, reduce conflict, and sometimes improve survival or later reproductive opportunities, while often carrying little or no detectable fitness cost [48,49]. Hence, same-sex sexual behaviour, although previously considered misdirected and maladaptive, can indeed lead to fitness benefits in animal populations.

Besides external factors, also internal states of animals can lead to unexpected behavioural responses. Many animals adjust their risk-sensitivity during foraging to their energetic state [50,51]. For example, social rank biases how animals evaluate risk, choose between competing actions, select partners, learn, and move or forage [52–54]. These effects are often flexible; when rank or social context changes, decision strategies and even underlying neural circuit activation shift [55]. In semi-free-ranging tonkean macaques (*Macaca tonkeana*), middle-ranking individuals displayed reduced risk aversion, and longitudinal analyses showed that changes in social rank were followed by corresponding shifts in risk attitudes [56]. Rank thus acts as a key organizing variable linking social structure to individual decision making and brain function.

**4) *Delayed rewards***

What seems like non-appropriate, erroneous behaviour, often is a prerequisite for achieving a later goal that will then provide fitness benefits either for focal individuals or future offspring. Indeed, at first glance, some behaviours may seem misdirected, with little to no immediate or short-term fitness benefits. However, when viewed across a longer time scale, behaviours that initially seemed erroneous may prove to be a form of adaptive investment into future gains. A typical example for such delayed returns is rooted in the concept of reciprocal altruism, where one individual exchange resources, or extends help to non-related individuals to receive similar aid later [57]. For instance, previous studies have shown that pied flycatchers (*Ficedula hypoleuca*) assist their neighbours in predator mobbing when said neighbour previously assisted them [58]. Similarly, Norway rats (*Rattus norvegicus*) are more helpful towards partners from which they had previously received help from [59].

Across many species, "errors" are key components that guide learning, strategic planning, and innovation. To learn, animals need to experience mismatches between what is expected and what actually happens, in the form of action prediction errors [60] and reward prediction errors [61]. For example, in maze navigation, mice that showed earlier trial-and-error exploration later solved routes faster and found better detours when paths were blocked, demonstrating that early failures improve future problem-solving [62]. Moreover, research from insects to mammals show that animals not only learn from their own mistakes, but also by watching others [63,64].

Many problems that animals face are solved through trial-and-error learning, where behaviour is gradually refined as individuals learn from the consequences of their actions. High levels of exploration and persistence, can promote the discovery of novel solutions or the development of novel actions, even when early attempts look like errors [65,66]. For example, spontaneous innovation in tool manufacture and use was identified in a Goffin's cockatoo (*Cacatua goffiniana*) [67], a species that exhibits high levels of neophilia and curiosity.

A safe or lower-stake opportunity for animals to explore, make "errors," and refine decision strategies is playing; although the exact definition of play behaviour itself is highly debated [68] and

therefore subject to observer interpretation biases. Play often involves self-handicapping and temporary loss of control (e.g. slips, falls, vulnerable positions) that simulate mistakes in a safe context. The "training for the unexpected" hypothesis [69] proposes that animals actively create such situations in play to practice recovery from shocks, imbalance, and stress, hence, building versatile motor and emotional responses to improve antipredator behaviours, foraging efficiency, and social skills.

**Misdirected behaviours from an evolutionary perspective**

As outlined above, there are multiple causes which might defy the observer's predictions, and such mismatch between predictions and observed behaviour might lead to the classification of animal's response as misdirected. Under this scenario, there is a temptation to classify the misdirected response as maladaptive. However, that classification must be avoided until its effects on the animal's fitness are estimated (Fig. 2).

A trait is considered adaptive when its expression increases survival or reproductive success, thereby moving animals closer to their fitness optimum [70]. Variation in such traits can be either neutral or negative depending on their effects on fitness, as either neutral or costly [71]. Maladaptation therefore refers to the prevalence of a trait that lowers the relative fitness among the available phenotypes in a population [70]. The same logic can also apply to behavioural traits. As behavioural responses may interact with or be constrained by an individual's performance capacities [7,72], variation in behavioural responses can potentially have positive, negative, or neutral effects on fitness [73].

Behavioural ecologists often assume that observed behaviours are shaped by natural selection and are therefore adaptive, overlooking their evolutionary histories. Trait variation arises through mutation, pleiotropy, drift [70], and in the case of behaviour, also through errors in perception and integration of socio-environmental cues. Crucially, the mechanisms which might lead to the expression of misdirected behaviour are also responsible for generating behavioural innovation, enabling organisms to adjust and potentially adapt to changing environments [74]. Hence, what we classify as misdirected behaviour also feeds into the overall diversity of behavioural responses which selection might act on.

As any other phenotypic trait, behavioural traits enable animals to adapt to the environment, exploit new niches and potentially diverge between populations. In Lake Victoria's haplochromine cichlids, assortative mating via mate choice is responsible for the reproductive isolation between distinct morphotypes, leading to their maintenance in the population and possibly speciation [75]. Also, some migratory birds have been adjusting their migration timing in response to environmental change through three distinct, but not mutually exclusive (e.g. [76]), processes: phenotypic flexibility, which allows reversible within-individual changes [77]; developmental plasticity, where environmental, physiological or social conditions experienced during ontogeny irreversibly shape adult migratory behaviour [9], leading to the new phenotype replacing older ones in the population over generations; and evolution, through longer term, inter-generational changes in the frequency of alleles controlling migratory behaviour [78].

One key factor to take into consideration is the frequency of which a behaviour is expressed, especially when investigating the ultimate consequences of misdirected behaviour. Relative fitness consequences of most behavioural responses, including misdirected behaviour, are dependent on the frequency of which the behaviour is expressed. Theoretical models predict selection to act on behavioural states in a frequency-dependent manner [79]. For instance, in wild regent honeyeaters (*Anthochaera phygia*), the emergence of an abbreviated song was initially associated with lower pairing success. However, the increase on the frequency of males singing the abbreviated song was associated with an increase in pairing success, suggesting that their associated fitness costs decreased as it became the dominant song type in the population [80]. Such examples not only highlight the relative importance of the frequency at which a behavioural response is expressed, but it also shows how the socio-environmental context in which behavioural responses are expressed must be considered when estimating their potential fitness consequences.

Depending on the effect that a behavioural response has on the animal's fitness, we can classify behaviour, including misdirected behaviour, as either adaptive, maladaptive or neutral. Evolutionary biologists consider that most genomic changes do not lead to changes in fitness and are hence neutral to selection [81]. Only changes which lead to either an increase or decrease in fitness are subject to natural

selection, where natural selection might fix adaptive traits or to purge the maladaptive traits through purifying selection [81,82]. As behavioural biologists, we should employ the same reasoning, especially when describing/studying misdirected behaviour or errors in the animal's behavioural response. This entails that similarly to other evolutionary fields, our starting point should be that such behaviours do not affect the animal's fitness and are neutral to selection. We should then investigate whether misdirected behaviour confers either a fitness advantage or disadvantage to the animal, being either adaptive or maladaptive, respectively. Employing this type of reasoning will enrich our field and our knowledge on the evolution and fixation of behavioural traits.

**Focus topic: Parental care**

Parental care is a widespread reproductive strategy across several animal taxa [83], that is costly to parents in terms of time and energy expenditure but enhances survival success in the recipients. Parental decision-making is affected by the trade-offs between current and future reproduction [84], which in turn are shaped by the condition and state of the caregiver, as well as the natural and social environment. Given the energetic demands and time investments associated with parental care, animals are expected to direct parental behaviours to related offspring (i.e. offspring from themselves or their relatives) to maximize their direct and/or indirect fitness. Yet, sometimes parental care is provided to non-genetically related offspring (hereafter referred to as 'foreign' offspring), or hostile behaviour directed towards own progeny. At first glance, such behaviours may appear "misdirected", raising the question of why selection has not purged such seemingly maladaptive behaviours [85]. Herein, we outline possible reasons that may account for some observed cases of such seemingly "misdirected" parental care behaviours, in the contexts previously discussed. We acknowledge that parental behaviours may appear misdirected also in other contexts, such as the choice of appropriate rearing habitats, and the timing of parental behaviours. However, we restrict this section to cases where care is provided to foreign offspring, or where harmful behaviours are exerted on own progeny due to its direct effect on the caregiver's fitness.

**(i) *Genetic background and developmental constraints***

Genetic background and developmental constraints can redirect parental behaviour toward offspring neglect or aggression in ways that appear maladaptive but might reflect evolved responses to conflict or stress [86,87]. In male African striped mice (*Rhabdomys pumilio*), the social environment (social isolation vs. group housing) affects expression of the Agouti gene, and changes in this gene alters parental behaviour towards high levels of pup-directed hostility [88]. Via cross-fostering of offspring and quantitative trait locus analyses, it has been shown that also offspring genomes themselves can affect the level and quality of parental care, as genetic (dis)similarity between foster-parent and offspring can distort care allocation [89].

Also, developmental constraints can lead to a mismatch between observed and expected parental behaviours. In azure-winged magpies (*Cyanopica cyanus*), offspring recognition is acquired gradually through parent–offspring association, and any factor disrupting that association during development causes parents to reject their own offspring or accept unrelated young [90]. Cross-fostering experiments further showed that the probability of provisioning unrelated young increased with greater age similarity between cross-fostered chicks [90].

**(ii) *Sensory perception and integration***

To avoid directing parental care towards the wrong target, parents may use different sensory information to inform their parental decisions. In some cases, individuals have been found to not differentiate between their own and foreign offspring, either due to the lack of kin recognition abilities and/or due to the high costs associated with the rejection of their own offspring [91,92]. If costs associated with rejecting own offspring are higher than the risk of caring for unrelated con- or even heterospecific offspring [92–94], then more relaxed offspring discrimination strategies can be expected to evolve. This is particularly evident in species where offspring are immobile and therefore parents employ the use of indirect cues (e.g. location) to identify their own offspring. For instance, in the brilliant thighed poison frog (*Allobates femoralis*), males also transport unrelated tadpoles experimentally added to their terrarium to the provided water bodies [94].

329 The low probability of encountering foreign offspring inside a male's own territory probably selected for
330 indirect spatial offspring discrimination in this species. It is also worth highlighting that the criteria for
331 including or excluding single individuals as "own offspring" are probably highly frequency dependent and
332 have led to a complex arms race between hosts and parasitic individuals/species [92,95,96]. It has even
333 been speculated that the lack of offspring discrimination may have eased the transition from solitary to
334 cooperative breeding in spiders [97] (but see also section on delayed rewards).
335
336 **(iii)** ***Socio-environmental context***
337 Changes in socio-environmental conditions can cause parents to redirect, reduce, or even reverse care in
338 ways that appear misdirected but may actually reflect context-dependent trade-offs. In unpredictable or
339 poor nutritional environments, parents may adjust parental behaviour based on offspring survival
340 probabilities and less on offspring needs. For example, in great tits (*Parus major*), parents were found to
341 conditionally adjust their response to offspring signals based on recent food availability. Under poor
342 conditions, parents paid less attention to offspring begging (i.e. hunger levels) and instead fed the biggest
343 chicks that begged less and neglected smaller chicks that begged more [98]. Also, Hihi (*Notiomystis cincta*)
344 parents when supplemented with food became less sensitive to their offspring's mouth color signals,
345 demonstrating that resource availability can fundamentally alter which offspring cues parents attend to [99].
346 Social environments are intrinsically dynamic and thus expected to considerably affect individual
347 behaviour, including parental care. For example, in African striped mice (*Rhabdomys pumilio*), social
348 isolation increases alloparental care in males to 65%, while group housing resulted in 29% of males
349 becoming infanticidal, with the Agouti signalling protein in the medial preoptic area mediating this context-
350 dependent switch [88].
351 In several fishes and spiders, adult individuals have been found to purposefully approach and care
352 (or pretend to do so) for foreign offspring (also labelled as 'kidnapping', 'egg stealing', 'thievery', or 'brood
353 take-over'; [100–102]. For example, in the threespine stickleback (*Gasterosteus aculeatus*), males steal
354 eggs from rivals' nests and deposit them in their own nest, increasing attractiveness to females, which

355 preferentially spawn in nests already containing eggs [103,104]. Hence, alloparental care can evolve as a
356 response to female preference for caring males [105,106], but see also [107].
357
358 **(iv) *Delayed rewards***
359 Individuals may care for non-related offspring because of future benefits. In cooperative breeders,
360 individuals that care for foreign offspring (i.e. "helpers") invest time and energy without receiving
361 immediate reproductive benefits. However, helpers are expected to benefit in the long run in the form of
362 increased chances of territory inheritance [108,109], lower punishment and avoidance of eviction by
363 dominant members of the group (pay-to-stay hypothesis [110], increased protection due to group
364 augmentation [111], and/or improved future offspring survival by enhanced parenting skills [112]. For
365 instance, comparative studies in cooperative breeding birds indicate that helpers provision foster offspring
366 more heavily when prospects for territory inheritance are high [113]. Also, in prairie voles (*Microtus*
367 *ochrogaster*), subadults who care for non-related neonates gain parental care experience, subsequently
368 enhancing the growth rate of their own pups [112].
369 Adult individuals may also provide care to foreign offspring as a mean of expending excess
370 resources (e.g. surplus milk) that would otherwise constrain the efficiency of other ecologically relevant
371 behaviours (i.e. milk evacuation hypothesis) [93,114]. Possible benefits to the foster parent include weight
372 loss and increased agility [115], both of which may be important when hunting fast moving prey or escaping
373 predation. For instance, female lions (*Panthera leo*) give a higher proportion of their milk to foreign
374 offspring as their own cubs increase in age, and switch to a more meat-based diet [116]. Similar
375 observations have also been reported for evening bats (*Nycticeius humeralis*) [117].
376
377

## Human-induced environments as promotors of misdirected behaviour

Human population growth is increasingly accelerating environmental change and often increasing the rate and complexity of environmental variability through urbanisation and climate change [118]. In these rapidly changing environments, animals may follow evolved "rules of thumb" based on cues that no longer reliably indicate real risks or rewards [119].

Different forms of pollution can modify the visual, acoustic, and olfactory properties of the environment, reducing the reliability or detectability of sensory cues [120]. For example, it has been shown that artificial light disrupts the orientation of hatchlings of many species of sea turtles by interfering with their movement towards the naturally bright seaward horizon, thereby affecting dispersal behaviours [121]. Also, urban noise masks low-frequency components of bird song and modifies their information content [122]. These noise perturbations can further affect social and reproductive decisions, as in females of Mediterranean field crickets (*Gryllus bimaculatus*), which prefer males with higher-quality songs under undisturbed conditions, do not show this response anymore under traffic or white noise [123].

Also, climate change has been disrupting the relationship between environmental cues and the ecological conditions they once reliably predicted [119]. In seasonal systems, for example, photoperiod has remained stable, while temperature and resource availability shifted, which resulted in many migratory species arriving too late at breeding grounds or become asynchronous with periods of peak food availability, resulting in reduced fitness [124,125], and thus maladaptation.

However, some species or populations have adjusted their behaviour responses, through mechanisms occurring over different timescales [126,127]. For example, one adjustment was starting migration earlier: bogong moths (*Agrotis infusa*) now arrive at aestivation sites approximately one month earlier than in the 1950s [128], and the Common tern (*Sterna hirundo*) advanced the arrival date in 9.3 days over 27 years [76]. The loss of migratory behaviour represents another form of adjustment, with, for example, the Iberian white stork (*Ciconia ciconia*) and some populations of the North American monarchs (*Danaus plexippus*) having shifted towards residency [129,130]. Importantly, these behavioural

adjustments could only be detected because these populations were monitored over sufficiently long periods to capture changes in behaviour over time.

Long-term studies that assess fitness consequences across ecological and evolutionary timescales are then necessary to determine whether an apparent mismatch reflects maladaptation or a transient response that populations can overcome. Understanding how individuals and species respond behaviourally to rapid human-induced environmental change has also important implications for conservation [119], as it could help predict which species are likely to remain vulnerable and inform management actions to mitigate population declines or, where relevant, control expanding pest species.

## Conclusions

Misdirected behaviour is a classification given to behavioural responses that violate the observer's predictions. In such instances, behavioural biologists must proceed with caution and investigate the potential fitness consequences of the observed misdirected behaviour in relation to the animals' (i) genetic and developmental background, (ii) sensory perception and integration abilities, (iii) socio-environmental context and potential (iv) delayed rewards. From an evolutionary perspective, the description and study of misdirected behaviours increase our knowledge on the variability of behavioural responses which selection might act on. However, the frequency in which animals express misdirected behaviour, and its fitness consequences, must also be considered. Only after estimating the fitness consequences of misdirected behaviour we can classify it as either, positive, negative or neutral, and expect misdirected behaviour with negative fitness consequences to be selected against in animal populations over time.

## Ethics

This work did not require ethical approval from a human subject or animal welfare committee.

## Data accessibility

This article has no additional data.

## Declaration of AI use

We have used Concensus.ai to assist with literature review and ChatGPT for language editing.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