Early life experiences have complex and long-lasting effects on behavior

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Some animal behaviors, such as escape and courtship, are often genetically determined. However, many behaviors are heavily influenced by learning and experience. In particular, early life experiences can have a lasting impact on adult behavior. This developmental plasticity acts as a means of fine-tuning an animal's behavior to its local environment. For example, the social environment during early development has a strong effect on social behavior throughout life in humans and other animals (1, 2). In addition to variation in social environments, animals may be exposed to different ecological environments during development, and these too can drive divergence in behavior. For example, exposure to sensory cues from predators can elicit a long-lasting increase in antipredatory behavior (3–5). Although both social and ecological factors can act early in development, their impacts on adult behavior have typically been studied in isolation. In PNAS, Fischer et al. (6) explore how social environment and perceived predation threat during early development act together to influence adult social behavior. Remarkably, they find that these two factors interact nonadditively to drive divergent behavioral phenotypes. The effect of the early social environment on adult behavior depends on the perceived predation threat during development, and vice versa.

Neolamprologus pulcher is a cooperatively breeding species of cichlid fish, meaning that offspring are cared for by their parents as well as additional "helpers" (Fig. 1*A*). In the wild, each group consists of a dominant breeding pair and as many as 30 nonbreeding subordinates who, in addition to caring for the young, also help maintain and defend the group's territory (7). Previous work showed that rearing *N. pulcher* in more complex social environments leads to increased social behavioral competence in the adults, making them better at territory defense, social integration, and conflict resolution (8–10).

This social organization is especially remarkable because, unlike many cooperatively breeding species, the largest subordinates are not related to the breeding pair, and therefore do not receive indirect genetic benefits from assisting kin. Instead, it seems that this particular group living arrangement has evolved due to extreme predation pressure (7). Serving as a subordinate affords protection from predation but comes at the expense of not reproducing. Thus, subordinates are faced with a choice: either stay with the group and wait for an opportunity to inherit the territory or leave the group in an attempt to breed independently. The latter is clearly a risky decision, one that would be well informed by knowledge of the relative threat from predation. However, previous studies had not addressed how information about local predation pressure during development might influence social behavior and the decision to disperse in *N. pulcher*. Fischer et al. (6) predicted that early exposure to predator cues would, much like early social enrichment, lead to increased behavioral competence. They also predicted that these two effects, social enrichment and ecological enrichment, would act additively in enhancing behavioral competence. Finally, they predicted that these changes in behavioral competence would affect the decision to disperse in adulthood.

To test these predictions, Fischer et al. (6) performed an impressive 3-y-long laboratory experiment. First, they manipulated the social environment and perceived predation threat during a 63-d period that started just after the newborn fish became free-swimming. Half of the fish were reared with their parents and a subordinate helper (+F), while the other half were reared without any older group members (−F). During this time, half of the fish in each of these groups were exposed to predator stimuli (visual and olfactory) twice a week (+P), while the other half were not (−P). Thus, there were four treatment groups: +F/+P, +F/−P, −F/+P, and −F/−P (Fig. 1*B*). They made several detailed observations of social behavior during this experience phase, and then they performed several different behavioral tests, the first 80 d after the end of the experience phase and the last 344 d after. Finally, when the fish reached 2.5–3.5 y of age, they performed a behavioral test in which females were given the choice to stay as a subordinate helper in their territory or leave to pair up with a male in a different territory.

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Author contributions: B.A.C. wrote the paper.
The author declares no conflict of interest.

See companion article 10.1073/pnas.1705934114.
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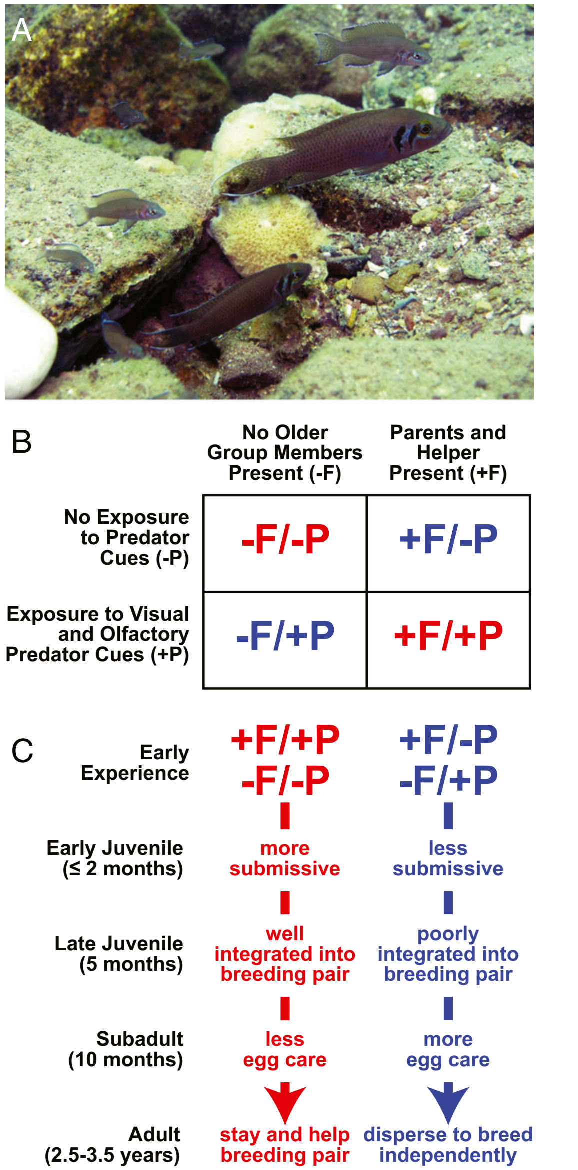

Fig. 1. (*A*) Picture of an *N. pulcher* breeding pair in Lake Tanganyika, alongside multiple smaller, subordinate fish that help with territory defense and upkeep, as well as rearing the pair's offspring. The newborn fry are hiding under the shelter. © Dario Josi. (*B*) Young fish were placed into four different groups during an "early experience" phase that started just when the fish became free-swimming and ended 63 d later. The groups differed in whether adult fish were present (+F vs. −F) and whether they were exposed to predator cues (+P vs. −P). (*C*) These forms of social and ecological enrichment interacted with each other in determining the developmental trajectory of the fish's social behavior, as seen through behavioral observations during the early experience phase (early juvenile) and subsequent behavioral experiments performed during the late juvenile, subadult, and adult stages.

As expected, fish reared in the presence of predatory cues later exhibited greater antipredator behavior, regardless of their early social experience. However, the other results were surprising. As expected, perceived predation threat during early development did indeed impact social behavior and dispersal decisions. However, the effects of early social and ecological experience were not additive; instead, these two effects interacted to shape behavior (Fig. 1*C*). Fish that were raised in an enriched social environment without predatory cues (+F/−P) showed behavioral patterns similar to those of fish raised with predatory cues but without social enrichment (−F/+P). Compared with the other two groups, these fish tended to be more submissive during the early experience phase. In subsequent behavioral tests they behaved more submissively and were better integrated socially into a breeding pair, and they tended to provide less help in caring for the dominant pair's eggs. Finally, these fish were more likely to stay as helpers with the dominant pair when given the opportunity to disperse years after the early experience phase. Thus, the specific combination of social and ecological enrichment during early development was predictive of future behavior in a way that each of these variables alone was not.

Importantly, these findings reveal that multiple factors acting during early development can have complex, unpredictable effects on behavior, and that considering these factors in isolation can be deeply misleading. For example, previous studies on the effects of early social enrichment in *N. pulcher* revealed that it led to increased social competence later in life (8–10), but these studies were all done in the complete absence of predatory cues (i.e., +F/−P vs. −F/−P). If, instead, the same experiments had been performed, but in the presence of predatory cues (i.e., +F/+P vs. −F/+P), then the exact opposite results would be obtained: Fish raised under social enrichment would show reduced social competence later in life. The general implications of this for understanding the evolution and development of social behavior are profound. What other biotic and abiotic factors affect the development of behavior but have yet to be identified? Might these unknown factors interact with early social experience and predatory cues to shape adult behavior in equally unpredictable ways?

It is likely that different behavioral strategies represent adaptive responses to natural variation in social and ecological environments. To explain their findings from this perspective, Fischer et al. (6) suggest that the different social trajectories they found are driven by two key factors: avoiding eviction by the dominant breeding pair and avoiding predation on the home territory. In the presence of dominant fish, submissive behavior may be a good strategy to avoid eviction in a low-risk environment (+F/−P), but helping behavior may be a better strategy in a high-risk environment (+F/+P) in which the breeding pair stands to gain more from this help (11). In a high-risk environment lacking a dominant breeding pair (−F/+P) submissive behavior will reduce conflict among peers (12), leaving more time to stay on the lookout for predators (13). By contrast, in a low-risk environment lacking a dominant breeding pair (−F/−P) submissive behavior would put an individual at a disadvantage in competing for resources (14).

That multiple factors acting early in development can influence behavior in complex, interacting ways is likely to hold as a general principle. Given a complex, multifaceted environment, individuals should integrate information from all relevant sources to generate a unified, adaptive phenotype (15–17). What's more, if the environment is stable, then it makes sense to restrict developmental plasticity to a relatively short, early window of time (17–20). However, it remains unclear just how applicable the specific findings of Fisher et al. (6) will be to better understanding behavioral development in species other than *N. pulcher*. Does early social enrichment and exposure to predators have similar effects on behavioral development in other cooperatively breeding animals, or might this only be true for species in which predation pressure was the primary driver in the evolution of cooperative breeding? How do early social and ecological experiences influence adult behavior in species that do not reach the same degree of social complexity as cooperative breeders? Comparative studies in a range of species are needed if we hope to develop predictive, generalizable theories of what factors influence behavioral development and how these factors interact with each other. Such studies would also likely shed light on the adaptive significance of these effects on behavioral development, as well as the evolutionary origins of cooperative breeding and other forms of social organization. Finally, what is the neuroendocrine basis by which different factors early in development interact with each other to drive divergent behavioral trajectories that persist throughout life? The unexpected findings of Fisher et al. (6) are sure to stimulate research in these exciting new directions.

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