

Nature and nurture

A step towards investigating their interactions in the wild

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The debate about the relative importance of nature versus nurture has been around for decades, but despite this, there has been very little evidence about how these might in fact interact to drive evolution in the wild. Recently, the identification of a comparable methodology for analyzing both genetic and social effects of phenotypic variation revealed that fitness variation in a free-living population of dolphin was driven by a strong social and genetic interaction. This study not only provides evidence that nature and nurture do interact to drive phenotypic evolution but also represents a step towards partitioning the effects of genetic, social, environmental factors and their multiway interactions to better understand phenotypic evolution in the wild.

Reproductive success is the key to the spread of any organism's genes, yet our understanding of the factors driving individual fitness variation in natural populations remains incomplete. Measuring fitness in the wild is not easy, but field studies provide us with the unique opportunity to investigate how genetic and environmental factors interact to influence fitness under natural conditions.¹ To date, some studies point to inherited genetic characteristics,^{2,3} while others show the benefits of social effects of unrelated helpers.^{4,5} Surprisingly, the genetic and social effects on reproduction have never been studied together in natural populations.

A recent study led by Frere et al.⁶ has shown that social and genetic effects

are both important for reproduction. A female's calving success is boosted either by social association with other females that had high calving success, or by the female having relatives who are good at calving. Not only that, but the social and genetic effects interact in an intriguing way: the benefits of social associates were more important for female pairs with lower genetic relatedness.

Why do female dolphins benefit by associating with other successful females? We do not know all the details, but this population is in Shark Bay, WA, where dolphins are attacked by sharks, so protection by other females^{7,8} may enhance calf survival. In addition, since females with calves may be more likely to associate with other mothers and calves,^{9,10} lowered predation risk, exchange of social and hunting information and social opportunities for calves may all contribute to female calving success. Sharks are not the only threat to females and calves: the females may need protection from members of their own species. Males are aggressive towards females, particularly when they are cycling.^{11,12} Recently,¹³ Frere showed that younger females are susceptible to inbred matings, which reduce their reproductive output because calves that are more inbred are slower to wean. We suggest that due to inexperience or vulnerability, young females may be less able to deter matings from related males. We have seen females risk injury by joining a female who is being herded by males. Sometimes these "helpers" are attacked in the process.

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This suggests that females might assist each other when they can.

Why has it taken so long for such a study to be done in any species when we know that evolutionary ecology cannot be fully understood without analyses of interactions between genetics, ecology and social behavior? First, it is only since 2008 that new analyses of molecular relatedness have allowed geneticists to track heritability in wild populations.¹⁴ Second, there was no comparable way of directly analyzing social interactions, until Frere et al.⁶ use of social association between pairs of females in the same analysis as the pairwise molecular relatedness. This represents only a first step towards addressing a critical gap in statistical modeling. In particular, we need analyses that allow incorporation of multiple pairwise matrices within a mixed model framework. Such advances would enable evolutionary ecologists and quantitative geneticists to start partitioning the effects of genetic, social, environmental factors and their multiway interactions to better understand phenotypic evolution

(e.g., fitness attributes). Genetic and social effects could be broken down into multiple types such as maternal and biparental relatedness,¹⁵ while social effects could include pairwise association, sharing of behaviors such as foraging and sexual advertisements.

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