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Too many people, women, men? The psychological effects of population density and sex ratio

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Has your environment become more crowded over time? Do you find yourself surrounded by mostly men or mostly women? Here, we review recent work on the psychological effects of two key ecological dimensions: population density—the number of people in a given space—and sex ratio—the relative proportion of men to women in a group. Higher population densities are associated with a future-oriented psychology, increased educational investment, and a focus on 'quality over quantity' in family size and relationship preferences. Unequal sex ratios are associated with increased competition and risky behaviors amongst individuals of the more prevalent sex, and a general shift toward the relationship preferences of the scarcer sex.

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How many children would you like to have? Burying beetles frequently face this difficult decision. To successfully reproduce, these beetles first need to find an animal carcass to lay their eggs near. Competition for desirable (i.e. larger) carcasses is intense, and beetles that are physically larger are more able to fight off competitors. When beetles live in dense ecologies (where there are lots of other beetles), they tend to have fewer, but physically larger, offspring [1,2]. Why? Dense environments foster greater competition, and in order for offspring to successfully compete in such ecologies, parents cannot afford to split their investment across too many children. Instead, it may be more adaptive to have fewer children, allowing more focused investment in each child, and ultimately increasing their competitiveness (in this case, by developing larger body sizes). The parent beetle's reproductive flexibility is one example of *phenotypic plasticity*—the adoption of different traits and behaviors depending on environmental conditions [3,4].

Why should we care about beetles (assuming you aren't one)? It turns out that density might have similar effects in our species, as we elaborate below. More broadly, organisms across species, including humans, have evolved forms of phenotypic plasticity because different traits facilitate survival and reproduction in different ecologies, and natural selection has selected for the ability to flexibly switch-specific behaviors depending on ecological conditions. A recent integrative framework draws upon phenotypic plasticity to generate predictions about the human psychological effects of six key ecological dimensions—population density, sex ratio, resources, pathogen prevalence, kin relatedness, and mortality likelihood [5•]. Given space constraints, we focus this review on the first two dimensions: population density and sex ratio (see Table 1 for a summary). The framework uniquely highlights new ways of thinking about the origins of psychological diversity, and aims to connect human literatures with non-human animal work, providing a unifying perspective across disciplines. It also complements existing ecological approaches, which highlight the importance of the objective environment, the consideration of multiple ecological dimensions, and the influence of culture [6,7,8].

Population density

The study of density's psychological effects was perhaps most popular in the 1960s and 1970s, in part due to Calhoun's work on overcrowding in rats. In these rats, living in highly dense conditions led to vivid social pathologies, such as cannibalism and hypersexuality [9]. Initial human work also seemed to find pathological effects of density in our species. For instance, living in dense conditions was associated with greater mortality rates, juvenile delinquency, and mental disorders [10]. However, subsequent work that took into account confounding factors, such as socioeconomic status and ethnicity, found little to no evidence for density's pathological effects [11]. With some exceptions [e.g. 6,12], interest in the psychology of density has diminished over time.

A framework from evolutionary biology offers a different perspective for thinking about density. *Life history theory* begins with the premise that all organisms face the problem of limited time and energy [13]. Given this, how might one best allocate limited resources to facilitate

Table 1

Summary effects of population density and sex ratio

Ecological dimension	Example effects
Population density	Higher density → Building of competitive skills/delayed reproduction Higher density → Investment in quality over quantity of children Higher density → Increased parenting/decreased mating effort
Sex ratio	Male-biased → Competition/risk-taking among males, restricted sociosexuality Female-biased → Competition/risk-taking among females, unrestricted sociosexuality

survival and reproduction? Trade-offs are inherent to all allocation decisions. So burying beetles that have more offspring will also have less to invest in each individual offspring, assuming parental resources are held constant. In contrast, beetles that have *fewer* offspring will have more resources to invest in each individual offspring. The same outcomes would be true for humans as well. This represents a trade-off between the *quantity* versus *quality of offspring*—more but less competitive offspring or fewer but more competitive offspring.

From life history theorizing, ecological dimensions such as population density may influence which trade-offs work best [14•]. As highlighted by the burying beetle example, given the greater competition in high density ecologies, it might be adaptive to have fewer children to allow greater investment in each child (quality over quantity). Two other life history trade-offs are relevant here [15]. The first is *mating* versus *parenting effort*. For individuals who already have children, they can invest time and energy into seeking additional mates (e.g. by finding and competing for new relationship partners), but this is time and energy taken away from caring for and investing in existing children. As mentioned above, higher densities favor increasing investment in offspring quality, and this also leads to a focus on parenting over mating effort. The final trade-off is that of *current* versus *future reproduction*. Individuals can choose to reproduce now, or delay reproduction to a later time. Delaying reproduction allows individuals to invest current resources into improving abilities (e.g. skills and knowledge), increasing social competitiveness, and enhancing resource-acquisition ability for the future. Given the need for greater competitive ability in dense ecologies, such environments may also favor a focus on delaying reproduction.

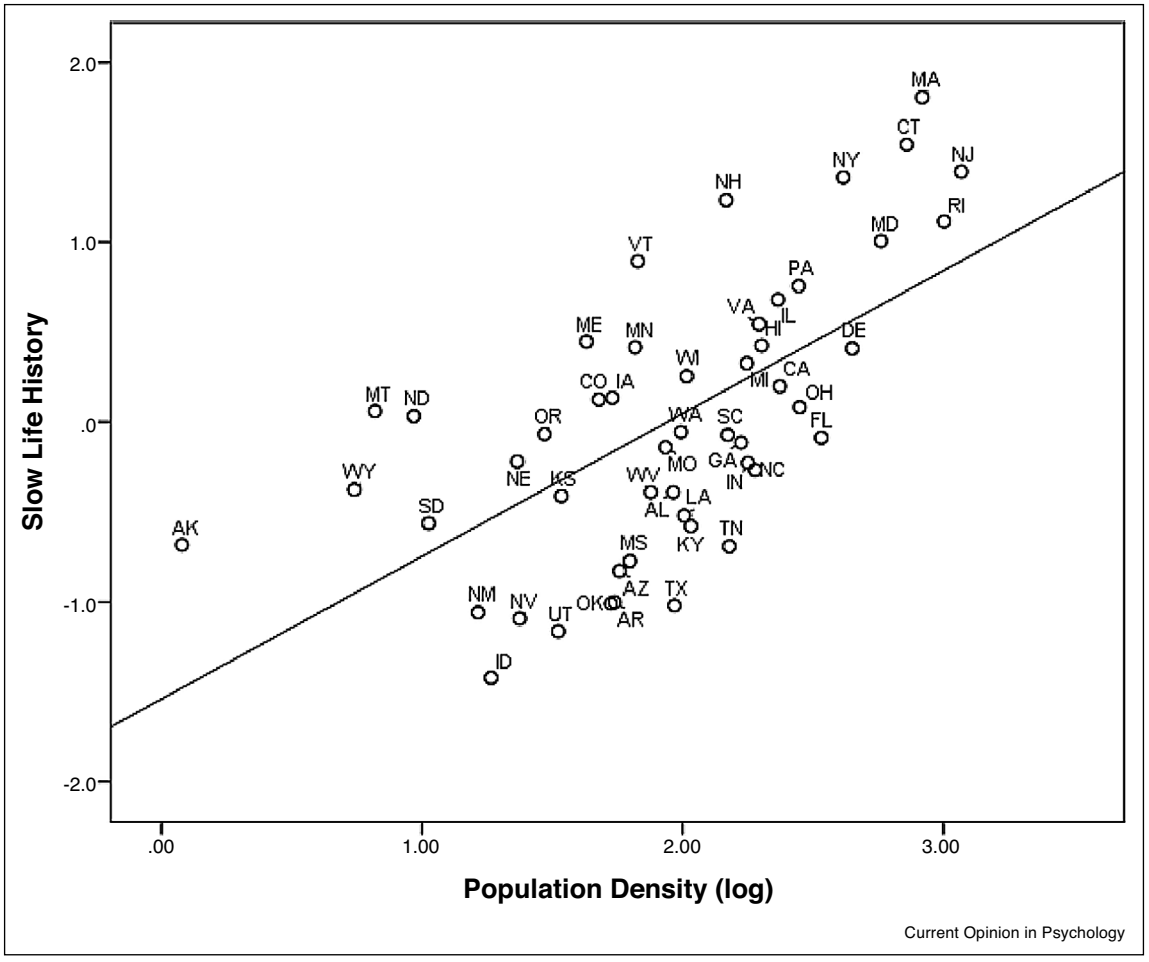
To summarize, higher densities might lead to a psychology that focuses on (1) quality over quantity of offspring, (2) parenting over mating effort, and (3) future over current reproduction. A recent series of correlational and experimental studies tested these predictions [16]. Across countries and the 50 U.S. states, people living in populations with higher social densities tend to have fewer children, but invest more in the education of their children (quality over quantity of offspring), prefer committed long-term relationships to casual short-term ones (parenting over mating effort), as well as marry later in life, plan for the future more, and invest more in their own education (future over current reproduction) (see Figure 1). These patterns generally hold controlling for potential confounds, including economic development, urbanization, and regions. Similarly, in experimental studies, when people were provided with information about increasing population density in their environment, they seemed to change their social preferences to prefer focusing their investment on fewer children and fewer romantic relationships. These findings converge with independent work in demography, which finds that increasing population density also predicts decreasing fertility over time [17]. Interestingly, in this work, density's suppressing effects on fertility seem strongest after a 20–25 year time lag. Note that these patterns may seem counterintuitive, especially given early research seeming to indicate that density leads to pathological behavior. However, reviews of this early work concluded that such conclusions were unfounded and created confusion in the literature [18]. We might also question whether an individual's own resources will influence how they react to density, with more resources potentially lessening the need to make strict trade-offs in investment. However, in analyses testing this possibility in the data sets reported earlier [16], there was no evidence of any consistent interaction of resource levels with density.

The life history perspective provides a novel way of thinking about the psychological effects of density. Using the three broad trade-off types outlined above, one can generate further predictions about other psychological effects. For instance, the 'quality over quantity' focus in reproductive choices and romantic relationships in high density conditions might also be observed in friendship patterns, with a preference for few close friendships versus many distant ones ('deep' versus 'shallow' strategies) [19].

Sex ratio

The presence of many other individuals in your ecology can shape your social behavior. Whether these others comprises *more men or more women* also has unique psychological effects. The proportion of males to females in a population is labeled the sex ratio, with female-biased

Figure 1



Population density and slow life history composite across the 50 U.S. states. Slow life history composite is created from standardized scores of seven state-level variables (parentheses represent higher scores on composite): (older) male and female marriage age, (lower) fertility, (lower) teenage birth rates, (higher) preschool enrollment rates, (higher) college degree completion rates, and (greater) retirement plan participation ($r = 0.63$; composite $\alpha = 0.89$). Adapted from Ref. [16].

ratios referring to ecologies where there are more females than males, and *vice versa* for male-biased ratios. Of particular importance is the operational sex ratio, which is the sex ratio of reproductive aged males to females.

Broadly, when sex ratios are biased toward one sex, heterosexual members of the more prevalent sex face greater competition for mates [20], and the sex that is scarcer can afford to be more selective when choosing partners. This can lead to a wide variety of psychological consequences. Consider sociosexuality—a 'restricted' sociosexuality refers to a preference for high commitment, long-term relationships. An '*un*restricted' sociosexuality, in contrast, reflects the opposite—a preference for casual short-term partners. Females are generally more restricted in sociosexuality than males [21]. And in ecologies with male-biased sex ratios—where there is greater competition between males for female partners, and females can impose their preferences on males—one observes more restricted sociosexuality (e.g. higher marriage rates, fewer out-of-wedlock births, increased paternal investment). Female-biased sex ratios promote the opposite process, leading to more unrestricted sociosexuality (e.g. lower marriage rates; [22,23]). Indeed, this pattern has been found across populations [21,24–26]. Experimental work also provides converging evidence, with manipulations of sex ratio perceptions leading to similar shifts in expressions of sociosexuality [27].

Beyond sociosexuality, biased sex ratios also implicate a variety of social behaviors. For instance, male-biased sex ratios are associated with higher rates of homicide and violent crime [28,29], presumably reflecting increased male–male competition. Female-biased ratios are associated with women prioritizing career advancement over starting a family [30], due to perceptions of greater

difficulty in finding desirable male partners. Finally, unfavorably biased sex ratios (i.e. more of one's own sex) can lead both women and men to make riskier but higher-return decisions [31•]. For instance, males perceiving more male-biased sex ratios concentrated their expenditures into a smaller number of funds when presented with investment options. Such behavior was driven by the motivation to impress potential romantic partners in the face of intense competition.

Summary and future directions

To summarize the effects of population density and sex ratio: (1) High population density leads to increased competition for resources, which influences key trade-offs in life, promoting a preference for future over current reproduction, quality over quantity of children, and parenting over mating effort. (2) Skewed sex ratios lead to increased competition for mates among the more prevalent sex, and increased selectivity in mate choice among the scarcer sex. Both ecological factors, objectively measured or subjectively perceived, exert unique psychological effects. The study of these dimensions has led to novel discoveries about influences on our psychology.

Going forward, researchers might examine how multiple ecological dimensions interact in shaping behavior. A common approach in existing work is to focus on only one dimension of interest while accounting for 'confounds' (e.g. controlling for economic development). However, confounds are often themselves ecological dimensions in their own right, and examining how they interact with dimensions of interest could shed useful insights. Ecological influences on our psychologies may not act like control variables in a regression. For instance, sex ratio and population density might interact to promote different forms of competition. High densities might amplify more male-typical competitive behaviors (e.g. physical aggression) under male-biased sex ratios, but amplify female-typical competition [e.g. indirect aggression; [32]] in female-biased ratios. Ecological dimensions might also interact by influencing perceptions of each other. For instance, recent work has found that cues to pathogen prevalence led people to perceive greater social density in their surroundings [33]. Considering how ecological factors interact is also likely to be critical when studying the influence of any single ecological dimension across different groups (e.g. different cultures). The hypothesized effects of a given ecological dimension in one group might not emerge, or might even reverse, in a second group due to interactions with another ecological dimension that differs in degree between these groups.

There has also been a relative lack of attention to *age-dependent* effects of ecologies [see Refs. [22,34•], for exceptions]. Take sex ratio, for example. A skewed sex ratio leads to increased competition for mates amongst the more prevalent sex. But how would skewed sex ratios influence the psychology of people who are in life stages where they are not yet, or no longer, competing for mates? For instance, parents who are no longer actively seeking mates might invest in enhancing their *children's* competitiveness if they perceive an unfavorable sex ratio for their child. More broadly, considering the goals of individuals at different life stages, and how these goals interact with ecologies, is likely to lead to important insights.

The current review has barely scratched the surface. The potential of ecological thinking for understanding the origins of our social behavior cannot be underestimated. Much work remains to be done, in both breadth (e.g. examining less explored ecological dimensions) and depth (e.g. understanding how and on whom a given ecological dimension exerts its effects).

Conflict of interest statement

Nothing declared.

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