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In Focus

Featured Articles in This Month's *Animal Behaviour*

Totally Stressed Out

Who hasn't felt a little stressed out when work demands or personal issues get to be too much to handle? Broadly considered, stress has evolved as an adaptive physiological response to adverse environmental conditions. A little stress is a good thing; it helps prepare an animal to fight or flee and an animal behaviourist to meet a deadline. Too much stress, however, can have long-term detrimental effects. These effects can be particularly negative if they occur during development, when physiological systems are being organized and limited resources are allocated in a careful choreography. In a paper in this issue (pp. XXX–XXX), Kim Schmidt and colleagues from the University of Western Ontario investigate the effects of early life stress on the learning and production of a well-studied communication signal, the song of male songbirds.

In 1998, Steve Nowicki, Susan Peters and Jeff Podos incorporated the concept of harmful early stress as the foundation of their developmental stress hypothesis (Nowicki et al. 1998). They suggested that stress experienced during early life could serve as a cost that later enforced the honesty of songs used by adult birds as a signal of quality. This hypothesis provided a neat solution for a problem that had been vexing those studying birdsong, namely what form of costs enforced its honesty? Theory suggested that advertisement signals given by a male should reliably indicate his quality for a female to bother attending to them, and there was plenty of evidence available that females paid attention to the songs of males. One obvious candidate cost was the energetic costs of song production, but the relatively few studies that had managed to document these costs suggested that they were actually rather low. The alternative proposed by Nowicki and colleagues was built on two key observations. First, the production of birdsong requires repeatedly executing motor patterns that are stereotyped, precise and often very elaborate. Second, in many species these motor patterns are learned early in life. Both these factors suggested that birdsong might be particularly susceptible to disruption by stressors experienced early in life.

Over the ensuing decade evidence has accumulated in support of the developmental stress hypothesis. A number of studies have shown negative effects of developmental stress on adult song traits; many of these also showed a corresponding decrease in the size of some of the neural regions involved in vocal production and learning, thus providing a mechanistic link to the behaviour of singing. Most of these studies, though, were conducted in species with small and simple song repertoires. Such species are the minority across oscine songbirds; the majority of species have larger repertoires. It also remained unclear the degree to which early life stress negatively affects aspects of song learning (e.g. amount or accuracy of learned song) versus aspects of song performance (e.g. the difficulty or stereotypy of song). Both song repertoire size and vocal performance have been shown to be traits to which females are particularly attuned. Thus it hasn't been clear that developmental stress affects those features of song that females cared about the most.

This gap has now been filled nicely by Schmidt et al. They employed for their study the song sparrow, a North American songbird with a moderately large repertoire of 5–12 songs composed of 20–50 unique syllables. They collected hatchlings (Fig. 1) from nests 3 days after hatching, brought them into a laboratory, and subjected males to one of three treatments: food restriction, orally administered corticosterone or unstressed controls. Birds received these treatments from day 7 to day 60 posthatch, corresponding to the period in which initial song learning is known to occur. Birds were tutored with song from day 16 to day 122 to provide a model for learning, then held for 1 year until their adult song could be recorded. The authors compared measures of song learning (song and syllable repertoire size, imitation accuracy) and song performance (song stereotypy and trill deviation, a function of bandwidth and speed) among the three treatments. Notably, they also examined the neural substrates underlying these behaviours by comparing size and neural density in the song control learning and production nuclei HVC, RA and Area X. They found that both food restriction and corticosterone enhancement diminished measures of song learning including song and syllable repertoire size; food restriction also decreased imitation accuracy. Food restriction, but not corticosterone enhancement, also resulted in a decrease in size of the brain nucleus RA. In contrast, there were no effects of either treatment on the size of nuclei HVC or Area X or on measures of singing performance such as song stereotypy and trill deviation. Intriguingly, trill deviation of experimental males was correlated with the song repertoire size of their fathers recorded in the field the previous year, suggesting that some aspects of song performance are heritable.

These results are consistent with the idea that early life stress negatively affects the quality of song learning by restricting the development of at least some of the neural centres that subsume learning behaviour. Such stress has less effect on the ability of males to produce the song they have learned, perhaps because the neural centres involved are inherently more plastic and can recover from early stress. These results nicely complement those from a parallel study by Schmidt and colleagues that found that early life stress also affects the song preferences of females (Schmidt et al. 2013). In that study female song sparrows subjected to the same food restriction and corticosterone enhancement treatments as nestlings showed decreased selectivity for playbacks of conspecific song over heterospecific song compared to untreated controls. This decreased selectivity

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Figure 1. A nestling song sparrow displays its vulnerability to early life stress. Photo: Dominique Potvin.

was mirrored, and perhaps driven by, a decrease in the number of cells in the auditory forebrain regions of stressed birds that were positive for the expression of *Zenk*, a key gene in determining responsiveness to song in both males and females. Thus both studies nicely link details of the signalling behaviour and the underlying neural mechanisms. Together, they provide the most integrative picture to date of how early life stress negatively affects both the ability of males to learn to produce song and the ability of females to learn to process it correctly. They also provide an important piece to the puzzle of how the honesty of an elaborate but energetically inexpensive signal such as birdsong is maintained over time.

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Timothy F. Wright
Editor

Human Mutual Mate Choice for Height Results in a Compromise

Pairing with a suitable mate for reproduction is a tricky business for many animals including humans. One has to contend not only with finding and choosing a mate, taking the rough with the smooth and outcompeting rivals, but also with the necessity to be the preferred mate for that chosen individual. Therefore, it is not surprising that mate preferences are unlikely to be satisfied and there may be a conflict of interest between any two potential mates. How are such conflicts resolved? The answer offered by a paper in this month's issue (pp. ?–?) is loud and clear: through compromise.

Gert Stulp (University of Groningen, The Netherlands), Abraham Buunk (University of Groningen and The Royal Netherlands Academy of Arts and Sciences), Robert Kurzban (University of Pennsylvania and University of Alaska, U.S.A.) and Simon Verhulst (University of Groningen) used data on human preference for height in both sexes. The authors analysed 174 speed-dating events, in which 3024 females and 2758 males made 128 104 choices resulting in 9072 matches. Height is a particularly useful trait to study because it can be measured quantitatively and objectively. Moreover, earlier work has demonstrated that both sexes show height preferences but that such preferences do not align and thus create a sexual conflict over this trait. Previous studies have also demonstrated that pairing with respect to height is nonrandom and both female and male height are related to the number of offspring. Compared to earlier self-reporting, questionnaire-based results, the speed-dating data studied by Stulp and co-authors have the crucial advantage of matching simultaneous preferences with choices and eventual pairings. It is this concurrency that allowed the authors to assess potential sexual conflict over partner height and its resolution.

On average women preferred a larger height difference with their partner than men. There was also a significant difference between the genders in terms of within-gender competition according to height. Short and tall women faced more competition than those of average height, although these differences were small. By contrast, short men had dramatically more competitors than tall men. As in women, men of average height had the smallest number of competitors. The analysis of the relationship between preferred height and choice showed that preference strength was stronger in women than in men. Furthermore, while women were much more unfavourable towards men who were shorter than preferred compared to men who were taller than preferred, men were exactly the opposite. They were more unfavourable towards women taller than preferred compared to those shorter than preferred, although in a less pronounced way. The higher preference strength in women was matched by their tendency to choose a narrower range of heights than men. On average men were less choosy than women. Taller men were more desirable and choosier. By contrast, female height was not related to choosiness but very short and very tall women were slightly less desirable than women of medium height. So how did these differences between the sexes in preference and choice affect eventual pairings? Men were most likely to choose a woman when she was on average 7.1 cm shorter than themselves, a value significantly lower than the 13.9 cm average height difference between the men and women taking part in the speed-dating events. By contrast, women were most likely to choose a man when he was on average 25.1 cm taller than themselves, a value significantly higher than the 13.9 cm average height difference. The greatest likelihood of a match was when the within-pair height difference was on average 19.2 cm. This value falls between 7.1 cm and 25.1 cm, the values representing the highest probabilities of choosing for men and women, respectively, and therefore represents a compromise between the preferences of the two sexes. It was also significantly higher than the average 13.9 cm height difference. Intriguingly, the authors found no evidence that couples somehow click with one another because neither men nor women were more likely to choose someone who chose them. Taller individuals from one gender tended to be matched with taller individuals from the other and this provides some evidence for assortative mating according to height. However, such assortative mating was tempered by women favouring men who were much taller than themselves. As a result, men of average height, rather than shorter men, were more likely to be matched with shorter women. This intriguing study demonstrates that conflict over height in human mate choice is resolved by a compromise resulting in a height difference that is between the preferences of the two genders. It also illustrates that human mate choice is best studied as a system of concurrent processes and that results are directly comparable to those for other species.

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