Figure 1 **The structure of the energy levels in a coupled qubit–oscillator system, as studied by Wallraff et al.[2] (left) and Chiorescu et al.[3] (right).**

As a further test, Chiorescu *et al.* induced and then analysed coherent Rabi oscillations between the energy levels of the coupled qubit–oscillator system; again, their data are in agreement with expectation. When they prepared the qubit in the ground state, only the Rabi processes associated with this state were visible; similarly, when the qubit was prepared in an excited state, only the Rabi oscillations involving that state were observed (Fig. 1). Although the coherence time was, at most, tens of nanoseconds, the demonstration of time-resolved coherent oscillations in this combined system is a remarkable achievement. The measured frequency of these processes, the Rabi frequency, passed the litmus test — it depended linearly on the amplitude of the microwave that induced the oscillations. Moreover, as the microwave power, and hence the Rabi frequency, was varied, the authors saw a resonance between the Rabi oscillations and the SQUID plasma oscillations, at exactly the position expected.

These experiments[2,3] show that a high level of coherence and control is possible in Josephson circuits, such that, on a single chip, qubits could be coupled through the oscillator to create a quantum computer (in the spirit of the coupling in ion-trap quantum registers[8]). This is also a step closer to

quantum communication — the transfer of quantum information between relatively distant stationary qubits via propagating waves. In both experiments, there is circumstantial evidence that the qubit and the oscillator were entangled; in future work with electronic qubit–oscillator or multi-qubit[7] circuits, it should be possible to observe the degree of entanglement directly. However, this would require the ability to carry out 'single-shot' measurements of both subsystems: although detectors are available that come close to achieving this[5,6,9], combining all the ingredients into a single circuit and operating it in a coherent regime is a challenge still to be faced. ■

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Animal behaviour

Relative size in the mating game

Malte Andersson and Johan Wallander

A common trend in size differences between males and females is a long-standing puzzle. A study of shorebirds shows that the type and strength of competition for mates may explain much of the pattern.

Five decades ago, the German evolutionary biologist Bernhard Rensch[1] presented an intriguing rule for the differing sizes of male and female animals. He found that in several groups (clades) that each contain related species, male size relative to female size increases with the body size of the species. Rensch's rule has since been verified in animals as diverse as arthropods, reptiles, birds and mammals, including primates[2]. The causes behind the rule, however,

have remained unclear[2–5]. Why are males much larger than females in many animals with large body size? And why, in the same clade, are males similar or even smaller than females in species with small body size[1,2]?

As they describe in *Proceedings of the National Academy of Sciences*, Székely *et al.*[6] have carried out a comparative analysis of shorebirds that show such trends, and have come up with some thought-provoking conclusions. They show that the trend in sexual

size difference (SSD) can be explained by two aspects of sexual selection (which arises from competition over mates), and the interaction between them. One aspect is the strength of sexual selection involved; the other is the agility of the male's display. The outcome of the analysis is similar whether it is based on body mass or wing length as a measure of size.

Males of many animals compete in fights for mates, and such contests favour large body size (Fig. 1). Through genetic correlations between the sexes[2,4,5], such competition may also lead to some increase in female body size, though less so than in males. In consequence, the mean size of each sex will increase, and so will the relative size difference between them. Increased male-biased SSD therefore tends to become associated with large body size. On the other hand, there are several smaller species in which sex roles are reversed and females compete strongly for males. Such species tend to have female-biased SSDs[5].

Some forms of male competition can favour smaller males. For example, in species where males compete by acrobatic aerial displays, there may be strong sexual selection for small male body size. For geometrically similar animals, agility increases with reduced body size[7], and this might lead to higher mating success of smaller males in certain birds[8,9]. Through genetic correlations it may also lead to some reduction in female body size. This in turn can help to explain why female-biased SSD increases with reduced body size in some birds and other animals with agile male display[5].

Székely *et al.*[6] tested the relative role of these mechanisms in producing SSD among 102 species of shorebirds and their allies (a clade named Charadriides). This is an ideal group for the purpose as it encompasses great variation in the traits of interest[6,8,10]. The analyses confirm Rensch's rule, showing that males are bigger than females in most large species, and that male-biased SSD increases with body size. In contrast, females are bigger than males in many small species.

The social mating system of a species can be used as a proxy for the strength of sexual selection in males. The strength increases from polyandry (where females compete to have several mates), through monogamy, to polygyny (where males compete to have several mates). As predicted, Székely *et al.* find that stronger sexual selection is associated with increasing male-biased SSD, and more agile aerial display is associated with increasing female-biased SSD. Notably, there are strong interactions between agility and strength of sexual selection. In polygynous species, the female is larger if male displays involve agility (Fig. 2); if they don't, males are the larger sex. Forms with less male competition (monogamy or polyandry) tend to have larger females regardless of male agility (Fig. 2). Such interactions may help to explain

Figure 1 **Competition at a mating arena. Males are the larger sex in many groups of animals in which males fight over females. Ruffs** *(Philomachus pugnax),* **for example, are shorebirds in which there is a great size difference between the sexes. Here, one of two (larger, collared) males mates with one of two females.**
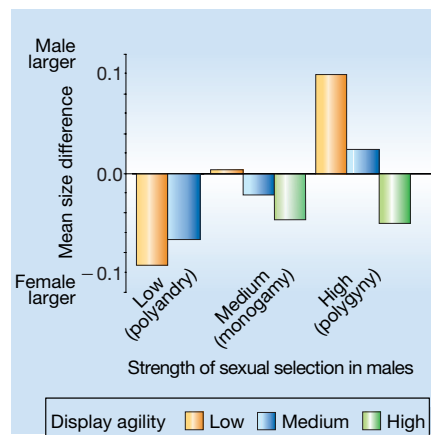

Figure 2 **Székely and colleagues' analysis[6] shows that the size difference between male and female shorebirds depends on the type as well as the strength of sexual selection. In species with strong male competition (polygyny) and non-agile display, males are larger than females. In species with agile aerial display, males are smaller than females. When competition over mates is weaker in males and strong in females (polyandry), females are the larger sex. The results are based on 75 species of shorebirds, with size differences measured as the mean of** $\log_{10}$**(male mass)** − $\log_{10}$**(female mass). (Modified after ref. 6.)**

why some groups with intense male competition show a range of SSD patterns, from female bias to male bias.

Sex difference in choice of habitat or food might also influence SSD. Székely *et al.* find that sexual difference in bill length — a trait of crucial importance for foraging — does not follow Rensch's rule. And when male and female body sizes are controlled statistically, sex difference in bill length is not associated with display agility or strength of sexual selection. So, unlike body size, which depends strongly on sexual selection, SSD in bill length is influenced mainly by other (probably ecological) selection pressures.

The generality of these conclusions can be explored by deriving predictions from them for tests in other animals. One prediction is that large males are favoured in species with large body size that compete for females in contests requiring strength or endurance[5] rather than agility. Moreover, among small species in the same clades, sex-role reversal and stronger competition among females, or male competition by agile[8] and energy-demanding[5] display, are expected to favour reduced male size, sometimes leading to female-biased SSD.

A review[2] of SSD in 40 groups shows that exceptions to Rensch's rule are rare and mostly occur in animals where females are the larger sex. There is much scope for testing the predictions in these and other groups. Advances in comparative and other analyses of SSD[2,6] open possibilities for clarifying the striking patterns in sexual size difference that have long puzzled biologists. Analyses of the form and strength of sexual selection are likely to be crucial in such work, as shown by Székely and colleagues' study of shorebirds. There is plenty of interesting work ahead — for instance, it is still not clear why, in most clades where some species show stronger sexual selection in females than males, this occurs mainly in its smaller forms. ∎

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