Diversity effects in reproductive biology

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In polyandrous species, such as most insects, the reproductive success of male parents is the outcome of competition via their gametes for resources that a female has invested in her ova and will provide to the developing offspring (Parker 1970). Resource partitioning among offspring and their genetic identity and diversity will also affect the reproductive success of female parents. These processes may be viewed as diversity effects in reproductive biology, which parallel diversity effects in community ecology (Loreau et al. 2001). We suggest that the analysis of potential effects of multiple paternity, or in principle also of multiple maternities, on reproductive success in animals and plants could benefit from ideas and experimental designs that have innovated community ecology, especially since diversity effects are being explored beyond the simple case of two or three interacting species (Kinzig et al. 2002, Loreau et al. 2002).

Recent experiments using randomly assembled plant communities ranging from 1 to over 10 species (e.g. Hector et al. 1999) have shown that biomass production increases linearly with the logarithm of species richness. This finding has been explained by two potential mechanisms referred to as “sampling” and “complementarity”. Sampling occurs when a large initial number of species in a community increases the probability that one or a few high-yielding species become dominant, thus resulting in high yield. Complementarity occurs for example when species differ in their resource requirements and therefore in combination extract more resources than a monoculture (or low-diversity mixture). These mechanisms are not mutually exclusive. However, even if they occur together, their relative contribution to the observed diversity effects can be separated with analytical approaches related to the Price-equation in evolutionary biology (Loreau and Hector 2001, Hector et al. 2002).

Sampling processes

Do sampling and complementarity also occur when diversity is among sires in animals and plants, especially where multiple paternity is not restricted to only two or three sires (Ellstrand 1984, Marshall 1991, Campbell 1998, Imhof et al. 1998)? The most obvious sampling effect in reproductive biology occurs among the many genetically related, yet usually not identical, male gametes of a single sire. In particular, if the mother can only carry one offspring, then sperm competition is about getting all or none of the female “resources”. More interesting sampling processes can arise through sperm or pollen competition among fathers in polyandrous matings of a female. The larger the number or genetic diversity of male parents, the greater becomes the female parent’s chance to sample a particularly good single father for her offspring.

Indeed, polyandry, mate choice and postcopulatory sexual selection are considered to play important roles in reproductive biology (Birkhead and Møller 1998, Yasui 1998, Baer and Schmid-Hempel 1999, Birkhead and Pizzari 2002). In animals in which fathers contribute only genes, the advantages of sperm competition and thus the benefits of polyandry to female fitness have been suggested in the opportunity to select the best among several fathers (with heritably higher viability, fertilization ability, or attractiveness), or in the defence against genetic incompatibility (Zeh and Zeh 2001) including inbreeding (Tregenza and Wedell 2002; for the additional advantage arising from genetically diverse offspring, see next section). In several taxa females re-mate more readily with novel partners (Archer and Elgar 1999). Furthermore, polyandry itself can intensify selection on sperm competitive ability (Bernasconi and Keller 2001, Hosken...
and Ward 2001), even leading to spectacular forms of altruistic cooperation among sperms of individual males (Moore et al. 2002). In flowering plants, where polyandry, due to the open pollination system, is probably more common and more synchronous than in animals, the fusion of carpels (syncarpy) is one key innovation that intensifies pollen competition and thus increases the chances of obtaining pollen from the best male parent by the sampling process (Mulcahy 1979, Endress 1982). A recent phylogenetic analysis estimates that syncarpy has evolved independently 17–26 times in the flowering plants (Armbruster et al. 2002).

Complementarity processes

Sampling processes may occur more frequently in reproductive biology than in community ecology. This is because there are many more male gametes than will eventually be allowed to use the resources offered by the female parent, i.e. her gametes and her later support of developing offspring, whereas in community ecology most individuals and species, at least initially, have direct access to resources. However, a single female often produces many gametes and supports many offspring, offering simultaneous access to male gametes from several male parents. It is thus conceivable that positive diversity effects in polyandrous species may also be due to processes involving complementarity.

First, genetic differences among female gametes within a maternal plant represent a “heterogeneous environment” which may best be “exploited” by a heterogeneous population of paternal gametes, if variability among paternal gametes increases the chances for compatible and viable matches. Thus, differential matching of gametes to form fitzygotes constitutes one possible process (potentially involving both sampling and complementarity) leading to positive diversity effects in reproductive biology. Second, even with a low genetic diversity of female gametes, a female could increase her fitness by mating with multiple males if this increases offspring diversity, leading to better resource exploitation in heterogeneous environments (Yasui 1998) or reduced sib-competition (Willson et al. 1987, Karron and Marshall 1990). The latter example would be the direct analogue to resource use complementarity reported from biodiversity experiments in community ecology (Hector et al. 2002). Under such a perspective potential fitness advantages for male parents of having offspring with many females (multiple maternity) might also be considered.

It is not obvious how to disentangle experimentally sampling and complementarity processes, but solutions have been found within community ecology and can be transferred to reproductive biology.

Analysing multiple-paternity as diversity effect

Most studies of sperm competition use 2-father matings (Birkhead and Møller 1998; for examples with 3-father matings see Zeh and Zeh 1994 or Lewis and Jutkiewicz 1998), rarely varying the genetic difference between fathers deliberately (Tregonzé and Wedell 2002). This corresponds to early competition experiments in community ecology which involved pure stands and two-species mixtures (de Wit 1960). General diversity effects were only detected when these experiments were expanded to larger ranges of species richness (Schmid et al. 2002). We suggest that a similar expansion of experimental designs should be considered for studies in reproductive biology. This should be particularly interesting for species with naturally high and variable numbers of male parents for each single female (and vice versa). This situations most likely to plants with their open pollination systems or to animals (such as ascidians and corals) with broadcast spawning and therefore the potential for simultaneous contribution of multiple mates to fertilization (Bishop 1998).

In a recent study using the rare plant Cochlearia bavarica (Paschke et al. 2002), we observed a strongly positive log-linear effect of the number of pollen donors, increasing from 1 to 3 to 9, on female reproductive success (Fig. 1). Total pollen load was held constant in this experiment. The positive diversity effect is relevant for the survival of the study species, because it can overcome the observed bi-parental inbreeding depression in small populations (Paschke et al. 2002). Although here the number of sires was greater than two, we do not know at present to which extent the effect of increased pollen diversity on reproductive success in C. bavarica resulted from sampling or complementarity. There are two additional requirements needed to disentangle the contributions of the two processes to diversity effects in reproductive biology, neither of which was fulfilled in our study. First, the proportion of the seeds of a maternal plant sired by each pollen donor or potential father should be measured. This could be relatively easily done in species where genetic markers are available (see Ellstrand 1984 for an early example of a paternity analysis in plants). Second, there is an experimental requirement, as in diversity studies in community ecology, namely that all fathers used in multiple-donor pollinations have also been tested in single-donor pollinations with the same female. If both requirements are fulfilled, methods using the Price-equation (Frank 1995) or diallel analysis (Cockerham and Weir 1977, Mather and Jinks 1982) may be developed to separate the individual and combined contributions of particular fathers to the total reproductive success of a multiply sired female. These approaches have been used by Loreau and Hector (2001) and McGilchrist and Trenbath (1971), respec-
two males compete for a female’s ova in the same reproductive period under natural competitive situations. Ideally, the number of sires should be varied below and above natural levels of polyandry (or polygyny) to explore the boundary of optimal mating rates (Baer and Schmid-Hempel 1999), which can differ between males and females (Rice 1996). Furthermore, morphological, physiological, and genetic differences among sires may be varied in a next step (Tregenza and Wedell 2002), corresponding to the use of different levels of functional diversity in ecological biodiversity experiments (Schmid et al. 2002). Perhaps, integrating concepts and methods from different fields and across different levels of biological organisation will eventually lead towards a general theory of diversity.

**Acknowledgements** – We thank Scott Armbruster, Andy Hector, Barbara Hellriegel, Michel Loreau, Owen Petchey and Io Skogsmyr for valuable comments on earlier versions of this paper, and the Swiss National Science Foundation (Swiss Priority Programme Environment, no. 5001–44628), Swiss Federal Program for Academic Recruitment (No. 409) and Forschungskredit der Universität Zürich (No. 560065) for financial support.

**References**


