

Reproductive interference

Emily R. Burdfield-Steel*
and David M. Shuker

What is reproductive interference?

Reproductive interference occurs when individuals of one species engage in reproductive activities with individuals of another species, and when these interactions reduce the fitness of one or both species (Figure 1). These interactions can vary from competition between males of different species for access to females through to matings between individuals of different species.

You mean animals trying to have sex with the wrong species? Yes! But not only animals; also plants and their promiscuous pollen or pollinators can cause reproductive interference between different plant species.

Why would they do that? In animals, reproductive interference is typically the result of incomplete species recognition. It occurs when animals fail to discriminate between individuals of their own species and those of another species. As this causes a reduction in fitness we would expect that such mistakes would be selected against and hence be rare in nature.

So, why does it occur? There are a number of reasons why species recognition may fail and lead to reproductive interference. Most straightforwardly, reproductive interference may just be a simple mistake. However, there may be a more systematic reason why animals are more permissive in their mate choice than we would first expect. Perhaps most importantly, classic mating systems theory predicts that one sex (usually males) will benefit more from mating with multiple partners and by being less choosy about mates, whilst the other sex (often females) may benefit from limiting matings to higher quality individuals (or individuals that control access to high quality resources). For the less choosy sex, this keenness to mate may lead to individuals being less discriminating when

choosing mates and therefore more likely to fail to differentiate between species. By 'trying it on' with any animal that vaguely looks, smells or sounds like your own species, weakly-discriminating males may end up successfully inseminating more partners than those that are more circumspect. Even for the choosy sex though, choosing a mate must be balanced with the importance of accepting at least one mate. Individuals that are too choosy may suffer equal fitness losses as those that are not choosy enough. It is these kind of trade-offs in male and female mating strategies that can result in reproductive interference. The extent to which reproductive interference typically results from simple errors, or is a side-effect of selection on mating strategies, remains to be determined however.

What types of reproductive interference are there? A whole range of reproductive behaviours can lead to reproductive interference. For instance, reproductive interference may take the form of heterospecific rivalry. In this, individuals, often males, mistakenly perceive members of another species as potential rivals for mates and thus behave aggressively towards them.

In terms of misplaced intersexual behaviour, there is a whole spectrum of possibilities. First, there is misdirected courtship behaviour towards an individual of a different species. In some cases, this may lead into another form of reproductive interference: heterospecific mating attempts (Figure 1). And finally heterospecific mating and hybridization may take place. It is expected that such heterospecific matings will carry the highest fitness costs. The exact cost will vary depending on the biology and reproductive strategy of the species involved. For example, in a species that mates only once, such a mistake would be disastrous and reduce the fitness of the affected individual to zero. For species that mate several times interspecific matings are expected to exact a lesser cost on lifetime fitness.

Other forms of reproductive interference include erroneous female choice, where females prefer heterospecifics as potential mates over conspecific males, and so-called 'signal jamming', whereby the behaviour or signals produced by one species in some way disrupt those necessary for successful reproduction in another species. An example would be the calls of one frog species



Figure 1. Examples of reproductive interference. Reproductive interference can be caused by transfer of pollen between different plant species by bees (top left); a young male fur seal attempts to mate with a king penguin (top right); reproductive interference between species of damselfly can drive the evolution of reproductive character displacement (bottom right); mating calls made by males of different species can overlap in frequency causing signal jamming as in the frog *Epipedobates trivittatus* (bottom left). Photo credits (clockwise from top left): David Shuker, P.J.N. de Bruyn, Martin Haddrill, and Brian Gratwicke.

interfering with the ability of a second species to locate mates. This could be the result of the one species' calls simply masking those of the other, or it could be that the calls confuse individuals of the second species and cause them to approach heterospecific callers rather than those of their own species. Such signal jamming can also occur within a sex. For instance, among two species of Amazonian frog, there is selection for decreased sensitivity in male *Allobates femoralis* to calls that fall within the range of *Epipedobates trivittatus* calls in areas where the two species overlap (Figure 1). That way *A. femoralis* might avoid interference resulting from the overlapping frequency range of *E. trivittatus* calls. As these calls form the basis of male–male communication in these territorial frogs, responses to *E. trivittatus* calls by *A. femoralis* males could represent both signal jamming and heterospecific rivalry.

But does reproductive interference really happen that often? There is evidence for reproductive interference in many species, particularly in invasive and closely related species. A recent review found 167 examples of reproductive interference, excluding studies of hybridization. Moreover, several types of reproductive interference can occur at the same time. For instance, when the two tick species *Aponomma hydrosauri* and *Amblyomma albolimbatum* were present on the same host reptile three forms of reproductive interference were recorded. First the mixing of female pheromones jams signals. Normally these pheromones cause males to cease feeding and search for females, but when females of both species were present males no longer responded. Second, males attempt to court females of the other species and thus spent less time courting and mating with females of their own species. Third, when *A. albolimbatum* males attempted to mate (unsuccessfully) with *A. hydrosauri* females, they remained attached to the females' ventral surface, preventing access to her genitals for conspecific males.

So how important is reproductive interference? Despite the growing body of empirical examples, the ecological and evolutionary effects

of reproductive interference are still poorly understood. While some reported cases may seem unlikely to have detectable effects on either the ecology or evolution of the species involved, such as those occurring between seals and penguins (Figure 1), reproductive interference by invasive species can contribute to the displacement of native species. And, there is increasing evidence of reproductive character displacement — the evolution of differences in reproductive behaviour between species — being driven by reproductive interference, for instance in damselflies. In addition, reproductive interference between naturally co-occurring species may have sufficient fitness effects to influence habitat use. One obstacle to determining the importance of reproductive interference is that it has often been studied as part of different evolutionary or ecological paradigms, e.g. hybridisation versus habitat use. Much like with other apparently non-intuitive mating behaviours, such as same-sex matings, the importance of reproductive interference may well lie in what it tells us about how and why organisms compete for mates, rather than as a consistently potent force of ecological or evolutionary change in its own right.

Where can I find out more?

- Amezquita, A., Hodl, W., Lima, A.P., Castellanos, L., Erdtmann, L. and De Araujo, M.C. (2006). Masking interference and the evolution of the acoustic communication system in the Amazonian Dendrobatid frog *Allobates femoralis*. *Evolution* 60, 1874–1887.
- Andrews, R.H., Petney, T.N. and Bull, C.M. (1982). Reproductive Interference between three parapatric species of reptile tick. *Oecologia* 52, 281–286.
- de Bruyn, P.J.N., Tosh, C.A., and Bester, M.N. (2008). Sexual harassment of a king penguin by an Antarctic fur seal. *J. Ethol.* 26, 295–297.
- Dame, E. A. and K. Petren (2006). Behavioural mechanisms of invasion and displacement in Pacific island geckos (*Hemidactylus*). *Anim. Behav.* 71, 1165–1173.
- Gröning, J. and Hochkirch, A. (2008). Reproductive interference between animal species. *Quart. Rev. Biol.* 83, 257–282.
- Mallet, J. (2005). Hybridization as an invasion of the genome. *Trends Ecol. Evol.* 20, 229–237.
- McLain, D.K. and Pratt, A.E. (1999). The cost of sexual coercion and heterospecific sexual harassment on the fecundity of a host-specific, seed-eating insect (*Neacoryphus bicrucis*). *Behav. Ecol. Sociobiol.* 46, 164–170.
- McLain, D.K. and Shure, D.J. (1987). Pseudocompetition - Interspecific displacement of insect species through misdirected courtship. *Oikos* 49, 291–296.

School of Biology, University of St Andrews, Harold Mitchell Building, St Andrews, Fife KY16 9TH, UK.

*E-mail: erb28@st-andrews.ac.uk

Primer

Antarctic marine biology

David K.A. Barnes
and Andrew Clarke

Antarctica is a continent of extremes: on average it is the highest, windiest, coldest and driest land mass on Earth. It also has the largest ice-mass, with less than 1% of its surface offering ice-free space for biology. Biology in the Southern Ocean surrounding Antarctica is also extreme in its isolation, light climate, water temperature and viscosity, continental shelf depth and, in the shallows, intense disturbance from scouring by icebergs. Being isolated and difficult of access, there are large areas which have never been sampled or even visited, and much of the biology is very poorly known away from the proximity of research stations.

Although there are a few similarities, in general the contrast between life in Antarctica on land and in the sea is amongst the strongest anywhere on Earth. Few higher taxa of organisms occur in Antarctica's deserts or lakes, and those which do are tiny and have species richness levels which would be dwarfed by any small island elsewhere. By contrast, in the marine environment, just 30 minutes using SCUBA (diving using Self Contained Underwater Breathing Apparatus) or a remote operated camera can reveal representatives of half of all known animal phyla. Ectotherms have had to adapt to very low, but stable temperatures, whereas most endotherms leave the polar regions in winter. Animals on the seabed (Figure 1) live life in the slow lane, exhibiting some of the slowest development and growth times known. The water column contrasts with both life on land and on the seabed, as although species-poor it is very productive in summer. It also includes some of the most numerous and largest macroscopic life on the planet.

History has played a dominant role in the explanation of why Antarctica's land, fresh-water, littoral and marine life is as it is. The most important factor has been the gradual long-term