CHAPTER 11

Evolutionary Game Theory in Biology

Peter Hammerstein[*], Olof Leimar[†]
[*]Institute for Theoretical Biology, Humboldt University Berlin, 10115 Berlin, Germany
[†]Department of Zoology, Stockholm University, 10691 Stockholm, Sweden

Contents

Abstract

This chapter reviews the origin and development of game-theoretic ideas in biology. It covers more than half a century of research and focuses on those models and conceptual advancements that are rooted in fundamental biological theory and have been exposed to substantial empirical scrutiny. The different areas of research—ranging from molecules and microbes to animals and plants—are described using informative examples rather than attempting an all-encompassing survey.

Keywords: Plant defenses, Sex ratios, Evolutionary dynamics, Animal fighting, Genetic conflict, Symbiosis, Cooperation, Biological markets, Animal signaling

JEL Codes: C73

11.1. STRATEGIC ANALYSIS—WHAT MATTERS TO BIOLOGISTS?

Biology is a natural science and as such it aims to understand the properties of real life. Its philosophy, therefore, differs fundamentally from that of conventional normative game theory (e.g., Hammerstein and Boyd, 2012), where central concepts rely on axioms of rationality and the consistency with these axioms matters more than empirical support. Neither rationality nor the consistency with any axiomatic system is a fundamental issue in biology. It is fundamental though that evolution acting on genes has shaped the biological properties of organisms on Earth.

Many of these properties can be conceived as strategies by which organisms interact adaptively with their living environment. To illustrate this, consider the morphological development of water fleas. In principle, these small crustaceans are capable of building a helmet–like structure that protects them from predators. Helmets are very costly to produce, however, and predation pressure can be large or small. When growing up, water fleas screen their aquatic environment for chemical traces left by predators. Based on the presence or absence of these chemical cues they grow large helmets only when predation is likely (Agrawal et al., 1999). What evolution has invented for these small crustaceans is more than just a protective device; it is the *strategy* to grow a helmet if there are predators around or else save this growth effort.

As demonstrated by the water flea example, the notion of a strategy can help biologists to simultaneously conceptualize traits and their contingencies. This creates an important interdisciplinary link with game theory, which can be quite fruitful for the broader understanding of phenomena involving conflict, cooperation, or signaling. It must be emphasized, however, that strategic analysis in biology often focuses on those details of interactions that do not fall within the traditional scope of game theory. The key to understanding strategic interaction in animals, plants, and microorganisms lies frequently in the sophisticated mechanisms and machineries involved. Where this is the case, the wisdom of biochemistry, molecular biology, or cognitive science can be of greater importance than that of game theory.

All identification of evolved strategies requires a thorough understanding of the biological context in which they occur. To give a simple example, falling coconuts sometimes kill humans that are relaxing under a palm tree. The dropping of coconuts, however, has not evolved as the tree's strategy to kill large mammals by throwing a solid object on their neck. It occurs instead as part of a seed dispersal strategy. Coconuts serve the seeds as vehicles and enable them to travel long distances in the sea. These vehicles need a sturdy design to act as a boat and let their passengers survive in saltwater. Hamilton and May (1977) were inspired by game theory when they argued that plants are usually under selection to send some of their propagules on a journey even if the "travel fee" is high and if habitats are stable and saturated. Launching sturdy vehicles is a response to this selection pressure and produces human casualties as a side effect.

In contrast, when nicotine kills insect larvae feeding on a tobacco plant, the larvae fall victim to a highly sophisticated strategy of plant defense against herbivores. Nicotine is one of the most powerful insecticides known today and it is also very toxic to mammals. Three tiny droplets of this substance would suffice to kill an adult human. It is an ingenious strategy of the tobacco plant to use nicotine for defenses because this toxin interferes with neuronal signaling systems that are widespread in the animal world. By partially mimicking the neurotransmitter acetylcholine and binding to receptors for this chemical signal, nicotine can very effectively disrupt vital regulatory processes in a multitude of animal species.

Plants in general have evolved a great variety of chemical defenses that manipulate animal nervous systems. Different plant compounds interfere with nearly every step in neuronal signaling (Wink, 2000), including neurotransmitter synthesis, storage, release, binding, and re-uptake. They also interfere with signal receptor activation, and with key enzymes involved in signal transduction. In many cases, plant compounds achieve these effects because they have evolved to resemble endogenous neurotransmitters of the targeted set of animal species.

Obviously, it would have been difficult for herbivores to stop such antagonistic interference through evolutionary modification of their own complex communication systems. They found other countermeasures instead (Karban and Agrawal, 2002;

Petzinger and Geyer, 2006). In turning the table, herbivores have evolved a number of compounds that interfere antagonistically with endogenous plant signaling. These compounds prevent or attenuate the induction of plant chemical defenses. In addition, herbivores evolved detoxification mechanisms—even through symbiotic relationships with microorganisms—and possess aversive learning mechanisms that permit feeding on less toxic tissues.

Has game theory played a significant role in revealing these strategic aspects of plant–herbivore interactions where conflict of interest is almost universal? The answer is no, and it is easy to explain why. In a figurative sense, plants act like programmers who "hack" the computers (neural systems) of target individuals (see Hagen et al., 2009, for a review). Conversely, the targets try to construct a firewall against these hacking attempts and may even "hack back." Needless to say that successful computer manipulation requires mainly the understanding of operating systems. Neither operating systems nor neural systems fall within the subject domain of traditional game theory but the latter have been studied extensively within the realm of biology.

There are many research areas, however, where game theory matters to biology. These include the study of sex ratios and sex allocation, animal fighting, intragenomic conflict, cooperation—or the frequent lack thereof—in microbes and higher organisms, market-like biological interactions, and honest versus deceptive signaling. In the following, we discuss these areas in turn, describe their affinities with game theory and highlight the lessons about nature biologists have learnt under the influence of game theory. Interestingly, the spirit of game theory appeared in biology already in the early work by Düsing (1883, 1884a,b) and Fisher (1930) on sex ratios. They foreshadowed evolutionary game theory in a way that is comparable to Cournot's well-known anticipation of classical game theory. We will address sex-ratio theory in the following to introduce some fundamentals of evolutionary game theory and describe the unexpected impact this theory had on empirical research and groundbreaking ideas in biology.

11.2. SEX RATIOS—HOW THE SPIRIT OF GAME THEORY EMERGED IN BIOLOGY

Many animal species produce male and female offspring in almost equal proportions. Intriguingly, this often happens even if males have lower chances than females to reach the age of sexual maturity, if they do not care for their young, and if competition among males is so strong that many of them will never reproduce. Shouldn't these aspects matter to sex-ratio evolution? No less than Charles Darwin (1874) felt that the frequent occurrence of approximate 1:1 sex ratios posed a serious challenge to his theory of adaptation through natural selection. He had to admit, however, that he himself could not master this challenge. What was so difficult about it?

11.2.1 There is a hitch with fitness

To understand the deeper nature of Darwin's difficulty, let us look at the relationship between a mother's offspring sex distribution $s = (s_f, \ s_m)$ and her fitness defined as the number u of her surviving adult offspring:

$$u = (s_f a_f + s_m a_m)n. \qquad [11.1]$$

Here, a_f and a_m are the sex-specific viabilities for females, males, respectively; n is the total number of the mother's newborn offspring, s_f is the relative frequency of her daughters, and $s_m = 1 - s_f$.

In order to demonstrate the hitch with [11.1], suppose that, as it is often the case, females are more likely than males to reach the age of sexual maturity ($a_f > a_m$). Mothers who produce only females would then have the largest number of surviving offspring— i.e., the highest fitness.

Here, we see a conceptual problem that relates to the question of how to define a biological notion of utility. Simple views on Darwinian evolution would suggest that in an evolving population where there are two competing traits, the one with the higher fitness u would be selected. From this perspective and with the assumptions made above, natural selection should be expected to create highly female-biased sex ratios and perhaps eradicate males from many populations on earth. Furthermore, in populations where there are no viability differences between males and females, the population sex ratio would be subject to random drift and could never stabilize. So, obviously there is something problematic about using the number of surviving offspring as a measure of success (utility, payoff) relevant to natural selection.

11.2.2 Düsing's solution—the first biological game

Only a few years after Darwin had given up his attempt to explain even sex ratios, the demographer Düsing (1883, 1884a,b) resolved Darwin's puzzle. Instead of looking at the number of surviving children, Düsing calculated a mother's reproductive success as the number of her grandchildren. This step toward a more far-sighted notion of reproductive success (utility) made it possible to identify the selective forces at work. Düsing realized that the expected number of grandchildren obtained through children of a given sex would depend on the overall sex ratio produced in a population. If the population on the whole produces one sex excessively, children of this sex will—on average—reward their mothers with fewer grandchildren than those of the opposite sex.

Düsing's insight follows from a *balance equation* which states that in a population with discrete nonoverlapping generations, the class of all males produces exactly the same number of offspring as the class of all females. This balance equation makes sense for genetically diploid organisms like mammals and birds because in this case individuals

have exactly one genetic father and one genetic mother. It does not hold, however, for haplodiploid organisms like ants, bees, and wasps, where males have no genetic father.

Using the balance equation, it is easy to calculate the number of grandchildren a mother would obtain through sons and daughters. This number depends on the population sex ratio and thus on the aggregate sex ratio "decisions" made by other mothers in the population. Obviously, the "flavor" of a game then appears if one considers the individual mother as a player in a population of players.

To be more concrete, let F_0, F_1, and F_2 denote the generations of a mother, her offspring, and her grandchildren. Suppose that for the entire population, the F_1-generation consists of N individuals, counted at the newborn stage, with fractions s_f, s_m of females, males, respectively, and that the F_2 population consists of M newborn individuals. On average, mothers would then obtain grandchildren as follows:

Expected number of a mother's grandchildren

$$(i)\ per\ daughter = \frac{M}{s_f N}, \tag{11.2}$$

$$(i)\ per\ son = \frac{M}{s_m N}. \tag{11.3}$$

From [11.2] and [11.3], it follows readily that a mother who wishes to maximize the number of her grandchildren would play a best response to the population by producing only sons if $s_f > s_m$ and only daughters if the inverse strict inequality holds. This game-theoretic reasoning serves biologists today as an important heuristic step toward a full-fledged dynamic theory of sex–ratio evolution (presented further later). It gives us the crucial hint about how natural selection pushes the offspring sex distribution in the direction of the equilibrium state s^* with $s_m^* = s_f^* = 0.5$, where according to [11.2] and [11.3] sons and daughters would on average be equally successful in producing grandchildren.

Düsing (1883, 1884a,b) phrased his sex–ratio arguments in a way very similar to the way we present them here, although he could of course not use the language of game theory. This language still had to be born but the spirit of game theory was definitely visible in his work. Sex–ratio theory can be regarded as both a precursor of evolutionary game theory and its current flagship if one considers the strong influence it has had for many decades on biological thought, experimentation, and field studies. We will describe this impact in Section 11.3.

11.2.3 Fisher's treatment of sex-ratio theory

The pioneering work by Düsing in the 19th century was long forgotten, partly because Fisher (1930), one of the most influential theoreticians of evolutionary biology, did not mention Düsing when he gave his own view on sex ratios in a classic monograph. Fisher draws primary attention to the "parental expenditure" made by parents when producing their young. To sketch his arguments informally, Fisher considers a "resource

cake" limiting this expenditure and asks how parents would divide the cake among sons and daughters if their resource allocation took place under the influence of natural selection. His answer is surprisingly simple. Evolved parents would split the cake in two equal halves, one for all the sons, and the other for all the daughters. Obviously, if the sexes differ in how big a slice of cake they need for development, this unbiased division of the cake requires a sex ratio biased toward the "cheaper" sex.

The derivation of Fisher's result requires no more than a tiny modification of [11.2] and [11.3]. Suppose that on average daughters and sons will obtain slices of cake with sizes c_f, c_m, respectively. The expected number of grandchildren per resource unit invested in a daughter is then expression (*i*) divided by c_f. The analogous calculation can be made for investment in sons, using (*ii*). At equilibrium, the return per invested resource unit must be equal for male and female offspring:

$$\frac{s_f}{s_m} = \frac{c_m}{c_f} \quad \textit{The Fisherian sex ratio.} \tag{11.4}$$

This equation captures one of the earliest quantitative predictions made in theoretical biology. It implies the equal split of the resource cake and is testable wherever one can measure the slices of the cake required by the sexes.

11.2.4 Does it suffice to count grandchildren—what is the utility?

In his reasoning about sex ratios Fisher (1930) did not explicitly talk of grandchildren as the measure of a parent's success. He suggested instead counting the children weighted by their reproductive value. In principle, this way of defining utility has a recursive flavor because in order to define the reproductive value of an offspring we would have to know the value of each of its offspring, etc. Taylor (1990), Charlesworth (1994a), McNamara and Houston (1996), and Grafen (2006) discuss the mathematical and conceptual intricacies of defining reproductive value. In Grafen's view, Fisher had the intuition that using reproductive value appropriately over one generation is the equivalent of looking an infinite number of generations ahead in order to obtain an asymptotic measure of fitness. This intuition—though often correct—needs careful examination (see Section 11.2.6).

If one does not fully trust the game-theoretic treatment of sex ratios or other biological phenomena, there are of course ways to invoke more mathematical rigor. This rigor is usually achieved at the expense of intuitive appeal. It seems to be the fate of game theory in biology that while it helps us tremendously in shaping our intuition and in generating insights, there is often the need to check these insights in a mathematical framework that captures more explicitly the dynamics of natural selection. In the following, we will give an example how this can be done for sex-ratio theory.

11.2.5 Evolutionary dynamics

In sex-ratio theory, populations are class structured because there are males and females. In principle, there could be more classes. Let $x_i(t)$ denote the number of individuals in class i at generation t. In a deterministic model with nonoverlapping generations, the evolutionary dynamics can be written as $x_i(t+1) = \sum_j a_{ij}x_j(t)$. The matrix A with elements a_{ij} is the so-called population projection matrix (Caswell, 2001), and if x is the vector of the x_i, we have $x(t+1) = Ax(t)$. Since we are dealing here with game-theoretic problems, the a_{ij} will depend on x and on the strategies present in the population. The elements a_{ij} are the per capita contributions of individuals in class j to class i in terms of offspring.

A common practice in evolutionary biology is to look for a stationary x for the case where all individuals use a strategy s. For such a stationary population one then examines whether initially rare mutant strategies s' would increase in number. Following this analytical program, we can now re-analyze the sex-ratio problem. Suppose that a mother has control over the sex ratio and produces a son with probability s_m and a daughter with probability $s_f = 1 - s_m$. Looking as before at nonoverlapping generations, and counting individuals at the newborn stage, the dynamics of x can be written as

$$\begin{pmatrix} x_f(t+1) \\ x_m(t+1) \end{pmatrix} = \begin{pmatrix} s_f b/2 & s_f bq/2 \\ s_m b/2 & s_m bq/2 \end{pmatrix} \begin{pmatrix} x_f(t) \\ x_m(t) \end{pmatrix}, \qquad [11.5]$$

where b is the expected number of offspring of a newborn female, bq is the corresponding reproductive output of a newborn male, and the factor $1/2$ accounts for the genetic shares of the parents in their offspring for diploid inheritance

Using the above mentioned balance equation again, the reproductive output of all males must equal that of all females. This implies $q = x_f(t)/x_m(t)$ and thus that $q = s_f/s_m$. In a stationary population $b = 1/s_f$ must hold, which could come about through a dependence of b on the total population size. Introducing now a mutant strategy s' and the matrix

$$B(s', s) = \frac{1}{2} \begin{pmatrix} s_f'/s_f & s_f/s_m \\ s_m'/s_f & 1 \end{pmatrix}, \qquad [11.6]$$

the population projection matrix for a stationary population is $A = B(s, s)$. The number of females and males, (x_f, x_m), in the stationary population is proportional to the leading eigenvector, $w = (s_f, s_m)$ of $B(s, s)$.

We now consider a mutant gene that causes a female to adopt the sex-ratio strategy s', but has no effect in a male. If the mutant strategy is rare, only the strategy of heterozygous mutant females needs to be taken into account, and the dynamics of the mutant subpopulation can be written as $x'(t+1) = A'x'(t)$ with $A' = B(s', s)$. Computation of the leading eigenvalue of A' shows that a mutant with $s_m' > s_m$ can invade if $s_m < 0.5$ and one with $s_m' < s_m$ can invade if $s_m > 0.5$, so there is an evolutionary equilibrium at $s^* = (0.5, \ 0.5)$.

11.2.6 Reproductive value

Intuitively, the reproductive value of an individual of class i measures the individual's expected genetic contribution to future generations. For the case of nonoverlapping generations, the value is proportional to the ith component of the leading "left eigenvector" v of the population projection matrix $A = B(s, s)$, i.e., the leading eigenvector of the transpose of A. This follows from the Perron-Frobenius theorem (we assume A is a primitive matrix with leading eigenvalue $\lambda = 1$ and leading left and right eigenvectors v and w, normalized such that $\sum_i v_i w_i = 1$). The theorem entails that for a dynamics $x(t + 1) = Ax(t)$ for $t = 0, 1, \ldots, x(t)$ will asymptotically approach $V_0 w$, where $V_0 = \sum_i v_i x_i(0)$ is the starting total reproductive value of the population.

For the sex-ratio problem, with $A = B(s, s)$ and B from [11.6], the leading left and right eigenvectors are $v = \frac{1}{2}(1/s_f, 1/s_m)$ and $w = (s_f, s_m)$. In this case, the reproductive value of a female is proportional to her expected number of offspring, $1/s_f$, and the same is true for a male. We see here the reason why Düsing's counting of grandchildren led to the correct conclusion, but his approach is not valid in general. For a mutant strategy s', the expected reproductive value per offspring is

$$V(s', s) = \frac{1}{2}\left(\frac{s'_f}{s_f} + \frac{s'_m}{s_m}\right),\qquad [11.7]$$

and this is sometimes used as a fitness or utility function, first introduced by Shaw and Mohler (1953). The fitness function gives the same conclusion, of an equilibrium for $s^* = (0.5, 0.5)$, as an examination of the leading eigenvalue. Although $V(s', s)$ differs from the leading eigenvalue $\lambda(s', s)$ of the mutant population projection matrix $A' = B(s', s)$, it is easy to see that V and λ have the same first order dependence on deviations of the mutant from the resident strategy, so V can be used to search for evolutionary equilibria. While reproductive value has the advantage of being a guide to intuition, it cannot fully replace a direct analysis of the evolutionary dynamics.

11.2.7 Haplodiploid sex-ratio theory

Let us repeat the analysis for haplodiploid insects, where haploid males develop from unfertilized eggs laid by their mother and diploid females develop from fertilized eggs. Given this mechanism of sex determination, a mother can readily influence the sex ratio among her offspring, by a choice of whether or not to fertilize an egg. In insects, eggs are fertilized one by one, right before they are laid. Corresponding to the dynamics [11.5], we then have

$$\begin{pmatrix} x_f(t+1) \\ x_m(t+1) \end{pmatrix} = \begin{pmatrix} s_f b/2 & s_f bq/2 \\ s_m b & 0 \end{pmatrix} \begin{pmatrix} x_f(t) \\ x_m(t) \end{pmatrix}\qquad [11.8]$$

for haplodiploids. Because each female has one mother and one father, $q = s_f/s_m$ must hold, and for a stationary population, we have $b = 1/s_f$, just as for the diploid case. For a rare mutant strategy s' and the matrix

$$B(s', s) = \begin{pmatrix} \frac{1}{2}s'_f/s_f & \frac{1}{2}s_f/s_m \\ s'_m/s_f & 0 \end{pmatrix}, \qquad [11.9]$$

the population projection matrix for the mutant subpopulation, consisting of female mutant heterozygotes and male haploid mutants, is $A' = B(s', s)$. The leading eigenvalue of $A = B(s, s)$ is $\lambda = 1$, with leading left and right eigenvectors $v = \frac{1}{2}(2/s_f, 1/s_m)$ and $w = (s_f, s_m)$. The expected number of offspring is $1/s_f$ for a female and s_f/s_m for a male, so counting grandchildren is not an appropriate measure of utility here. Instead, one needs to extend the accounting into the future, keeping track of genetic contributions at each step. Even so, the expected reproductive value per offspring, weighted by the genetic share, is proportional to $V(s', s)$ in [11.7], so the equilibrium sex–ratio strategy for the haplodiploid case is $s^* = (0.5, 0.5)$, just as for the diploid case. It is in a sense fortuitous that diploid and haplodiploid patterns of inheritance lead to the same sex–ratio equilibrium. In general, we should expect that evolutionary equilibria depend on the details of how genes are passed on to future generations.

11.3. THE EMPIRICAL SUCCESS OF SEX-RATIO THEORY

As persuasive as the Düsing–Fisher theory of sex ratios and sex allocation may be, some caution always needs to be exercised when evaluating functional explanations. In their famous "pamphlet" criticizing the "adaptationist program," Gould and Lewontin (1979) argued that many apparent adaptations may not have evolved for their seeming benefits, but may instead exist as part or by-product of another trait that has its own evolutionary logic. For example, in species with sex chromosomes like our human X and Y, where males are typically XY and females XX, the even sex ratio might simply occur as an unavoidable consequence of the sex determination system. Mendelian segregation of chromosomes implies an equal production of X- and Y-bearing sperm, so sex–ratio evolution could be constrained by an XY sex-determination mechanism if there are no genes that can modify it. Toro and Charlesworth (1982) showed indeed for an outbred population of the fruit fly *Drosophila melanogaster* that genetic variation in the sex ratio was effectively absent in that population.

11.3.1 Experimental evolution

Such observations do not decide the issue, however. The absence of genetic variation may actually result from natural selection for an even sex ratio (Bull and Charnov, 1988). By starting from a situation where there is genetic variation in the sex-ratio trait and

observing evolution in the laboratory, it is possible to investigate empirically whether frequency-dependent selection stabilizes the 1:1 ratio as soon as it has genetic material to work on. Carvalho et al. (1998) and Blows et al. (1999) created lab populations with genetic variation in the sex ratio and an initial mean deviation from an even sex ratio, using species of *Drosophila*. By tracing the evolution of their lab populations, both were able to demonstrate an approach towards an even sex ratio. In addition, the specific design of their experiments made it possible to examine the selective forces hypothesized in the Düsing-Fisher model.

Conover and Van Voorhees (1990) conducted a similar experiment with fish. They studied the Atlantic silverside, which has temperature-dependent sex determination, and kept several populations for half a decade in artificial constant-temperature environments, either constant low or constant high temperature. Initially this caused the sex ratio to be strongly biased—toward females in low and males in high temperatures—but the proportion of the minority sex increased over the years until a balanced sex ratio was established.

11.3.2 Measuring the slices of the cake

In order to test Fisher's cake model for sex allocation [11.4], one needs to measure the different amounts of resources invested in sons and daughters. For many solitary wasps, it is possible to literally see these slices of Fisher's cake. These wasps produce an individual brood cell for each of their offspring, fill the cell almost completely with captured insect larvae, and lay one egg in it. The captured larvae serve as food provisioning for the wasp larva emerging from the egg. Cell size can thus be used to quantify the slice of cake. Krombein (1967) investigated this size and its relation to offspring sex for a substantial number of wasp species. His data enabled Trivers and Hare (1976) to provide empirical support for Fisher's result [11.4], namely that the sex ratio is the inverse of the investment ratio. Furthermore, Trivers and Hare analyzed sex-allocation data for a variety of ant species where, in principle, there is an evolutionary conflict between the queen and her workers over the investment ratio. Their study shows that workers often provide a larger portion of the cake to the queen's daughters than what would have been optimal from the queen's point of view. This is what haplodiploid sex-ratio theory (introduced in 11.2.7) predicts under appropriate conditions (Bulmer and Taylor, 1981)

Torchio and Tepedino (1980) also present support for the Fisherian sex ratio, but in the solitary bee they studied the investment pattern varies through the season and requires, in principle, a more detailed life-history model. More generally, it has to be said that the sex ratio can be biased for various reasons other than those captured by [11.4], some of these will be given in the following. More information can, for example, be found in Charnov's (1982) classic monograph and in West's (2009) detailed evaluation of various sex-ratio results and observations.

11.3.3 Local mate competition

The theory outlined so far tacitly assumes random mating and an unstructured population. In a publication now considered as one of the founding works of evolutionary game theory, Hamilton (1967) highlighted the fact that mating often occurs locally in more or less isolated groups. He suggested that local mate competition (LMC) would favor the evolution of female-biased sex ratios and substantiated his theoretical argument with a long list of insect examples where sib mating is frequent and the typical batch of offspring strongly female biased. The basic idea is seen most readily in the extreme case where mating only occurs between sibs. The mother's genetic contribution to future generations is then directly proportional to the number of her daughters that go on to produce new batches of offspring, so the mother ought to produce the minimum number of sons needed to fertilize her daughters. This is true for Hamilton's perhaps most exotic case, which is not an insect but the live-bearing mite *Acarophenax tribolii*. As Hamilton points out, males of this species usually die before they are born, and they mate with their sisters in the mother's body. Hamilton lists a mother's typical batch of offspring as 1 son and 14 daughters, which is perfectly in line with the extreme form of LMC.

Many empirical studies have supported Hamilton's theory of LMC. Herre (1985), for example, studied varying degrees of LMC in fig-pollinating wasps. Here, a few females—referred to as foundresses—enter a fig nearly simultaneously, pollinate the flowers, lay eggs, and die. As the fruit ripens, the wasps' offspring emerge and mate inside the fruit. The number of foundresses can be used to estimate the intensity of LMC. As this number decreases, LMC increases, and one should expect the female bias to increase as well. Herre's empirical findings are qualitatively and quantitatively in good agreement with a sex-ratio model designed for this kind of biological system.

11.3.4 Environmental sex determination and the logic of randomization

The performance of males and females is sometimes differentially influenced by environmental conditions, such as local temperatures. If so, environmental sex determination has a chance to evolve (Charnov and Bull, 1977). This is nicely illustrated by Pen et al. (2010), who analyzed data from snow skink lizard populations from low- and highland regions of Tasmania. In the warmer lowlands, there is temperature-dependent sex determination (TSD), and females with good local basking opportunities give birth to mostly female offspring, usually born earlier in the season. This could be adaptive, because snow skink females benefit more than males from being born early and having a longer period to grow. A possible drawback of TSD, on the other hand, is that large-scale temperature fluctuations, for instance between years, might result in population-level fluctuations in the sex ratio, which can be detrimental to members of the majority sex.

If the fluctuations are large enough, it would be better for an individual, or its mother, to ignore the environment and instead randomize the sex. Mendelian segregation is a kind of random number generator, so genetic sex determination (GSD) might then evolve if temperature fluctuations are large (Bulmer and Bull, 1982; Van Dooren and Leimar, 2003). In agreement which this idea, Pen et al. (2010) found GSD in highland snow skink populations, for which temperatures are lower and much more variable from year to year. Using a model that included details of snow skink life history and plausible sex–determination mechanisms, they found good agreement between field data on sex ratios and the model output.

We can compare such evolved strategies of environmental sex determination with Harsanyi's (1973) famous conception of the "purification of mixed strategies." If each decision maker, be it the mother or the developing individual itself, experiences a random and independent deviation in temperature from an overall mean, and this deviation influences the relative advantages of becoming a male or a female in a monotone manner, the equilibrium strategy is evidently to develop as male on one side of a threshold and as a female on the other. Harsanyi showed that, in the limit of the payoff perturbations conditional on the experience or observation of a decision maker being small, these pure threshold strategies approach a mixed equilibrium of the unperturbed game. For the sex–ratio case, the limit would be a 50-50 male-female randomization. The snow skinks, however, seem not to approximate the mixed equilibrium through such pure strategies with sharp thresholds. In the lowlands, there is instead a gradual change of the chance of becoming female with temperature (Pen et al., 2010), and in the highlands Mendelian segregation imposes randomization even though the relative payoff effects most likely still are present. So what can one say about these other ways of approximating a mixed strategy equilibrium of an "unperturbed game"?

Leimar et al. (2004) suggest a reason for the frequent lack of bang-bang like solutions in nature. In the "purification of mixed strategies" paradigm, the players of a game each observe an independent, private variable that has some influence on their payoff. Instead of, for example, tossing a coin to play a random mixture of two pure strategies, the players make their actions dependent on the realization of the private variable and play one option for low values, the other for high values—bang-bang. As long as there is statistical independence of private information, this could possibly work in nature. Returning to the snow skinks, however, we see a case of statistical dependence among the private variables. Why? The snow skink's private variable is its estimate of the temperature during a sensitive period. Obviously, this information lacks statistical independence because of large–scale temperature fluctuations. Leimar et al. (2004) point out that the applicability of Harsanyi's purification idea to biology is limited to the case of statistically independent private variables. When these variables of interacting individuals are correlated, randomized, or even complex, oscillating strategies might instead be the outcome.

11.4. ANIMAL FIGHTING AND THE OFFICIAL BIRTH OF EVOLUTIONARY GAME THEORY

For more than half the 20th century, a number of empirical biologists were guided by the intuition that natural selection favors essentially those animal traits that increase the "well-being" of the species. As a child of his time, Lorenz (1963, 1966) aimed to explain the biological patterns of aggression with this idea in mind. He emphasized three ways in which aggression would benefit the species: it causes its members to be widely distributed in space, it ensures that the strongest individuals propagate the species, and it serves to protect the young. He even went as far as to postulate for animals an innate inhibition to kill members of their own species. Impressive fights such as occur in stags, appeared to him like "ritualized contests" where the opponents respect hidden rules to avoid serious injury, while still selecting the better fighter. It could be said that Lorenz looked at fighting animals as if they were humans in a fencing tournament.

There are two major problems with this view of aggression. First, stags are not as well behaved as Lorenz described them. When given a chance, they can target the vulnerable parts of their opponents and even kill them. Second, natural selection tends to act far more efficiently at the individual level than at the level of the species. With some important exceptions, individual rather than species benefits dominate the selection pressures on phenotypic traits. Methodological individualism is indeed of great importance to biology and here lies the potential for exchange of ideas with game theory.

Maynard Smith and Price (1973) realized this potential and explored how animal conflict can be studied in a formal game-theoretic model. Their aim was to explain the frequent observation of "limited war" in animal contests, without appealing to group or species benefits. The work triggered an avalanche of research activities in biology and founded evolutionary game theory as a field. Their paper centers on a model that depicts a conflict over a resource between two animals. The simplest, unburdened version of this model is now well known as the "Hawk-Dove" game, in which either player has two extreme behavioral options, namely to "be ready for escalation, use weapons, and fight it out" or "avoid escalation, display your interest and go for a peaceful conflict resolution." These strategies were later called "escalate" and "display" by Maynard Smith (1982). The model looks as follows:

$$
\begin{array}{c|cc}
 & \text{Escalate} & \text{Display} \\
\hline
\text{Escalate} & (V-C)/2,\ (V-C)/2 & V,\ 0 \\
\text{Display} & 0,\ V & V/2,\ V/2
\end{array}
\qquad [11.10]
$$

Parameter V is the benefit of winning and C the cost of being wounded.

11.4.1 The basic idea of an evolutionary game

How does a game like Hawk-Dove relate to a dynamic model of evolution? The idea is that strategies are heritable traits that evolve in a given population and are subject to

natural selection. For a matrix game, for instance, the trait would be a mixed strategy. The game is played every generation between animals who find themselves in a conflict depicted by the game. The animals play inherited strategies and their reproductive success depends at least partly on the game payoff. In a sense, natural selection makes the choice of strategy, not the animal that we can observe as an actor in the game.

An important question is, who meets whom in the population. Maynard Smith and Price (1973) and more explicitly Maynard Smith (1982) make a 'mass action assumption' and assume that strategies are randomly paired so that the probability of encountering a strategy q is its frequency x_q. This assumption would, of course, be violated in games between close genetic relatives.

Suppose now that two strategies p and q occur at population frequencies x_p and x_q so that the population distribution of strategies is $x = (x_p, x_q)$. Let $E(p, q)$ denote the expected game payoff for playing a strategy p against strategy q. In an otherwise simple biological world, we are justified to define the fitness of strategy p as follows:

$$w_p(x) = w_0 + x_p E(p, p) + x_q E(p, q) \quad \text{Frequency-dependent fitness} \qquad [11.11]$$

Here, w_0 is the animal's basic fitness expectation that is altered by the game payoff. Maynard Smith and Price were not explicit about how this payoff shows up in a selection equation but the simplest such equation fitting their approach is the following, which describes exact inheritance in a population with discrete, nonoverlapping generations:

$$x_p' = x_p w_p(x) / \bar{w}(x) \quad \text{Discrete replicator equation} \qquad [11.12]$$

Here, $\bar{w}(x) = x_p w_p(x) + x_q w_q(x)$ is the mean population fitness and x_p' is the frequency of p in the next generation.

11.4.2 The concept of an evolutionarily stable strategy

As already discussed in Section 11.2, a common practice in evolutionary biology is to look at a population state where all individuals play the same strategy and to examine whether initially rare mutant strategies would be able to invade. Maynard Smith and Price called a strategy p evolutionarily stable if according to [11.12] no initially rare mutant strategy q can invade. It is easy to show that—for the given model of frequency-dependent selection—this corresponds to the following characterization of an Evolutionarily Stable Strategy (ESS).

A strategy p is evolutionarily stable if and only if it fulfills the following two criteria:

$$[11.13]$$

 (i) $E(p, p) \geq E(q, p)$ for all strategies q.
(ii) All strategies q with $q \neq p$ and $E(q, p) \geqq E(p, p)$ satisfy $E(p, q) > E(q, q)$.

To gain some perspective on this characterization, let us consider a finite, symmetric matrix game with n pure strategies, defined by the matrix A and its transpose, and define

frequency-dependent fitness by [11.11] with $E(p, q) = \sum_{ij} p_i a_{ij} q_i$. If the population frequency of p is $1 - \varepsilon$ and that of q is ε, the difference ΔW in fitness between strategies p and q can be written as follows:

$$\Delta w = w_p(x) - w_q(x)$$

$$= (1 - \varepsilon)[E(p, p) - E(q, p)] + \varepsilon[E(p, q) - E(q, q)]. \qquad [11.14]$$

Looking at the two square brackets and their weights we see conditions (i) and (ii) emerge. On the one hand, (i) means that the pair of strategies (p, p) is a symmetric Nash equilibrium, and condition (ii) can be seen as a refinement of that equilibrium. This creates a well-founded link between biology and classical game theory. On the other hand, the fitness [11.11] and dynamics [11.12] relate to a rather simple world of models, which could limit the scope of the link.

The ESS concept addresses primarily the uninvadability of a population that is monomorphic for the strategy p, and the versatility of this general idea, linking game theory to evolutionary dynamics, might be the most important reason for its success. In biology, polymorphic populations are also of great interest, and the monomorphism/polymorphism distinction is important. Seen in this light, the combination of a mass action assumption and bilinear payoff is a special, degenerate case, where the ESS condition characterizes population states that are averages of distributions of strategies. Maynard Smith and Price (1973) were aware of this degeneracy.

What Maynard Smith and practically everyone else did not know in the 1970s is that Nash himself had offered a mass action interpretation of game-theoretic equilibrium in his PhD thesis. Unfortunately, this did not appear in the publication (Nash, 1951) of his doctoral work. As a result, it was buried for more than 40 years in the archives of Princeton University. The scientific community noticed Nash's mass action argument only in the 1990s when he was considered for a prestigious award. Once a Nobel laureate, Nash (1996) finally published the missing bit.

11.4.3 What does the Hawk-Dove game tell us about animal fighting?

If escalated fights are costly in relation to resource value (i.e., if $C > V$), the Hawk–Dove game has a mixed evolutionarily stable strategy, which is to "escalate with probability V/C and display otherwise." The main wisdom gained from this toy model is, therefore, that individual selection will limit the amount of aggression when only low fitness gains are at stake. So far, the model goes some way toward what Lorenz (1963) wanted to explain but without resorting to a group selection or species benefit argument. For high fitness gains (i.e., $V > C$), however, the model makes nature look "red in tooth and claw," in sharp contrast with the ideas expressed by Lorenz.

Opponents may differ in size, age, sex, or status, as well as in many other aspects that possibly influence the costs and benefits of a biological game. Some asymmetries can be payoff irrelevant, such as the random order of arrival at a site of conflict. Maynard Smith and Parker (1976) studied an asymmetric version of the Hawk-Dove game in which one player is the first to be present at this site, the other second. They showed that if $V < C$, the so-called Bourgeois strategy would be an ESS, which is to "escalate when first" and "display when second." Hammerstein (1981) extended their model and investigated contests that are asymmetric in more than one aspect. He decomposed the genuinely symmetric evolutionary game into asymmetric role games (subgames) where, for example, the role "weaker owner" is confronted with the opposite role "stronger intruder." With this decomposition, and using a result by Selten (1980), the ESS can be characterized as a combination of strict Nash equilibria for the role games. Hammerstein's analysis of the Hawk-Dove game with two asymmetric aspects shows that—within limits—the Bourgeois strategy remains evolutionarily stable even if this means that a weaker owner escalates and a stronger intruder avoids escalation (see Hammerstein and Riechert, 1988, for a possible example in the world of spiders). So here could be a second explanation for limited aggression: asymmetries might lead to conflict settlement without dangerous fighting but based on the logic of deterrence (see Hammerstein and Boyd, 2012, for the role of emotions in this context and Kokko et al. 2006 for the role of feedback between individual level behavior and population dynamics).

A third explanation (Parker, 1974), not well represented by the Hawk-Dove game, is that opponents gain information about their fighting abilities (size, strength, weapons, etc.) during a contest and use this information in deciding whether to withdraw or persist (Enquist and Leimar, 1983).

11.4.4 The current view on limited aggression

The qualitative conclusion by Maynard Smith and Price (1973) that a low resource value relative to the cost of escalating fighting limits aggression, still stands and has strong empirical support. There is also now an understanding that the value of a contested resource should be put into a life-history perspective. If a large part of the remaining lifetime opportunities for reproduction are at stake in a single contest, dangerous and even fatal fights are the expected consequence (Grafen, 1987, Enquist and Leimar, 1990), whereas limited aggression is expected when there are many reproductive opportunities beyond the current contest. As an example of the former, males of certain species of fig wasps have evolved into extreme fighters, with armored bodies and huge mandibles, and they often fight to the death inside the figs where they emerge. A comparison of a range of species of fig wasps showed that limited future mating opportunities for the males was the most important factor explaining this extreme form of fighting (West et al., 2001).

Over the years, a great number of studies of animal contests have accumulated, and overall it is the case that winners differ from losers in morphological and physiological characteristics that might indicate fighting ability, with higher values for winners (Vieira and Peixoto, 2013). It is also established that contestants generally acquire information, both in the current contest and from previous contests, and use this in deciding whether to withdraw or persist (Hsu et al., 2006), so some assessment of fighting abilities is widespread. This acts to limit the seriousness of aggression, because information is effectively used to predict the outcome of all-out fights, without paying the cost of entering those serious fights.

The importance of clear-cut asymmetries in contest settlement, as suggested by the Bourgeois strategy for the Hawk–Dove game, is a more controversial topic in the study of animal contests. There is no doubt that "owners" of territories or other resources often win contests, but the reason could at least partly be that these individuals have higher fighting ability or place a higher value on the resource (Leimar and Enquist, 1984). So, for instance, the conclusion from a classical study on contests in male Speckled wood butterflies over sunspot territories (Davies, 1978), supporting the Bourgeois strategy, is now in doubt. Effects of the motivation of a male to persist in the contest, for instance because he has private information about the chances of encountering females in the territory, could instead be the main factor explaining contest outcomes (Bergman et al., 2010). Even so, the possibility that owners and intruders could use different strategies also when they have identical information about fighting abilities and resource values cannot be ignored, but it is not yet settled how important this effect might be.

11.5. EVOLUTIONARY DYNAMICS

The strongest and most productive link between game theory and evolutionary dynamics lies in the study of the invasion of a rare mutant into a resident population. In many cases, the dynamics of the mutant subpopulation is approximately linear in the mutant frequencies, as long as the mutant is rare. The asymptotic rate of growth of the mutant subpopulation can then be employed as a measure of the fitness of the mutant strategy in the environment given by the resident strategies. If this linear problem allows a description of the rate of growth in terms of reproductive value, which we saw in Section 11.2 is connected to the Perron-Frobenius theorem, there is an even closer link involving the concept of utility or payoff in game theory. This approach is a general recipe that can be applied in many situations. For instance, the mutant could be an allele at some particular genetic locus, with the analytical machinery of population genetics, involving Mendelian segregation and recombination with genes at other loci, put to use to study the change in mutant frequency. Alternatively, one might make the simplifying assumption of exact, asexual inheritance of strategies. As soon as the situation of the mutant and the resident population is specified, one needs essentially to bring to bear

the relevant mathematical tools to the problem. A main goal of the analysis is to find resident strategies such that no mutant can invade. An equally important question is in which directions and towards which strategies such evolution through mutant invasion leads.

11.5.1 The replicator equation

Instead of the discrete-generation replicator equation [11.12], a continuous-time version is sometimes used to establish a link between game theory and evolutionary dynamics that goes beyond the question of the invasion of a rare mutant into a resident population. Assuming the population has strategies p_k with frequencies x_k, $k = 1, \ldots, N$, we define the fitness of p_k from the game payoffs as

$$f_k(x) = \sum_l E(p_k, \, p_l)x_l. \qquad [11.15]$$

The continuous-time replicator equation is then

$$dx_k/dt = x_k[f_k(x) - \bar{f}(x)], \qquad [11.16]$$

with $\bar{f}(x) = \sum_k x_k f_k(x)$. This equation is extensively discussed in an impressive book by Hofbauer and Sigmund (1998). For matrix games, the dynamics [11.16] specifies the change in the mean strategy, $\bar{p} = \sum_k x_k p_k$ and the payoff $E(p, q)$ can be expressed in terms of a payoff matrix. Hofbauer and Sigmund (1998) show that a strategy $\hat{p}$ is an ESS of the matrix game if and only if it is strongly stable, in the sense that under the dynamics [11.16], the mean strategy converges to $\hat{p}$ provided that it starts out at a point sufficiently close to $\hat{p}$. So for the continuous-time replicator equation, an ESS corresponds to a dynamically stable population strategy. As we shall see, however, for other kinds of evolutionary dynamics this form of stability is not a general property of uninvadable strategies.

11.5.2 Adaptive dynamics and invasion fitness

Any evolutionary dynamics where natural selection plays a role could be described as an adaptive dynamics, but the term has come to be used in particular for evolutionary sequences of steps where in each step a mutant strategy has a chance to invade and replace a resident strategy, or possibly, invade without ousting an alternative, thus creating polymorphism (Geritz et al., 1998; Hofbauer and Sigmund, 1998; Metz et al., 1996). A basic tool for the study of adaptive dynamics is the concept of invasion fitness, which plays the role of determining the probability with which a mutant can invade. Let s denote a strategy or trait, which we take to be an n-dimensional real vector. For a population monomorphic for s, the invasion fitness $F(s', s)$ of a mutant trait s' has the interpretation of a dominant Lyapunov exponent (Metz et al., 1992), corresponding to the mean rate of change of the logarithm of the size of the (small) mutant gene

subpopulation. So, when the mutant is the same as the resident, we have $F(s, s) = 0$. In the examples of sex-ratio evolution discussed in Section 11.2, invasion fitness would be the logarithm of the leading eigenvalue of the mutant population projection matrix. A mutant with $F < 0$ has no chance of invading (in a large population), whereas one with $F > 0$ might invade. If one takes into account that this mutant could go extinct during an initial phase of low mutant copy number, one finds that the probability of invasion is proportional to $F(s', s)$ (Dieckmann and Law, 1996).

   If a population is at an ESS, the adaptive dynamics cannot lead away from it, but it is also of interest to ask if trait-substitution sequences will lead toward the ESS. For one-dimensional trait spaces, this question of so-called convergence stability has been much studied (e.g., Eshel, 1983; Taylor, 1989). A basic idea is that the selection gradient

$$\partial F(s', s)/\partial s'|_{s'=s} \qquad [11.17]$$

should point toward a convergence stable point, resulting in the criterion that

$$\frac{\partial^2 F(s', s)}{\partial^2 s'^2} + \frac{\partial^2 F(s', s)}{\partial s' \partial s} < 0 \quad \text{at } s' = s \qquad [11.18]$$

should hold for a convergence stable s. This criterion is not equivalent to uninvadability, so there can be an uninvadable s that evolutionary change does not approach but rather moves away from. Furthermore, there can be local fitness minima that are convergence stable. These are called branching points (Metz et al., 1996; Geritz et al., 1998) and are associated with the evolutionary emergence of polymorphism.

   In multidimensional strategy spaces, the distinction between uninvadability and evolutionary convergence is even greater (Leimar, 2009), in that genetic correlations between strategy components can influence evolutionary trajectories. It is a general phenomenon that evolutionary change is guided by, but not fully determined by fitness. The possible influence of the mutation process in directing evolutionary change will be greater in higher-dimensional phenotype spaces, simply because with genetic correlations there are more possibilities for bigger gains in some trait component to trade off against smaller gains or even losses in other components.

11.5.3 Gene-frequency dynamics and the multilocus mess

Short-term evolutionary change is often not the result of natural selection operating on new mutations, but rather the consequence of selection on already existing genetic variation, sometimes called standing genetic variation. This variation is also important in artificial selection, so the matter of responses to selection that only involve gene- and genotype-frequency dynamics, without new mutations entering a population, is of great practical importance. In practical applications, quantitative genetics (Falconer and Mackay, 1996) is often used to investigate and predict the response to selection, and the approach has also been extended to study long-term evolution (e.g., Lande, 1981). The

basic idea is that the response to selection depends on the presence of additive genetic variation in the traits in question. Over the longer term, new mutations can replenish the supply of additive variation. Evolutionary quantitative genetics is an often used modeling alternative to adaptive dynamics.

There is, however, a difficulty that appears if one wants to base a theory of adaptive change solely on gene- and genotype-frequency dynamics, without considering new mutations. Quite some time ago, Moran (1964) and Karlin (1975) showed that one can readily find two-locus systems where the mean fitness of a population decreases over time. As a sort of resolution of this seeming dilemma, Eshel (1996), Hammerstein (1996), and Weissing (1996) pointed out that if one allows for a sufficiently wide range of mutations, long-term evolution is not constrained by the idiosyncrasies of multilocus genotype-frequency dynamics.

11.5.4 Finite populations and stochasticity

In finite populations, the randomness of reproduction and survival can have a noticeable influence on gene-frequency dynamics. The study of genetic drift at selectively neutral loci is a major endeavor in population genetics. Random changes in gene frequencies can also modify and even act in opposition to natural selection. This could be particularly important if, for instance, genetic drift allows a population to move from a local fitness peak to another higher peak, with chance events driving it across the fitness valley between peaks. There are many variants on this theme in the history of evolutionary thinking, with Wright's (1932, 1977) shifting balance theory being the most prominent. There is no consensus in biology about the importance for long-term evolution of random movements between selective equilibria (e.g., Coyne et al., 1997, question the importance of the shifting balance theory), but even so one should keep in mind what these processes might achieve.

In game theory, the idea that external shocks or an intrinsically noisy learning process can correspond to equilibrium selection (Young, 1993) has been put forward, and more recently this kind of thinking gained support in biologically oriented game theory (e.g., Nowak et al., 2004). Lacking decisive empirical studies, the contribution of random shifts to long-term evolution remains an open question. One should however keep in mind that the probability of a random shift from one equilibrium to another will depend very strongly on population sizes, so for these processes to play a major role, important evolutionary changes should sometimes happen in very small populations, and this is a significant constraint.

11.6. INTRAGENOMIC CONFLICT AND WILLFUL PASSENGERS

Although most genes probably have a function that serves the organism as a whole, some genetic elements (genes or larger parts of DNA) have properties that enhance

their own transmission relative to the rest of an individual's genome. These are called selfish genetic elements and are excellently reviewed by Werren et al. (1988) and Burt and Trivers (2006). Selfish elements are in conflict with the rest of the genome and thus fall within the domain of evolutionary game theory. Conceptually speaking now, what is a genetic conflict? Hurst et al. (1996) proposed the following definition: "Genes are in conflict if the spread of one gene creates the context for the spread of another gene, expressed in the same individual, and having the opposite effect." Evolutionary game theory can be helpful in identifying genetic conflict as such. For instance, applying the concept of reproductive value as a measure of Darwinian utility (as was done in Section 11.2) to a genetic element that is transmitted to a mother's daughters but not to her sons, it is evident that sons have zero utility, seen from the strategic perspective of the element. Even so, it usually makes little sense to offer anything like a "solution concept" for genetic conflict. The power of the players in genetic games depends too much on mechanistic detail (*cf.* Section 11.1), and there is often a never-ending arms race.

11.6.1 Meiotic drive

In organisms that carry pairs of chromosomes, each of these chromosomes usually has a 50% chance of transmission to offspring. Some chromosomes contain "selfish regions" that enhance this percentage at the expense of the paired chromosome's transmission, a phenomenon called meiotic drive. These regions may contain "killer genes" and "target genes," which protect the selfish element from killing itself. An example is the so-called t-haplotype found in in natural populations of the house mouse. Males carrying a chromosome with this selfish genetic element transmit the chromosome to approximately 90% of their offspring. Males carrying two copies of the t-haplotype are sterile. Furthermore, both males and females have reduced viability if they carry two copies of the t-haplotype As a consequence, this particular selfish element cannot spread to fixation in a population (e.g., Charlesworth, 1994b)

Meiotic drive genes are known from many animal species, including fruit flies and mosquitos. The vast majority of driving genetic elements are located on sex chromosomes, in which case they bias the sex ratio (see Jaenike, 2001, for a review). Many theory-guided sex-ratio studies have therefore led to the discovery of previously unknown selfish genetic elements—an unforeseen triumph for Düsing, Fisher, Charnov, and other developers of sex-ratio theory.

11.6.2 Example of an ultraselfish chromosome

Werren (1991) made an exciting discovery that even tops the story of meiotic drive. In the parasitoid wasp *Nasonia vitripennis*, he found small parasitic chromosome fragments—referred to as *PSR*, which stands for "paternal sex ratio"—and investigated their basic properties and population dynamics. These fragments are so-called B-chromosomes and exhibit the maximal degree of genetic selfishness found in nature. Werren and

Stouthamer (2003), therefore, called them "the ultimate selfish genetic elements." In a male, *PSR* first coexists peacefully with the wasp's regular chromosomes. But the peace is hollow. As soon as these regular chromosomes are passed on to a female's egg, a "magic hand" destroys them all with great efficacy. The presence of *PSR* is thus detrimental to the male's entire genome.

As a game theorist one has to wonder about the strategic advantage of this massive destruction. There is a hidden benefit. *PSR*—not being a regular chromosome—has problems with transmission through the female's germ line. The obstacle lies in the detailed mechanics of how ova are generated, and *PSR* would often get stranded during meiosis. By destroying the paternal chromosome after fertilization it acts as a "gender bender" and transforms the diploid female organism into a haploid organism that—according to the sex-determination system of wasps—develops into a male. This individual's sperm will carry *PSR* into the next generation and *PSR* will again transform daughters into sons, starting a new reproductive cycle of this selfish "player."

11.6.3 Endosymbionts in conflict with their hosts

Many organisms have microbial passengers. Humans, for example, have more bacterial symbionts than their bodies have cells. Our individual survival depends strongly on microbial cooperation. Even mitochondria, now known as "organelles" and as the "power plants" of animal and plant cells, used to be microbial passengers. About two billion years ago, they still were "autonomous" bacterial organisms. At some point, they became endosymbiotic partners of other kinds of bacteria that evolved into nucleated cells. The endosymbionts subsequently lost much of their genetic autonomy and are now largely controlled by genes located in the nucleus of the eukaryotic cell.

Mitochondria and some intracellular bacteria are transmitted via eggs from mother to offspring but are not transmitted via sperm. Such uniparental transmission has a remarkable theoretical consequence, highlighted by Cosmides and Tooby (1981). Whenever mitochondria are passed on to a male organism, this results in a dead end for their own reproduction. They should thus be under strong selection to manipulate the reproductive system of the host and increase as much as possible the fraction of females in host offspring. Taking into account, however, that mitochondria have very few genes left in their own genomes, it seems hardly possible for them to respond evolutionarily to the selection pressure just described. Yet, in plants, such as corn and rye, mitochondrial variants do exist that target the pollen-producing anthers and disrupt their development (Burt and Trivers, 2006). The otherwise highly cooperative mitochondria act here as enemies of male tissue—a striking example of how the sex ratio conflict described by Cosmides and Tooby can manifest itself in nature.

For us humans, the conflict between mitochondria and their hosts has an irritating aspect. Since men do not transmit mitochondria, the latter would not be punished by natural selection if they harmed the former. Frank and Hurst (1996) suspect that this

could play an important role in the understanding of human male diseases, such as the widely observed aberrations in sperm motility and male fertility. They opened a still underexplored research area where evolutionary game theory meets medicine and thus takes part in a broader scientific endeavor initiated by Nesse and Williams (1994) as "evolutionary medicine."

11.6.4 *Wolbachia*—master manipulators of reproduction

As manipulators of their hosts, mitochondria look like beginners compared to *Wolbachia*, their closest living relatives in the bacterial world. *Wolbachia* are intracellular passengers of insects, mites and other arthropods. They share their mode of inheritance with that of mitochondria and have found several impressive ways to alter the sex ratio, which puts them in conflict with the nuclear genome of their hosts. Their repertoire of manipulative skills (Werren et al., 2008) includes *feminization,* the transformation of genetic males into egg producers, *induction of parthenogenesis,* a mode of reproduction that leads to the exclusive production of daughters, and *male killing*, a destructive interference with male embryonic development. With respect to evolutionary medicine, it is of interest that the most typical manipulation exerted by *Wolbachia* is a modification of sperm causing male infertility in matings with uninfected females.

   Koehncke et al. (2009) explore the strategic options for hosts to counter the adverse action of their bacterial passengers. It turns out from their analysis that – in an evolutionary arms race – host populations would have a fair chance of driving *Wolbachia* to extinction. This seems inconsistent with the empirical estimate that 40 percent (Zug and Hammerstein, 2012) or even more of all arthropod species are infected. Zug et al. (2012) resolve this puzzle by considering an epidemiological model in evolutionary time, where *Wolbachia* can infect new species before becoming extinct in a given one, and where resistance against *Wolbachia* attenuates over time in an uninfected species. This way the master manipulator can save its neck, and the host–parasite game can finally be understood on a long time scale in a species-overarching context. The games *Wolbachia* play happen at different time scales.

11.7. COOPERATION IN MICROBES AND HIGHER ORGANISMS

Game theorists have used models like the Prisoner's dilemma and related empirical paradigms to demonstrate the obstacles to cooperation in a world where players act entirely according to their self-interest. For animals, plants, and microbes, however, these obstacles are often removed through the effect of genetic relatedness. When participants in a cooperative endeavor are genetic relatives, they may individually obtain a substantial share of their partners' success through indirect transmission of genes. This is the core argument of classical kin selection theory (Hamilton, 1964a,b) and enables us, for example, to understand the high degrees of sociality found in ants, wasps, and

bees. In fact, kin selection often "steals the show" from game theory when cooperative phenomena are to be explained. With this caveat in mind, let us now focus on the wisdom of game theory.

11.7.1 Reciprocal altruism

Evolutionary biologists use the term "altruism" for acts that are costly to the actor and beneficial to others. Their notion of altruism is solely based on the fitness consequences of behavior and leaves open the psychological question of whether there is a true concern for others. Consider now the case of an altruistic "donor" who provides support to a "receiver" in need of help. When there is some degree of genetic relatedness between donor and recipient, kin selection might elegantly explain this altruism by showing that the indirect fitness benefits compensate the direct fitness losses of the donor. In contrast, when there is no genetic relatedness, altruism remains a puzzle.

Can game theory help us resolve this puzzle? Trivers (1971) created in biology the paradigm of "reciprocal altruism," which closely relates to the theory of repeated games also addressed by Axelrod and Hamilton (1981), and more critically by Selten and Hammerstein (1984) as well as Boyd and Lorberbaum (1987). Trivers recognized that altruism has a chance to evolve in the context of repeated interactions if the roles of donor and recipient alternate between interacting, unrelated organisms. He considered the strategy of "reciprocal altruism," which is to help "by default" the partner in a repeated game but mirror refusal of help with a refusal to help. Assuming that the cost of a donor's help is smaller than the benefit to a receiver, that there are many repeated interactions, and that a sufficient share of a population plays reciprocal altruism, this very strategy will not be punished by negative selection. It simply pays donors to help because help begets help—this is how Trivers made helping lose its altruistic flavor.

Wilkinson (1984) presented a vampire bat example of reciprocal altruism that received much attention in biology and the social sciences. As the name indicates, vampire bats feed on blood, mostly from mammals. They live in colonies and hunt with varying success in the dark. After about three days of fasting a bat would die from starvation but hungry bats often receive help through a "blood donation," in which a donor regurgitates food to the hungry receiver. In his experiment, Wilkinson used bats from two colonies and controlled experimentally the access to food (blood). He showed that donations were more likely to come from those individuals that had already received a donation from the receiver than from those that had not.

The vampire bat example may look like reciprocal altruism. There are major problems, however, with Wilkinson's otherwise fascinating study. He did not provide any evidence for internal "bookkeeping" of help refusals, and we do not know from his experiment to what extent a refusal to help would be mirrored at all. Furthermore, the bats live in kin groups and help occurred mainly within the kin groups used in the

experiment. Perhaps, this study provided evidence for kin selection rather than reciprocal altruism. Based on a recent experiment, Carter and Wilkinson (2012) argue that kin selection may not be as important as it looked in the original study but they do not tackle the crucial bookkeeping issue. Hammerstein (2003) and Clutton-Brock (2009) criticize Wilkinson's example and come to the more general conclusion that the evidence for Trivers's reciprocal altruism is extremely scarce in nature. We think that the theory of repeated games has largely failed in biology. There are possible exceptions in the world of primates were the evidence for reciprocal altruism is so mixed and imprecise that it would be too cumbersome to present them here.

11.7.2 Indirect reciprocity

Nowak and Sigmund (1998) studied a model in which the entire population consists of only 100 individuals. Each generation 500 interactions take place where a randomly chosen "recipient" asks a randomly chosen "donor" for help. The donor can refuse to help but the entire community observes everyone's behavior. Individuals each have a reputation, which increases whenever the individual helps and decreases whenever help is refused. Given the high degree of stochasticity in their model, Nowak and Sigmund asked how much helping would on average be seen if one lets this population evolve on a long time scale. They found the average helping rate to be high and this was due to the frequent occurrence of a so-called "image-scoring strategy," which is to help those with sufficiently high reputation and not to help otherwise.

Leimar and Hammerstein (2001) pointed out that in the given model the image-scoring strategy contains an unexplained altruistic element because every time an individual refuses help it loses some of its reputation. They investigated a similar model with a more realistic, sizeable population that consists of 100 groups of 100 individuals, and where migration between groups occurs. As expected, the image-scoring strategy does not evolve in this model. The study by Nowak and Sigmund demonstrates a basic insight from population genetics, namely that selection works differently in populations with a small compared to a large "effective population size."

Sugden (1986) made the earliest suggestion of how indirect reciprocity might actually work. His approach differs from Nowak and Sigmund (1998) mainly in how reputation is updated. Sugden's players do not lose reputation when they fail to help those with a bad reputation. Engelmann and Fischbacher (2003) conducted a human experiment where Sugden's reputational logic seemed to work. This logic might be cognitively too demanding, however, to be realistic for animals. Wedekind and Milinski (2000) and Milinski et al. (2001) showed in experiments with humans that image scoring can occur but it remains an open question why this is so. In a theoretical study, Panchanathan and Boyd (2004) explored cost-free ways of punishing that would allow indirect reciprocity to work. Yet, outside the human world and perhaps with some primate exceptions, indirect reciprocity has not been shown to be broadly significant in biology.

11.7.3 Tragedy of the commons

In nature, iron is essential for elementary processes such as DNA synthesis. Bacteria have found an efficient method by which they can supply themselves with this metal. They secrete compounds that have a chemical affinity to iron and "grab" it. These so-called siderophores enable the bacteria to "fish" for the resource under discussion. A catch is then consumed via reuptake of the iron-catching molecules. If anything in biology looks like a "tragedy of the commons" in the sense of Hardin (1968), this is it. The production of siderophores is costly and serves producers as well as scroungers as a "meal."

How can this iron fishery work if it offers a strong incentive for free riding? This is an interesting conceptual question. As Ostrom (1990) explained so beautifully in her work on the tragedy of the commons, human societies have found many ways to counter free riding through institutions that change the structure of the game. Needless to say, for example, that an efficient police controlling resource use will make free riding unprofitable. But bacteria are different from human societies. They cannot easily design institutions. Kin selection, however, is a candidate process that might restrict the amount of free riding.

Griffin et al. (2004) studied a soil bacterium, *Pseudomonas aeruginosa*, to examine the role of kin selection in limiting the amount of free riding. They used an experimental evolution approach and used lab populations with different compositions of clones, so that the degree of relatedness varied between evolving populations. Griffin et al. showed that higher levels of siderophore production evolved in the higher relatedness treatments.

As in many other bacterial systems, kin selection plays here the dominant role in explaining cooperation. Without the influence of game theory, however, biologists would have been much less inclined to engage in experimental activities like the one presented here.

11.7.4 Common interest

Kin selection is very important but the biological theory of cooperation has more "tricks up its sleeve," and one is the effect of common interest. Following now Leimar and Hammerstein (2010), the basic idea of common interest is that individual organisms have a stake in the success of others or in the success of a joint project. This idea is translatable into the world of genes or larger genetic elements. Joint projects can be as simple as cooperative hunting in carnivores or as elaborate as the contribution of different genes and regulatory elements to the development of a multicellular organism. The common interest perspective plays an important role in biological attempts to understand the evolution of organismality (Queller and Strassmann, 2009; Strassmann and Queller, 2010).

How can common interest as such evolve? First, if partners are likely to stay together in the future, for instance because of costs associated with partner change, common

interest would typically become greater. The coupling of reproduction is another general reason for greater common interest. The extreme form of cooperation found in the genes operating in an organism provides an example. A comprehensive survey on selfish genetic elements (Burt and Trivers, 2006) confirms the view that most genes act most of the time to the benefit of the organism. This high degree of intragenomic cooperation is based on the genes' shared interest to "keep the organism running" that carries them into the next generation and "delivers" its passengers in a rather fair way. Fair transmission of genes in animals and plants occurs partly because gene movements are strictly regulated during mitotic and meiotic cell divisions. Molecular devices, such as the "spindle check point," supervise these "passenger movements." The alignment of gene interests through molecular control mechanisms represents one of the major transitions in evolution (Maynard Smith and Szathmáry, 1995).

It is important to understand how evolution can increase the dependence of partners on each other. The following plant–animal symbiosis documents this impressively. *Acacia* plants house mutualistic ants as their "body guards" and possess specific glands to provide them with extrafloral nectar, a sucrose-free nutritive product (Heil et al., 2005; Kautz et al., 2009). Due to the absence of sucrose the *Acacia's* nectar is unattractive to ants in general. The mutualistic *Pseudomyrmex* ants, however, are specialized to live on *Acacia* and depend strongly on this plant's specific nectar. They have even lost the capability to digest sucrose (Kautz et al., 2009). The dependence most likely evolved because the plant was under selection to become less attractive to nonmutualistic ants, and the mutualistic ants were forced to adapt to the evolutionarily changing *Acacia* to be efficient in their main habitat.

11.7.5 Common interest through lifetime monogamy

In the evolutionary view of the animal world, a female and her mate share an interest in their joint offspring but interests typically diverge when it comes to the question of how to split the work involved in raising that offspring (see Houston et al., 2005, for a review of modeling approaches to conflict between parents over care). Males may even benefit from actively harming female partners. The fruit fly *Drosophila melanogaster* is a naturally promiscuous species where males add toxic components to their seminal fluid. When they mate, these toxic components increase the fertilization chances of their sperm at the expense of the female's long-term reproduction and survival (Chapman et al., 1995). In the absence of mate fidelity, it is indeed possible for such harmful behavior to evolve because the male's reproductive success does not depend on the female's long-term survival. This makes *D. melanogaster* an interesting study object for experimental evolution of cooperation.

What if the fruit flies showed more partner fidelity? Holland and Rice (1999) conducted an evolutionary experiment to explore how monogamy can alter the harm males inflict on their female partners. In the evolving lab population, they imposed

monogamy by letting each female house individually with one randomly assigned male. After 47 generations, males had evolved to be less harmful to their mates and females where less resistant to male-induced harm. This demonstrates impressively the role monogamy can play in the evolution of cooperation.

Lifetime monogamy is likely to have played a key role in the evolution of social insects. As Boomsma (2009) reports, "all evidence currently available indicates that obligatory sterile eusocial castes only arose via the association of lifetime monogamous parents and offspring." This is extremely interesting because lifetime parental monogamy induces a reliable common interest between parents and their offspring. This is so because the average genetic relatedness between siblings is then equal to the relatedness between parent and offspring. Children may then stay with their parents as helpers at the nest if their positive effect on parental reproductive success is a little higher than the gains possible through own reproductive attempts (a standard kin selection argument). After presenting this simple but highly consequential argument, Boomsma discusses the possible counterargument that his line of reasoning makes eusociality "too easy to evolve." The rare occurrence of lifetime monogamy in nature and various other facts weaken this counterargument.

11.8. BIOLOGICAL TRADE AND MARKETS

As described by Leimar and Hammerstein (2010), social partner choice (Bull and Rice, 1991) and the concept of a biological market (Noë et al., 1991; Noë and Hammerstein, 1994, 1995) have gained increasing attention of researchers who explore the evolutionary stability of cooperation among microbes, animals, and plants. This may seem surprising because conventional market models in economics rely on idealizations that biologists cannot refer to (Bowles and Hammerstein, 2003). For example, many market models describe interactions in which the goods and services traded are subject to complete contracts that are enforceable at no cost. These models do not apply to biology since nonhuman organisms do not sign contracts and even if they did, these contracts could not be enforced. Under such circumstances, one cannot expect biological markets to clear in the sense that supply matches demand at evolutionary equilibrium.

The most basic aspect of a biological market is the possibility to choose between offers in trade-like interactions where some exchange of "commodities" takes place. There is ample evidence for such choices, and this is important for the understanding of cooperation. Trades in nature often take place in mutually beneficial interactions between members of different species (interspecific mutualism). These interactions tend to follow the pattern of "hosts" offering food or shelter to "visitors" while gaining benefits from the latter (Cushman and Beattie, 1991). If visitors are sufficiently mobile, this enables them to exert choice between potential hosts.

11.8.1 Pollination markets

Pollination biology has a long tradition of thinking in terms of market analogies. Perhaps the first use of this analogy was made by Von Frisch (1967), who wrote about "regulation of supply and demand on the flower market." A large body of work now supports the view that, on a rather short time scale, insect-flower systems may approach an equilibrium with approximately equal profitability for visitors to different hosts (Schaffer et al., 1983). We know in addition that the choosiness of pollinators can strongly influence the composition of host communities. Dramatic changes in community structure occur, for example, when an invading plant outcompetes the residents, offering a particularly rich nectar to lure pollinators away from the native plants (Chittka and Schürkens, 2001). There is also evidence from experiments with artificial flowers showing the dramatic impact rewards can have on pollinator visitation rates (Internicola et al., 2007). Many other systems exist where visitors choose among hosts. These include ants visiting aphids (Fischer et al., 2001; Völkl et al., 1999) and client reef fish visiting cleaner wrasse stations (Bshary and Noë, 2003; Bshary and Schäffer, 2002).

11.8.2 Principal-agent models, sanctioning and partner choice

The reverse choice occurs when a stationary individual can accept or reject incoming "applicants" for a "position." For example, the power of strong males to keep weak males off their territory enables them to act as if they were "principals" in trades with the less strong "agents" applying for entry to their territory. Bowles and Hammerstein (2003) have therefore likened certain biological scenarios to principal–agent problems in economics. Among possible examples are the males of a songbird called lazuli bunting (the name alludes to a well-known gemstone). Bright-plumaged males, the principals, allow less competitive dull-plumaged males, the agents, to settle at the periphery of their high-quality territories (Greene et al., 2000). This deal is beneficial to both principal and agent because the latter will attract a new female to the territory and both will mate with her. Note that the principal can enforce his share of the mating activities but if he goes too far and monopolizes access to this female, the agent will have no reason to care for her offspring. In this way, the trade works without an enforceable contract.

Other possible examples are large male fiddler crabs accepting smaller territorial neighbors for help with territorial defense (Backwell and Dennions, 2004; Detto et al., 2010). There are also indications of choosiness by hosts in legume–rhizobium mutualism (Heath and Tiffin, 2009). *Rhizobium* is a soil bacterium that forms an association with the roots of legumes and fixes nitrogen. Admittedly, the mechanisms by which a plant could recognize and choose a beneficial *Rhizobium* are currently unknown. Termination of interactions with unprofitable visitors is frequently thought of as a form of sanction resulting in partner choice (Bull and Rice, 1991; Kiers et al., 2003; Kiers and Denison, 2008; Simms et al., 2006).

From the range of empirical data, it seems that choice in biological markets is a widespread and basic mechanism that stabilizes cooperation in nature. This mechanism can operate in situations where there is little or no common interest and where partners only meet once. Note, however, that choosiness will often be costly and there must be sufficient variability to choose from in order to offset such costs (McNamara and Leimar, 2010; McNamara, 2013).

11.8.3 Supply and demand

Even if biological markets cannot be generally expected to clear, there are a number of examples that show some similarity to the influence of variation in supply and demand in idealized markets (Noë and Hammerstein, 1994, 1995). This is nicely demonstrated by mutualisms where ants protect the larvae of lycaenid butterflies from enemies and receive food in return. It has been found that a larva will sharply increase its delivery of food when it perceives itself to be under attack from enemies or when ants return to it after an interruption in attendance, i.e., when the larva's need for ant protection is particularly high (Agrawal and Fordyce, 2000; Axén et al., 1996; Leimar and Axén, 1993).

This kind of influence of the availability and value of partners may also be present in cleaning mutualisms, where members of the cleaner fish species "run cleaning stations" and a number of client fish species visit these stations to be purged from skin parasites. As reviewed by Bshary and Noë (2003), local clients for which long-distance moves are very costly receive less thorough cleaning than visitors from further away, who might more readily switch between cleaning stations and thereby exert partner choice. This is what the economic theory of monopolistic competition would predict: buyers with few alternative sources of supply will have less advantageous transactions than those who can shop around (Bowles and Hammerstein, 2003). There is also data showing that cleaner service quality improves when clients become scarce (Soares et al., 2008). A similar phenomenon has also been found in the social behavior of vervet monkeys, where the providers of food items were found to receive more grooming when the food was scarce (Fruteau et al., 2009). Such adjustments are potentially general properties of biological markets and are therefore of broad interest.

11.9. ANIMAL SIGNALING—HONESTY OR DECEPTION?

Honest communication sometimes looks like a good in limited supply. Generations of school children, for example, were tricked by their teachers who, perhaps unwittingly, used a fake citation from the classical roman literature to underscore the importance of their educational efforts. In the fake, it is said that education serves to prepare us for our future lives and is not intended to just get us through school. What Seneca really said is the exact opposite: *Non vitae, sed scholae discimus.*

11.9.1 Education and the Peacock's tail

Spence (1973) elaborated on Seneca's caricature of education. In an article that laid the foundation of signaling games in economics, he asked the following question about job markets: Can the acquisition of higher levels of education lead to higher wages even if education fails to improve a person's productivity? Spence's model hinges on the idea that those who apply for a job know more about themselves than the hiring company can easily observe. In real life, this private information can be on anything like health, learning ability, talent, or the efficiency in getting long-term projects done. In the model, there are simply more or less talented "types of persons." A random move assigns the talent to a person. The person can then choose a level of education conditional upon its talent, it being less costly for the more talented to continue in school. Following completion of schooling, firms observe the person's education and make wage offers.

As is well-known today, Spence found that a game-theoretic equilibrium can exist in which education signals talent and higher education implies higher wage. The reason is that only the talented persist in long years of schooling, so employers use years of schooling as a signal of the unobservable trait, talent. This result is remarkable because education is costly in the model and does not increase a person's productivity.

There is a striking parallel between Spence's original signaling game in economics and the so-called "handicap principle" in biology. Without knowing signaling games, the behavioral biologist Zahavi (1975) claimed that animals acquire costly handicaps, such as the peacock's tail, just to impress others. He emphatically maintained that the credibility of signals hinges on their costliness. Zahavi first failed to convince the community of theoretical biologists (e.g., Maynard Smith, 1976). Subsequently, however, Pomiankowski (1987), Grafen (1990a,b), and others showed that Zahavi's verbal idea can be expressed in coherent mathematical models.

In these models—like in Spence's job market—the animal (e.g., a peacock) chooses the size of its handicap (e.g., a giant tail) depending on private information (e.g., body condition). The size of the handicap is the signal perceived by a receiver who aims to gain information about hidden qualities of the sender (e.g, a female checking a potential mate). Bowles and Hammerstein (2003) demonstrated how a few lines of "heuristic algebra" lead to the core of the biological handicap principle—circumventing a number of important technical issues. Their shortcut of Grafen's (1990a,b) approach makes the link with Spence's theory particularly transparent. Grafen himself confronted certain biological aspects of signaling theory that economists are usually unfamiliar with. For example, it is known from Fisher's (1930) model of "runaway selection" that in the context of sexual selection a genetic covariance can build up between (a) genes relevant to mate choice and (b) genes relevant to the traits that are favored through mate choice. Such covariance is of importance because if males carry a trait that is preferentially chosen, their sons will propagate the genes for the attractive trait as well as the genes

for the preference for this trait. This alone can drive the evolution of exaggerated male characteristics (Lande, 1981; Kirkpatrick, 1982).

11.9.2 Does the handicap principle work in practice?

To confront the handicap principle with reality, let us now have a closer look at the signaling games played between male and female widowbirds. Male long-tailed widowbirds are rather small but have an extreme sexual ornament; their tails are about half a meter long. In a famous field experiment, Andersson (1982) truncated the tails of some males and glued the obtained snippets to the tails of others. He showed that males with more than normal-sized tails attract more females. More recently, Pryke and Andersson (2005) did a similar experiment and manipulated the tails of red-collared widowbirds. They demonstrated in particular that (a) females use tail length as the primary mate choice cue, (b) tail length is an indicator of body condition, and (c) tails are costly. Their results confirm the role of mate choice and quality advertising as the main selection pressures behind elongated tails in widowbirds. So here, the handicap principle might indeed be at work and the widowbirds' tails lend empirical support to the basic theory of signaling games.

The analysis of widowbird signaling does not end here though. Do we, for example, understand the evolutionary origin of this system? In their open grassland and savanna habitats, male widowbirds make themselves conspicuous by displaying their impressive tails. Pryke and Andersson (2005) argue that the evolution of elongated tails probably started because it increased conspicuousness (visibility of the male) and that simultaneously or subsequently the exaggerated tail might have become an indicator of male condition and quality. This is an important argument because only those handicaps can evolve that are not a handicap to begin with. For example, female birds would never prefer males that chop off one of their legs just to please Spence, Grafen, and Zahavi. The set of handicaps that can evolve is limited but signaling games are blind to this issue.

Female mate choice in stalk-eyed flies is another possible application of Zahavi's handicap principle (David et al., 2000). Males of these flies have long eyestalks, so their eyes are far apart. Because flies in general do not have this trait, the eyestalks most likely come at some cost. Nevertheless, high phenotypic quality, either from high nutrition or from genes, cause stalk-eyed fly males to develop longer eye stalks. Female stalk-eyed flies prefer to mate with these males thus providing a selective force that might maintain the long eyestalks.

11.9.3 The rush for ever more handicaps, has it come to an end?

Powerful ideas are seductive. Many researchers were mining for examples of Zahavian handicaps like diggers in search for a vein of gold. During this rush, efforts were also made to scrutinize the applicability of the handicap principle. From these efforts, we know that apparently costly signals can be surprisingly cheap and far from a serious handicap. To

illustrate this, consider the so-called parent-offspring conflict (Trivers, 1974). This is a conflict about the allocation of resources from parent to offspring. From a mother's genetic point of view, she is equally related to all her children. The children, however, are more related to themselves than to their brothers and sisters. As a consequence, one would expect individual offspring to always want a little more provisioning from a mother than the mother would want to give—an evolutionary conflict within the family that, in principle, always exists. Signaling plays a role in this conflict because the need for food varies over time, and this need is to some extent private information. It is tempting to interpret the begging behavior of nestling birds as a costly signal because it may, for example, attract predators.

Haskell (1994) tested this idea by playing back begging calls from radios placed in artificial nests. This way he could measure changes in predation rates with changes in begging. Haskell found no effect of begging on predation for nests positioned at sites where the recorded calls might have naturally occurred. McCarty (1996) measured energetic expenditure associated with begging in starlings and tree swallows and found this expenditure surprisingly low. These and many other behavioral studies led various biologists to emphasize the limited scope of the handicap principle (Zollman, 2013). Recent advances in experimental methodology enabled researchers, however, to demonstrate a cost of begging for a few bird species. Haff and Magrath (2011) and similarly Ibáñez-Álamo et al. (2012) showed that elevated nestling calling attracts predators to active, natural nests. Moreno-Rueda and Redondo (2011) found that intensive begging decreases simultaneously the nestlings' growth rate and intensity of immune reactions.

11.9.4 Warning signals and mimicry

Certain animals who, based on their size and general life style, would be regarded as prey by some predators are actually unpalatable to these predators. Larvae of the monarch butterfly (*Danaus plexippus*), for instance, feed on milkweed plants that contain cardiac glycosides, which are toxic to many animals. The monarch larvae, however, do not suffer from ingesting these substances, but sequester them in their bodies. The defense substances are passed on to the adult butterflies, who otherwise would be suitable prey for insectivorous birds. The toxin in the butterflies instead turns them into a powerful emetic, producing extreme nausea when ingested (Brower, 1969). Both the larvae and the adults of the monarch have a distinctive and conspicuous coloration, serving as warning to predators. This type of warning, or aposematic coloration is widespread in nature (Poulton, 1890; Ruxton et al., 2004). An interesting question is then if, and for what reason, the coloration is an honest signal of unpalatability.

The traditional view on warning coloration dates back to discussions between Charles Darwin and Alfred Russel Wallace in the 1860s and proposes that aposematism works because predators learn through experience to associate the coloration with

unpalatability. Naturally, such learning could only happen if, on the whole, there is a statistical correlation between the appearance and the palatability of prey. The correlation need not be perfect, as illustrated by the phenomenon of Batesian mimicry, in which a palatable species is similar in appearance to an aposematic model species, and gains protection through identification mistakes by predators. For the monarch butterfly, the viceroy (*Limenitis archippus*) is a well-studied example of a Batesian mimic (Van Zandt Brower, 1958).

Both Zahavi (1991) and Grafen (1990b) interpret warning coloration as handicap signaling. Grafen develops the idea that palatable prey would often suffer costs if they were conspicuous, because predators find them more readily and learn that they are good to eat, so the honesty of the signal is tested. While this might well be true, the idea that aposematism is best understood as handicap signaling is not widely accepted (e.g., Guilford and Dawkins, 1993), basically for two reasons. First, the strongest and most direct application of the handicap principle would state that only potentially very unpalatable animals have the capacity to produce strong warning signals. To a large extent, the empirical evidence rejects this possibility. For monarch butterflies, Brower (1969) showed that they can be reared on plants that do not contain cardiac glycosides, which makes them palatable to birds but does not change their appearance. Also, studying wild-caught monarchs, Brower (1972) found that there is much variation in the concentration of cardiac glycosides in adult butterflies, both between different areas in North America and between individuals sampled from the same area, such that some individuals would be suitable as prey. There is thus no direct link between unpalatability and appearance, so the signal is not honest in this sense. Second, there is the question of how natural selection in fact has molded warning signals. If this process embodied the handicap principle and conspicuousness is the cost of signaling, there ought to be selection for conspicuousness per se when the signal evolves. The general view is instead that warning signals have been shaped by their role in the learning process, for instance to promote rapid learning and high memorability, and conspicuousness appears mainly as a side effect (Ruxton et al., 2004).

Even so, constraints on the success of Batesian mimics, from being sampled and found to be tasty by predators, throw light on why warning signals are not everywhere corrupted by mimicry, and can maintain an overall correlation between unpalatability and appearance. Mimics are often less numerous than their aposematic models, or show mimetic polymorphism, such that only some individuals are mimetic or that different individuals mimic different models (Mallet and Joron, 1999). In this way, the mimics avoid being too common. There is a frequency dependence in Batesian mimicry, with an advantage of being rare, because predators then have less opportunity, and reason, to learn about the palatable mimics.

As an aside, polymorphic Batesian mimicry appears to be the first biological example to which the term "theory of games" was applied. In his discussion of the nature of

genetic polymorphism, Fisher (1958) elaborated on his early work (Fisher, 1934) on randomized strategies in card play and suggested that such strategies could evolve in prey, to improve their chances of escaping predation. It is perhaps curious that Fisher, who evidently had a strong interest in game theory (he saw himself as one of the originators of this theory), did not propose a link to sex-ratio theory, which seems so natural today, but instead compared polymorphic Batesian mimicry with a mixed equilibrium of a game.

The study of warning coloration in evolutionary biology shows why one may need to understand particular biological mechanisms and how they shape the evolutionary process (cf. section 11.1), and that the usefulness of game theory is primarily as a tool to sharpen the analysis and guide the intuition. So, knowing about signaling games affords us some understanding of the evolution of aposematism – that some factor must limit the proliferation of palatable mimics – but the understanding remains incomplete without deeper insights into the interaction between predators and prey.

Warning coloration is the result of the evolutionary interaction of two complex systems, the developmental machinery producing prey coloration and the neural, cognitive machinery responsible for the learning and generalization of prey appearances by predators. When predators learn to discriminate between unpalatable and palatable prey, the most salient (i.e., striking) aspects of the differences in appearance will act as a focal point of learning; the importance of the salience of stimuli for learning was investigated already by Pavlov (1927). Having learned to discriminate, predators will tend to generalize to new prey appearances in a biased manner, for instance acting as if prey whose appearance further accentuates the learned characteristics of unpalatable prey are even more unpalatable.

This biased response from learned discrimination was first studied by animal psychologists (Spence, 1937; Hanson, 1959), and is a quite general and carefully investigated phenomenon. Leimar et al. (1986) proposed that it could drive the evolution of warning coloration. Together with similar cognitive properties such as memorability, there is thus a plausible account of how warning colors evolve (Ruxton et al., 2004). From this perspective, we can ascribe an evolutionary function to the appearance of the monarch butterfly. The striking and even beautiful coloration has evolved so that—after some learning by a predator—it is effective in evoking in this predator a feeling of revulsion. This insight derives, at least in terms of the ideas it builds on, from outside of game theory.

More generally, there is a trend in contemporary biology to integrate function and mechanisms (Hammerstein and Stevens, 2012; McNamara, 2013; McNamara and Houston, 2009). It is still too early to tell what this trend means for the future of game theory in biology. Perhaps the role of game theory will be diminished, but there is also an alternative, that game theory enriches its framework by incorporating mechanisms. This way it could enter into a more direct confrontation with empirical observation—and with biology.

REFERENCES

Agrawal, A.A., Fordyce, J.A., 2000. Induced indirect defence in a lycaenid–ant association: The regulation of a resource in a mutualism. Proc. R. Soc. B 267, 1857–1861.

Agrawal, A. A., Laforsch, C., Tollrian, R., 1999. Transgenerational induction of defences in animals and plants. Nature 401, 60–63.

Andersson, M., 1982. Female choice selects for extreme tail length in a widowbird. Nature 299, 818–820.

Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. Science 211, 1390–1396.

Axén, A.H., Leimar, O., Hoffman, V., 1996. Signalling in a mutualistic interaction. Anim. Behav. 52, 321–333.

Backwell, P.R.Y., Dennions, M.D., 2004. Animal behaviour: Coalition among male fiddler crabs. Nature 430, 417.

Bergman, M., Olofsson, M., Wiklund, C., 2010. Contest outcome in a territorial butterfly: The role of motivation. Proc. R. Soc. B 277, 3027–3033.

Blows, M.W., Berrigan, D., Gilchrist, G.W., 1999. Rapid evolution towards equal sex ratios in a system with heterogamety. Evol. Ecol. Res. 1, 277–283.

Boomsma, J.J., 2009. Lifetime monogamy and the evolution of eusociality. Philos. Trans. R. Soc. B 364, 3191–3207.

Bowles, S., Hammerstein, P., 2003. Does market theory apply to biology? In: Hammerstein, P., (Ed.), *Genetic and Cultural Evolution of Cooperation*, MIT Press, Cambridge, MA, pp. 153–165.

Boyd, R., Lorberbaum, J.P., 1987. No pure strategy is evolutionarily stable in the repeated Prisoner's Dilemma game. Nature 327, 58–59.

Brower, L.P., 1969. Ecological chemistry. Sci. Am. 220, 22–29.

Brower, L.P., 1972. Variation in cardiac glycoside content of monarch butterflies from natural populations in Eastern North America. Science 177, 426–429.

Bshary, R., Noë, R., 2003. Biological markets: The ubiquitous influence of partner choice on the dynamics of cleaner fish–client reef fish interactions. In: Hammerstein, P., (Ed.), Genetic and Cultural Evolution of Cooperation, MIT Press, Cambridge, MA, pp. 167–184.

Bshary, R., Schäffer, D., 2002. Choosy reef fish select cleaner fish that provide high-quality service. Anim. Behav. 63, 557–564.

Bull, J.J., Charnov, E., 1988. How fundamental are Fisherian sex ratios? Oxford Surv. Evol. Biol. 5, 96–135.

Bull, J.J., Rice, W.R., 1991. Distinguishing the mechanisms for the evolution of co-operation. J. Theor. Biol. 149, 63–74.

Bulmer, M.G., Bull, J.J., 1982. Models of polygenic sex determination and sex ratio control. Evolution 326, 13–26.

Bulmer, M.G., Taylor, P.D., 1981. Worker-queen conflict and sex ratio theory in social hymenoptera. Heredity 47, 197–207.

Burt, A., Trivers, R., 2006. Genes in Conflict: The Biology of Selfish Genetic Elements. Harvard University Press, Cambridge, MA.

Carter, G.G., Wilkinson, G.S., 2012. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. Proc. R. Soc. B 280, 2012–2573.

Carvalho, A.B., Sampajo, M.C., Varandas, F.R., Klaczko, L.B., 1998. An experimental demonstration of Fisher's principle: Evolution of sexual proportion by natural selection. Genetics 148, 719–731.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Second Ed. Sinauer, Sunderland, MA.

Chapman, T., Liddle, L.F., Kalb, J.M., Wolfner, M.F., Partridge, L., 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. Nature 373, 241–244.

Charlesworth, B., 1994a. Evolution in Age-Structured Populations. Cambridge University Press, Cambridge, UK.

Charlesworth, B., 1994b. The evolution of lethals in the t-haplotype system of the mouse. Proc. Biol. Sci. 22, 101–107.

Charnov, E.L., 1982. The Theory of Sex Allocation. Princeton University Press, Princeton, NJ.

Charnov, E.L., Bull, J., 1977. When is sex environmentally determined? Nature 266, 828–830.

Chittka, L., Schürkens, S., 2001. Successful invasion of a floral market. Nature 411, 653.

Clutton-Brock, T., 2009. Cooperation between non-kin in animal societies. Nature 462, 51–57.

Conover, D.O., Van Voorhees, D.A., 1990. Evolution of a balanced sex ratio by frequency-dependent selection in a fish. Science 250, 1556–1558.

Cosmides, L.M., Tooby, J., 1981. Cytoplasmic inheritance and intragenomic conflict. J. Theor. Biol. 89, 83–129.

Coyne, J.A., Barton, N.H., Turelli, M., 1997. Perspective: A critique of Sewall Wright's shifting balance theory of evolution. Evolution 51, 643–671.

Cushman, J.H., Beattie, A.J., 1991. Mutualisms: Assessing the benefits to hosts and visitors. Trends Ecol. Evol. 6, 193–195.

Darwin, C., 1871. The Descent of Man and Selection in Relation to Sex, 2nd Ed., John Murray, London; 1874.

David, P., Bjorksten, T., Fowler, K., Pomiankowski, A., 2000. Condition-dependent signalling of genetic variation in stalk-eyed flies. Nature 406, 186–188.

Davies, N.B., 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): The resident always wins. Anim. Behav. 26, 138–147.

Detto, T., Jennions, M.D., Backwell, P.R.Y., 2010. When and why do territorial coalitions occur? Experimental evidence from a fiddler crab. Am. Nat. 175, E119–E125.

Dieckmann, U. Law, R., 1996. The dynamical theory of coevolution: A derivation from stochastic ecological processes. J. Math. Biol. 34, 579–612.

Düsing, C., 1883. Die Factoren welche die Sexualität entscheiden. Jenaische Zeitschrift für Naturwissenschaft 16, 428–464.

Düsing, C., 1884a. Die Regulierung des Geschlechtsverhätlnisses bei der Vermehrung der Menschen, Tiere und Pflanzen. Jenaische Zeitschrift für Naturwissenschaft 17, 593–940.

Düsing, C., 1884b. Die Regulierung des Geschlechtsverhältnisses bei der Vermehrung der Menschen, Tiere und Pflanzen. Gustav Fischer: Jena.

Engelmann, D., Fischbacher, U., 2003. Indirect reciprocity and strategic reputation building in an experimental helping game. Games Econ. Behav. 67, 399–407.

Enquist, M., Leimar, O., 1983. Evolution of fighting behaviour: Decision rules and assessment of relative strength. J. Theor. Biol. 102, 387–410.

Enquist, M., Leimar, O., 1990. The evolution of fatal fighting. Anim. Behav. 39, 1–9.

Eshel, I., 1983. Evolutionary and continuous stability. J. Theor. Biol. 103, 99–111.

Eshel, I., 1996. On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. J. Math. Biol. 34, 485–510.

Falconer, G.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, Fourth ed. Addison Wesley Longman, Harlow, Essex, UK.

Fischer, M.K., Hoffmann, K.H., Völkl, W., 2001. Competition for mutualists in an ant-homopteran interaction mediated by hierarchies of ant attendance. Oikos 92, 531–541.

Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.

Fisher, R.A., 1934. Randomization, an old enigma of card play. Math. Gaz. 18, 294–297.

Fisher, R.A., 1958. Polymorphism and natural selection. J. Ecol. 46, 289–293.

Frank, S.A., Hurst, L.D., 1996. Mitochondria and male disease. Nature 383, 224.

Fruteau, C., Voelkl, B., van Damme, E., Noë, R., 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. Proc. Natl. Acad. Sci. USA 106, 12007–12012.

Geritz, S.A.H., Kisdi, É., Meszena, G., Metz, J.A.J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evol. Ecol. 12, 35–57.

Gould, S.J., Lewontin, R.C., 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. Proc. R Soc. B 205, 581–598.

Grafen, A., 1987. The logic of divisively asymmetric contests – respect for ownership and the desperado effect. Anim. Behav. 35, 462–467.

Grafen, A., 2006. A theory of Fisher's reproductive value. J. Math. Biol. 53, 15–60.

Grafen, A., 1990a. Biological signals as handicaps. J. Theor. Biol. 144, 517–546.

Grafen, A., 1990b. Sexual selection unhandicapped by the Fisher process. J. Theor. Biol. 144, 473–516.

Greene, E., Lyon, B.E., Muehter, V.R., Ratcliffe, L., Oliver, S.J., Boag, P.T., 2000. Disruptive sexual selection for plumage coloration in a passerine bird. Nature 407, 1000–1003.

Griffin, A.S., West, S.A., Buckling, A., 2004. Cooperation and competition in pathogenic bacteria. Nature 430, 1024–1027.

Guilford, T., Dawkins, M.S., 1993. Receiver psychology and the design of animal signals. Trends Neurosci. 16, 430–436.

Haff, T.M., Magrath, R.D., 2011. Calling at a cost: Elevated nestling calling attracts predators to active nests. Biol. Lett. 7, 493–495.

Hagen, E.H., Sullivan, R.J., Schmidt, R., Morris, G., Kempter, R., Hammerstein, P., 2009. Ecology and neurobiology of toxin avoidance and the paradox of drug reward. Neuroscience 160, 69–84.

Hamilton, W.D., 1964a. The genetical evolution of social behaviour. I. J. Theor. Biol. 7, 1–16.

Hamilton, W.D., 1964b. The genetical evolution of social behaviour. II. J. Theor. Biol. 7, 17–52.

Hamilton, W.D., 1967. Extraordinary sex ratios. Science 156, 477–488.

Hamilton, W.D., May, R.M., 1977. Dispersal in stable habitats. Nature 269, 578–581.

Hammerstein, P., 1981. The role of asymmetries in animal contests. Anim. Behav. 29, 193–205.

Hammerstein, P., 1996. Darwinian adaptation, population genetics and the streetcar theory of evolution. J. Math. Biol. 34, 511–532.

Hammerstein, P., 2003. Why is reciprocity so rare in social animals? A protestant appeal. In: Hammerstein, P., (Ed.), Genetic and Cultural Evolution of Cooperation, MIT Press, Cambridge, MA, pp. 84–93.

Hammerstein, P., 2012. Towards a Darwinian theory of decision making: Games and the biological roots of behavior. In: Binmore, K., Okasha, S., (Eds.), Evolution and Rationality, Cambridge University Press, Cambridge, NY, pp. 7–22.

Hammerstein, P., Boyd, R., 2012. Learning, cognitive limitations, and the modeling of social behavior. In: Hammerstein, P., Stevens, J.R., (Eds.), Evolution and the Mechanisms of Decision Making, MIT Press, Cambridge, MA, pp. 319–343.

Hammerstein, P., Riechert, S.E., 1988. Payoffs and strategies in territorial contests: ESS analyses of two ecotypes of the spider *Agelenopsis aperta*. Evol. Ecol. 2, 115–138.

Hammerstein, P., Stevens, J., (Eds.)., 2012. Evolution and the Mechanisms of Decision Making. MIT Press, Cambridge, MA.

Hanson, H.M., 1959. Effects of discrimination training on stimulus generalization. J. Exp. Psychol. 58, 321–333.

Haskell, D., 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. Proc. R. Soc. B 257, 161–164.

Hardin, G., 1968. The tragedy of the commons: The population problem has no technical solution; it requires a fundamental extension in morality. Science 162, 1243–1248.

Harsanyi, J., 1973. Games with randomly disturbed payoffs: A new rationale for mixed-strategy equilibrium points. Int. J. Game Theory 2, 1–23.

Heath, K.D., Tiffin, P., 2009. Stabilizing mechanisms in a legume-rhizobium mutualism. Evolution 63, 652–662.

Heil, M., Rattke, J., Boland, W., 2005. Postsecretory hydrolysis of nectar sucrose and specialization in ant/plant mutualism. Science 308, 560–563.

Herre, E.A., 1985. Sex ratio adjustment in fig wasps. Science 228, 896–898.

Hofbauer J., Sigmund, K., 1998. Evolutionary Games and Population Dynamics. Cambridge University Press, Cambridge.

Holland, B., Rice, W.R., 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. Proc. Natl. Acad. Sci. USA 96, 5083–5088.

Houston, A.I., Székely, T., McNamara, J.M., 2005. Conflict between parents over care. Trends Ecol. Evol. 20, 33–38.

Hsu, Y., Earley, R.L., Wolf, L.L., 2006. Modulation of aggressive behavior by fighting experience: mechanisms and contest outcomes. Biol. Rev. 81, 33–74.

Hurst, L.D., Atlan, A., Bengtson, B.O., 1996. Genetic conflict. Q. Rev. Biol. 71, 317–364.

Ibáñez-Álamo, J.D., Arco, L., Soler, M., 2012. Experimental evidence for a predation cost of begging using active nests and real chicks. J. Ornithol. 153, 801–807.

Internicola, A.I., Page, P.A., Bernasconi, G., Gigord, L.D.B., 2007. Competition for pollinator visitation between deceptive and rewarding artificial inflorescences: An experimental test of the effects of floral colour similarity and spatial mingling. Funct. Ecol. 21, 864–872.

Jaenike, J., 2001. Sex chromosome meiotic drive. Annu. Rev. Ecol. Syst. 32, 25–49.

Karban, R., Agrawal, A.A., 2002. Herbivore offense. Annu. Rev. Ecol. Syst. 33, 641–644.

Karlin, S., 1975. General two-locus selection models: Some objectives, results and interpretations. Theor. Pop. Biol. 7, 364–398.

Kautz, S., Lumbsch, H.T., Ward, P.S., Heil, M., 2009. How to prevent cheating: A digestive specialization ties mutualistic plant-ants to their ant-plant partners. Evolution 63, 839–853.

Kiers, E.T., Denison, R.F., 2008. Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. Annu. Rev. Ecol. Syst. 39, 215–236.

Kiers, E.T., Rousseau, R.A., West, S.A., Denison, R.F., 2003. Host sanctions and the legume-rhizobium mutualism. Nature 425, 78–81.

Kirkpatrick, M., 1982. Sexual selection and the evolution of female choice. Evolution 36, 1–12.

Koehncke, A., Telschow, A., Werren, J.H., Hammerstein, P., 2009. Life and death of an influential passenger: *Wolbachia* and the evolution of CI-modifiers by their hosts. PLoS One 4:e4425.

Kokko, H., López-Sepulcre, A., Morell, L.J., 2006. From hawks and doves to self-consistent games of territorial behavior. Am. Nat. 167, 901–912.

Krombein, K., 1967. Trap-Nesting Wasps and Bees: Life Histories, Nest and Associates. Smithsonian Press, Washington.

Lande, R., 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA 78, 3721–3725.

Leimar, O., 2009. Multidimensional convergence stability. Evol. Ecol. Res. 11, 191–208.

Leimar, O., Axén, A.H., 1993. Strategic behaviour in an interspecific mutualism: Interactions between lycaenid larvae and ants. Anim. Behav. 46, 1177–1182.

Leimar, O., Enquist, M., 1984. Effects of asymmetries in owner-intruder conflicts. J. Theor. Biol. 111, 475–491.

Leimar, O., Enquist, M., Sillén Tullberg, B., 1986. Evolutionary stability of aposematic coloration and prey unprofitability: A theoretical Analysis. Am. Nat. 128, 469–490.

Leimar, O., Hammerstein, P., 2001. Evolution of cooperation through indirect reciprocity. Proc. R. Soc. B 268, 745–753.

Leimar, O., Hammerstein, P., 2010. Cooperation for direct fitness benefits. Philos. Trans. R. Soc. B 365, 2619–2626.

Leimar, O., Van Dooren, T.J.M., Hammerstein, P., 2004. Adaptation and constraint in the evolution of environmental sex determination. J. Theor. Biol. 227, 561–570.

Lorenz, K., 1963. Das sogenannte Böse. Zur Naturgeschichte der Aggression. Borotha-Schoeler, Wien.

Lorenz, K., 1966. On Aggression. Methuen, London.

Mallet, J., Joron, M., 1999. Evolution of diversity in warning color and mimicry: Polymorphisms, shifting balance, and speciation. Annu. Rev. Ecol. Syst. 30, 201–233.

Maynard Smith, J., 1976. Sexual selection and the handicap principle. J. theor. Biol. 57, 239–242.

Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Maynard Smith, J., Parker, G.A., 1976. The logic of asymmetric contests. Anim. Behav. 24, 159–175.

Maynard Smith, J., Price, G., 1973. The logic of animal conflict. Nature 246, 15–18.

Maynard Smith, J., Szathmáry, E., 1995. The Major Transitions in Evolution. Oxford University Press, Oxford.

McCarty, J.P., 1996. The energetic cost of begging in nestling passerines. The Auk 113, 178–188.

McNamara, J.M., 2013. Towards a richer evolutionary game theory. J. R. Soc. Interf. 10, 20130544.

McNamara, J.M., Houston, A.I., 1996. State-dependent life histories. Nature 380, 215–221.

McNamara, J.M., Houston, A.I., 2009. Integrating function and mechanism. Trends Ecol. Evol. 24, 670–675.

McNamara, J.M., Leimar, O., 2010. Variation and the response to variation as a basis for successful cooperation. Philos. Trans. R. Soc. B 365, 2627–2633.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A., Van Heerwaarden, J.S., 1996. Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S.J., Verduyn Lunel, S.M., (Eds.), Stochastic and Spatial Structures of Dynamical Systems, Elsevier, North-Holland, pp. 183–231.

Metz, J.A.J., Nisbet, R., Geritz, S.A.H., 1992. How should we define 'fitness' for general ecological scenarios? Trends Ecol. Evol. 7, 198–202.

Milinski, M., Semmann, D., Bakker, T.C.M., Krambeck, H.J., 2001. Cooperation through indirect reciprocity: Image scoring or standing strategy? Proc. R. Soc. B 268, 2495–2501.

Moran, P.A.P., 1964. On the nonexistence of adaptive topographies. Ann. Hum. Genet 27, 383–393.

Moreno-Rueda, G., Redondo, T., 2011. Begging at high level simultaneously impairs growth and immune response in southern shrike (*Lanius meridionalis*) nestlings. J. Evol. Biol. 24, 1091–1098.

Nash, J.F., 1951. Non-cooperative games. Ann. Math. 54, 286–295.

Nash, J.F., 1996. Essays on Game Theory. Edward Elgar, Cheltenham, UK.

Nesse, R.M., Williams, G.C., 1994. Why We Get Sick: The New Science of Darwinian Medicine. Vintage, New York.

Noë, R., Hammerstein, P., 1994. Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behav. Ecol. Sociobiol. 35, 1–11.

Noë, R., Hammerstein, P., 1995. Biological markets. Trends Ecol. Evol. 10, 336–339.

Noë, R., van Schaik, C.P., van Hooff, J.A.R.A.M., 1991. The market effect: An explanation for pay-off asymmetries among collaborating animals. Ethology 87, 97–118.

Nowak, M.A., Sasaki, S., Taylor, C., Fudenberg, D., 2004. Emergence of cooperation and evolutionary stability in finite populations. Nature 428, 646–650.

Nowak, M.A., Sigmund, K., 1998. Evolution of indirect reciprocity by image scoring. Nature 393, 573–577.

Ostrom, E., 1990. The Evolution of Institutions for Collective Action. Cambridge University Press, Cambridge, UK.

Panchanathan, K., Boyd, R., 2004. Indirect reciprocity can stabilize cooperation without the second-order free rider problem. Nature 432, 499–502.

Parker, G.A., 1974. Assessment strategy and the evolution of animal conflicts. J. Theor. Biol. 47, 223–243.

Pavlov, I.P., 1927. Conditioned Reflexes: An investigation of the physiological activity of the cerebral cortex. Translated and edited by G. V. Anrep. Oxford University Press, London.

Pen, I., Uller, T., Feldmeyer, B., Harts, A., While, G.M., Wapstra, E., 2010. Climate-driven population divergence in sex-determining systems. Nature 468, 436–438.

Petzinger, E., Geyer, J., 2006. Drug transporters in pharmacokinetics. Naunyn. Schmied. Arch. Pharmacol. 372, 465–475.

Pomiankowski, A., 1987. Sexual selection: The handicap principle does work - sometimes. Proc. R. Soc. B 231, 123–145.

Poulton, E.B., 1890. The Colours of Animals: Their Meaning and Use, Especially Considered in the Case of Insects. Kegan Paul, London.

Pryke, S.R., Andersson, S., 2005. Experimental evidence for female choice and energetic costs of male tail elongation in red-collared widowbirds. Biol. J. Linnean Soc. 86, 35–43.

Queller, D.C., Strassmann, J.E., 2009. Beyond society: The evolution of organismality. Philos. Trans. R. Soc. B 364, 3143–3155.

Ruxton, G., Sherratt, T., Speed, M., 2004. Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry. Oxford University Press, Oxford.

Schaffer, W.M., Zeh, D.W., Buchmann, S.L., Kleinhans, S., Schaffer, M.W., Antrim, J., 1983. Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 64, 564–577.

Selten, R., 1980. A note on evolutionarily stable strategies in asymmetric animal conflicts. J. Theor. Biol. 83, 93–101.

Selten, R., Hammerstein, P., 1984. Gaps in Harley's argument on evolutionarily stable learning rules and in the logic of 'tit for tat'. Behav. Brain Sci. 7, 115–116.

Shaw, R.F., Mohler, J.D., 1953. The selective significance of the sex ratio. Am. Nat. 87, 337–34.

Simms, E.L., Taylor, D.L., Povich, J., Shefferson, R.P., Sachs, J.L., Urbina, M., Tausczik, Y., 2006. An empirical test of partner choice mechanisms in a wild legume-rhizobium interaction. Proc. Biol. Sci. 273, 77–81.

Soares, M.C., Bshary, R., Cardoso, S.C., Côté, I.M., 2008. Does competition for clients increase service quality in cleaning gobies? Ethology 114, 625–632.

Spence, K.W., 1937. The differential response in animals to stimuli varying in a single dimension. Psychol. Rev. 44, 430–444.

Spence, M., 1973. Job market signaling. Q. J. Econ. 87, 355–374.

Strassmann, J.E., Queller, D.C., 2010. The social organism: congresses, parties, and committees. Evolution 64, 605–616.

Sugden, R., 1986. The Economics of Rights, Co-operation and Welfare. Basil Blackwell, Oxford, UK.

Taylor, P.D., 1989. Evolutionary stability in one-parameter models under weak selection. Theor. Pop. Biol. 36, 125–143.

Taylor, P.D., 1990. Allele-frequency change in a class-structured population. Am. Nat. 135, 95–106.

Trivers, R.L., 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35–57.

Trivers, R.L., 1974. Parent-offspring conflict. Am. Zool. 14, 249–264.

Trivers, R.L., Hare, H., 1976. Haplodiploidy and the evolution of the social insects. Science 191, 249–263.

Torchio, P.F., Tepedino, V.J., 1980. Sex ratio, body size and seasonality in a solitary bee, *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). Evolution 34, 993–1003.

Toro, M.A., Charlesworth, B., 1982. An attempt to detect genetic variation in sex ratio in *Drosophila melanogaster*. Heredity 49, 199–209.

Van Dooren, T.J. Leimar, O., 2003. The evolution of environmental and genetic sex determination in fluctuating environments. Evolution 57, 2667–2677.

Van Zandt Brower, J., 1958. Experimental studies of mimicry in some North American butterflies: Part I. The monarch, *Danaus plexippus*, and viceroy, *Limenitis archippus archippus*. Evolution 12, 32–47.

Vieira, M.C. Peixoto, P.E.C., 2013. Winners and losers: A meta-analysis of functional determinants of fighting ability in arthropod contests. Funct. Ecol. 27, 305–313.

Völkl, W., Woodring, J., Fischer, M., Lorenz, M.W., Hoffmann, K.H., 1999. Ant-aphid mutualisms: The impact of honeydew production and honeydew sugar composition on ant preferences. Oecologia 118, 483–491.

Von Frisch, K., 1967. The Dance Language and Orientation of Bees. Harvard University Press, Cambridge, MA.

Wedekind, C., Milinski, M., 2000. Cooperation through image scoring in humans. Science 288, 850–852.

Weissing, F.J., 1996. Genetic versus phenotypic models of selection: Can genetics be neglected in a long-term perspective? J. Math. Biol. 34, 533–555.

Werren, J.H., 1991. The paternal-sex-ratio chromosome of *Nasonia*. Am. Nat. 137, 392–402.

Werren, J.H., Baldo, L., Clark, M.E., 2008. Wolbachia: master manipulators of invertebrate biology. Nat. Rev. Microbiol. 6, 741–751.

Werren, J.H., Nur, U., Wu, C., 1988. Selfish genetic elements. Trends Evol. Ecol. 3, 297–302.

Werren, J.H., Stouthamer, R., 2003. PSR (paternal sex ratio) chromosomes: the ultimate selfish genetic elements. Genetica 117, 85–101.

West, S., 2009. Sex Allocation. Princeton University Press, Princeton, NJ.

West, S., Murray, M.G., Machado, C.A., Griffin, A.S., Herre, E.A., 2001. Testing Hamilton's rule with competition between relatives. Nature 409, 510–513.

Wilkinson, G.S., 1984. Reciprocal food sharing in the vampire bat. Nature 308, 181–184.

Wink, M., 2000. Interference of alkaloids with neuroreceptors and ion channels. Stud. Natl. Prod. Chem. 21, 3–122.

Wright, S., 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proceedings of the 6th International Congress on Genetics 1, 356–366.

Wright, S., 1977. Evolution and the Genetics of Populations. Vol. 3: Experimental Results and Evolutionary Deductions. University of Chicago Press, Chicago.

Young, H.P., 1993. The evolution of conventions. Econometrica 61, 57–84.

Zahavi, A., 1975. Mate selection – a selection for a handicap. J. Theor. Biol. 53, 205–214.

Zahavi, A., 1991. On the definition of sexual selection, Fisher's model, and the evolution of waste and of signals in general. Anim. Behav. 42, 501–503.

Zollman, K.J.S., 2013. Finding alternatives to handicap theory. Biol. Theory 8, 127–132.

Zug, R., Koehncke, A., Hammerstein, P., 2012. Epidemiology in evolutionary time: The case of *Wolbachia* horizontal transmission between arthropod host species. J. Evol. Biol. 25, 2149–2160.

Zug, R., Hammerstein, P., 2012. Still a host of hosts for *Wolbachia*: Analysis of recent data suggests that 40% of terrestrial arthropod species are infected. PLoS ONE 7(6), e38544.