Optimal foraging theory and economics: a historical note

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Abstract. This study sheds a light on economic roots of optimal foraging and optimal mating theory. Two examples show graphical optimisation models of behavioural ecology that are identical to much older ones of economics. The knowledge transfer has been conscious and explicit in some cases, but also less visible in others. This does no imply plagiarism or misconduct but merely shows how knowledge can diffuse along obscure, sometimes unconscious, routes of non-public and private communication.

Key-words: marginal value theorem, marginal utility theory, optimal foraging, optimal mating, predator switching

1 Introduction

Vromen (2011) detailed an episode in the history of economics that also happens to bear on the history of optimal foraging and optimal mating theory in ecology. He showed that some scholars of the first generation of the Chicago school of economics (e.g., Alchian 1950; Friedman 1953) considered selection arguments in defence of marginal analysis. The so-called marginalist controversy emerged in the 1940s and lasted until the end of the 1960s (Screpanti and Zamagni 2005, 413). This marginalist theory was based on the assumption that individuals (firms) acted rational so as to maximise their utility (profit). Tintner (1941a, b) denied that this even made any sense as a guide for action in an unpredictable economic system. That would require a foresight that cannot be had. Alchian and Friedman employed a selection argument in defence of the established economic theory. In the long run, only the firms that did maximise profits will survive economically and only the individuals that did maximise their utility will rise in the hierarchy and become affluent. The result looks *as if* individuals and firms maximise utility or profits, even if their actions were random and their foresight nill.

> "Let the apparent immediate determinant of business behavior be anything at all—habitual reaction, random chance, or whatnot. Whenever this determinant happens to lead to behavior consistent with rational and informed maximization of returns, the business will prosper and acquire resources with which to expand; whenever it does not, the business will tend to lose resources and can be kept in existence only by the addition of resources from outside. The process of "natural selection" thus helps to validate the [maximization-of-returns] hypothesis—or, rather, given natural selection, acceptance of the hypothesis can be based on the judgement that it summarizes appropriately the conditions for survival." (Friedman 1953, 22)

At that point economics was the receiver and evolutionary biology the source delivering an argument for economic selection.

Some of the second generation of the Chicago school took the validity of economic theory for granted and used it as a base for expanding the domain of economics into ecological territory. Thus, Tullock (1970; 1971a, b) applied marginal utility theory, demand-supply diagrams, and externalities to explain the prey switching of general predators, the food patch exploitation of coal tits, and pasture management respectively; Becker (1974, 1976) applied *social income* (instead of inclusive fitness) to sociobiological problems and Hirshleifer (1977) expanded on this. Ecologists, however, had not been sleeping and were already on the fast lane by that time.

Ecologists sometimes speak of a *parallel development of theories in economics and ecology* (MacArthur and Pianka 1966, 603, Martin Cody pers. comm.), in which behavioural ecology developed similar to but independent of economics (Schoener 1987, 31-36), and point to the rarity of references to economic literature in research articles on behavioural ecology. Here, I show that this is wrong for optimal foraging[1] theory in two respects. First, the economic theory that has been defended by applying an argument of selection to economics stems from the *marginalist revolution* around the 1870s (Screpanti and Zamagni 2005, chap. 5). Its optimisation models are about a century older than similar models of behavioural ecology. Sharon Kingsland (1995, 41-44) has already detailed how Alfred Lotka used this neo-classical economics for his modelling and concluded that it has been an intellectual deadend, because Lotka failed to connect his economic modelling of biological systems to natural selection. This connection has eventually been made by economists like Alchian and Friedman in the 1950s. (Sections 4, 5.1 and 8 illustrate the isomorphism of some graphical models of optimal foraging theory with much older ones of microeconomics.)

Second a lack of citations of economic literature is no proof of a lack of influence. Many routes of knowledge transfer are never recorded in the form of citations, because the knowledge is taken for granted in peers or not taken to be part of the research in question, for example, common knowledge, social background, undergraduate training, personal conversations. Also, the scaffolds and tools used in modelling are often removed before publishing the final result. (Sections 5.2, 6 and 7 exemplify the influence of economics on pioneers of behavioural ecology that are not readily visible from inspecting citations.) The following sections 2-3 chronicles a waning awareness of the economics heritage in the literature on optimal foraging theory.

A disclaimer is in order first. The following only illustrates how economic knowledge spread, sometimes unnoticed, into ecology. It does not mean to diminish anybody's deed. Scientific advance is often achieved by a unique and new combination of old knowledge (theories, methods, technologies etc.) that can be applied in new ways previously unthought of. Notorious examples are Darwin's combining knowledge from breeding (artificial selection) with natural history (natural selection), the makers of the neo-Darwinian synthesis fusing knowledge about mutations and Mendelian inheritance with Darwinism, or molecular biologists applying the method of X-ray crystallography to the study of biological molecules like DNA. It does neither suggest that the particular publications of economics or operations research presented below were the specific source of inspiration for behavioural ecologists of the 1970s, except those acknowledged by the authors. In particular, it does not insinuate plagiarism of any party.

2 Roots of behavioural ecology

In the 1970s the new research field of behavioural ecology was staked out by pioneering research publications (Gross 1994; Drickamer 1998; Parker 2001, 2010; Owens 2006; Birkhead and Monaghan 2010; Birkhead 2014). The historical writing on this science is in its infancy and mainly concerned with its roots in ethology, ecology, populaton biology and evolution or with its own development after inauguration (e.g., Alcock 2003; Altmann and Altmann 2003; Birkhead and Monaghan 2010; Bolduc 2012; Burkhardt 2005, 2016; Cézilly 2008; Krebs 1985, 2010, 390-2; Owens 2006; Schoener 1987); or it is concerned with the controversy about strong adaptationism and the question whether organisms are really optimal (e.g., Kitcher 1987 and subsequent comments; 1990; Orzack and Sober 1994a, b; Driscoll 2009, Potochnik 2009; Bolduc and Cézilly 2012).

The history of behavioural ecology has more than these dimensions, however. The most obvious transfer from economics is probably that the *evolutionarily stable strategy* (ESS) is based on game theory, which was developed with economic choices of humans in mind (Kalmus 1969; Potochnik 2012). "The theory of games was first formalised by Von Neumann & Morgenstern

1 If not mentioned otherwise, *optimal foraging* means to include *optimal mating* theory in the following.

(1953) in reference to human economic behaviour" (Maynard Smith 1982, 1).[2] Levins and Lewontin (1985, 25)[3] agreed: "In fact, some forms of optimization theory, including the theory of games, have been taken over from economics and political science as techniques for prediction and explanation in organic evolution."

Beyond game theory, Levins (1962) was a further pioneer that has consciously used economic tools for ploughing ecological ground (Eric Charnov, pers. comm.).[4] Edward O. Wilson (1977, 136) stated: "Already, models in ecology and sociobiology have borrowed heavily from the graphical methods of economics," and he continued to anticipate a growing overlap and unification of these sciences. The book of Oster and Wilson (1978) was an explicitly economic analysis of social insect states. At page 294 they mention *operations research* as a particular source of inspiration: "The most recent impetus to optimization modeling in ecology has come from engineering, and especially operations research. Indeed, most of the models we have developed in this book employ mathematical techniques developed to solve problems in engineering and industrial design." To wit, George F. Oster got his bachelor of science from the *U.S. Merchant Marine Academy*.[5]

Concerning optimal foraging theory, the relationship seems to have been obvious at the beginning. Rapport and Turner (1977) explicitly introduced marginal analysis (see section 5) as the historical basis for studying similar trade-offs in the foraging behaviour of animals. McFarland (1985, 443-454) explicitly applied consumer theory to animals. Stephens and Krebs (1986, 104) mention that both biologists and psychologists have recognised that "the theory of economic allocation of a limited budget can be used to study animal choices" and proceeded to outline the relevant economic theory in their chapter 5.

3 A token of oblivion in foraging theory?

Contrary to the clear links of various ecological theories with economics given above, Schoener (1987, 31-36) addressed the question of inspiration and parallels between optimal foraging ecology on the one hand and anthropology, psychology, and economics on the other, and his conclusion concerning economics was (Schoener 1987, 35f):

2 Richard Lewontin (1961) applied game theory and population genetics. This may have been the source from which Maynard Smith took his lead to apply it to behavioural ecology.

3 *The Dialectical Biologist* of Levins and Lewontin (1985) contains the English originals of articles first published in Italian translation in the *Enciclopedia Einaudi* (1977, edited by Giulio Einaudi, Turino).

4 It is clear from Levins and Lewontin ([1977]1985, 84) that they were well versed in economics because of their political background: "The ideology of equilibrium and dynamic stability characterizes modern evolutionary theory as much as it does bourgeois economics and political theory; Whig history is mimicked by Whig biology."

John Maynard Smith (1992, 33), himself a Marxist in youth who got disillusioned with communism later, remembered: "Levins was a Marxist before he was a biologist, and all his work shows it. His book *Evolution in a Changing Environment* [of 1968], although it avoids the usual jargon, is the work of a conscious Marxist. […] It is perhaps ironic that he made extensive use of mathematical techniques borrowed from capitalist economic theory: I cannot criticise because I have done the same."

5 In an essay originally published in *The New York Review of Books*, 6 Nov. 1986, Maynard Smith (1992, 114) even described the habit of biologists borrowing theory from other sciences as pervasive: "The formal similarities between biological evolution and human history have repeatedly tempted students of one topic to borrow ideas from the other. The most famous and fruitful example of borrowing by biologists of an idea from the human sciences was the use made, by both Darwin and Wallace, of Malthus's picture of human competition for resources as a foundation for their own theory of evolution by natural selection. At a less exalted level, I have myself spent much of the last fifteen years applying the mathematical theory of games, first developed for use in economics, to solve problems in evolution. *Indeed, I am by no means the only recent biologist to exploit mathematical economics as a source of ideas.* Biologists have, by and large, been eager to borrow ideas from the human sciences. Borrowing in the other direction is less well regarded. The reason for this ill repute is not far to seek: biological ideas have too often been used, not as potentially valuable research tools, but as a moral justification of policies that might otherwise seem dubious." (Emphasis added)

> “Almost everyone would agree that there are striking resemblances between OFT [optimal foraging theory] and certain aspects of economic theory. To what extent are these resemblances convergences and to what extent are they casual?[sic]—the direction of course being from economics to ecology.
>
> The answer appears fairly clear when one considers who the principal early theorists were. Except for papers by Rapport (1971), Covich (1972), and in part Hamilton and Watt (1970), explicit reference to economic theory is largely lacking (Rapport & Turner 1977), very likely because most of the other papers’ authors did not know much, if anything, about it. This is despite the appearance of such phrases as “the economics of consumer choice” (MacArthur 1972), “marginal value theorem” (Charnov 1976), or “currency” (Schoener 1971). It is hard to verify the ignorance in most cases, but speaking for myself, I can confirm its near totality. For example Joel Cohen pointed out to me that a graphical model in Schoener (1969b) is a “production function,” and Rapport and Turner (1977) say that the tradeoff between time and energy in Schoener (1971) is a rediscovery of the economist’s notion of marginal costs. Pianka (personal communication) also notes the ignorance for himself, and probably, for MacArthur: “I recall telling a Princeton economics grad student our theory and having him say it was ‘old hat’!” One striking exception to the generalization exists, however: Belovsky received his undergraduate degree in economics.
>
> Not only have nearly all ecologists been chronically ignorant of economic analyses, but to go a step farther, it seems that when the latter were directly appropriated, they were less influential. […] Hence had economics never been invented, optimal foraging concepts would likely exist virtually unchanged, albeit with more biological terminology.”

Schoener’s testimony, however, must be taken with a grain of salt or two. First, even if all ecologists were ignorant about economics, this does not mean that no influence existed. The case of Geoffrey A. Parker illustrates one such unnoticed influence (see section 8). Second, Eric L. Charnov graduated in fisheries and resource management including classes in economics and operations research (pers. comm., see also section 6).

The next to publicly disassociate from economics appears to have been Rapport (1991). He who had previously been most up-front about the economic sources of his studies of animal behaviour, completely recanted the usefulness of economic models and the optimisation approach for behavioural ecology. Rapport (1991) denied the use of laboratory experiments as tests of the validity of these models for nature, where Ydenberg (1994, 5), for example, noted: “In the study of foraging risk-sensitivity began as a strictly theoretical construct borrowed from microeconomics and initially seemed so unlikely that it was hardly expected to hold in real animals. Its existence was quickly confirmed in laboratory experiments.” Apparently, laboratory experiments could convince one but disenchant the other. An irony in Rapport’s change of mind is that he severely criticised the assumption of perfect knowledge and rational behaviour of the actors in the models. He, thereby, recycled criticisms, which had been raised decades earlier, against the marginalist models applied to human economic behaviour. The irony is that this very criticism had been answered by borrowing an argument from evolutionary theory, of all sciences: The result only looks as if actors were rational and in the know, so the anser, because those that happen do behave that way (despite their ignorance and irrationality) tend to survive the selection process (see introduction).

Next to recant, economics in general for ecology in general, was Ed Wilson (1998). Contrary to his gleaming embrace of 1977, his *Consilience* was no longer a vision of confluence with the social sciences (Wilson 1998, ch. 9), but a take-over bid. Ironically, he decried the very models, on which much of ecological theorising has been based, as “Newtonian” (too simple) and “hermetic” (sealed off from reality). Hence the comment of Segerstråle (2000, 355):

> “Interestingly, it is economics that is most severely criticized. Economics is said to be totally on the wrong track, not having a realistic view of human nature and not factoring in the

> environment in its overall calculations. Here Wilson is in agreement with many other critics of economics, including sociobiologists and political scientists! But look at the irony here. Neo-classical economists typically use models of self-interest, optimization strategies, and the like—and these are exactly the models that underlie much of sociobiological reasoning, too."

Admittedly, Ydenberg et al. (2007, 3f) still mentioned Tullock (1971a) as illustrating the historically new thrust of economic thinking among foraging ecologists in comparison with earlier ethologists, without claiming that the economist had originated the approach. This balancing act of conceding the influence but denying the supremacy of economics, however, seems to have tilted towards ignoring or forgetting the initial inspiration from economics by and by. The tide has turned and the narratives of behavioural ecology have grown rather dim on economics.[6]

For example, tracing out the various roots of behavioural ecology from antiquity onwards, Cézilly (2008, 25) uses the term *economic* only once in 25 pages—and not in reference to the science of economics[7] at that:

> "The synthesis between the evolutionary analysis of social behaviour and the economic analysis of exploitation of resources by animals, two approaches that share the same theoretical foundations (Krebs 1985), came about quickly and gave birth to behavioural ecology."

Reading Krebs (1985) makes it clear that Cézilly (2008) used *social behaviour* to mean sociobiology and *economic analysis* to mean foraging theory, not economics. Birkhead and Monaghan (2010) did mean economics—the science—the one time they used that term: "Combining economics and population biology, they developed elegant mathematical theories to understand the choices animals make when moving between food patches (MacArthur and Pianka 1966)." Given Pianka's testimony to Schoener (1987, 35f, see quote above) of his own ignorance of economics and his suggestion that MacArthur had been equally ignorant, however, some historical context is obviously getting lost in these reminiscences and textbook introductions.[8] Finally,

6 Published and personal communications suggest a field divided between those utterly ignorant of economics (e.g., Schoener and Pianka in Schoener 1987; Martin Cody, Geoff Parker and Nick Davies in pers. comm.) and those that regard the connection as a matter of course (e.g., Eric Charnov, Alan Covich and Dennis Lendrem in pers. comm.).

7 Language is ambiguous and the use of terms like *economic ideas* or *economic analysis* can sometimes mean anything from based in economics as a science to merely that behaviour should be parsimonious, efficient or profitable. The divergence in opinion about the question whether MacArthur directly transferred economic theory into ecology or not may be largely due to his own ambiguous formulations. For example, the first sentence *On optimal use of a patchy environment* (MacArthur and Pianka 1966, 603) reads: "There is a close parallel between the development of theories in economics and population biology." Many readers may have taken this opening to imply their knowledge of economics. Again, the book that MacArthur (1972) published as a legacy, when already terminally ill with cancer, contains a chapter headed *The economics of consumer choice*, but it contains no reference to any economics literature. Similarly, Krebs and Davies (1978, 2) seem to imply economics and no other science, like psychology, sociology, or pure mathematics, by using *optimal choice* and *efficient predator* in the following statement: "MacArthur first used the idea of optimal choice in the context of foraging behaviour. He proposed that one could work out from first principles a set of rules for the behaviour of an efficient predator, an idea which has since produced a substantial body of work." But all these statements suffer from the above mentioned ambiguity. They might mean economics—the science—or just efficiency or profitability. Unfortunately, the correspondence of Robert MacArthur held in the archive of the library of Yale University is sealed until 2035.

8 Geerat J. Vermeij (2009, 42, see also footnote 5) even implied Schoener, of all ecologists, of having partaken in the introduction of ideas from economics into behavioural ecology: "Robert MacArthur and his associates introduced ideas from microeconomics to explain how animals allocate resources among such competing functions as growth, reproduction, and defense. Thomas Schoener considered costs and benefits when asking under which circumstances animals looking for food should maximize energy intake or should minimize search time." This ambiguity may again be due to the following statement by MacArthur (1972, 66, see also footnote 5): "Schoener (1969), deriving his results by a different pathway, relates convergence of body size to the economics." Did MacArthur, here, say that Schoener related to economics—the science—or simply that he related body size to evolutionary efficiency or parsimony? Probably the latter, but that easily gets lost in the Chinese Whispers game of citation.

focussing on the ethological roots of behavioural ecology, Bolduc (2012) only got a whiff of a peculiar "economical thinking" that distinguished the new field from its ethological heritage. However, he did not inquire into the provenience of this economic thinking.[9]

If this signifies a trend of forgetting the economics heritage of optimal foraging theory, then a historical note may be in place. The following only suggests some models of economics as sources for models of behavioural ecology. It does not vindicate any of the models, economic or ecological. Alan Covich (pers. comm.) said that "economics was in the air," but it was also in the heads and often also made it into print as Covich's publications prove best (see section 5.1). But even when it did not make it into the primary research literature on optimal foraging in the form of citations to economics literature, some traces of influence can sometimes still be found.

4 Marginal utility

As marginal values are particularly relevant to optimal foraging, the *marginal utility theory* of economics is a good place to start searching for roots. Therefore, the following takes a closer look at early proponents of marginal utility theory before discussing ecologists' use of it for solving problems of behavioural ecology. Gossen (1854) stated, as a law, that the utility of a good diminishes with its consumption. Gossen conceived this diminishing gain in psychological terms of pleasure (Genuss) rather than caloric intake or fertilisation success, but later economists replaced pleasure by utility.

> "Die Größe eines und desselben Genusses nimmt, wenn wir mit Bereitung des Genusses ununterbrochen fortfahren, fortwährend ab, bis zuletzt Sättigung eintritt." (Gossen 1854, 4f)
> "The magnitude of one and the same pleasure diminishes continually, if we keep enjoying it incessantly, until satiation eventually commences." (My translation)

Gossen's second law stated that a consumer should stop enjoying any one good, when it still just gives the same marginal pleasure as any of the other goods would.

> "Der Mensch, dem die Wahl zwischen mehren Genüssen frei steht, […] muß, […] um die Summe seines Genusses zum Größten zu bringen, sie alle theilweise bereiten, und zwar in einem solchen Verhältnis, daß die Größe eines jeden Genusses in dem Augenblick in welchem seine Bereitung abgebrochen wird, bei allen noch die gleiche bleibt." (Gossen 1854, 12)
> "In order to maximise the sum of its pleasure, the person that can chose between several goods has to enjoy each one only partially, in such a proportion that the pleasure at the moment of terminating to enjoy one good is of the same magnitude as of all the others." (My translation)

Replacing several goods by only one resource type that occurs in patches will transform this statement into the *marginal value theorem* of behavioural ecology: an individual should leave one resource patch, when the marginal gain rate in that patch drops to the average gain rate for the habitat (Charnov 1976).

A graphical model derived from marginal utility theory (Pareto 1919, 180), which is by now a standard model of optimal consumer choice (e.g., Friedman 1953, 100-113; Becker 1962), represents indifference curves with tangential budget lines defining ratios of goods that yield optimal utility to a consumer. Indifference curves map ratios of goods, for example apples, *A*, and bananas, *B*, that will have the same utility for consumers and hence render them indifferent to the variation in ratio (fig 1).

9 A paradox situation exists in some compendia with chapters written by different authors. The community endowing historical narrative in the introduction may deny (e.g., Schoener 1987) or ignore (e.g., Cézilly 2008) the import of economics, but later chapters teach certain models or techniques with explicit reference to the economic source theory (e.g., Caraco 1987; Cézilly, Danchin and Giraldeau 2008, 65; Giraldeau 2008, 234).

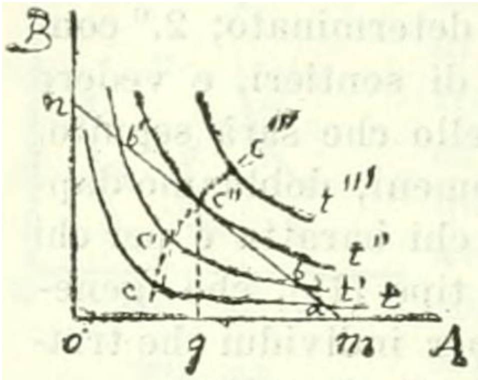

Figure 1
Indifference map with a tangential budget line (*m, n*) touching one indifference curve (*t”*) at a ratio (*c”*) of two goods (*A* and *B*) that yields the optimal utility for the consumer. The dotted line through the optimal ratios *c*, *c’*, *c”*, and *c’”* is the consumption curve (from Pareto 1919, 180)

Indifference curves are convex to the origin because a consumer that has a lot of bananas and no apples (*n*) will trade more bananas for one apple than one that already has apples and vice verse for one that has many apples (*m*) and no bananas. An *indifference map* is the cluster of indifference curves for varying utility levels. A *budget line* represents the ratios of the goods a consumer can actually afford with a certain budget. The tangential point where the budget line touches one of the indifference curves defines the optimal ratio of goods that will maximise utility for that consumer. Unlike in figure 1, budget lines will often be concave to the origin, because the price of a good rises with its consumption as an adjustment to either increased demand or decreased supply. Finally, the *consumption curve* that connects the optimal ratios c^i (fig. 1) curls away from good *B* meaning that people will consume relatively less of that good as their affluence rises.[10]

5 Economics as a tool shed

5.1 Scaffolds remain in publication

Rapport (1971; 1980) took big chunks of marginal utility theory and introduced them to an ecological context keeping economic terms like indifference curve, welfare etc. Just like consumers should chose a combination of different goods yielding the optimal utility, so generalist predators should switch between different prey species yielding the optimal food gain. He only dropped the *consumption curve* through the optimal ratios c^i (cf. fig. 1) and plotted a concave time budget line assuming that the search-time required to catch a prey item increases as the predator becomes more specialised (see fig. 2 in Rapport 1971). Rapport (1971, 585) mentioned a textbook on microeconomics as a particular source of inspiration in the discussion: “The model here derives from consideration of models found useful in microeconomic analysis (Watson 1963).” He also mentioned Baumol (1961), *Economic Theory and Operations Research*, and Rosen (1967), a textbook applying optimisation tools from physics, engineering, and economics to biological problems.

Covich (1972) independently applied the same theory to the food choice of mice species and later to pollinator insect (Covich 1974). The introduction of the theory by Covich (1972) is more comprehensive than in Rapport (1971) and so are his references to relevant publications of economics. He even mentions “F. Y. Edgeworth in 1881” and “I. Fisher in 1892” in the main text though not in the reference list. His study of 1972 is not just theoretical modelling but also attempts

10 Friedman (1953, 101, footnote 3) points out that indifference maps with consumer budget lines have been widely used in economics to argue that income taxes are better than excise taxes yielding equal revenue, because the latter were assumed to skew the budget line so as to meet a lower indifference curve. Friedman (1953, 103) features the graphical model.

to test some predictions of the theory experimentally.[11] For further examples of behavioural ecologists using ready-made microeconomic theories see Charnov and Orians (1973, 3) and Rapport and Turner (1977).

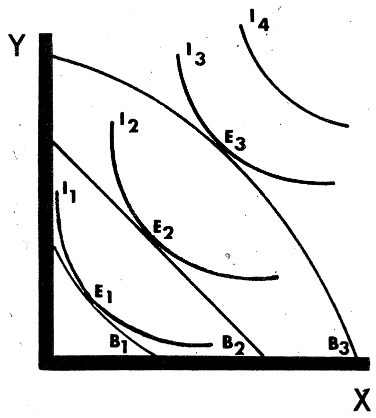

Figure 2
Animal preference map for the optimal choice of food items *X* and *Y*. Three different kinds of budget lines are illustrated: B_1 is concave to the origin, B_2 straight, and B_3 convex. As always, the indifference curves I_i are convex to the origin. The optimal ratios of food items are at the points E_i (from Covich 1972, 73)

5.2 Scaffolds removed before publication

Dennis Lendrem, a student of Tinbergen's successor, McFarland, in Oxford and a direct observer of the research groups around David McFarland and John Krebs from 1979 to 1982, provided a peek through the keyhole. He has written an introductory textbook on *Modelling in behavioural ecology* (Lendrem1986) that was not sanitised on purpose: "I was intrigued at the contrast between the highly sanitized accounts of modelling that make it into the literature, and the more haphazard model development pathway I observed, and experienced, in real life" (Lendrem pers. comm.).

The book distinguishes a top-down from a bottom-up modelling approach. Top-down modelling started from theory of another area—engineering or economics—and explored their implications in behavioural ecology. Bottom-up modelling started in the lab or the field and initiated a search for a branch of theory (usually economic) capable of capturing the essential features of the data. "Looking back I think the best work flowed back and forth between the two" (Lendrem pers. comm.).

Lendrem (1986, x) thanked many of the pioneers "for free and frank discussion of their models ('warts and all' as one of them put it)" and the main text mentions the related models throughout, for example, from economics (Lendrem 1986, 2, 44, 59, 80, 81, 192, 203) or other sciences like psychology or engineering (Lendrem 1986, 81, 118, 192). He rated the awareness of the relationship of behavioural ecology with economics among the pioneers (e.g., John Krebs, Alex Kacelnik, Tom Caraco, David McFarland, Ron Ydenberg, William Hamilton) as very high and some modelling concepts, like elasticity, resilience, and risk-sensitivity in animal behaviour as direct applications of economic thinking (Lendrem, pers. comm.).

After having fully quoted Schoener's opinion that economics had no significant influence on pioneering research in behavioural ecology (see section 3), it is only fair to contrast it with Lendrem's opposite observations made from inside the Oxford research groups that were hot spots of this pioneering research:

> "If my memory serves me correctly Richard Sibly, Robin McCleery and David McFarland all extended ideas around economic resilience to resilience in behaviour and its implications for time-budgeting in animals. McFarland's book on Quantitative Ethology is quite explicit. David Stephens applied the idea of risk indifference curves to optimal foraging theory to

11 Covich (1976) referred to the economists Losch and Isard as sources of inspiring research on the shapes of foraging territories of animals that were bound to a central place, like a nest, in analogy to humans being bound to a home.

build with John Krebs ideas around risk-sensitive foraging. John Krebs was a big influence and acted as my internal examiner for my PhD viva.

Richard Dawkins, Alan Grafen and Mark – not Matt – Ridley were busy with games theory applications. And Matt – not Mark – Ridley was busy working on games and the evolution of sex and moving between his supervisor John Krebs in the Institute of Ornithology and Richard Dawkins in David McFarland's Animal Behaviour Research Group. You are probably aware that Matt "Red Queen" Ridley left Oxford to join *The Economist* magazine as science correspondent?

Both groups worked closely. One of the key driving ideas underlying behavioural ecology was the notion of understanding animal decisions. Whether through games theory – decisions around aggressive contests, decisions to cooperate, decisions around conflicting behaviours – or optimality theory eg. feeding and vigilance." (Dennis Lendrem, pers. comm.)

6 Economics as a college to graduate from

Even without such explicit use, economic knowledge could have diffused to behavioural ecology in less visible ways. The case of Geoffrey A. Parker (section 8) illustrates an unnoticed influence. Between the explicit use of economic tools and the unconscious influence along obscure routes, however, there is the *alma mater* type of influence that can be strong but invisible in publications. Naturally, graduate research applies knowledge from undergraduate training but the lecturers and textbooks are usually not cited, because their knowledge can be taken for granted in the peers. For example, modern genetics research papers are full of terms and concepts like *gene, DNA, mutation, linkage disequilibrium* without even once giving a reference to the originators (except for deep reviews, papers dealing with particularly recalcitrant issues, or indeed historical analyses). Each time and place has its common knowledge that can be taken for granted and needs no references. This does not exclude the possibility of individual misjudgements of the peers' knowledge.

Eric Charnov graduated in fisheries and resource management including classes in economics and operations research (pers. comm.). Calling his optimal foraging theory the *marginal value theorem* (Charnov 1976) was a conscious reminiscence to the many marginalist economics he had learned of as an undergraduate, but he did not mean to refer to the marginal utility theory described in section 4 in particular (pers. comm.). Apparently, Charnov had taken a knowledge of economics as evinced by Rapport (1971) or Covich (1972) as a matter of course. However, Charnov (1976, 132) did cite a book on operations research by Taha (1971) on "the second derivative conditions for a multidimensional optimization problem to be an optimum" (pers. comm.), which was definitely more than he could take for granted in peers.

7 Economics strewing useful gadgets about

Non-public communication is an obscure route for the diffusion of knowledge. Here, *non-public* means any communication that does not reach beyond the direct participants, like private conversations or lectures that do not get recorded and published. Unlike Charnov, Parker ran through the classical zoology curriculum with no training on economics whatever (Parker 2001). The crucial tip for solving the optimal persistence problem of Parker (1974) came from his father, Dr. Alan Parker, who was an industrial chemist and microbiologist working on antibiotics production and knew this method from his job.

> "I talked over the problem with my father, and he saw a parallel in industrial economics. The situation resembled a process where there was a fixed "setting up" time before the process could begin, and where the cumulative yield showed diminishing returns with the time that the process ran. To maximize the yield rate, the optimal run time was given graphically by a tangent drawn to the curve of cumulative yield with time, the tangent starting from a point

> on the time axis to the left of the origin a distance equal to the setting up time." (Parker 2001, 14, see also Parker 1974, 164; 2010, 443)

When Geoffrey Parker wanted to analyse this optimisation model more generally, he recruited the electrical engineer Robert A. Stuart. They applied their model to the yellow dung fly, *Scathophaga stercoraria* (Parker and Stuart 1976). Around oviposition sites, dung pats, the males either search for females, copulate with a female or guard it after copulation, while the female is laying eggs. The guarding prevents any other male from mating after him, who would otherwise displace his sperm and reduce his fertilisation success from over 80 to under 20% of the next batch.

Parker and Stuart (1976, 1060) apportioned the three behavioural patterns of male dung flies to the two sides of their trade-off as follows:

> "However, extra time invested in copulation means missed opportunities to capture new females. The mean search cost *S* for a new female is approximately 140 min (Parker 1970b), to which must be added the 16.5 min guarding time during oviposition."

The reason for adding the guarding to the searching time was that they assumed that they were both mandatory expenditures (Parker, pers. comm.) and that all three patterns were important for reproductive success (could not be dropped from the trade-off). While this reflects the economic convention of dividing the *full costs* into *fixed costs* on the one hand and *variable costs* on the other, such economic reasoning did not inform their choice (Parker, pers. comm.).

A comparison with other approaches can sharpen the analogy with economics. Take the biological functions for example: searching is for finding a mate, copula for transferring sperm, and guarding for ensuring the fertilisation success of that sperm. Reasoning about biological functions, the three patterns either form one unit or the copula and guarding form a sub-unit with closely related functions in fertilisation—the copula for transferring sperm and the guarding for ensuring the fertilisation success of that sperm. Other forms of modelling do also suggest other choices. For example, genetic models often assume that drift or recombination would make no difference and therefore ignore them, no matter whether they are fixed or variable. Given the above assumption that all three patterns are relevant for fitness, a genetic model could drop none, but it would not be structured like a trade-off either. Even in game theory, initially a possession of economics, the fixed costs that all players need to pay anyway do not even enter the payoff matrix. The apportioning of Parker and Stuart (1976) is therefore comparatively similar to marginalist economics conventions, even if this was not the conscious reason of their choice.

8 Marginal productivity

As the tip to draw the tangent intersecting the x-axis at -*S* reached Parker via the private communication with his father, who knew it from industrial economics, it may well have an economic template not yet discovered. If so, the emblematic diagram of the marginal value theorem in behavioural ecology (fig. 3) should also exist somewhere in the economics literature.[12] The earliest use I found was by Knut Wicksell's *Über Wert, Kapital und Rente* originally published in 1893 in German. An English translation was first published in 1954. He analysed a case, in which workers borrow all the capital required to set up a production process, so that the rate of interest on that capital, *z*, equals their fixed costs. He then asked "how long a period of production these workers are to choose with most advantage to themselves" (Wicksell 1954, 120). Wicksell actually wanted to maximise the wages *l* of the workers by finding the optimal production time *t*. He illustrated his analysis in the form of a graphic (fig. 4), wich is strikingly similar to those illustrating the marginal value theorem in behavioural ecology (fig. 3).

Wicksell (1934, 180) used a similar graphic model in order to illustrate the relationship between capital, interest and time using the example of wine gaining value with time. Joan Robinson adapted Wicksell's model in in order to predict the effects of technical progress on wages

12 A hopeless quest at first sight, lead to success by the reverse image-search function of modern search engines.

and profit (see Robinson 1953-54, fig. 2; 1956, 411-420). Hirshleifer (1967, 191) called Wicksell's formalisation of a theory relating wages, capital stock, interest and the period of production "one of the most famous developments in the history of economic thought."

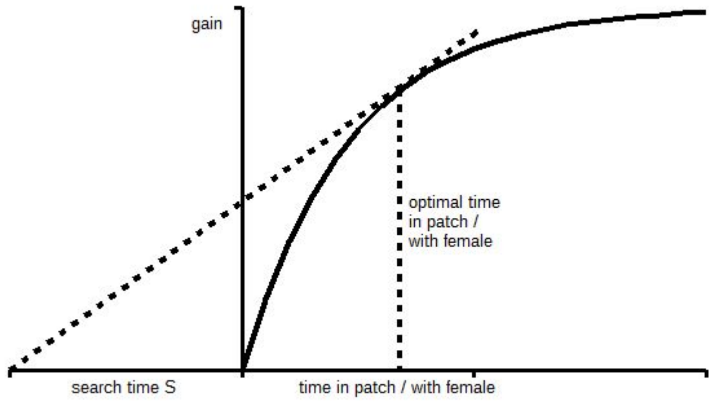

Figure 3
Emblematic representation of the *marginal value theorem* in behavioural ecology. Either females or food occurs in patches. The optimal time spent in a patch or with a female is given, where the tangent that intersects the x-axis at *-S* touches the gain function.

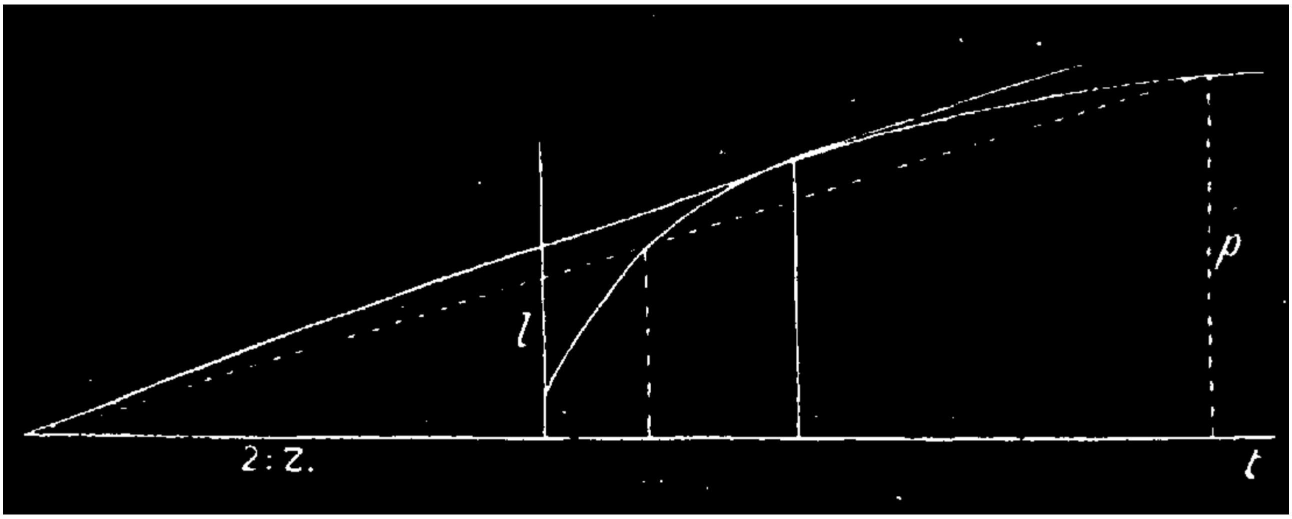

Figure 4
Optimal run-time for a production process. Here, *t* is the length of the period of production; the intersection with the y-axis *l* divides the profit into the portion that can be spent on the wages of the workers (from 0 to *l*) and the portion that must be spent on the fixed costs (from *l* to *p*); *p* is the average production of the workers; *z* is the annual interest rate on capital invested (= fixed costs). The optimal period for the process is *t* at the continuous perpendicular (from Wicksell 1970[1954], 122)

Two things about Wicksell's analysis and graphic model differ from those of Parker (1974), Smith and Fretwell (1974), Charnov and Krebs (1974), Charnov (1976), or Parker and Stuart (1976). First, Wicksell used an inverse of the fixed costs, *2/z,* to determine the intersection point of the tangent with the x-axis.[13] This suggests that the workers should terminate the process earlier as the interest rate on invested capital rose. It makes sense, however, because the workers should not even borrow the money to start the endeavour, if the interest rates were too high. In foragers or

13 As the annual interest rate is an inverse of time (percent per year) any inverse of it will yield a quantity in years. For the analytic derivation of *2/z* as the interception point see Wicksell (1970, 121f). Robinson (1954-54, fig. 2; 1956, 411-420) interpreted the line-segment from the origin to the left, where the tangent intersects the x-axis, as the simple inverse of the rate of interest (1/rate-of-interest). In the optimal case, the rate of profit should just cancel the rate of interest and the rest of the revenue be spent on wages.

males, on the other hand, an exceptionally long search time does not mean that the individual should not even start exploiting/mating a found resource patch/female.

Second, Wicksell determined the portion of the revenue that can be apportioned to wages as the value, *l*, from the origin to the intersection of the tangent with the y-axis, the remainder going to pay the fixed costs. This is not possible for mating or foraging behaviour, because the costs and benefits have different currencies. In optimal mating theory, for example, the gain is in terms of fertilised eggs, the expenditure in time used for searching. This difference in currencies was a formidable problem for behavioural ecology (Ydenberg et al. 2007, 15) and the solution was to find trade-offs in state variables instead (e.g., time spent searching vs. time spent mating).

The above mentioned differences suggest that Wicksell has not been a direct source of inspiration for optimal foraging theory. Furthermore, the graphical model of Wicksell has not become as emblematic in economics as figure 3 has in foraging theory. Nevertheless, this model seems to have entered operations research or industrial engineering and thus reached Parker's father[14] or the undergraduate courses of Charnov without either of them having ever consciously seen such a graph in its economic context.

9 Independent discoveries

The last and least concrete indications that some undercurrent fuelled a gold rush into the newfound field of behavioural ecology are some striking instances of independent but similar achievements. Schoener (1987, 5) and many other behavioural ecologists (e.g., Ydenberg et al. 2007) think that their field was born the moment that MacArthur and Pianka (1966) published back-to-back with Emlen (1966). Both promoted the idea that time spent in a behavioural pattern is an investment or cost and energy uptake the return or benefit, and that organisms should be selected to optimise that in a trade-off. And both used graphical model representations.[15]

From the above examples, Rapport (1971) and Covich (1972) independently applied marginal utility theory to derive optimal ratios of different food items. Likewise, Charnov and Krebs (1974), Parker (1974), as well as Smith and Fretwell (1974) independently applied the method of finding the optimal investment (in clutch size, mating, and offspring size respectively) by drawing the tangent to the gain function.

10 Conclusion

Scientific advances often result from previously unthought of combinations of knowledge and the new applications resulting therefrom. The above suggests that such a research advancing combination joined an optimisation approach from microeconomics with evolutionary ethology. While it probably facilitated the exploration of the newfound field of behavioural ecology and had an igniting effect on what has been called the *explosive growth* of behavioural ecology (e.g., Krebs 1985; Schoener 1987; Parker 2001, 2010), the influence on the pioneers was highly variable and individual. Some used microeconomics as a fort from which to ride out and occupy new territory for economics. Some used it as a tool shed from which to borrow equipment to cultivate a new piece of land for ecology. Some regarded it as a school from which to graduate and emancipate. And still others did not even see the building but tripped up on a useful microeconomic gadget left lying about, or inherited one from an elder without knowing its ultimate provenience.

The economists among these pioneers (e.g., Becker 1962, 1977; Tullock 1970, 1971a, b; Hishleifer 1977) received relatively few citations from behavioural ecologists (Vromen 2011; Charnov pers. comm.). Why? The first behavioural ecologists did not try to explain human behaviour but the foraging or mating behaviour of animals. Economic substitutes of genetic success like utility or social income were, therefore, of no use to them. Conversely, the first generation economists (e.g., Alchian 1950; Friedman 1953) were really interested in defending their

14 Unfortunately, the source of Geoffrey Parker's father, Alan Parker, remains unknown (G.A. Parker, pers. comm.).

15 For more examples of independent but analogous achievements see Schoener (1987).

marginalist approach against criticism from inside economics, and the second generation, Becker, Tullock, Hishleifer, expanded it to animals without abandoning the economic proxies for success. Nevertheless, the above analysis suggests that foraging theory has deeper roots in economics than these imperialistic attempts at colonialization by economists of the 1960-70s.

References

Alchian, Armen A. 1950. Uncertainty, evolution and economic theory. *Journal of Political Economy* 58: 211-222.

Alcock, John. 2003. A textbook history of animal behaviour. *Animal Behaviour* 65: 2-10.

Atmann, Stuart A., and Jeanne Altmann. 2003. The transformation of behaviour field studies. *Animal Behaviour* 65: 413-423.

Baumol, William J. 1961. *Economic theory and operations analysis*. Englewood Cliffs, NJ: Prentice-Hall.

Becker, Gary S. 1962. Irrational behavior and economic theory. *Journal of Political Economy* 70: 1-13.

Becker, Gary S. 1974. A theory of social interactions. *Journal of Political Economy* 82: 1032-1093.

Becker, Gary S. 1976. Altruism, egoism, and genetic fitness: economics and sociobiology. Journal of Economic Literature 14: 817-826.

Birkhead, Tim R. 2014. Reflections. *Behavioral Ecology* 25: 239-241.

Birkhead, Tim R., and Pat Monaghan. 2010. Ingenious ideas: the history of behavioral ecology. In *Evolutionary Behavioral Ecology*, eds. David F. Westnead, and Charles W. Fox, 3-15. Oxford Univ Press.

Blumler, Mark A., Anthony Cole, John Flenley and Udo Schickhoff. 2011. History of Biogeographical Thought. In *Handbook of Biogeography*, eds., Andrew Millington, Mark Blumler, and Udo Schickhoff, 23-42. London: SAGE Publications.

Bolduc, Jean-Sébastien. 2012. Behavioural ecology’s ethological roots. *Studies in History and Philosophy of Biological and Biomedical Sciences* 43: 674-683.

Bolduc, Jean-Sébastien, and Frank Cézilly. 2012. Optimality modelling in the real world. *Biology and Philosophy* 27: 851-869.

Boulding, Kenneth E. 1966. *Economics Analysis, vol. I, Microeconomics*. New York: Harper and Row.

Burkhardt, Richard W. 2005. *Patterns of behavior: Konrad Lorenz, Niko Tinbergen, and the founding of ethology*. University of Chicago Press.

Burkhardt, Richard W. 2016. Niko Tinbergen: a message in the archives. *Journal of the History of Biology* 49: 685-703.

Caraco, Thomas. 1987. Foraging games in a random environment. In Foraging behavior, eds., Alan C. Kamil, John R. Krebs, and H. Ronald Pulliam, 389-414. New York: Plenum Press.

Cézilly, Frank. 2008. A history of behavioural ecology. In *Behavioural Ecology*, eds., Etienne Danchin, Luc-Alain Giraldeau, and Frank Cézilly, 3-27. Oxford Univ Press.

Cézilly, Frank, Ètienne Danchin, and Luc-Alain Giraldeau. 2008. Research methods in behavioural ecology. In *Behavioural Ecology*, eds., Etienne Danchin, Luc-Alain Giraldeau, and Frank Cézilly, 55-96. Oxford Univ Press.

Charnov, Eric L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129-136.

Charnov, Eric L., and Gordon H. Orians. 1973. *Optimal foraging: some theoretical explorations*. Lobo Vault, University of New Mexico. http://hdl.handle.net/1928/1649. Accessed 26 January 2017.

Charnov Eric L., and John R. Krebs. 1974. On clutch size and fitness. *Ibis* 116: 217-219.

Cody, Martin L. 1966. A general theory of clutch size. *Evolution* 20: 174-184.

Cody, Martin L. 1974. Optimization in ecology. *Science* 183: 1156-1164.

Cody, Martin L., and Diamond, Jared M. 1975. Ecology and evolution of communities. Cambridge MA: Harvard University Press.
Covich, Alan P. 1972. Ecological economics of seed consumption by *Peromyscus*: a graphical model of resource substitution. *Transactions of the Connecticut Academy of Arts and Sciences* 44: 71-93.
Covich, Alan P. 1974. Ecological economics of foraging among coevolving animals and plants. *Annals of the Missouri Botanical Garden* 61: 794-805.
Covich, Alan P. 1976. Analysing shapes of foraging areas: some ecological and economic theories. *Annual Review of Ecology and Systematics* 7: 235-257.
Drickamer, Lee C. 1998. Vertebrate behavior: integration of proximate and ultimate causation. *American Zoologist* 31: 39-42.
Driscoll, Catherine. 2009. On our best behavior: optimality models in human behavioral ecology. *Studies in History and Philosophy of Biology and Biomedical Sciences* 40: 133-141.
Emlen, J. Merritt. 1966. The role of time and energy in fool preference. *American Naturalist* 100: 611-617.
Friedman, Michael T. 1953. *Essays in positive economics*. Chicago University Press.
Luc-Alain Giraldeau. 2008. Solitary foraging strategies. In *Behavioural Ecology*, eds., Etienne Danchin, Luc-Alain Giraldeau, and Frank Cézilly, 233-256. Oxford Univ Press.
Gossen, Hermann H. 1854. *Entwicklung der Gesetze des menschlichen Verkehrs und der daraus fließenden Regeln für menschliches Handeln*. Friedrich Vieweg und Sohn, Braunschweig. https://books.google.de/books?id=BzFGAAAAYAAJ. Accessed 20 January 2017
Gross, Mart R. 1994. The evolution of behavioural ecology. Trends Ecol Evol 9:358-360
Hirshleifer, Jack. 1977. Shakespeare vs. Becker on altruism: the importance of having the last word. *Journal of Economic Literature* 15: 500-502.
Kalmus, Hans. 1969. Animal behaviour and theories of games and language. *Animal Behaviour* 17: 607-617.
Kingsland, Sharon E. *Modeling nature. Second edition*. University of Chicago Press.
Kitcher, Philip. 1987. Precis of Vaulting Ambition: Sociobiology and the Quest for Human Nature. *Behavioral and Brain Sciences* 10: 61-71.
Kitcher, Philip. 1990. Developmental decomposition and the future of human behavioral ecology. *Philosophy of Science* 57: 96-117.
Krebs, John R. 1985. Sociobiology ten years on. *New Scientist* 108(1476): 40-43.
Krebs, John R., and Nicholas B. Davies. 1978. Behavioural ecology: an evolutionary approach. Oxford: Blackwell Scientific Publications.
Krebs, John R., and Nicholas B. Davies. 1997. Behavioural ecology: an evolutionary approach. Fourth edition. Oxford: Blackwell Science.
Lendrem, Dennis. 1986. *Modelling in behavioural ecology*. London: Croom Helm.
Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *American Naturalist* 96: 361-373.
Levins, Richard, and Richard Lewontin. 1985. *The dialectical biologist*. Cambridge MA: Harvard University Press.
Lewontin, Richard (1961). Evolution and the theory of games. Journal of Theoretical Biology 1: 382-403.
MacArthur Robert H., and Eric R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100: 603-609.
MacArthur, Robert H. 1972. *Geographical ecology: Patterns in the distribution of species*. Princeton University Press.
McFarland, David. 1985. Animal behaviour. London: Pitman.
Maynard Smith, John. 1982. *Evolution and the Theory of Games*. Cambridge Univ Press.

Maynard Smith, John. 1992. Did Darwin get it right? Essays on games, sex and evolution. New York: Chapman & Hall.
Odenbough, Jay. 2013. Searching for pattern, hunting for causes: Robert MacArthur, the mathematical naturalist. In *Outsider scientists: routes to innovation in biology*, eds. Oren Harman, and Michael R. Dietrich, 181-198. Chicago University Press.
Orzack, Steven H., and Elliott Sober. 1994a. How (not) to test an optimality model. *Trends in Ecology and Evolution* 9: 265-267.
Orzack, Steven H., and Elliott Sober. 1994b. Optimality models and the test of adaptationism. *American Naturalist* 143: 361-380.
Oster, George F., and Edward O. Wilson. 1978. *Caste and ecology in social insects*. NJ: Princeton University Press.
Owens, Ian P. F. 2006. Where is behavioural ecology going? Trends in Ecology and Evolution 21: 356-361.
Pareto, Vilfredo. 1919. *Manuale di economia politica con una introduzione alla scienza sociale*. Milano: Società Editrice Libraria. https://archive.org/details/manualedieconomi00pareuoft. Accessed 21 January 2017.
Parker, Geoffrey A. 1974. Courtship persistence and female-guarding as male time investment strategies. *Behaviour* 48: 157-184.
Parker, Geoffrey A. 2001. Golden flies, sunlit meadows: a tribute to the yellow dungfly. In *Model Systems in Behavioral Ecology*, ed., Lee A. Dugatkin, 3-26. NJ: Princeton Univ Press.
Parker, Geoffrey A. 2010. Reflections before dusk. In *Leaders in Animal Behaviour: The Second Generation*, eds., Lee C. Drickamer, and Donald A. Dewsbury, 429-464. Cambridge Univ Press.
Parker, Geoffrey A., and Robert A. Stuart. 1976. Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. *American Naturalist* 110: 1055-1077.
Potochnik, Angela. 2009. Optimality modeling in a suboptimal world. *Biology and Philosophy* 24: 183-197.
Potochnik, Angela. 2012. Modeling social and evolutionary games. *Studies in History and Philosophy of Biological and Biomedical Sciences* 43: 202-208.
Rapport, David J. 1971. An optimization model for food selection. American Naturalist 105: 575-587.
Rapport, David J. 1980. Optimal foraging for complementary diets. American Naturalist 116: 324-346.
Rapport, David J., and James E. Turner. 1977. Economic models in ecology. *Science* 195: 367-373.
Rapport, David J. 1991. Myths in the foundations of economics and ecology. *Biological Journal of the Linnean Society* 44: 185-202.
Robinson, Joan. 1953-54. The production function and the theory of capital. *Review of Economic Studies* 21(2): 81-106.
Robinson, Joan. 1956. *The accumulation of capital*. Homewood, IL: Richard D. Irwin.
Rosen, Robert. 1967. *Optimality principles in biology*. Butterworths, London
Schoemaker, Paul J. H. 1991. The quest for optimality: a positive heuristic of science? *Behavioral and Brain Sciences* 14: 205-245.
Schoener, Thomas W. 1969. Optimal size and specialization in constant and fluctuating environments: an energy-time approach. *Brookhaven Symposia in Biology* 22: 103-114.
Schoener, Thomas W. 1987. A brief history of optimal foraging ecology. In *Foraging Behavior*, eds., Alan C. Kamil, John R. Krebs, and H. Ronald Pulliam, 5-67. New York: Plenum Press.
Screpanti, Ernesto, and Stefano Zamagni. 2005. *An outline of the history of economic thought*. Second edition. Oxford University Press.
Segerstråle, Ullica. 2000. *Defenders of the truth*. Oxford University Press.

Slack, Nancy G. 2010. G. *Evelyn Hutchinson and the invention of modern ecology*. New Haven: Yale University Press.
Smith, Christopher C., and Stephe D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108: 409-506.
Stephens, David W., and John R. Krebs. 1986. *Foraging theory*. Princeton University Press.
Taha, Hamdy A. 1971. *Operations research. An introduction*. New York: Macmillan.
Tintner, Gerhard. 1941a. The theory of choice under subjective risk and uncertainty. *Econometrica* 9: 298-304.
Tintner, Gerhard. 1941b. The pure theory of production under technological risk and uncertainty. *Econometrica* 9: 305-311.
Tullock, Gordon (1970) Switching in general predators. *Bulletin of the Ecological Society of America* 51: 21-23.
Tullock, Gordon. 1971a. The coal tit as a careful shopper. *American Naturalist* 105: 77-80.
Tullock, Gordon. 1971b. Biological externalities. *Journal of Theoretical Biology* 33: 565-576.
Vermeij, Geerat J. 2009. Nature: an economic history. Princeton University Press.
Vromen, Jack. 2011. Allusions to evolution: edifying evolutionary biology rather than economic theory. In *Building Chicago economics. New perspectives on the history of America's most powerful economics program*, eds., Robert van Horn, Philip Mirowski, and Thomas A. Stapleford, 208-236. Cambridge University Press.
Watson, Donald S. 1972[1963]. *Price theory and its uses*. *Third edition*. Boston: Houghton Mifflin Company.
Wicksell, Knut. 1934. *Lectures on political economy, volume I: General theory*. Reprinted 1977 in Fairfield, NJ: Augustus M. Kelley Publishers. https://mises.org/library/lectures-political-economy-volume-i-general-theory. Accessed 21 June 2017
Wicksell, Knut. 1954. *Value, Capital and Rent*. Translated by S. H. Frowein, reprinted 1970 in New York: Augustus M. Kelley Publishers. https://mises.org/library/value-capital-and-rent-0. Accessed 25 January 2017
Wilson, Edward O. 1977. Biology and the social sciences. *Daedalus* 106(4): 127-140.
Wilson, Edward O. 1998. *Consilience: the unity of knowledge*. New York: Alfred A. Knopf.
Wilson, Edward O. 2006. *Naturalist*. Washington DC: Island Press.
Ydenberg, Ronald C. The behavioral ecology of provisioning in birds. Ècoscience 1(1): 1-14.
Ydenberg, Ronald C., Joel S. Brown, and David W. Stephens. 2007. Foraging: an overview. In *Foraging: behavior and ecology*, eds., D.W. Stephens, J.S. Brown, and R.C. Ydenberg, 1-28. University of Chicago Press.