

## “It Felt More like a Revolution.” How Behavioral Ecology Succeeded Ethology, 1970–1990

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**Summary:** As soon as ethology’s status diminished in the early 1970s, it was confronted with two successor disciplines, sociobiology and behavioral ecology. They were able to challenge ethology because it no longer provided markers of strong disciplinarity such as theoretical coherence, leading figures and a clear identity. While behavioral ecology developed organically out of the UK ethological research community into its own disciplinary standing, sociobiology presented itself as a US competitor to the ethological tradition. I will show how behavioral ecology took the role of legitimate heir to ethology by rebuilding a theoretical core and an intellectual sense of community, while sociobiology failed to use its public appeal to reach disciplinary status. Meanwhile, ethology changed its disciplinary identity to encompass all biological studies of animal behavior.

**Keywords:** ethology, behavioral ecology, sociobiology, behavioral biology, animal behavior, Konrad Lorenz, Nikolaas Tinbergen, Edward O. Wilson, John Krebs, Mike Cullen

### 1. Disciplinary Identities: People, Places, Publications


“Many of us have been surprised at the unconventional decision of the Nobel Foundation to award this year’s prize [...] to three men who had until recently been regarded as ‘mere animal watchers,’”<sup>1</sup> began Nikolaas Tinbergen his Nobel Prize Lecture, delivered in Stockholm on 23 December 1973. Fellow ethologists saw the award of the Nobel Prize in Physiology or Medicine to Konrad Lorenz, Nikolaas Tinbergen, and Karl von Frisch as honoring them for

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<sup>1</sup> Tinbergen 1974, on 20.

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creating the discipline of ethology, celebrating it as a fresh and distinctly biological perspective on animal behavior that far surpassed the subjective impressions of “mere animal watching” in the past, transforming natural history into proper science.<sup>2</sup> However, as the Nobel Prize outwardly celebrated a strong discipline with charismatic leaders and clear conceptual content, ethology had already lost a lot of its disciplinary strength.

The ascension of ethology to the status of a discipline in the early 20<sup>th</sup> century and its prime in the 1940s and 1950s were soon memorialized and analyzed by ethologists, ethologists turned historians, and historians of science.<sup>3</sup> There is vast scholarship on how ethology was purposefully established as a discipline, the influence and idiosyncrasies of its founding figures, and the distinct approach it took to animals as its subjects.<sup>4</sup> Richard Burkhardt examined it from a disciplinary perspective, asking: “How did the science of ethology come into being?”<sup>5</sup> However, the disciplinary trajectory of ethology in the last quarter of the 20<sup>th</sup> century has received less interest. This paper examines a period when the field of animal behavior studies became more crowded and ethology experienced the threat of disciplinary competition and asks: How did the discipline of ethology move out of being?

It is not possible to answer this question by exclusively looking at ethology. There is agreement on two points regarding ethology’s decline: It occurred by the mid-1970s and involved the rise of two other disciplines, sociobiology and behavioral ecology. The conventional wisdom goes that ethology was replaced by either sociobiology or behavioral ecology, or both. This is a compelling narrative, as both sociobiology and behavioral ecology have their roots in ethology and animal behavior.<sup>6</sup> However, there is a more complex relationship between these disciplines than a simple matter of succession. This complicated process of disciplinary reconfiguration has received little attention and the changing tides of these disciplines, their core theoretical and methodological content, and their personnel, as well as how these materialized in their publication structure have yet to be analyzed. This paper aims to close this gap in historiography while following a disciplinary perspective approach where

<sup>2</sup> Hinde and Thorpe 1973, on 346.

<sup>3</sup> Early examples of historical scholarship include: Burkhardt 1981; Burkhardt 1983; Dewsbury 1986a; Dewsbury 1986b; Dewsbury 1992a; Dewsbury 1992b; Dewsbury 1995; Dewsbury 1997; Durant 1981; Durant 1986a; Durant 1986b. Recollections and biographies by ethologists include: Thorpe 1979; Halliday and Dawkins 1991; Klopfer 1999; Kruuk 2003; Schurig 2014.

<sup>4</sup> Examples of more recent monographs: Munz 2016; Beale 2008; Burkhardt 2005; Röell 2000; Taschwer and Föger 2001; Crist 1999. See also the recent articles by Paul Griffiths: Griffiths 2008a (essay review); Griffiths 2008b; Griffiths 2004.

<sup>5</sup> Burkhardt 2005, on 1.

<sup>6</sup> This narrative is represented in Greenblatt 2012, who claims ethology was reborn as sociobiology. Recently, more nuanced examinations of the intertwined histories of sociobiology, ethology and behavioral ecology have been undertaken by Bolduc 2012 or Levallois 2018. Milam 2022 (in this issue) traces the impact behavioral ecology had on creating long-term research projects, while Dhein 2022 and Odenwald 2022 show how human ethology as well as neuro-ethology relate to the ethological research paradigm.

disciplines as a whole rather than individual contributions are examined by focusing my analysis on selected disciplinary publications.

Tracing the development of one or even several disciplines requires taking a bird's eye view of developments. This is done by looking at signature publications as well as their reception within the community from the macro level rather than examining the specific practices or results of any given researcher or group. Burkhardt explores the disciplinary beginnings of ethology along the central categories people, places, practices, politics; my approach here replaces the latter two categories with publications.<sup>7</sup> While people make disciplines, publications make disciplines visible to the larger scientific community. Establishing journals, writing textbooks and monographs, and organizing conferences and publishing their proceedings, therefore, can be understood as strategic moves in achieving disciplinarity. Not all publications are created equal when it comes to disciplinary reflections. Certain types of publications stand out: My focus is on textbooks, as they form the basis of a discipline, as well as long-running series, proving a thorough line of disciplinary reflection on different themes and trends. Book reviews play an extraordinary part in disciplinary transformation as they allow for more explicit disciplinary reflections and boundary work<sup>8</sup> since a reviewer is invited to place the scholarship into its context. The disciplinary politics of the time are reflected in these publications.

The intertwined histories of sociobiology, behavioral ecology, and ethology are a ripe field for investigating the dynamics of disciplinary rearrangement and competition. There are different ways to define disciplinarity, and even though the scholarship has not settled on one definition, there is a consensus that it involves uniting a set of scholars with a subject matter and a research method.<sup>9</sup> The following section (2.) assesses the disciplinary status of ethology at what seems to be its disciplinary peak. Then, each of the following sections explores how strengthening an element of disciplinarity – social coherence (3.), unifying theoretical core (4.), and advancing through competition (5.) – leads to

<sup>7</sup> Burkhardt 2005 also analyzes the role of publications extensively without making an explicit category. Other scholars have similarly stressed the importance of factors such as publication practices, conferences and personal meetings, and institution building for the foundation of ethology, such as Schurig 2014, or for evolutionary biology more generally, such as Smocovitis 1996.

<sup>8</sup> Boundary work as Thomas Gieryn defines it in Gieryn 1987, on 788 does not only refer to the practice of demarcating science from non-science, but also for “excluding others as pseudoscientists.” While the debates in animal behavior studies did not get heated to the point of accusing others of pseudo-science (unlike the debates about applications of adaptive frameworks on humans), the logic of boundary work can be applied to disciplinary competition.

<sup>9</sup> Chandler 2009, on 734 captures the dialectical nature of a discipline between its social-institutional and substantive (e.g., theoretical and methodological) elements: “For a discipline to do its work it must have a home base and a sense of its identity over time; it must have a local habitation and a name [...]. At the same time, to imagine that disciplines are nothing more than their institutional arrangements is to deny the possibility that a disciplinary system can evolve beyond the structure [...] that is meant to administer it.” Features of disciplinarity are discussed in countless publications, some helpful overviews are: Becher and Trowler 2001; Becher 1989; Guntau and Laitko 1987; Whitley 1984.

discipline formation. The final section (6.) answers the question of what happened to ethology and if, indeed, it ceased to be.

## 2. An Insecure Discipline: Ethology Beyond the Nobel Prize, 1973–1976

The perception of disciplinary coherence at the time of the Nobel Prize was in stark contrast to the true state of the discipline. Looking deeper into the ethological community, feelings about the state of the discipline were not unequivocally celebratory and were, in fact, more insecure. However, this was not always the case. Ethology had its roots in the 1920s and 1930s and its most impressive successes in the following decades and in its prime, ethologists knew precisely what they stood for: During this time, especially Lorenz and Tinbergen had crafted the image of ethology as a merger of the naturalist tradition with more scientific approaches, theoretical foundations, and exact terminology, providing complex causal mechanisms to explain animal behavior.<sup>10</sup> Central concepts revolved around ideas of innateness and instinct, behavior that animals did not learn.<sup>11</sup> This focus on the innate was used to present ethology as an alternative to the branch of psychology interested in animal behavior and learning: comparative psychology. These two disciplines were thought of as competitors, often based on a caricature of their actual complexities and nuances: Here was American-based comparative psychology, preoccupied with just one species in the confines of the laboratory, running white rats through mazes, exclusively focused on behavior modification through punishment and reward; there was European ethology, observing instinctive behavior in natural settings, without interventions and dealing with the whole of the animal world.<sup>12</sup> Comparative psychology provided an optimal adversary to early ethology's emerging identity. However, by the time of the Nobel Prize in 1973, the boundaries between ethology and comparative psychology had become porous as core concepts of ethology, such as “instinct”; they were first questioned and then dismantled, especially in the English-speaking part of the ethological landscape.

Ethologists' disciplinary insecurity was reflected in two edited volumes that appeared in the 1970s: *Perspectives in Ethology* (1973),<sup>13</sup> edited by ethologists Patrick Bateson and Peter Klopfer, and, three years later, *Growing Points in*

<sup>10</sup> Crist 1999, on 89.

<sup>11</sup> Lorenz 1937; Tinbergen 1942; Tinbergen 1951. For the role of instinct, see also Brigandt 2003; Durant 1981; Griffiths and Linquist 2021.

<sup>12</sup> This opposition between comparative psychology and ethology left a lasting impact on historiographical record and is still recreated in the literature: Jaynes 1969; McBride 1987; Crist 1999, on 89; Burghardt 2009; Greenblatt 2012. However, in fact, the relationship was more complicated from the beginning, see Dewsbury 1992a; Dewsbury 1997; Burkhardt 2005, on 362.

<sup>13</sup> Bateson and Klopfer 1973. This anthology was the first volume of what became the long-running *Perspective in Ethology* series with 13 volumes published between 1973 and 2000.

*Ethology* (1976),<sup>14</sup> edited by Bateson again, this time with Robert Hinde. All three of them were leading figures in establishing ethology at Madingley Field Station of Cambridge University beginning in the 1950s.<sup>15</sup> Despite the recent Nobel Prize, these volumes did not set a jubilant and self-confident tone, distancing themselves from ethology's past, stating dissatisfaction with the current status quo and offering little future perspective beyond "encouraging scientists [...] to let their hair down a little and write in a less inhibited way."<sup>16</sup> They seemed unsure of ethology's future potential, or, as Hinde and Bateson phrased it with the metaphor of growth: "As things stand, the roots ethology has put down seem healthy. But are they growing towards soil that will continue to nourish them? Are the shoots heading toward the light?"<sup>17</sup>

In exploring ethology's future, Bateson and Klopfer wanted to leave its past behind as back then, "much of the evidence was anecdotal, much of the thinking intuitive," and Bateson and Hinde were equally keen to "not to review past achievements or reenact past battles."<sup>18</sup> This dismissal was mainly directed at Konrad Lorenz. As early as the 1950s, his theory of instinct, a central concept for ethology, underwent scrutiny and criticism that eventually turned into outright rejection. This process started as an external critique from the other side of the Atlantic and disciplinary divide, spearheaded by Daniel Lehrman,<sup>19</sup> an American comparative psychologist, which initially could be attributed to the larger disciplinary rivalry. However, while Lorenz stood firm against Lehrman's arguments, Tinbergen and his colleagues at Oxford and Cambridge embraced both Lehrman and his critique and turned away from early ethological theories.<sup>20</sup> Lorenz perceived this intellectual development as a personal attack and publicly declared his unhappiness with the modern field of ethology in the UK, declaring it had unduly given up on innateness in the introduction to his long-awaited textbook.<sup>21</sup>

This marked a rift in the development of UK and continental ethology. In the UK, Tinbergen's group had grown more interventionist, so the differences to comparative psychology were lessening.<sup>22</sup> His circle, including Robert Hinde, became open advocates of integrating comparative psychology into ethology; the latter even wrote a book in 1966 that was an explicit synthesis of

<sup>14</sup> Bateson and Hinde 1976.

<sup>15</sup> Robert Hinde and Patrick Bateson stayed there until their retirement in 1994 and 2005 respectively, while Peter Klopfer, a postgraduate student at the University of Cambridge, became professor at Duke University in 1958 and an influential ethologist in the US.

<sup>16</sup> Bateson and Klopfer 1973, on v–vi.

<sup>17</sup> Bateson and Hinde 1976, on 1.

<sup>18</sup> Bateson and Klopfer 1973, on v; Bateson and Hinde 1976, on 1.

<sup>19</sup> Lehrman 1953. For background, see: Beer 1975a; Burkhardt 2005, on 384–390; Wunsch 2016.

<sup>20</sup> Burkhardt 2005, on 428–431; Griffiths 2004, on 628.

<sup>21</sup> Lorenz 1965. Additionally, John B. S. Haldane opposed Lorenzian influence in the UK; Griffiths 2004, on 626.

<sup>22</sup> For a detailed history of the shift in Tinbergen's and his students research activities: Beale 2008. From the perspective of his students or colleagues, see Kruuk 2003 and Klopfer 1999. See further the chapters by Dawkins, Krebs, Hinde, Davies, Parker, Clutton-Brock, and Tinbergen himself in: Dewsbury 1985; Drickamer and Dewsbury 2010.

these two disciplines,<sup>23</sup> which is credited with having “swept away much of the old theorizing by Lorenz and Tinbergen.”<sup>24</sup> Lorenz’s status in UK ethology had degraded.<sup>25</sup> While Klopfer and Bateson did not call out Lorenz by name, Arthur Riopelle was direct and brutal in his conclusion that ethology had no use for Lorenzian thought anymore: “This superb collection of essays doesn’t afford much solace to tired old notions. The old Lorenzian notions of causation of behavior and evolutionary functions are passed over with scarcely a glance.”<sup>26</sup>

With Lorenz firmly in the past, ethologists in the 1970s were looking to forge a future path for ethology.<sup>27</sup> However, in their assessment, the current state of the discipline did not provide a satisfactory basis: They contrasted the intuitive thinking of early ethology with the current focus on more rigorous and sophisticated quantitative methodology, which they saw as an overcorrection to the point of stifling the innovative and creative energy of the discipline: “Radical or novel theories must be fully formed if they are not to be laughed to scorn, and as new ideas peep out of the ground in the conceptual flowerbed, it is easy enough to shout ‘Weeds!’ and dig them up by the roots,”<sup>28</sup> wrote Klopfer and Bateson in *Perspectives*. Hinde and Bateson make a similar point: “Vast mounds of impeccably collected data could easily overwhelm creative thinking and a preoccupation with method could displace a concern for problems.”<sup>29</sup> Cambridge psychologist Michael Morgan agreed with their concern in his reviews: “There is thus a great deal of heart searching and a striving to put the subject on what a mathematician would call ‘a sound axiomatic footing,’” but he is not impressed with the results: “One feels not altogether sure about the value of this search for rigor.”<sup>30</sup>

Older ethologists articulated a tension between, on the one hand, wanting to re-create the sense of excitement of earlier days, but this time with more scientific rigor and less loose thinking, and on the other hand being overwhelmed by the new increasingly data-driven and mathematical methodology. Ethology seemed to be stuck, having lost its conceptual identity and doubting its ability to forge a new one. In his review, George Barlow picks up on this: “One does well to ask: Who is an Ethologist? It is hard to say.”<sup>31</sup> Several reviewers also note with astonishment how hollow former adversarial distinctions have become. “The title of the book could equally be *Perspectives in Psychology*,” writes Riopelle;<sup>32</sup> Beer provides a more vivid description:

<sup>23</sup> Hinde 1966.

<sup>24</sup> Krebs 2010, on 390.

<sup>25</sup> Griffiths 2004, on 628. For US ethology, see Dewsbury 1995.

<sup>26</sup> Riopelle 1975, on 714.

<sup>27</sup> Bateson and Klopfer 1973, on vii: “Advice to potential contributors: If this volume does mark the start of a series, it is our intention that it be a series that stimulates and directs new lines of research rather than chronicles the past.”

<sup>28</sup> *Ibid.*, on v.

<sup>29</sup> Bateson and Hinde 1976, on 1.

<sup>30</sup> Morgan 1977, on 496.

<sup>31</sup> Barlow 1974, on 675.

<sup>32</sup> Riopelle 1975, on 715.

“Perspective drawing is a way of making parallel lines appear to meet. This book illustrates admirably how the distinction that used to be easy to make between European ethology and American comparative psychology has diminished almost to a vanishing point.”<sup>33</sup> In order to re-establish a disciplinary identity around a shared but not too complicated theory in the future, the editors suggested that ethology was merely in need of an intellectual energy burst, a forum where scholars can be more speculative to re-invigorate the discipline as “embryonic ideas which have tremendous potential may not be easily distinguishable from embryonic nonsense.”<sup>34</sup> However, the results were not convincing. While reviewers lauded the volumes for their high quality, it remained unclear “where ethology is headed today.”<sup>35</sup>

Where does this leave ethology in 1973? Both *Growing Points* and *Perspectives* made it clear that the honors of the present represented the intellectual past of the discipline. The foundational figures and theories were in the past, and the future direction of the discipline was unclear, with especially the older generation questioning the push for more mathematical approaches. With methodology and theory changing and one of the defining characteristics, the line between ethology and comparative psychology, eroded, the question was urgent: What about exploring animal behavior shaped ethology into a coherent discipline?

### 3. A New Golden Age: Young Ethologists at Cambridge and Oxford, 1975–1978

While these publications reflect the weaknesses of ethology in the mid-1970s – a conceptual identity lost between the overhaul of classical ethology and the spread of more mathematical and quantitative methods<sup>36</sup> – surprisingly, they reveal an ongoing strength of ethology: its strong social identity.

Cambridge social psychologist Martin Richards ruminates on this phenomenon extensively in his review of *Growing Points*. Like many reviewers of this volume, he notes the lack of conceptual coherence. “The diversity begs the question of the definition and scope of ethology – what makes the ‘growing points’ that are discussed ethology rather than comparative psychology, genetics or developmental psychology among many possible contenders?”<sup>37</sup> and then answers his own question: social belonging. “What is perhaps remarkable about ethology is the way in which workers of such varied interests continue to identify with one another and form a cohesive social group.”<sup>38</sup> Richards himself is familiar with the close-knit ethological community as he did his Ph.D. under

<sup>33</sup> Beer 1975b, on 460.

<sup>34</sup> Bateson and Klopfer 1973, on v.

<sup>35</sup> Barlow 1974, on 675.

<sup>36</sup> These developments are represented in the contributions of John Krebs and Richard Dawkins to *Growing Points* and *Perspectives*.

<sup>37</sup> Richards 1977, on 374.

<sup>38</sup> *Ibid.*

Hinde's supervision at Madingley Station in Cambridge, one center of ethological sociality. Several of these centers were a key factor in creating a sense of community that was strong enough to secure the disciplinary identity through a phase of theoretical insecurity. As Peter Klopfer puts it: "The history of 20<sup>th</sup>-century ethology is essentially contained in the reports and records of three institutions,"<sup>39</sup> Lorenz' Max-Planck-Institute in Starnberg, Tinbergen's Animal Behavior Group in Oxford, and the Madingley Field Station at the University of Cambridge.<sup>40</sup>

The *Growing Points* volume was, in fact, dedicated to one of these central institutions: It consisted of papers presented in 1975 in celebration of the research station in Madingley of the Cambridge department. Madingley became a focal point for UK ethology, a pet project of William Thorpe, founded in 1950 with Robert Hinde as its first director. Thorpe was heavily influenced by Lorenz and Tinbergen<sup>41</sup> and while Hinde was not officially supervised by Tinbergen, he can still be counted as a Tinbergen student.<sup>42</sup> Thorpe and Hinde were instrumental in establishing ethology with an ornithological perspective at Cambridge; Hinde and his student Bateson were responsible for creating a focus on neuroscience, physiology, and development at Cambridge that stressed complicated interrelations between different ecological and behavioral factors.<sup>43</sup> And beyond Cambridge, Hinde's synthetic account of animal behavior became the "great blue bible" of ethology.<sup>44</sup>

The anniversary of this foundational institution provided ethologists in the 1970s with a chance to strengthen their social ties as well as reflect on the direction of the discipline. Since the theoretical approaches of the participants of the conference at this time were diverse, it was the personal connection that decided who was an ethologist and could contribute to the conversation, as Richards noted in his review:

Despite the fact that the contributions are in no sense a cross-section of ethologists (all are people who have worked at Cambridge or have been closely associated with the Sub-Department and, for instance, no continental researchers are represented) the diversity of work discussed is enormous and a summary is impossible in the space available.<sup>45</sup>

Therefore, *Growing Points* as a conference proceeding, in particular, reflects the social dimension of the discipline. And in this social dimension, ethology at Cambridge was going strong to the point where Klopfer identifies it as the place where "signs of ethological ferment are most in evidence."<sup>46</sup> Despite Klopfer's assessment of Cambridge as the center for a movement of transforming ethology, Oxford soon overtook Cambridge in relevance. Over the course

<sup>39</sup> Klopfer 1977, on 366.

<sup>40</sup> This list ignores the ethological tradition in the Netherlands, especially at the universities in Groningen and Leiden.

<sup>41</sup> Durant 1986a, on 1610. See also Durant 1986b.

<sup>42</sup> Beale 2008, on 283.

<sup>43</sup> Davies 2010, on 145.

<sup>44</sup> Clutton-Brock 2010, on 112.

<sup>45</sup> Richards 1977, on 374.

<sup>46</sup> Klopfer 1977, on 366.



of the 1970s, it leveraged its social cohesion and strong group identity into leading the charge in both an intellectual and generational change within ethology.

When Tinbergen came to the University of Oxford in 1948, first as a university lecturer and then, as of 1966, as Professor for Animal Behaviour, his focus was twofold: Firstly, supervising students and building a vibrant research community; secondly, shifting ethology towards questions of the evolutionary significance of behavior. Since the late 1960s, Tinbergen became increasingly concerned that there was too much physiological work and too little on evolution and function work, which required intense investment of time and energy out in the field.<sup>47</sup> Tinbergen, himself a keen field naturalist, made it his priority to steer modern ethology toward the study of behavior and environmental pressures, named behavioral ecology.<sup>48</sup> There was allegedly even an informal understanding that Thorpe's and Hinde's Field Station at Madingley was to focus on behavioral mechanisms while Tinbergens's group at Oxford was to focus on behavioral function.<sup>49</sup> Oxford's overzealous adoption of the adaptationist outlook was soon lovingly mocked by Cambridge ethologists, ascribing Oxford the motto: "Never use a causal explanation if a teleological one will do instead."<sup>50</sup> Even though his own research interests turned increasingly toward human behavior in the late 1960s and did not display the overriding adaptationist focus Oxford became famous for, Tinbergen had firmly established his Oxford research group as a place for connecting evolution, ecology, and ethology.<sup>51</sup> This research group was instrumental in transforming ethology from within over the course of the 1970s.

Who was this group that was ringing in a new era of ethology? The generational and intellectual transformation is best represented by Tinbergen's right-hand man, Mike Cullen. Cullen had completed his Ph.D. under Tinbergen, married fellow postdoctoral group member Esther Sager<sup>52</sup>, and became "an extraordinary influence on the development of the scientific discipline of ethology."<sup>53</sup> This assessment is taken from Cullen's obituary in *The Guardian*, penned by Richard Dawkins and John Krebs, where they also name him "the unsung hero of that golden age."<sup>54</sup> That this little-known ethologist has such a prominently penned and placed obituary is a testament to the depth of gratitude the authors felt they owed him.

Cullen increasingly took over the mentoring role from Tinbergen since the mid-1960s, when Tinbergen became less involved with his students and

<sup>47</sup> Burkhardt 2005, on 407.

<sup>48</sup> Burkhardt 1983, on 439–440; Burkhardt 2005, on 439.

<sup>49</sup> Durant 1986a, on 1612, quoting a personal communication with Robert Hinde.

<sup>50</sup> Bateson 2006, on 167.

<sup>51</sup> For an in-depth look at Tinbergen's Oxford years, see Burkhardt 2005, Chapters 7 and 10; Kruuk 2003, Chapters 6 to 9. See also Durant 1986a, on 1612.

<sup>52</sup> Beale points out the importance of Esther Sager's (later Cullen) work for the direction of the group; Beale 2009, on 152–160; Burkhardt 2005, on 414–420.

<sup>53</sup> Krebs and Dawkins 2001a; Krebs and Dawkins 2001b.

<sup>54</sup> Krebs and Dawkins 2001b.

increasingly focused on his work on autism in children,<sup>55</sup> often interrupted by bouts of depression.<sup>56</sup> Luckily, Cullen was a born mentor for this group of talented youngsters and almost all members of the group mention his enormous influence. He was widely admired for his mathematical abilities<sup>57</sup> and analytical rigor: Tim Clutton-Brock recalls him as a “continuous source of stimulation challenging us to focus on testing hypotheses rather than on description.”<sup>58</sup> Strict but humorous<sup>59</sup> and extremely dedicated to his students, “he would spend whole days on a student’s problems, designing new methods to solve them and coming up with elegant mathematical solutions.”<sup>60</sup>

Cullen’s influence led to a shift in approach that is exemplified by an anecdote from Krebs: When choosing a Ph.D. topic, Krebs was interested in focusing on a theoretical question from population ecology. At the time, an important debate was raging between David Lack from Edward Grey Institute of Field Ornithology and Vero Wynne-Edwards: Was population size limited by external ecological or internal evolutionary factors? Wynne-Edwards was proposing a group-selectionist evolutionary argument that population was self-regulating its size for the good of the species, while Lack was categorically opposed to this view, pointing instead to ecological factors such as food shortages as imposing external limitations on population size. Krebs had seeds of an idea for an alternative evolutionary argument that did not rely on group selection and proposed the project to Lack himself. As Krebs did not know what animal he wanted to work on, Lack introduced him to his group as “This is David Krebs. He wants to do a D.Phil., but he doesn’t know what he wants to work on.” While Krebs had a clearly defined problem, this did not count in Lack’s eyes, as his approach was based on picking a species first. Krebs concludes: “My approach of defining a problem and not a species did not fit comfortably with the Edward Grey Institute in the mid-1960s.”<sup>61</sup> Working from a theoretical problem was, however, indicative of Cullen’s influence, who ended up supervising Krebs’ Ph.D. project.

Despite Cullen’s enormous social impact on the direction of ethology, he did not succeed Tinbergen when he officially retired in 1974 and did not rise to particular ethological fame. Whereas other stages of disciplinary development are visible in signature publications, in Cullen’s case, his signature was his lack of publications. This is often cited as a reason he did not succeed Tinbergen<sup>62</sup> and yet as Krebs and Dawkins put it: “If he had followed what is now a common practice of putting his name on all the papers of his students

<sup>55</sup> Davies 2010, on 146–147; Kruuk 2003, on 274–278.

<sup>56</sup> Kruuk 2003, esp. Chapters 8 and 9 for recollections from a Tinbergen student.

<sup>57</sup> Davies 2010, on 148.

<sup>58</sup> Clutton-Brock 2010, on 117.

<sup>59</sup> Davies 2010, on 148 recounts an anecdote, where he presented research that included “hope” as an analytical factor. Cullen suggested that the model might provide an even better fit if it also included “charity and faith.”

<sup>60</sup> Kruuk 2003, on 260.

<sup>61</sup> Krebs 2010, on 380–381.

<sup>62</sup> *Ibid.*, on 385.

and co-workers that he had helped, he would have stood out as one of the most prolific ethologists of his time.”<sup>63</sup> Cullen’s influence is typical for a mentor figure, essential to discipline building in giving younger generations a voice without taking credit.

Mike’s entire life revolved around student projects. But he never asked for credit, and rarely even put his name on a paper. He was much more involved in the thesis of almost every single student than Niko [Nikolaas Tinbergen] ever was, and without him, the scientific activity of Niko’s group would not have been anywhere near the level it reached with Mike.<sup>64</sup>

The Oxford group became a central location for ethological intellectual exchange and discussion. Tinbergen was known for his exacting and demanding questions for speakers and exerted his intellectual influence in colloquia and seminars on their scientific thinking.<sup>65</sup> “In the actual discussions, the younger members tended to be much more hard-hitting than Niko himself; they were a merciless, highly intelligent, and very articulate audience.”<sup>66</sup> A new generation of ethologists was being raised in the group and their work was soon to be commended for its quality.<sup>67</sup> The later generation of Tinbergen’s group included future leaders of the field, such as Richard Dawkins, John Krebs, Nicholas Davies, Hans Kruuk, Colin Beer, Nicholas Blurton-Jones and Tim Clutton-Brock.<sup>68</sup> This generation of Tinbergen profited from an extremely stimulating set of guest speakers that presented what was the cutting edge of ethological, evolutionary, and ecological theory. Robert Trivers presented his work on parent-offspring conflict in the early 1970s, William Hamilton spoke on kin selection, and John Maynard Smith and Geoffrey Parker were there to elucidate their newest work on using game theory in evolutionary biology. As John Davies remembers: “It wasn’t necessary to travel to meet stars of behaviour – we simply had to wait in Oxford for them to visit.”<sup>69</sup> Rigorous questioning and examination of guest speakers was par for the course, as was the intensive exchange of ideas between graduate students, taking inspiration from the new and exciting theoretical work.

Davies recalls his time at Oxford in the late 1970s as knowing no art, only artists, meaning that their sense of group identity was based on their shared interests and activities, the new research direction being best described by what people were doing, and only then finding the thematic common ground.<sup>70</sup> With hindsight, one can see that slowly the group identity was forming into a discipline centering around behavior, ecology, and evolution. A decisive factor was the young and dynamic research community that Tinbergen had established in Oxford. By the mid-1970s, George Barlow noted in his review

<sup>63</sup> Krebs and Dawkins 2001a.

<sup>64</sup> Kruuk 2003, on 261.

<sup>65</sup> *Ibid.*, Chapter 7, on 207–266; Krebs 2010, on 381.

<sup>66</sup> Kruuk 2003, on 260.

<sup>67</sup> Hailman 1977, on 618; Thompson 1975, on 113.

<sup>68</sup> See Beale 2008, on 283, annex 1 for a list of Tinbergen’s students.

<sup>69</sup> Davies 2010, on 147.

<sup>70</sup> *Ibid.*, on 150.

of *Growing Points* what had become “ethology’s most rapidly growing and potentially most important area: behavior as a mechanism in ecology.”<sup>71</sup> And despite the social continuation of ethology, the theoretical innovations of the younger generation “felt more like a revolution than a gentle gradual metamorphosis.”<sup>72</sup>

#### 4. A Discipline Emerges: Assembling Behavioral Ecology, 1978

Throughout the 1970s, this new approach to animal behavior, increasingly relying on mathematical models adopted from population ecology and population genetics, more informed by evolutionary theory and population thinking, formed a distinct disciplinary identity that would eventually lead it to overshadow ethology itself. This transformation realized some of the fears of earlier ethologists that complex theory and inaccessible mathematical formulations were taking over the discipline. However, the researchers at Oxford saw these developments as necessary steps to revitalize ethological research. Richard Dawkins’ contribution to *Growing Points* makes this clear. He identifies the main problem of ethology as not having produced any “great explanatory principles of late.”<sup>73</sup> With this diagnosis and the will to fix the problem, Dawkins was right at home in Oxford. There they shared an air of excitement at the rapid pace of change and felt that they were at the “cusp of a new wave of behavior studies.”<sup>74</sup> Much like earlier ethologists, members of this group were later to credit themselves that the late 1960s and 1970s were truly the time “that led natural history to blossom into a formal science.”<sup>75</sup> Looking back in 1981, Nicholas Davies summarizes behavioral ecology and its progress in the 1970s in the following manner: “During the last decade behavioral ecology has emerged as an exciting field of study, so named because the way in which behavior contributes to survival and reproduction depends on an animal’s ecology, the food it eats, its predators, the architecture of its habitat, and so on.”<sup>76</sup>

What catalyzed a lot of this progress was the above-mentioned debate about the viability of group selection as a means of population size regulation, as proposed by Vero Copner Wynne-Edwards. Wynne-Edwards’ arguments for group selection provoked objections in equal measure from ecologists like David Lack, and evolutionary theorists like George Williams.<sup>77</sup> Both argued forcefully against the group selectionist logic that birds controlled their reproduction due to altruistic behavioral tendencies, explaining that such

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<sup>71</sup> Barlow 1974, on 676.

<sup>72</sup> Parker 2006, on 48.

<sup>73</sup> Dawkins 1977, on 8.

<sup>74</sup> Davies 2010, on 147; Clutton-Brock 2010, on 120.

<sup>75</sup> Parker 2006, on 24.

<sup>76</sup> Davies 1981, on 1341.

<sup>77</sup> Clutton-Brock, on 120; Klopfer 1999, on 95. For a vindication of Wynne-Edwards group-selectionist stance as a precursor to modern multi-level selection, see Borello 2003.

altruism would be mercilessly rooted out by the logic of natural selection. Williams', Lack's, and William Hamilton's work on this logic became central to the theory of kin selection or inclusive fitness that circulated in the discussions of the Oxford group and inspired Dawkins to work on what was to become the international bestseller *The Selfish Gene* (1976).<sup>78</sup> With its publication, Oxford was soon the center for what came to be known as the gene's eye view of evolution.<sup>79</sup> This logic of how genes for certain behavioral tendencies increased or decreased within a population strongly informed research questions in behavioral ecology.<sup>80</sup> Behavioral ecology focused on understanding selective forces that have shaped behavior over evolutionary time in its current ecological context.<sup>81</sup> The logic of the gene's eye view also lent itself to being connected with a second trend of understanding animal behavior as if it were a strategic choice in order to increase reproductive success within a population. In this view, strategies for reproductive success depended not only on the ecological factors surrounding a given population but also the behaviors of others, turning the quest for optimal outcomes into a social game. These behavioral choices and strategies could best be understood by adopting models from economics, game theory and cost-benefit analysis optimality theory.<sup>82</sup> John Maynard Smith, George Price, Geoffrey Parker, John Krebs, and Nicholas Davies all made pioneering contributions in applying these theories and methods to animal behavior in the late 1960s and early 1970s.<sup>83</sup>

Both of these trends created an understanding of natural selection as an optimizing process that yielded results in behaviors that were optimally adapted to their ecological and social environments, applying this thinking to behaviors such as foraging or mating. Parker describes these theoretical advances as the "two stages of ethology's metamorphosis into behavioral ecology."<sup>84</sup> Both trends shift the focus away from ethology's interest in species-typical behavior to research questions that switch between a gene-centered and population-based perspective: The individual animal became the vessel for scheming and strategic genes and its behavior was seen as a means to resolve conflicts and competition to further its inclusive fitness.

These theoretical innovations based on a population-focused, gene-centered and strategic view of animal behavior allowed the development of clear and specific hypotheses that could be tested by collecting long-term data sets and analyzing them with statistical methods.<sup>85</sup> Davies recounts that the theories were merged with the Tinbergian tradition of extensive field studies, careful

<sup>78</sup> For background, see Grodwohl 2019. For more on inclusive fitness and William Hamilton, see Swenson 2015 and Segerstrale 2015.

<sup>79</sup> For a history of gene-selectionism, see Ågren 2020.

<sup>80</sup> Ågren 2020, on 192 describes the relationship: "Countries where behavioural ecology has been strong also seemed to have embraced the gene's-eye view faster."

<sup>81</sup> Parker 2006, on 24.

<sup>82</sup> For more on the "family resemblance" between game theory and optimal-foraging theory, see Bolduc 2012, on 682.

<sup>83</sup> Parker 2006, on 27; Davies 2010, on 147; Owens 2006, on 356.

<sup>84</sup> Parker 2006, on 27.

<sup>85</sup> Krebs 2010, on 383.

experimentation, and a comparative perspective to create the foundation of behavioral ecology.<sup>86</sup> Davies and Krebs laid the foundations of this new discipline in their defining 1978 textbook: *Behavioral Ecology: An Evolutionary Approach*<sup>87</sup>.

There is a general consensus that behavioral ecology as a discipline was shaped by the Krebs and Davies textbook (Figure 1).<sup>88</sup> While there were other textbooks at the time that covered similar ground, *Behavioural Ecology* was by far the most reprinted and widely used.<sup>89</sup> As one reviewer put it:

The names Krebs and Davies are virtually synonymous with the term behavioral ecology in the eyes of most undergraduate students. References to one author or both in various associations litter the examination answers of uncertain candidates on the (half reasonable) assumption that they must have said something about the topic at hand somewhere.<sup>90</sup>

Unlike the edited volumes earlier in the decade that showed a diversification of the discipline of ethology that lacked a coherent core, in 1978 Krebs and Davies could present a unity of conceptual viewpoint in behavioral ecology that was remarkable.<sup>91</sup> While this continuation of ethology was too theoretical for some,<sup>92</sup> its origins and identity were clearly represented. Reviewers knew where it came from: “Between 1965 and 1975, theoretical ecology, population genetics, ethology, and theoretical evolutionary biology fused,”<sup>93</sup> and what it stood for: “emphasis is laid on the theoretical development of quantitative predictions which can be tested, and are tested, by observation and experiment both in field and laboratory.”<sup>94</sup>

One ambition Krebs and Davies had for their textbook becomes clear in a review by Davies of Douglass H. Morse’s textbook *Behavioral Mechanisms in Ecology* (1980). While he is generally complimentary, he complains that it “does not convey excitement, because it does not present empirical data in light of theory.”<sup>95</sup> This makes clear that behavioral ecology as it was conceived in Oxford was not only about new theory or methodology but also about a communal feeling of excitement about these discoveries. The textbook was not only meant to serve as an introduction but also as an induction into the Oxford vibe. The textbook and its shorter companion piece, *Introduction to Behavioral Ecology* (1981), written jointly by Krebs and Davies and aimed at an undergraduate audience, were received as intended: “A textbook that kindles

<sup>86</sup> Davies 2010, on 145.

<sup>87</sup> Krebs and Davies 1978.

<sup>88</sup> For instance: Parker 2006, on 25; Owens 2006, on 356.

<sup>89</sup> *Behavioural Ecology: An Evolutionary Approach* had four reprintings in its first edition.

<sup>90</sup> Barnard 1984, on 345.

<sup>91</sup> See reviews by Millikan 1979 and Matthew 1984. Wilbur 1979 warns readers of the three “dogmata” contained in the book, inclusive fitness theory, game theory and optimality theory.

<sup>92</sup> Waage 1981, on 128.

<sup>93</sup> Stearns 1980, on 240.

<sup>94</sup> Matthews 1984, on 285, adding: “Sometimes, as in much science, there is a flavour of proving the obvious. Sometimes one has the feeling of reading a modern Aesop’s fable.”

<sup>95</sup> Davies 1981, on 1341.

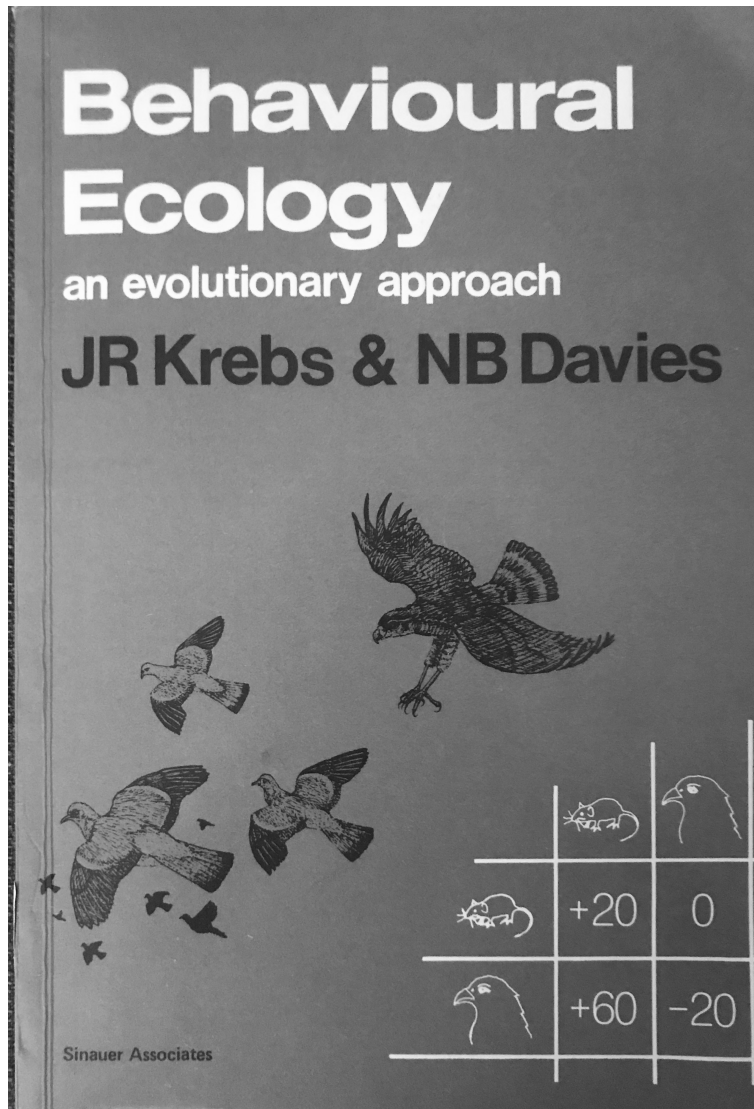


Figure 1. Cover of the first edition of *Behavioural Ecology: An Evolutionary Approach*. The cover shows a hawk chasing doves and a game-theoretic matrix with hawks and mice, thereby emphasizing the analytical approach of behavioral ecology. Krebs, John and Nicholas Davies, *Behavioural Ecology: An Evolutionary Approach* (Oxford: Blackwell Scientific Publications, 1978). Copyright © 1978 by Blackwell Scientific Publications. Used by permission. All rights reserved.

enthusiasm,<sup>96</sup> representative of “a hot field,”<sup>97</sup> full of recent discoveries, and, overwhelmingly British.

In addition to its content, *Introduction to Behavioral Ecology* also represented the disciplinary identity of behavioral ecology as a vivid scholarly community with its center in the UK. The textbook was a collaborative effort by multiple authors, most of them British. Each author provided a chapter that was most closely related to their individual research, providing their own perspective rather than being summarized. Krebs stressed this sense of community when he recalls that they “built around exciting ideas and people that we knew,”<sup>98</sup> and as the field was small enough, it was easy to be “on top of the literature and know all key people personally.”<sup>99</sup> Readers quickly gained a sense that a tight-knit group of scientists was at work here, maybe even overly so to the point of being somewhat exclusionary: Reviewers complained about the frequent use of nicknames and cliquish jargon, that was hard to understand for “non-English workers – or even non-Oxford behavioral ecologists.”<sup>100</sup> Donald Dewsbury, an ethologist and historian of ethology, wrote in a review: “Heavily British in tone, this work provides a valuable and exciting set of sociobiological investigations that should be on the bookshelf of every specialist in the area.”<sup>101</sup> While he correctly identifies the British roots of the textbook, this sentence is indicative of a problem that behavioral ecology had to confront: Their intellectual agenda was subsumed under the banner of sociobiology, a new discipline proposed by Edward O. Wilson in 1975.

## 5. Dealing with the Competition: The Challenges of Sociobiology, 1975–1985

When Edward O. Wilson published *Sociobiology: The New Synthesis* in 1975,<sup>102</sup> he did not take aim against behavioral ecology as a discipline. Quite the opposite: Wilson saw sociobiology and behavioral ecology as two distinct disciplines that would together succeed ethology. His famous dumbbell

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<sup>96</sup> Ormond 1983, on 662.

<sup>97</sup> Millikan 1979, on 749; Pullam 1979, on 1279: “A quick survey indicated that almost two-thirds of the papers cited have been published in the last 10 years, and nearly one half in the last 5 years!”

<sup>98</sup> Krebs 2010, on 391.

<sup>99</sup> *Ibid.*, on 392.

<sup>100</sup> Greene 1980, on 169: “Will non-English workers – or even non-Oxford behavioral ecologists! – immediately grasp the meaning of hustling, salesmanship, sales resistance, ‘Beau Geste hypothesis,’ cowardly, ‘British Museum algorithm,’ and green fingers in the present context? I think not, and, although it might make for good textbook style, this practice reflects a cliquishness that has no place in the formal writing of international science.” See also Kroodsma 1983, on 785: “This informality is further reinforced by use of the first names, or even nicknames, of some scientists, but the rules of use are not always clear.” Other reviewers remarked on the British origins, e.g., Pullam 1979; Dewsbury 1979.

<sup>101</sup> Dewsbury 1979, on 437.

<sup>102</sup> Wilson 1975.



diagram showed ethology stagnant, whereas behavioral ecology and sociobiology were to grow in originality and, by extension, relevance (Figure 2). He predicted ethology was “destined to be cannibalized by sociobiology and

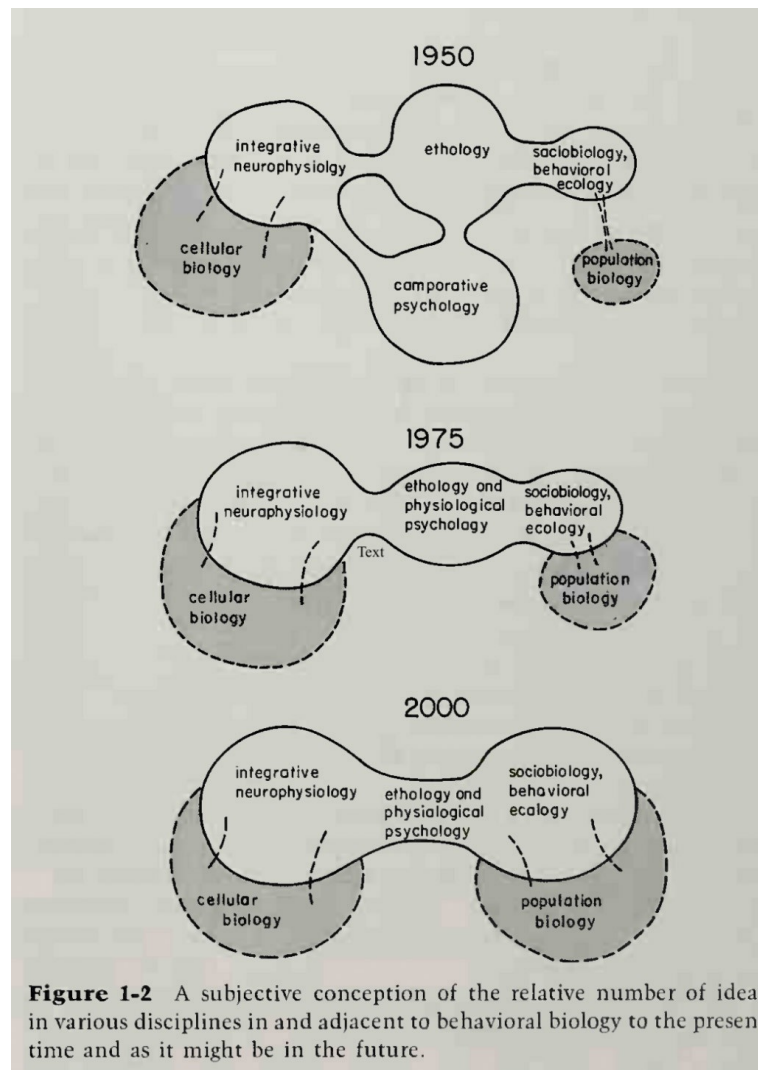


Figure 2. The dumbbell diagram from *Sociobiology: The New Synthesis*. Although read by many as a prediction about disciplinary development, the diagram’s heading clarifies that this represents Wilson’s subjective take on the amount of important ideas generated in these fields. This leaves the future disciplinary status of ethology open, while making the claim that ethology has run out of important ideas to contribute to the study of behavioral biology. Wilson, Edward O., *Sociobiology: The New Synthesis* (Cambridge, MA: The Belknap Press of Harvard University Press, 1975). Copyright © 1975 by the President and Fellows of Harvard College. Used by permission. All rights reserved.

behavioral ecology.” At first glance, this should put behavioral ecologists and the burgeoning group of sociobiologists on the same page, ready to take over from ethology. However, most behavioral ecologists strongly identified with the ethological tradition and Wilson’s book included an open attack on ethology as using outdated methodology, lacking mathematical rigor and theoretical grounding.<sup>103</sup> His view of ethology is scathing: “The future, it seems clear, cannot be with the ad hoc terminology, crude models, and curve fitting that characterize most of contemporary ethology.”<sup>104</sup>

This attack did not sit well with ethologists in general and alienated the group of Oxford scholars who were turning to behavioral ecology: As Wilson was ready to plunge the dagger into the heart of ethology and take over, behavioral ecology presented itself to be the “legitimate heir” to ethology,<sup>105</sup> drawing heavily from the Tinbergian tradition. Sociobiology, therefore, was seen as competition by behavioral ecologists: Their disciplines were similar enough to be confused with each other from the outside but different enough from the inside to insist on distinction. The challenge that behavioral ecology faced was to represent its distinct disciplinary identity when sociobiology’s huge popular and media appeal gave the impression that it was, in fact, a new revolutionary discipline. Writing about sociobiology, behavioral ecologists were quick to distance themselves from the Wilsonian project.

When asked to review *Sociobiology: The New Synthesis* for the journal *Animal Behavior*, most of them commented on Wilson’s disciplinary ambitions. Robert Hinde dedicated almost his entire review to a defense of ethology’s achievements and ended by criticizing Wilson for the “sales talk with which Wilson dishes up the discipline of sociobiology.”<sup>106</sup> John Crook similarly accused Wilson of disciplinary politics: “This naming and renaming of fields is of course a political game [...]. Nominal matters such as these are matters of fashion and his treatment of them reveals the nature of Wilson’s advocacy.”<sup>107</sup> They made the point that Wilson was pursuing other, non-scientific goals, such as gaining public acclaim due to being considered the father of a discipline. Mary-Jane West-Eberhard even devotes the introduction to her review to what she calls “The sociobiological fairytale.” It is worth reading in full how she humorously accuses Wilson of unnecessarily trying to create a discipline by public proclamation:

Once upon a time there was a small community of modest scholars called natural historians, who devoted their lives to philosophy and the contemplation of humble plants and animals. With the passage of time and the invention of Science they began to take on new names. Some called themselves Systematists; others Ecologists; and still others Population Biologists and Ethologists. Only their enemies called them natural historians.

<sup>103</sup> Wilson 1975, on 6, trying to soften the blow: “I hope not too many scholars in ethology and psychology will be offended by this vision of the future of behavioral biology.” Despite his harsh words, the differences between Wilson and the ethologists were later blurred in crossfire of public debate and Wilson aligned much more closely with pop ethology; Weidmann 2021.

<sup>104</sup> Wilson 1975, on 6.

<sup>105</sup> Pullam 1979, on 1279.

<sup>106</sup> Hinde 1976, on 706.

<sup>107</sup> Crook 1976, on 703.

All of the new sciences grew and became rich. However, there was one small group without a name. They went about dressed in the castoff clothing of the titled sciences, and often failed to recognize each other, even when they hurried along the same paths. So they suffered greatly. Sometimes they had to learn to collect birds or identify ants in order to get jobs. Then one day there rose up a man from among them. He had been called Entomologist, Ecologist, and even Biochemist. But that was not enough. All grew quiet as he raised his golden pen: “There shall be a new science,” he said, “and it shall be called SOCIOBIOLOGY.”

She goes on:

Edward Osborne Wilson, the kindly bespectacled father of sociobiology, has assumed god-like powers with this book [...]. It is enough to make any working animal behaviorist-ecologist tremble a bit with anticipation (what treasures of information will it hold?), with fear (will I be codified in? or out?), and with the athletic strain of holding its flopping five pounds at reading level.<sup>108</sup>

Behavioral ecologists shared this impression of unnecessary spectacle. To them, Wilson’s work was hardly new or original; he was just re-packaging elements of earlier disciplines under a new label.<sup>109</sup> While they appreciated the effort Wilson put into organizing the scattered empirical literature on animal behavior, they were often confused about the way Wilson arranged the theoretical framework. His synthesis was exceedingly idiosyncratic from the point of view of the Oxford orthodoxy. For instance, while Wilson included kin selection, it did not function as a central organizing principle of the book. He also did not exclude the possibility of group selection and, worst of all, even classified kin selection as a case of group selection, which Hamilton and Krebs pointed out in their review.<sup>110</sup> Krebs also noted a lack of modern methodological apparatus: for instance, the incorporation of optimality models and game theory. While the former is completely missing, the latter warranted only a brief mention in the section on ritualized combat.<sup>111</sup> Krebs concluded: “A biochemist recently asked me to define sociobiology. The only simple answer to the question was ‘The branch of biology covered in E. O. Wilson’s book.’”<sup>112</sup>

As they felt that Wilson was not representative of their work, they did not want to use the moniker “sociobiology.” In general, they felt that their ambitions were broader, focusing on all behavior in relation to the environment, whereas Wilson limited himself to social behavior. And even when UK-based scholars actually worked on the topic of social behavior, they were

<sup>108</sup> West-Eberhard 1976, on 89.

<sup>109</sup> Kruuk 1976, on 710: “Sociobiology is not a new field, of course, its activities used to be carried out under the heading ‘behavioural ecology,’ or ‘natural history’”; Crook 1976, on 704: “His decision to name this complex area of interfaced investigations ‘sociobiology’ feels more or less timely, even if by so nominal a change he undercuts the developing status of ‘social ethology.’” Similarly: Eisenberg 1976; Barlow 1976; Hinde 1976.

<sup>110</sup> Krebs 1976, on 710; Hamilton 1977. I am, therefore, inclined to believe Wilson’s own account, where he denies being inspired by Williams’ and Hamilton’s work to write *Sociobiology*, as reported in Levallois 2018, on 421 (fn. 3).

<sup>111</sup> Wilson 1975, on 129.

<sup>112</sup> Krebs 1976, on 709.

apprehensive of calling it sociobiology due to the political controversy attached to this term.<sup>113</sup> For instance, as Patrick Bateson writes, the King's College Sociobiology Study Group at the University of Cambridge were initially uncomfortable with using the label sociobiology, since "in many places 'Sociobiology' is either a battlecry or a term of abuse."<sup>114</sup> In this climate, the decision by Krebs and Davies to call their textbook *Behavioural Ecology* was seen as a competitive ploy against sociobiology.<sup>115</sup> The authors deny that the book was written to spite Wilson and that the name was chosen to evade the controversy and to reflect the broader scope, but other ecologists had different opinions and suggested it was part of an Anglo-American rivalry: "John Krebs spearhead[ed] a hostile takeover of E.O. Wilson's 'new synthesis' almost before the paint could dry, successfully usurping and greatly improving the emerging field we now perceive."<sup>116</sup>

And yet, despite their conscious effort to present the discipline of behavioral ecology in its own right, in the popular perception, especially in the US, the disciplinary lines between sociobiology and behavioral ecology were blurred. Even though Krebs and Davies did not describe *Sociobiology* in their introduction as an inspiration, but only mention it to differentiate their own project,<sup>117</sup> this did not preclude reviewers from repeatedly naming Wilson as an influence on its development.<sup>118</sup> The confusion is especially present in the reviews of the undergraduate textbook *Introduction to Behavioural Ecology*. US reviewers described it as a great introduction to sociobiology,<sup>119</sup> a defense of sociobiology,<sup>120</sup> were openly confused about the differences between the fields,<sup>121</sup> or saw them as irrelevant<sup>122</sup>. Looking back in 2005, Parker concedes

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<sup>113</sup> Segerstrale 2001.

<sup>114</sup> King's College Sociobiology Study Group 1982, on x.

<sup>115</sup> Davies 2010, on 148–150; Krebs 2010, on 390.

<sup>116</sup> Parker 2006, on 25 quotes this as an answer from an anonymous behavioral ecologist to a questionnaire he distributed about the development of the field.

<sup>117</sup> Krebs and Davies 1978, on ix: "We have not attempted a global synthesis on the scale of Wilson's monumental tome."

<sup>118</sup> Grant 1979, on 820; Dewsbury 1979, on 436.

<sup>119</sup> Wells 1981, on 217.

<sup>120</sup> Rubenstein 1981, on 271: "With these excesses sociobiology acquired a bad name, and far from becoming the discipline that would cannibalize the related fields of anthropology and psychology, it became a subject to be scoffed at, or ignored, by many biologists and nonbiologists alike. Now a short new text by John Krebs and Nick Davies should do much to correct this faulty impression."

<sup>121</sup> Waage 1983, on 128: "It also does little to clear up present confusion over the distinctions among behavior, ethology, behavioral ecology, and sociobiology"; Brown 1981, on 421: "Behavioral ecology means different things to different people. For Krebs and Davies, 'The book is about the survival value of behaviour,' and the subject matter is overwhelmingly sociobiological."

<sup>122</sup> Barash 1982, on 57: "Britain may have lost her empire, but for what it is worth, she seems to be doing just fine in producing good, young behavioral ecologists (or evolutionary ecologists, or sociobiologists, call them what you will)."

that the distinction between the fields was not clear, many saw them as synonyms, and that in the late 1970s, sociobiology was used more.<sup>123</sup>

But while sociobiology created immense attention in the mid to late 1970s, it subsequently failed to catch on. Sociobiology provoked countless pages of articles in newspapers and journals, books and reviews to be written. It was the topic of panels and entire conferences, of films and documentaries, but all the press and public attention overshadowed the fact that substantially hindered sociobiology's establishment as a discipline: There were very few actual practitioners in animal behavior calling themselves "sociobiologists."<sup>124</sup> Wilson himself did not establish sociobiological research projects or sites, recruited few researchers to the discipline<sup>125</sup> and almost immediately moved on to work on modeling gene-culture co-evolution with Charles Lumsden. Wilson was not really in the business of social discipline building. Meanwhile, behavioral ecologists, maybe due to their overwhelming British heritage, kept calm and carried on, strengthening their disciplinary identity over time. The recipe for success was the commitment of the entire disciplinary community. While Wilson hid for four years to produce *Sociobiology* as a single author monograph, Krebs and Davies mention directly in the introduction that the multiple author approach was a conscious choice: "We felt that the sort of book we had in mind would have to be written by a number of authors currently working in the field rather than as a single author text."<sup>126</sup> While *Sociobiology* was one big monograph published in 1975, never to be updated,<sup>127</sup> both textbooks by Krebs and Davies became living documents that were updated and substantially revised in each edition: "They have done it again! [...] They do not just sit back and update the earlier edition. Instead [...] the new edition is an almost completely rewritten book."<sup>128</sup> This meant that new scholarship was being generated, included in the disciplinary canon and then disseminated to the next generation. While sociobiology remained static, behavioral ecology became a dynamic discipline.<sup>129</sup> As the second edition of *Introduction to Behavioural Ecology* was published in 1981, there was no mention of sociobiology in the reviews anymore.

By the mid-1980s, behavioral ecology had successfully sharpened its disciplinary identity against its competitor, best summarized by an article that

<sup>123</sup> Parker 2006, on 25.

<sup>124</sup> One exception is John Alcock, professor at Arizona State University since 1972.

<sup>125</sup> According to his CV, Edward O. Wilson mainly stuck to supervising PhDs on social insects during the 1970s and 1980s.

<sup>126</sup> Krebs and Davies 1978, on ix.

<sup>127</sup> An abridged edition was published in 1980 and an anniversary edition was published in 2000, but other than a short preface, these editions did not revise or add any material: Wilson 1980; Wilson 2000.

<sup>128</sup> Gustaffson 1992, on 170.

<sup>129</sup> Other markers of an active disciplinary community include the foundation of the International Society for Behavioral Ecology in 1986, which hosts a biennial conference and has published the journal *Behavioral Ecology* since 1990, Gross 1994. Another journal *Behavioral Ecology and Sociobiology*, founded in 1976, united the adaptationist disciplines in one journal on equal footing.

came out in celebration of *Sociobiology's* ten-year anniversary in the *New Scientist* written by John Krebs. He made it clear that sociobiology was merely a means to bring “the study of animal behavior from an ecological and evolutionary perspective into the public eye,” and not an original research effort: “E.O. Wilson’s book *Sociobiology* [...] was by no means the start of sociobiology and behavioural ecology.”<sup>130</sup> Again, he dismissed Wilson’s idiosyncratic synthesis as “an eclectic compendium of facts with little theorising.”<sup>131</sup> After this assessment, he quickly moved away from the topic of sociobiology – he did not even mention the term again – and used the rest of the text to celebrate the achievements of behavioral ecology and provide more information on “What behavioral ecology is all about.”<sup>132</sup> The article conveyed to the reader that the real scientific field to be celebrated is behavioral ecology, and sociobiology is merely its public relations campaign. While sociobiology was a public spectacle, behavioral ecology was a serious discipline. But did behavioral ecology’s succession mean that ethology had died?

## 6. What Is Dead May never Die: Ethology in the 1980s

In the early 1980s, the role of ethology in animal behavior studies was precarious: “Some years ago, a prominent biologist dared to ask ‘Is ethology dead?’”<sup>133</sup> The rise of functional studies, in the guise of both sociobiology and behavioral ecology, left behind an “embattled ethology”<sup>134</sup> that increasingly ceded territory and started a strategic retreat to a minimal disciplinary definition. Even though Konrad Lorenz claimed in 1980: “Ethology, the comparative study of behavior, is easy to define,” he himself gives a minimal and vague definition of a discipline that “applies, to the behavior of animals and humans, all those questions asked and those methodologies used as a matter of course in all the other branches of biology since Charles Darwin.”<sup>135</sup> Similarly, in 1981 Samuel Anthony Barnett published a textbook that defines ethology as a major branch of biology, not limited to a certain method or school, but simply “the science of animal behavior.”<sup>136</sup> This *Modern Ethology* had rid itself of the conceptual baggage of the past. When the *Zeitschrift für Tierpsychologie* was renamed *Ethology* in 1986, the editorial stressed the importance of the comparative approach to animal behavior, but also limited its definition of ethology to a minimal consensus: “The concept ‘Ethology’ can certainly be defined as a program, separated from the concept ‘Behavio-

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<sup>130</sup> Krebs 1985, on 40.

<sup>131</sup> Ibid.

<sup>132</sup> Ibid., on 42.

<sup>133</sup> Pullam 1979, on 1279.

<sup>134</sup> Colgan 1979, on 148; for a nuanced perspective on the “triumph of adaptationism” rather than a “triumph of sociobiology,” see Griffiths 2008b, on 398–401.

<sup>135</sup> Lorenz 1980, on 171.

<sup>136</sup> Barnett 1981, on v.

rism.”<sup>137</sup> Finally, in an article for the *New Scientist*, John Durant only requires that ethology is the “study of animal behavior under more-or-less naturalistic conditions.”<sup>138</sup> During the 1980s, the term ethology lost its original meaning and became a conceptually empty vessel for different forms of animal behavior studies that were connected to natural behaviors, a comparative and evolutionary approach, and that were not behaviorism. But it ceased to refer to the specific type of underlying theory, method, or set of concepts of classical ethology.

By the end of the decade, ethologists had become accustomed to their new disciplinary understanding and took a mostly pragmatic view on defining ethology. When the 1989 volume of *Perspectives in Ethology*, titled *Wither Ethology?*,<sup>139</sup> came out, its editors (once again Patrick Bateson and Peter Klopfer) recognized the futility of providing a coherent definition of ethology: “It is possible to agonize too much about the true nature of ethology,” but recognized the need for a basic consensus to provide institutional and social identification: “Even so, people who call themselves ethologists have to live in a harsh competitive world in which funding agencies need recognizable fields to which they can allocate money and universities want subjects around which courses can be organized.”<sup>140</sup>

They and others in the same volume, such as George Barlow, suggested basing ethology around a definition Tinbergen provided in his famous 1963 paper, “On aims and methods of Ethology.”<sup>141</sup> In it, he lists aspects of behavior that ethologists are interested in: causation, survival value, evolution, and development. Most commonly, there are four questions derived from these areas: What is the physiological cause of the behavior? What is its survival value (or: how is it adaptive/functional)? How did it evolve? And finally: How does it develop in the individual? This paper resulted from Tinbergen’s disciplinary anxieties in the 1950s, and while it provided an analytical view of the discipline, it also stressed the importance of jointly examining these aspects of behavior.<sup>142</sup> It was soon used as anchoring points for ethology when it had to face conceptual uncertainty. Already in 1976, Hinde and Bateson structured the contributions along these “questions traditional to ethological research.”<sup>143</sup> Rather than being an entirely empty vessel, invoking the term ethology meant invoking a specifically structured approach to animal behavior research and ethology’s continued importance was due to its all-encompassing matrix to understand animal behavior.

<sup>137</sup> Another journal *Sociobiology and Ethology* was founded in 1979, but overwhelmingly concerned with human sociobiology and was renamed *Evolution and Human Behavior* in 1997.

<sup>138</sup> Durant 1986b, on 41.

<sup>139</sup> Klopfer and Bateson 1989.

<sup>140</sup> *Ibid.*, on v.

<sup>141</sup> Tinbergen 1963. For historical background on the paper: Burkhardt 2005, on 426–434; Griffiths 2008b, on 397–398.

<sup>142</sup> For more on the paper, see Burkhardt 2014.

<sup>143</sup> Hinde and Bateson 1976, on 2.

Other contributions in the volume used the same definition: When American ethologist George Barlow asked the question “Has sociobiology killed ethology or revitalized it?” and answered: “Ethology is dead, or at least senescent. That is, if you think of ethology in the narrow sense.”<sup>144</sup> The ethology he refers to means only classical ethology; ethology as the broader project of pursuing the four questions set out by Tinbergen is alive and well. With this framework at hand, the overwhelming focus of functional studies became a mere temporary aberration of the original ethological project, not a permanent disciplinary displacement. Especially Marian Stamp Dawkins in a short contribution bemoans the one-sided focus in recent years: “There was a time when ethology could fairly claim to be a four-question science,” but now “Ethology may still be a four-legged animal, but it is an animal hopping around on one big leg, with the other three dangling somewhat ineffectively.” Therefore, she advocates for more studies in the other areas of ethology as “it is difficult to be dynamic and to run fast in the one-legged manner that ethology seems often to adopt as its mode of progression.”<sup>145</sup> However, when invoking the four-question paradigm of ethology, all adaptationist work done in behavioral ecology was still ethology in essence. Therefore, it makes sense to retain ethology as the umbrella term for biological studies of animal behavior, as Barlow argues: “But what shall we call this field? Sociobiology is too narrow, even when it includes behavioral ecology, and so is socioecology. [...] As the reader might have predicted, I would prefer retaining ethology.”<sup>146</sup> Earlier ethologists had already subsumed the adaptive discipline of behavioral ecology and sociobiology under the term ethology, and it became common practice to refer to all of animal behavior studies simply as “ethology.”<sup>147</sup>

How did ethology move out of being? It didn't, really. It advanced to a changed state of being: By defining its later disciplinarity along a meta-theoretical structure and redefining its scope to be very broad, it lives on as a term for animal behavior research from a biological perspective, with few limitations applied.

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<sup>144</sup> Barlow 1989, on 2.

<sup>145</sup> Stamp Dawkins 1989, on 47–48.

<sup>146</sup> Barlow 1985, on 37.

<sup>147</sup> For earlier examples, see Crook 1976, on 703: “W. D. Hamilton may like to see himself as an evolutionary ethologist”; Durant 1986b, on 44: “Sociobiology grand word for one branch of evolutionary ethology.” For later reflections, see Hinde 1985, on 200: “Ethology and its subdiscipline of sociobiology”; Krebs 2010, on 390: “field of animal behavior (ethology)”; Klopfer 1999, on 95: Behavioral ecology “is the most active domain in which ethologists (in the broad sense) operate.”



## References

- Ågren, Arvid, *The Gene's Eye View of Evolution* (Oxford: Oxford University Press, 2020).
- Barash, David, review of *An Introduction to Behavioural Ecology*, by J.R. Krebs and N.B. Davies, *Ethology and Sociobiology* 3, no. 1 (1982): 57–58.
- Barlow, George, “Ethology Today,” review of *Perspectives in Ethology*, by Patrick Bateson and Peter Klopfer (eds.), *Science* 184, no. 4137 (1974): 675–676.
- Barlow, George, “Multiple Review of Wilson’s Sociobiology,” review of *Sociobiology: The New Synthesis*, by E.O. Wilson, *Animal Behaviour* 24 (1976): 700–701.
- Barlow, George, “Has Sociobiology Killed Ethology or Revitalized It?,” in *Whither Ethology?*, Perspectives in Ethology, vol. 8, ed. Patrick Bateson and Peter Klopfer (New York and London: Plenum Press, 1989), 1–45.
- Barnard, Chris, review of *Behavioural Ecology: An Evolutionary Approach*, 2nd edition, by J.R. Krebs and N.B. Davies (eds.) *Animal Behaviour* 33, no.1 (1985): 345–346.
- Bateson, Patrick, and Peter Klopfer (eds.), *Perspectives in Ethology*, vol. 1 (New York and London: Plenum Press, 1973).
- Bateson, Patrick and Peter Klopfer (eds.), *Whither Ethology?*, Perspectives in Ethology, vol. 8 (New York and London: Plenum Press, 1989).
- Bateson, Patrick, and Robert Hinde (eds.), *Growing Points in Ethology* (Cambridge: Cambridge University Press, 1976).
- Bateson, Patrick, “The Nest’s Tale: Affectionate Disagreements with Richard Dawkins,” in *Richard Dawkins: How a Scientist Changed the Way We Think*, ed. Alan Grafen and Matthew Ridley (Oxford: Oxford University Press, 2006), 164–175.
- Beale, Robert Graeme, “Tinbergian Practice, Themes and Variations: The Field and Laboratory Methods and Practice of the Animal Behaviour Research Group under Nikolaas Tinbergen at Oxford University” (PhD thesis, University of Edinburgh, 2008).
- Becher, Tony, *Academic Tribes and Territories: Intellectual Enquiry and the Culture of Disciplines* (Milton Keynes: Open University Press, 1989).
- Becher, Tony, and Paul Trowler, *Academic Tribes and Territories: Intellectual Enquiry and the Culture of Disciplines* (Philadelphia: Open University Press, 2001, 2nd edn. of Becher 1989).
- Beer, Colin, “Was Professor Lehrman an Ethologist?,” *Animal Behaviour* 23 (1975a): 957–964.
- Beer, Colin, review of *Perspectives in Ethology*, by Patrick Bateson and Peter Klopfer (eds.), *BioScience* 25, no. 7 (1975b): 460.
- Bolduc, Jean-Sébastien, “Behavioural Ecology’s Ethological Roots,” *Studies in History and Philosophy of Biological and Biomedical Sciences* 43 (2012): 674–683.
- Borrello, Mark, “Synthesis and Selection: Wynne-Edwards’ Challenge to David Lack,” *Journal of the History of Biology* 36 (2003), 531–566.
- Brigandt, Ingo, “The Instinct Concept of the Early Konrad Lorenz,” *Journal of the History of Biology* 38, no. 3 (2005): 571–608.
- Brown, Jerram, “Behavioral Ecology for Sophomores,” review of *An Introduction to Behavioural Ecology*, by J.R. Krebs and N.B. Davies, *Evolution* 36 no. 2 (1982): 421–422.
- Burghardt, Gordon M., “Darwin’s Legacy to Comparative Psychology and Ethology,” *American Psychologist* 64, no. 2 (2009): 102–110.
- Burkhardt, Richard, “On the Emergence of Ethology as a Scientific Discipline,” *Conspectus of History* 1, no. 7 (1981): 62–81.
- Burkhardt, Richard, “The Development of an Evolutionary Ethology,” in *Evolution: From Molecules to Men*, ed. Derek S. Bendall on behalf of Darwin College, Cambridge (Cambridge: Cambridge University Press, 1983), 429–444.
- Burkhardt, Richard, *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology* (Chicago: University of Chicago Press, 2005).
- Burkhardt, Richard, “Tribute to Tinbergen: Putting Niko Tinbergen’s Four Questions into Historical Context,” *Ethology* 120, no. 3 (2014): 215–223.
- Chandler, James, “Introduction: Doctrines, Disciplines, Discourses, Departments,” *Critical Inquiry* 35, no. 4 (2009): 729–746.

- Colgan, Patrick, "Embattled Ethology", review of *Perspective in Ethology*, vol. 8, by Patrick Bateson and Peter Klopfer (eds.), *BioScience* 40, no. 2 (1990): 148–149.
- Crist, Eileen, *Images of Animals: Antrophomorphism and Animal Mind* (Philadelphia: Temple University Press, 1999).
- Crook, John, "Multiple Review of Wilson's Sociobiology," review of *Sociobiology: The New Synthesis*, by E.O. Wilson, *Animal Behavior* 24 (1976): 703–704.
- Davies, Nicholas, review of *Behavioral Mechanisms in Ecology*, by Douglass H. Morse, *Science* 211, no. 4488 (1981): 1341.
- Dawkins Stamp, Marian, "The Future of Ethology: How many Legs Are We Standing on," in *Whither Ethology?*, Perspectives in Ethology, vol. 8, ed. Patrick Bateson and Peter Klopfer (New York and London: Plenum Press, 1989), 47–54.
- Dewsbury, Donald A., review of *Behavioral Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *Contemporary Psychology* 24, no. 5 (1979): 436–437.
- Dewsbury, Donald A., "The Making of Ethology: The Association for the Study of Animal Behaviour, 1936–1986," *Animal Behaviour* 34, no. 6 (1986a): 1601–1616.
- Dewsbury, Donald A., "The Ontogeny and Evolution of Ethology," *Contemporary Psychology: A Journal of Reviews* 31, no. 12 (1986b): 967–969.
- Dewsbury, Donald A., "Triumph and Tribulation in the History of American Comparative Psychology," *Journal of Comparative Psychology* 106, no. 1 (1992a): 3–19.
- Dewsbury, Donald A., "Comparative Psychology and Ethology: A Reassessment," *American Psychologist* 47, no. 2 (1992b): 208–215.
- Dewsbury, Donald A., "Americans in Europe: The Role of Travel in the Spread of European Ethology after World War II," *Animal Behaviour* 49, no. 6 (1995): 1649–1663.
- Dewsbury, Donald A., "Rhetorical Strategies in the Presentation of Ethology and Comparative Psychology in Magazines after World War II," *Science in Context* 10, no. 2 (1997): 367–386.
- Dhein, Kelle, "From Karl von Frisch to Neuroethology: A Methodological Perspective on the Friscean Tradition's Expansion into Neuroethology," *Berichte zur Wissenschaftsgeschichte* 45, no. 1–2 (2022).
- Durant, John, "Innate Character in Animals and Man: A Perspective on the Origins of Ethology," in *Biology, Medicine and Society, 1840–1940*, ed. Charles Webster (Cambridge: Cambridge University Press, 1981), 157–192.
- Durant, John, "The Making of Ethology: The Association for the Study of Animal Behaviour, 1936–1986," *Animal Behaviour* 34, no. 6 (1986a): 1601–1616.
- Durant, John, "From Amateur Naturalist to Professional Scientist," *New Scientist*, 24 July 1986b: 41–44.
- Eisenberg, John, "Multiple Review of Wilson's Sociobiology," review of *Sociobiology: The New Synthesis*, by E.O. Wilson, *Animal Behaviour* 24 (1976): 705–706.
- Gieryn, Thomas, "Boundary-Work and the Demarcation of Science from Non-Science: Strains and Interests in Professional Ideologies of Scientists," *American Sociological Review* 48, no. 6 (1983): 781–795.
- Grant, Peter, review of *Behavioural Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *The Auk* 96, no. 4 (1979): 819–821.
- Greenberg, Gary, "Comparative Psychology and Ethology," in *Encyclopedia of the Sciences of Learning*, ed. Norbert Seel (Boston, MA: Springer, 2012), 658–661.
- Greene, Harry, review of *Behavioral Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *Journal of Mammalogy* 61, no.1 (1980): 168–169.
- Griffiths, Paul E., "Instinct in the '50s: The British Reception of Konrad Lorenz's Theory of Instinctive Behavior," *Biology and Philosophy* 19, no. 4 (2004): 609–631.
- Griffiths, Paul E., "History of Ethology Comes of Age," review of *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen and the Founding of Ethology*, by Richard Burkhardt, *Biology & Philosophy* 23, no. 1 (2008a): 129–134.

- Griffiths, Paul E., "Ethology, Sociobiology, and Evolutionary Psychology," in *A Companion to the Philosophy of Biology*, ed. Sahotra Sarkar and Anya Plutynski (New Jersey: John Wiley & Sons, 2008b), 393–414.
- Griffiths, Paul E., and Stefan Linquist, "The Distinction between Innate and Acquired Characteristics," in *The Stanford Encyclopedia of Philosophy* (Winter 2021 Edition), ed. Edward N. Zalta, <https://plato.stanford.edu/archives/win2021/entries/innate-acquired/> (accessed 30 March 2022).
- Grodwohl, Jean-Baptiste, "Animal Behavior, Population Biology and the Modern Synthesis (1955–1985)," *Journal of the History of Biology* 52, no. 4 (2019): 597–633.
- Gross, Mart, "The Evolution of Behavioural Ecology," *Trends in Ecology and Evolution* 9, no. 10 (1994): 358–360.
- Guntau, Martin, and Hubert Laitko, "Entstehung und Wesen wissenschaftlicher Disziplinen," in *Der Ursprung der modernen Wissenschaften: Studien zur Entstehung wissenschaftlicher Disziplinen*, ed. Martin Guntau and Hubert Laitko (Berlin: Akademie Verlag, 1987), 17–89.
- Gustaffson, Lars, review of *Behavioural Ecology: An Evolutionary Approach*, 3rd edition, by J.R. Krebs and N.B. Davies (eds.), *Trends in Ecology and Evolution* 7, no. 5 (1992): 170.
- Hailman, Jack, "A Comprehensive Look at Ethology's Growth," review of *Growing Points in Ethology*, by Patrick Bateson and Robert Hinde (eds.), *BioScience* 27, no. 9 (1977): 618.
- Halliday, Timothy, and Richard Dawkins (eds.), *The Tinbergen Legacy* (London: Chapman & Hall 1991).
- Hamilton, William, review of *Sociobiology: The New Synthesis*, by E.O. Wilson, *Journal of Animal Ecology* 46, no. 3 (1977): 975–977.
- Hinde, Robert, *Animal Behaviour: A Synthesis of Ethology and Comparative Psychology* (New York: McGraw-Hill, 1966).
- Hinde, Robert, "Multiple Review of Wilson's Sociobiology," review of *Sociobiology: The New Synthesis*, by E.O. Wilson, *Animal Behaviour* 24 (1976): 706–707.
- Hinde, Robert, "Ethology in Relation to Other Discipline," in *Studying Animal Behavior: Autobiographies of the Founders*, ed. Donald Dewsbury (Chicago: University of Chicago Press, 1985), 193–203.
- Hinde, Robert, and William Thorpe, "Nobel Recognition Ethology," *Nature* 245, no. 5425 (1973): 346.
- Jaynes, Julian, "The Historical Origins of 'Ethology' and 'Comparative psychology,'" *Animal Behaviour* 17 no. 4 (1969): 601–606.
- King's College Sociobiology Study Group, *Current Problems in Sociobiology* (Cambridge: Cambridge University Press, 1982).
- Klopfer, Peter, review of *Growing Points in Ethology*, by Patrick Bateson and Robert Hinde (eds.), *American Scientist* 65, no. 3 (1977): 366.
- Klopfer, Peter, *Politics and People in Ethology: Personal Reflections on the Study of Animal Behavior* (Lewisburg, PA: Bucknell Press, 1999).
- Krebs, John, "Multiple Review of Wilson's Sociobiology," review of *Sociobiology: The New Synthesis*, by E.O. Wilson, *Animal Behaviour* 24 (1976): 709–710.
- Krebs, John, "Luck, Chance and Choice," in *Leaders in Animal Behavior: The Second Generation*, ed. Lee Drickamer and Donald Dewsbury (Cambridge: Cambridge University Press, 2010), 375–404.
- Krebs, John, and Nicholas Davies, *Behavioural Ecology: An Evolutionary Approach* (Oxford: Blackwell Scientific Publications, 1978).
- Krebs, John, and Nicholas Davies, *An Introduction to Behavioural Ecology* (Oxford: Blackwell Scientific Publications, 1981).
- Krebs, John, and Richard Dawkins, "Obituary John Michael (Mike) Cullen (1927–2001)," *Ibis* 143 (2001a): 704–705.
- Krebs, John, and Richard Dawkins, "Obituary Mike Cullen: The Unsung Hero of a Golden Age in the Development of Understanding Animal Behaviour," *The Guardian*, 10 April 2001b.

- Kroodtsma, Donald, review of *An Introduction to Behavioural Ecology*, by J.R. Krebs and N.B. Davies, *The Auk* 100, no. 3 (1983): 784–786.
- Kruuk, Hans, “Multiple Review of Wilson’s Sociobiology,” review of *Sociobiology: The New Synthesis*, by E.O. Wilson, *Animal Behaviour* 24 (1976): 710–711.
- Kruuk, Hans, *Niko’s Nature* (Oxford: Oxford University Press, 2003).
- Lehrman, Daniel, “A Critique of Konrad Lorenz’s Theory of Instinctive Behaviour,” *Quarterly Review of Biology* 28 (1953): 337–363.
- Levallois, Clement, “The Development of Sociobiology in Relation to Animal Behavior Studies, 1946–1975,” *Journal of the History of Biology* 51 (2018): 419–444.
- Lorenz, Konrad, “Über die Bildung des Instinkt begriffes,” *Die Naturwissenschaften* 25, no. 19 (1937): 289–300, 307–318, 324–331.
- Lorenz, Konrad, *Evolution and Modification of Behavior* (Chicago: University of Chicago Press, 1965).
- Lorenz, Konrad, “A Personal Introductory History of Ethology,” *The Journal of Mind and Behavior* 1, no. 2 (1980): 171–182.
- Matthews, Geoffrey, review of *Behavioural Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *Oryx* 16, no. 3 (1982): 284–285.
- McBride, Glen, “Ethology and Comparative Psychology,” *Journal of Comparative Psychology* 101, no. 3 (1987): 272–274.
- Milam, Erika, “Landscapes of Time: Building Long-Term Perspectives in Animal Behavior,” *Berichte zur Wissenschaftsgeschichte* 45, no. 1–2 (2022).
- Millikan, George, review of *Behavioural Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *BioScience* 29, no. 12 (1979): 749.
- Morgan, John, “Promising Approaches,” review of *Growing Points in Ethology*, by Patrick Bateson and Robert Hinde (eds.), *Contemporary Psychology: A Journal of Reviews* 22, no. 7 (1977): 496–497.
- Munz, Tania, *The Dancing Bees* (University of Chicago Press, 2016).
- Odenwald, Jakob, “Ethologists in the Kindergarten: Natural Behavior, Social Rank, and the Search for the ‘Innate’ in Early Human Ethology (1960s–1970s),” *Berichte zur Wissenschaftsgeschichte* 45, no. 1–2 (2022).
- Ormond, Rupert, review of *Behavioural Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), and *An Introduction to Behavioural Ecology*, by J.R. Krebs and N.B. Davies, *Journal of Animal Ecology* 52, no. 2 (1983): 660–662.
- Owens, Ian, “Where is Behavioural Ecology Going?,” *Trends in Ecology and Evolution* 21, no. 7 (2006): 356–361.
- Parker, Geoff A., “Behavioural Ecology: Natural History as Science,” in *Essays in Animal Behaviour: Celebrating 50 Years of Animal Behaviour*, ed. Jeffrey Lucas and Leigh Simmons (London: Elsevier Academic Press, 2006), 23–56.
- Pulliam, H. Ronald, review of *Behavioural Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *Animal Behaviour* 27, no. 4 (1979): 1279.
- Richards, Martin, review of *The Biology of Human Action*, by Vernon Reynolds, *Growing Points in Ethology*, by Patrick Bateson and Peter Klopfer (eds.) and the *Selfish Gene*, by Richard Dawkins, *Journal of Biosocial Science* 9, no. 3 (1977): 373–377.
- Riopelle, Arthur, “Review of Perspectives in Ethology,” *The American Journal of Psychology* 88, no. 4 (1975): 709–715.
- Röell, David Rene, *The World of Instinct: Niko Tinbergen and the Rise of Ethology in the Netherlands (1920–1950)* (Assen, NL: Van Gorcum, 2000).
- Rubenstein, Daniel, “Toward a Realistic Sociobiology,” review of *An Introduction to Behavioural Ecology*, by J.R. Krebs and N.B. Davies, *Contemporary Psychology* 28, no. 4 (1983): 271–272.
- Schurig, Volker, *Problemgeschichte des Wissenschaftsbegriffs Ethologie* (Rangsdorf: Basiliken-Press, 2014).
- Segerstråle, Ullica, *Defenders of the Truth* (Oxford: Oxford University Press, 2001).

- Segerstråle, Ullica, *Nature's Oracle: The Life and Work of W. D. Hamilton* (Oxford: Oxford University Press, 2015).
- Smocovitis, Vassiliki Betty, *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology* (Princeton: Princeton University Press, 1996).
- Stearns, Stephen, review of *Behavioural Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *American Scientist* 68, no. 2 (1980): 214.
- Swenson, Sarah, "From Man to Bacteria: W. D. Hamilton, the Theory of Inclusive Fitness, and the Post-War Social Order," *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 49 (2015): 45–54.
- Taschwer, Klaus, and Benedikt Föger, *Die andere Seite des Spiegels: Konrad Lorenz und der Nationalsozialismus* (Vienna: Czernin Verlag, 2009).
- Thompson, Nicholas, review of *Perspectives in Ethology*, by Patrick Bateson and Peter Klopfer (eds.), *The Quarterly Review of Biology* 50, no. 1 (1975): 113.
- Thorpe, William Homan, *The Origins and Rise of Ethology: The Science of the Natural Behaviour of Animals* (London: Heinemann Educational Books, 1979).
- Tinbergen, Nikolaas, "An Objectivistic Study of the Innate Behaviour of Animals," *Bibliotheca Biotheoretica* 1 (1942): 39–98.
- Tinbergen, Nikolaas, *The Study of Instinct* (London: Oxford University Press, 1969; reprint, with a new introduction, of the original edn. published in 1951).
- Tinbergen, Nikolaas, "On Aims and Methods of Ethology," *Zeitschrift für Tierpsychologie* 20, no. 4 (1963): 410–433.
- Tinbergen, Nikolaas, "Ethology and Stress Diseases," *Science* 185, no. 4145 (1974): 20–27.
- Waage, Jonathan, review of *Behavioural Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *Journal of Animal Ecology* 50, no. 1 (1981): 332–333.
- Waage, Jonathan, review of *An Introduction to Behavioural Ecology*, by J.R. Krebs and N.B. Davies, *Quarterly Review of Biology* 58, no. 1 (1983): 128.
- Wells, Kentwood, review of *An Introduction to Behavioural Ecology*, by J.R. Krebs and N.B. Davies, *American Scientist* 70, no. 2 (1982): 217.
- West-Eberhard, Mary Jane: "Born: Sociobiology," review of *Sociobiology: The New Synthesis*, by E.O. Wilson, *The Quarterly Review of Biology* 51, no. 1 (1976): 89–92.
- Whitley, Richard, *The Intellectual and Social Organization of the Sciences* (Oxford and New York: Clarendon Press, 1984).
- Wilbur, Henry, "Views of Behavior," review of *Behavioural Ecology: An Evolutionary Approach*, by J.R. Krebs and N.B. Davies (eds.), *Science* 205, no. 4408 (1979): 781.
- Wilson, Edward O., *Sociobiology: The New Synthesis* (Cambridge, MA: The Belknap Press of Harvard University Press, 1975).
- Wilson, Edward O., *Sociobiology: The Abridged Edition* (Cambridge, MA: The Belknap Press of Harvard University Press, 1980).
- Wilson, Edward O., *Sociobiology: The New Synthesis. Twenty-Fifth Anniversary Edition* (Cambridge, MA: The Belknap Press of Harvard University Press, 2000).
- Wunsch, Matthias, "Instinktverhalten bei Tieren: Die Debatte zwischen Konrad Lorenz und Daniel Lehrman," in *Methoden und Programme: Philosophie der Tierforschung*, vol. 1, ed. Martin Böhnert, Kristian Köchy, and Matthias Wunsch (Freiburg and Munich: Verlag Karl Alber, 2016), 277–340.