NOTES AND RECORDS

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CELEBRATING A SCIENTIST: JOSUÉ A. NÚÑEZ'S PASSION FOR INSECT PHYSIOLOGY, ENGINEERING AND EVOLUTION

by

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On the tenth anniversary of his passing and the hundredth anniversary of his birth, this article honours Josué A. Núñez (1924–2014), a pioneering Argentine biologist remembered for his groundbreaking work in insect physiology and behaviour. Núñez's seminal papers are recognized for their rigorous experimentation and his skill in crafting instruments. Known for his humility and sense of humour, he taught and conducted research at prestigious institutions worldwide. The article traces Núñez's career through key milestones, beginning with his foundational studies in insect anatomy and physiology. It then explores his formative years in Buenos Aires, where he conducted innovative independent experiments, and his influential early career research in Germany. Núñez's initial interest in the relationship between flowers and honeybees developed into a profound exploration at the intersection of biology, evolutionary theory, and engineering principles. A major focus of this tribute is his integration of engineering concepts to examine the roles of honeybees as both nectar carriers and information channels. By emphasizing Núñez's meticulous data analysis and systemic approach, the article not only highlights his significant contributions but also challenges traditional Eurocentric perspectives, advocating for a more inclusive understanding of global scientific achievements.

Keywords: Josué A. Núñez; insect physiology and behaviour; honeybee; biology and engineering integration; global scientific contributions; systemic research approach

INTRODUCTION

In the scientific community, some figures leave an indelible mark not just through their contributions, but through the lives they touch and the ideas they inspire. Josué Antonio Núñez (figure 1) was one such individual. Born on 11 November 1924 in Tapalqué, Buenos Aires Province, Argentina, Núñez became an expert in the anatomy, physiology and behaviour of insects. His pioneering contributions spanned groundbreaking discoveries in insect physiology. Over his prolific career, Núñez published more than a hundred articles and was recognized for his exceptional observational skills, self-learning abilities,

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originality and passion for scientific inquiry, all complemented by a desire for crafting his own instruments, leaving an indelible mark on the field.

I first met Núñez many years ago when I was an eager undergraduate in Argentina, drawn to his lab by our shared passion for science. What began as a traditional student–mentor relationship evolved into a profound and enduring connection that transcended the boundaries of the laboratory. Over the course of nearly two decades, we met and talked regularly, cooked together, travelled together, conducted both homemade and formal experiments, and engaged in countless discussions ranging from the complexities of insect physiology to the philosophical underpinnings of scientific inquiry. These experiences were not merely academic exercises—they were transformative, shaping my understanding of both science and life. The memories and reflections shared in this tribute are deeply rooted in the rich tapestry of direct interactions and conversations I had with Núñez over the years. On the tenth anniversary of his passing, I feel compelled to document some of the landmarks of his remarkable academic journey and scientific contributions, not only as a testament to his enduring legacy but also as a reflection of the profound influence he had on all who had the privilege of knowing him. This tribute is more than a recounting of his achievements. It is a celebration of the life and wisdom of a mentor, colleague and dear friend who left an indelible mark on both science and the lives he touched.

Also, as I reflect on the impact of Núñez's mentorship and the depth of our conversations, it becomes clear that his scientific legacy extends beyond his pioneering research. His thoughtful critiques of modern biology, including his reflections on various aspects of the field, offer valuable insights that remain relevant today. Sharing these perspectives in this tribute serves not only to honour his memory but also to provide future generations with a nuanced understanding of the challenges and opportunities within contemporary science.

In his later years, Núñez's critique of contemporary biology was incisive, asserting that it often neglects fundamental concepts. He expressed concern that there is a tendency to uphold significant speculations by notable figures, past and present, simply because of their prominence, which he viewed as reflecting an outdated philosopher's approach. He emphasized that modern science operates differently, with hypotheses holding significant weight. His concerns extended beyond what new generations were learning; he worried about what they were not learning, particularly in epistemology. Núñez pointed out that contemporary biology often disregards established principles, potentially owing to an epistemological deficit, which he found concerning. For instance, he referenced Norbert Wiener's demonstration in the 1940s that emergent properties are systemic and holistic, not merely manifestations of a system's parts. Yet today, many biologists focus narrowly on constituent molecules without fully understanding their systems of interest, an oversight that he found problematic. I once casually asked him about his thoughts on ontological damage justified by medical arguments, such as when imperfect vaccines derived from ideological reductionism are used to reduce the incidence of serious diseases. His response was insightful:

> Are solutions facilitated by such tools always more effective? The example is intriguing. However, Western medicine, lacking emphasis on prevention, relies on elements discovered by indigenous populations through holistic approaches or random discovery. Consider antibiotics—discovered by chance! Yet, their mechanisms and benefits have not yet been grasped in full, contributing to resistance issues. Novelty emerges from

> quasi-random research—seeking one thing and discovering another. This reflects the need for a systemic view; otherwise, we risk finding only what we seek, or nothing at all.

The following sections trace key milestones in Núñez's extraordinary journey, emphasizing his profound curiosity and interest in merging biology and engineering. It begins with his early fascination with insect physiology and meticulous anatomical studies, which set the stage for his pioneering research on insect water balance and regulatory pathways. The narrative then explores Núñez's formative years at the Natural Sciences Museum in Buenos Aires, where independent experimentation refined his scientific approach, and his impactful postdoctoral research in Germany. A key aspect of this tribute is how Núñez integrated information theory, cybernetics and engineering principles into his fascination with the relationship between flowers and honeybees, providing novel insights into the roles of honeybees as both nectar carriers and information channels. This article not only highlights Núñez's dedication to rigorous data analysis and systemic research but also stresses its contributions to a more inclusive history of science. By challenging traditional Eurocentric narratives, it aims to recognize and value diverse scientific contributions, particularly those emerging from non-Western contexts.

Approaching the physiology of insects

Núñez fondly recalled his early days at the University of Buenos Aires when biology attracted little interest. He started in 1944 with two classmates who soon dropped out. In his first year at the Faculty of Exact and Natural Sciences, he studied physics, mathematics, chemistry and natural drawing. By the second year, the curriculum included botany and zoology, with no courses on evolution or statistics. Lecturers mainly repeated early twentieth-century textbook content. Despite these limitations, Núñez believed those early years strengthened his understanding of fundamental concepts in physics and chemistry. Furthermore, studying alongside geologists and chemists broadened his perspective on biology. During his second year, one of his lecturers asked him about his primary area of interest, and Núñez responded that it was the physiology of insects, although he could not explain why even years later. The lecturer then introduced him to Alejandro A. Ogloblin, a Russian-born Argentine entomologist, whom he considered to be the only true entomologist in Argentina.[1] Ogloblin led the Institute of Acridiology located outside Buenos Aires. Thus began Núñez's routine of travelling three times a week to a remote lab outside the city after classes. He vividly recalled the train ride from downtown, arriving at the lab with eyes blackened by the smoke of the wood-burning locomotive. Josué Antonio Núñez's initial task under the guidance of Ogloblin, who was accustomed to precise work with micro-hymenopterans, was to prepare sections of the small tarsal gland of Embioptera. Demanding as it was, this task boosted Núñez's passion for anatomy and precise instrumentation. Núñez worked

1 Alejandro A. Ogloblin (1891–1967), originally from Kiev, obtained his PhD in Prague and conducted research on multiembryony in parasitic flies. He collaborated with Boris Uvarov (1886–1970), a renowned Russian entomologist who later led the Anti-Locust Research Centre in London. Ogloblin relocated to Argentina owing to his fascination with locust swarm dynamics. His primary interest was in controlling locust populations using parasitic insects, although this approach faced challenges due to the increasing use of chlorinated compounds during his time. His work included verifying the correct doses of chlorinated compounds used by industrialists. He devised a simple method involving an old phonograph plate: fixing a locust, spraying it with the compound and calculating the revolutions required for mortality.

Figure 1. Josué A. Núñez at age 84, taking a brief pause while conducting fieldwork with honeybees.

with Ogloblin for over five years, until 1950. Eventually, he earned his PhD in 1953, thanks to a meticulous description of the pygidial gland system in *Anisotarsus cupripennis* Germ., which he had independently carried out during those years in Ogloblin's lab.

Learning in the shadows

In 1948, while fulfilling his compulsory conscription, Núñez continued his studies and collaboration with Ogloblin. In need of an income, a botany professor recommended him for a position at the Natural Sciences Museum in Buenos Aires. With limited roles available, Núñez initially worked 'undercover' as a maintenance assistant (janitor). This marked the beginning of his 12-year tenure at the museum, where he later became affiliated with the Laboratory of Entomology and Zoophysiology. Working alone on the nearly abandoned fourth floor, Núñez enjoyed the freedom to design and conduct experiments. During this time, he met Lothar Szidat (1892–1973), a former professor from Königsberg who had arrived in Argentina one year earlier.[2] Struggling with Spanish, Szidat sought to discuss his work with Núñez in German. In Ogloblin's lab, Núñez discovered the existence of a German book on invertebrate histology published by Gustav Fischer. Fischer's widow requested food supplies in exchange for a copy of the book that had survived the Second World War. Núñez sent the supplies and received the book. To understand it, he began learning German with Szidat's assistance, while Szidat improved his Spanish in return. These were formative years. Szidat's influence and the solitude of the isolated room in the museum shaped Núñez's character profoundly. Reflecting on the significant influences on his scientific practice, he attributed much to Szidat. Engaging in debates on various

2 Lothar Szidat was born in Illowo, East Prussia (now Ilowo, Poland). He studied natural sciences in Königsberg, obtained his PhD in 1920 and became the director of the Zoological Station at Rositten (now Rybachi, Russia) in 1925. After spending three years in a Danish camp, he arrived in Argentina with his family in 1947, where he worked at the Museum of Natural Sciences in Buenos Aires. Szidat pioneered helminthology in both Europe and Argentina, being one of the first to establish links between parasites and host ecology.

topics, Núñez designed and conducted experiments that not only challenged but occasionally disproved Szidat's views, forging profound learning and growth.

Early career

Two years after completing his PhD and already established at the Natural Sciences Museum, Núñez set his sights on working in England, inspired by the pioneering research of Sir Vincent Wigglesworth (1899–1994), widely regarded as *the* insect physiologist. However, owing to limited funds, Núñez redirected his efforts toward applying for a postdoctoral scholarship from the Alexander von Humboldt Foundation, which was then in its second round. Núñez successfully secured the scholarship with the support of Alfred Kühn (1885–1968), a prominent figure in physiology and developmental genetics. During his doctoral studies, Núñez had independently explored the regulation of water balance in Coleoptera as a side project, developing his own laboratory instruments and conducting numerous experiments. With Szidat's assistance, he had written a manuscript in German and sent it to Kühn. Impressed by its quality, Kühn invited Núñez to join his laboratory.

To fund his journey, Núñez borrowed money and embarked on the modest ship *Yapeyú*, eventually arriving in war-torn Germany. After a brief stay in an old bunker in Essen, he travelled to the Max Planck Institute of Biology in Tübingen, led by Kühn. In Tübingen, Kühn encouraged Núñez to publish his 'side project', which later became a significant milestone.[3] At that time, neither Wigglesworth nor others had explored the regulation of water balance in insects, underscoring the significance of Núñez's pioneering findings, which were later recognized by his peers. His research revealed that diuresis in insects is triggered by a diuretic hormone and he proposed a potential regulatory pathway. Initially underestimating its importance, Núñez later regarded this contribution as one of his most original works.

These pivotal events—beginning in a remote lab in the countryside outside Argentina's capital, unfolding in an abandoned museum room and culminating in a prestigious postwar institute in Germany—marked the start of a distinguished career defined by significant and rigorous publications. Within 15 years of completing his doctoral thesis in 1953, Núñez had already published groundbreaking discoveries in insect physiology. He identified the prothoracic glands responsible for ecdysone production and demonstrated the neuroendocrine regulation of water excretion in beetles.[4] He further elucidated the nervous control of diuresis and the mechanical properties of the cuticle in blood-sucking bugs, as well as the neural regulation of ingestion in dipterans.[5] As interest in the behaviour of foraging honeybees grew, Núñez conducted the first analysis of how the energetic properties of nectar sources influence honeybee nectar gathering, advancing the study of both individual and

3 J. A. Núñez, 'Untersuchungen über die Regelung des Wasserhaushaltes bei *Anisotarsus cupripennis* GERM'. *Z. Vergl. Physiol*, **38**, 341–354 (1956) (https://dx.doi.org/10.1007/BF00340417).

4 *Ibid*.; J. A. Núñez, 'Über das Vorkommen der Prothoraxdrüsen bei *Anisotarsus cupripennis* (Coleoptera, Carabidae)'. *Biol. Zbl*. **73**, 602–610 (1954).

5 J. A. Núñez, 'Central nervous control of the mechanical properties of the cuticle in *Rhodnius prolixus*'. *Nature* **199**, 621–622 (1963) (http://dx.doi.org/10.1038/199621a0). J. A. Núñez, 'Regulation of water economy in *Rhodnius prolixus*'. *Nature* **194**, 704 (1962) (http://dx.doi.org/10.1038/194704a0); J. A. Núñez, 'Trinktriebregelung bei Insekten'. *Naturwissenschaften* **51**, 419 (1964) (http://dx.doi.org/10.1007/BF00609055).

collective foraging—a topic that will be explored in much greater detail in subsequent sections.[6] He also discovered that honeybees optimize foraging by marking empty nectar sources with repellent pheromones.[7]

Over the course of his career, Núñez made numerous other significant discoveries, including the perception of infrared radiation by haematophagous bugs—likely too many achievements to fully capture in a brief summary. He conducted experiments and taught at top-tier institutions, including the Max Planck Institute of Biology in Tübingen, the University of Göttingen, the University of Freiburg, the Free University of Berlin, the University of California, the University of São Paulo, the Venezuelan Institute for Scientific Research and the University of Buenos Aires, where he pioneered the field of behavioural physiology in Argentina. Núñez's life and work offer a compelling counter-narrative to traditional histories of science, which often overlook the contributions of non-Western scientists. His achievements are a reminder of the importance of recognizing and valuing the diverse ways in which scientific knowledge is produced and shared globally. This will be further discussed below. Notably, Núñez's early research paralleled significant advancements in evolutionary theory and engineering.

The engineering perspective

Núñez's early career coincided with the modern synthesis and the emergence of information theory, cybernetics and bionics, a context that shaped his future perspectives. Shannon's work separated information as an abstract quantity from matter and energy, setting the stage for cybernetics.[8] This field provided biologists with new frameworks to understand goal-directed behaviours, while the concept of complex systems challenged scientists to predict properties from component behaviours alone.[9] By the mid-twentieth century, integrating goal-directed processes with physicochemical explanations signalled a shift from mechanistic biology to studying complex organismal properties. Concurrently, bionics emerged in the 1950s, focusing on mimicking nature's adaptations to enhance technology. This compound approach simulated communication and goal-directed behaviour in artificial systems, reshaping biological research from traditional structural analysis to integrating insights from technical disciplines into physiological studies. Núñez found these new perspectives compelling and incorporated them into his own research. He believed it was crucial to assess systems holistically, applying concepts from control theory and an engineer's perspective to identify fundamental principles and regulatory mechanisms.

To Núñez, engineering and biology shared operational principles. Both disciplines draw upon common knowledge to construct and comprehend intricate systems. Engineers synthesize elements with diverse properties following principles in mechanics, chemistry or electronics, while biologists analyse living systems using methods from physics and

6 J. A. Núñez, 'Quantitative Beziehungen zwischen den Eigenschaften von Futterquellen und dem Verhalten von Sammelbienen'. *Z. Verl. Physiol.* **53**, 142–164 (1966) (http://dx.doi.org/10.1007/BF00343733).

7 J. A. Núñez, 'Sammelbienen markieren versiegte Futterquellen durch Duft'. *Naturwissenschaften* **54**, 322–323 (1967) (http://dx.doi.org/10.1007/BF00640625).

8 C. E. Shannon, 'A mathematical theory of communication'. *Bell Syst. Tech. J.* **27**, 379–423 (1948) (http://dx.doi.org/10.1002/j.1538-7305.1948.tb01338.x). N. Wiener, *Cybernetics, or communication and control in the animal and the machine* (MIT Press, Cambridge, MA, 1948).

9 K. L. von Bertalanffy, *General system theory: foundations, development, applications* (George Braziller, New York, 1968).

chemistry. Technology aids biologists in modelling and understanding technically analogous systems. In discussions with Núñez about any biological topic, two concepts inevitably emerged: energy optimization from engineering and the principle of economy from biology (a term he frequently used to encapsulate the Darwin–Wallace ideas on natural selection). He viewed these concepts as inseparable, guiding effective organization and resource-efficient outcomes. His explanation of Darwin's and Wallace's ideas on common descent and natural selection was succinct: adaptation involves adjusting form and function to fit a variable environment, ensuring the survival of the unit of selection. This process optimizes energy use by aligning systems with their surroundings. Living systems experiment with energy to form new assemblies (morphological, functional or both) that prove more efficient, with successful assemblies forming the basis for evaluation. Critically, for evaluation and selection, a population of assemblies must exhibit variability, showcasing a range of alternatives. This diversity is essential for developing strategies that enable efficient resource use and biomass increase. Over time, systems with substantial diversity gain an enhanced capacity to adapt and compete in varying environments. Núñez believed this capacity catalysed the emergence of diversity-safeguarding mechanisms like heterosis, achieved through cross-fertilization. Despite lacking formal training in evolutionary theory, he attributed enough significance to this overall strategy to explain the diversity of technical solutions found in nature, extending his fascination to engineering success.

Understanding evolution through engineering

Evolution strategy (ES), pioneered in the 1960s by Ingo Rechenberg (1934–2021), is a biologically inspired engineering algorithm that leverages mutation and selection principles derived from Darwinian evolution.[10] Alongside genetic algorithms, introduced by John Holland in 1975 (1929–2015), ES applies evolutionary concepts to solve complex optimization problems.[11] Rechenberg's method involves systematically altering variables in a system and discarding changes that worsen performance, mimicking natural evolution. Despite initial scepticism about its efficiency, ES proved remarkably successful, requiring fewer iterations than anticipated, owing to its ability to handle the complexity and indeterminacy of systems with numerous nonlinear interactions. Central to ES is the mutation strength (MS), which dictates the rate of optimization progress and remains effective across varying dimensions of search space. ES optimizes both the system and the optimization process itself by fine-tuning MS, mirroring evolutionary mechanisms that enhance variability and adaptability within populations. This aligns with evolutionary biology, where genetic turnover and adaptation enable populations to navigate changing environments.

Encountering Rechenberg's work proved fortuitous and enlightening for Núñez, who had been largely unaware of advancements in evolutionary thought. This technical interpretation of the Darwin–Wallace ideas offered a practical approach to addressing the indeterminacy of the living world. When presented in technical terms, Núñez quickly grasped the fundamentals of evolution through natural selection, despite his lack of formal training. These new perspectives would guide his insights into countless biological systems. He

10 H. G. Beyer and H. P. Schwefel, 'Evolution strategies: a comprehensive introduction'. *Nat. Comput.* **1**, 3–52 (2002) (http://dx.doi.org/10.1023/A:1015059928466).

11 J. H. Holland, *Adaptation in natural and artificial systems* (University of Michigan Press, Ann Arbor, 1975).

saw the relationship between modern flowers, trading sugary rewards for reproduction, and honeybees, surviving harsh winters with robust colonies, as a striking example of both energy optimization and the principle of economy. He often challenged his students: task an engineer with designing a flower attractive to pollinators or a biologist with creating an artificial nectar-gathering bee. Good luck! He believed true breakthroughs occur when these disciplines collaborate, devising efficient methods to enhance pollination and biomass production for plants and bees alike.

Flowers and bees: opposing control systems

Focusing on the plant's perspective, Núñez consistently emphasized key landmarks in the early stages of entomogamy. He argued that cross-fertilization in higher plants was justified from an engineering perspective owing to operational benefits. Initially, it was mediated by wind, causing gymnosperms to produce large amounts of pollen owing to environmental unpredictability. Gymnosperms dominated until the early Lower Cretaceous, but their pollen was not a significant energy source for insects. About 130 million years ago, angiosperms evolved floral structures, and early anthophilous insects, such as Coleoptera, began visiting flowers for pollen, establishing mutualism. This insect-mediated pollination likely started in tropical regions, fostering novel strategies. During the Tertiary era, this pollination allowed plants to reduce pollen production per seed, optimizing energy use. Flowers catered to insects using pollen as food but evolved to offer nectar, a cheaper energy source than proteins, leading to reduced stamen numbers. Flowers also enhanced their energy value by reducing pollinator uncertainty with scents and colours. They adjusted traits and timing to align with pollinator activity. *Ophrys* orchids were Núñez's favourite landmark. They mimic female *Gorytes* (Hymenoptera) pheromones and appearance, attracting males and ensuring efficient pollination. The plant provides only essential information to the insect pollinator, achieving extreme material efficiency by attracting male wasps solely through simulation.

From the pollinator's perspective, Núñez would emphasize to his students that the relationship between modern flowers and honeybees that we observe is the result of millions of years of coevolution between two complex and opposing control systems. Plants aim to optimize pollination efficiency while conserving pollen and nectar, whereas pollinators seek to maximize food intake by improving foraging techniques and reducing handling time. This interaction has led to a sophisticated network of flower–pollinator systems that are energetically efficient both in relation to each other and within their specific habitats. The honeybee, extensively studied for its high foraging specialization, served as an ideal case for him to analyse the interaction between these opposing control systems through an engineering lens.

The dual roles of foraging honeybees

Núñez's lifelong interest in honeybees began with an unfortunate yet serendipitous event, exemplifying the role of contingency in science. In 1964, with renewed support from the Alexander von Humboldt Foundation, he returned to Germany as an assistant researcher at the Zoological Institute of the University of Freiburg, led by Bernhard Hassenstein (1922–2016).[12] However, the reduviid bugs he had transported from Argentina for his research did not survive the journey. Faced with this unexpected setback, Núñez had to find a new organism for his studies on ingestion, water balance and regulatory pathways. Honeybees, which were readily available in Freiburg, presented themselves as an unplanned but fortuitous alternative. Unaware of Karl von Frisch's (1886–1982) pioneering work or Aristotle's extensive coverage of honeybees in *Historia Animalium*, Núñez's initial foray into honeybee research was driven by necessity rather than design.[13] Yet, this chance encounter with honeybees led him to design the first flower simulator to study honeybee nectar gathering quantitatively, setting the foundation for his subsequent groundbreaking contributions to the field. This shift in focus exemplifies how scientific progress can sometimes hinge on unforeseen circumstances, where contingency plays a pivotal role in guiding researchers toward new and fruitful directions.

Núñez's simulator featured artificial flowers with varying flows of sugary solutions and sucrose concentrations. Honeybees conditioned to use it behaved similarly to how they did at natural sources, enabling Núñez to make a series of critical observations.[14] Later in life, he fondly recalled surprising local colleagues with his ability to predict, several minutes in advance, the exact time of a honeybee's departure from his simulator down to the second. This precision was achieved through meticulous control of sugar solution flow and detailed behaviour measurements. These measurements exposed, for the first time, a quantifiable balance between individual foraging efficiency and the overall efficiency of the colony. Núñez identified two roles for foragers: as carriers transporting nectar into the hive and as information channels relaying data between nectar sources and the forager task force. He uncovered the function linking these two roles. Here is a summary.

When the sugar solution flow rate at the simulator exceeds 10 μl min^{-1}, a foraging honeybee stays until its crop is full, typically holding about 70 μl. A single visit for high-flow solutions lasts no more than 7 minutes. The bee then returns to the hive, transfers the nectar to other bees (keeping a small amount for energy) and heads back for another collection. At flow rates below 10 μl min^{-1}, even as low as 0.3 μl min^{-1}, the crop load a honeybee gathers is directly linked to the logarithm of the nectar supply. At a flow rate of 0.2 μl min^{-1}, a visit usually results in an empty crop. However, this is rare as honeybees avoid such low-flow sources, opting to stay in the hive and take long breaks. During the appropriate season and without competing flowers, trained foragers stay loyal to the simulator even at flows as low as 0.3 μl min^{-1}, similar to their in-flight intake (about 0.18 mg sugar min^{-1}). At this low threshold, foraging drive decreases, leading to longer breaks between visits. If low flow persists, the bee may eventually stop visiting the simulator. However, by continuously injecting sugary solutions during breaks, more nectar becomes available, mimicking natural accumulation. This intermittent pattern causes fluctuations in foraging behaviour but keeps bees engaged with the nectar source, ensuring effective nectar collection and pollination if the flower becomes profitable again. Natural sources often have low nectar flows but remain attractive to honeybees, likely reducing navigational demands by using familiar routes.

12 Bernhard Hassenstein (1922–2016) was a pioneering German biologist and cyberneticist known for his research in behavioural physiology, especially in visual processing and motion perception in insects, which significantly influenced the field of neuroethology.

13 Karl von Frisch (1886–1982) was an Austrian ethologist whose pioneering work in sensory physiology and animal behaviour included studies on colour vision, olfaction, and communication in bees, particularly their "waggle dance". Aristotle, Historia Animalium, trans. A. L. Peck, Loeb Classical Library, Cambridge, MA: Harvard University Press, 1965.

14 Núñez, op. cit. (note 6). J. A. Núñez, 'Quantitative Beziehungen zwischen den Eigenschaften von Futterquellen und dem Verhalten vonSammelbienen'. *Z. Ver. Physiol.* **53**, 142–164 (1966). (doi:10.1007/BF00343733).

Núñez was intrigued by the duration of visits as nectar flow exceeded 10 μl min^{-1}, which typically fills the crop completely. Under these conditions, visit duration—and crop load—decreases as flow rate increases, the opposite of what happens at flow rates below 10 μl min^{-1}, where visit duration increases with flow. This shows that when the nectar source is highly profitable, honeybees prioritize faster returns to the hive without fully replenishing their capacity. This behaviour remains consistent across specific honeybee strains, acting as a distinct behavioural parameter.[15] As nectar flow in the simulator increases further, source exploitation intensifies, prompting the recruitment of additional foragers from the hive. Group foraging reduces individual collection but ensures efficient transport of all nectar back to the hive. Decades of research show that even during peak nectar seasons, honeybee colonies respond to increased nectar flow at specific spots by sending out many foragers to outperform competitors. Two key observations emerge: as nectar flow increases, both the number of foragers and the total nectar collected increase. Additionally, the maximum number of bees visiting the simulator for the same nectar flow varies seasonally, peaking towards the end of the main nectar flow period.[16] This suggests that future versions of Núñez's simulator, combined with weather sensors, could provide valuable tools for monitoring and managing crop pollination.

In summary, a collector bee's efficiency as a carrier depends on its ability to transport sugar in a single trip, which is determined by its crop capacity and foraging duration. Reduced nectar flow extends the time bees spend at sources, disrupting information exchange among bees and diminishing colony efficiency. This is because the bee's efficiency as an information channel directly depends on the time it spends in the hive between trips. Núñez saw this 'hive time' as the most sensitive indicator of the strength of the ongoing foraging communication network. The dual role of collector bees is crucial in eusociality, linking nectar flow and visit duration. It highlights both individual efficiency and the bee's capacity to share information. While recruiting new bees for nectar collection might not be efficient individually, intra-hive competition significantly enhances the colony's responsiveness to nectar availability. Once a collector honeybee fills its crop, additional flow does not increase its nectar-gathering ability. However, a group of collectors can detect and respond to larger flow variations, collectively saturating crop loads at higher rates. This collective ability directs more bees to productive nectar sources, optimizing the colony's energy use as a whole. It illustrates how individual foraging behaviours are finely tuned to enhance overall colony efficiency. Fundamentally, recruitment amplifies the link between sugar flow and individual intake. Núñez recognized the implications of this for studying eusociality and encouraged students to explore these concepts in other social insects. Personally curious after these observations, he sought to compare honeybee variants with different crop capacities, always eager to challenge hypotheses. He was particularly intrigued by the Italian (*Apis mellifera ligustica* Spinola) and African (*Apis mellifera adansonii* Latri) honeybees in Brazil.

15 J. A. Núñez, 'Estudio cuantitativo del comportamiento de *Apis mellifera ligustica* Spinola, y *Apis mellifera adansonii* Latreille. Factores energéticos e informacionales condicionantes y estrategia del trabajo recoletor'. *Cienc. Cult. São Paulo* **26**, 786–797 (1974).

16 J. A. Núñez, 'Nectar flow by melliferous flora and gathering flow by *Apis mellifera ligustica*'. *J. Insect Physiol.* **23**, 265–275 (1977) (http://dx.doi.org/10.1016/0022-1910(77)90041-5).

Variants with different crop capacity

In 1956, African honeybees were introduced to Brazil to enhance commercial beekeeping, but escaped control efforts, displacing the European strain. In competitive tropical conditions, African hives outperformed others in food gathering, exerting increasing pressure on different bee populations over time. They consistently produced more honey than European hives. Núñez introduced his simulator and examined how the function linking nectar availability and food intake related to the enhanced performance of the African colonies. Here is a summary of his findings. African bees made shorter collection visits and carried smaller crop loads per trip. While some of this disparity was attributable to their smaller size, the gap widened as nectar flow rates decreased. When flow rates dropped below 1 μl min^{-1}, African bees sometimes carried only 30% of the load that Italian bees managed. As nectar scarcity intensified, both the average crop load and individual yield of African bees declined.[17] Despite African honeybee colonies being energetically more efficient overall, individual foragers were less efficient carriers compared with Italian bees. Núñez found this dynamic particularly intriguing. The African bee colony demonstrated a superior adaptability to fluctuations in nectar availability alongside increased hive visits by its foragers, in line with the idea that this facilitated improved dissemination of nectar information. Unlike the more homogeneous floral populations of temperate regions, tropical habitats are rich in diverse flower species. Tropical strains such as the African honeybee can show polylectic behaviour, enabling them to switch between different flower species for nectar. This behaviour likely enhances the availability of nectar-related cues within the hive, reducing uncertainty for foragers. Núñez hypothesized that this enhanced communication and cooperation would align with statistical expectations under the Nyquist–Shannon sampling theorem, ensuring efficient resource exploitation by the colony despite individual efficiency challenges.

Pursuing data integrity beyond debates

Núñez's approach to honeybee ergonomics reveals another facet of his profile. He consistently demonstrated a commitment to thorough examination of procedures and data while actively avoiding fruitless debates. For him, meaningful scientific discussion could only occur when proper procedures were followed and reliable data were available. An example of this commitment can be seen in his treatment of the research surrounding the famous waggle dance of honeybees, widely recognized as one of the most remarkable communication systems in the animal kingdom. This topic has long sparked debates about how foragers interpret the dance.[18] Núñez always maintained a distance from such disputes, which he believed often arose from incomplete or biased data sets.

A comprehensive account of the disputes over the waggle dance is beyond the scope of this article and would likely require multiple volumes to cover in full. It is hard to imagine any other behaviour that has generated such a consistent stream of publications over the

17 J. A. Núñez, 'Times spent on various components of foraging activity: comparison between European and Africanized honeybees in Brazil'. *J. Apic. Res.* **18**, 110–115 (1979) (http://dx.doi.org/10.1080/00218839.1979.11099953).

18 J. Tautz, *Communication between honeybees: more than just a dance in the dark* (Springer, New York, 2022) (http://dx.doi.org/10.1007/978-3-030-99484-6).

years. The following is a brief summary of the issue, focusing on well established aspects rather than providing an exhaustive list of references, which would be too numerous to include. This summary is intended solely to illustrate the primary reason Núñez chose to distance himself from these debates. Briefly, the waggle dance for sugary rewards (honeybees also dance for nest sites, pollen and water) allows humans to pinpoint the location of specific areas by indicating the endpoint of a vector within a two-dimensional coordinate system, guiding us to where active foragers are likely to be found around the colony. This groundbreaking discovery by Karl von Frisch is one among many made by an extraordinary scientist.[19] However, whether honeybees themselves interpret this spatial information in the same way has puzzled biologists for decades.

Despite almost eight decades of research since von Frisch's original discovery, our understanding of how spatial information is transferred from dancers to followers remains incomplete. Significant challenges persist in assessing the redundancy and precise functions of various dance signals, as well as the roles of different cues—such as olfactory and visual cues—that contribute to local recruitment (the number of bees eventually reaching a target advertised by the dances). Moreover, research on recruitment through dances has shown that local recruitment rates are often much lower than expected if bees were simply following the dance directly to the indicated goal. This discrepancy is typically attributed to the redundancy of dance signals and the inherent imprecision in encoding and decoding spatial information. Two key aspects further complicate things. First, while communication involves the reproduction of a symbolic signal by the sender, the received signal can be influenced by the receiver's prior experiences. Both the response to the dance and navigation are significantly shaped by these experiences. Honeybees use a sky compass for directional cues and estimate distances through self-induced optic flow. They navigate with both path integration and familiar landmarks: path integration coordinates track direction and distance during flight, while familiar views help with orientation based on stored coordinates. To fully understand the waggle dance's role in local recruitment, it is essential to examine how these communication and navigation processes interact, particularly how navigational memories are shared or not shared between dancers and followers.

Addressing all these issues involves several key methodological considerations. First, continuous monitoring of all interactions between dancers and followers, both inside and outside the hive, is crucial for accurately tracking stimulus-triggered actions. Second, controlling the number of dancers is essential, ideally keeping it small (preferably just one), as local recruitment rates closely correlate with the number of dancers simultaneously flying between the hive and the advertised goal. Third, followers should be exposed only to dances for unfamiliar goals to clearly distinguish between current dance information and past experiences. Fourth, varying the locations of these goals is necessary to analyse how discrepancies affect follower responses. Fifth, using unscented rewards and maintaining unscented feeding stations are vital, though achieving perfectly unscented conditions is nearly impossible. This involves consistently removing recruited bees from the feeding station to minimize olfactory cues, creating an open-loop system for better control. Finally, placing both past and present goals far from the hive reduces the likelihood of followers locating the goals through solitary searches.

19 T. Munz, *The dancing bees: Karl von Frisch and the discovery of the honeybee language*. (University of Chicago Press, 2016) (http://dx.doi.org/10.7208/chicago/9780226021058.001.0001).

Núñez was acutely aware that experiments rarely, if ever, met all these requirements simultaneously, leaving much of the debate unresolved owing to insufficient or unreliable data. While he admired von Frisch's work, especially his discoveries in sensory physiology, Núñez was less interested in the various interpretations of how followers 'read' the waggle dance that arose from subsequent research. Moreover, Núñez generally focused on understanding the recruitment system as a whole rather than its individual components. He viewed each means of recruitment as just a small part of a larger system. The waggle dance for nectar and pollen, which is relatively infrequent under natural conditions for most of the year, was just one element in a complex series of interconnected components, the relationships among which are still not fully understood. (Perhaps one exception was on-flight following. This phenomenon captured his interest, likely owing to the significant methodological challenges it presents, and it remains largely unexplored.) His focus was on the fundamentals, seeking parameters that could explain how individual actions contribute to the collective, accounting for the emergent properties of complex systems such as insect societies. For Núñez, a key issue in the dance debates was that researchers often overlooked crucial aspects of behaviour and sensory physiology related to recruitment that operate alongside the dancing displays. Additionally, isolating and accurately controlling the stimuli embedded in the dance have proven challenging, complicating the interpretation of recruitment outcomes, especially under less-than-ideal experimental conditions. In the collective effort to study group foraging in honeybees, his true puzzle lay beyond the dance. He could never fully grasp why so many researchers interested in group foraging continued to use *ad libitum* feeders, a practice they still uphold. He believed this practice inevitably hampers the analysis of how honeybees work collectively for the benefit of the group, as flowers rarely provide *ad libitum* nectar. Even when they do, it is typically only very briefly during the peak of the nectar season and often limited to part of the day.

Challenging the centre–periphery model: a key part of Núñez's legacy

Núñez's career offers a valuable perspective on the dynamics of knowledge production and circulation within the broader history of science in Latin America. His contributions to insect physiology and behaviour not only reflect individual brilliance but also illustrate the complex interplay between local scientific traditions and global networks. Núñez's scientific journey embodies key aspects of Latin American science during the mid-twentieth century, a period marked by increasing integration of Latin American scientists into international scientific networks.

Despite the peripheral position often attributed to Latin American science in global narratives, Núñez's work challenges the simplistic centre–periphery model.[20] His research, conducted in Argentina, had a profound international impact, demonstrating that significant scientific contributions can emerge from peripheral contexts. Núñez's early training under Ogloblin and his collaboration with Szidat illustrate how scientific knowledge in Argentina was developed in unique environments, often in resource-constrained settings like an isolated lab outside Buenos Aires or an abandoned room in the Natural Sciences Museum. These conditions did not hinder innovation; rather, they fostered a distinct

20 G. Basalla, 'The spread of Western science: a three-stage model describes the introduction of modern science into any non-European nation'. *Science* **156**, 611–622 (1967) (http://dx.doi.org/10.1126/science.156.3775.611).

approach characterized by ingenuity, self-reliance and a profound engagement with both local biodiversity and broader scientific questions.

At the same time, Núñez's career reflects the broader dynamics of Latin American science, which often involve navigating between peripheral and central scientific environments. His trajectory (from Argentina to leading institutions in Europe and back) illustrates both the common patterns of Latin American science and how individual achievements can disrupt and enrich our understanding of these patterns. While his path might seem to follow a conventional narrative of moving from the periphery to the centre, the reality is more nuanced. Núñez's pioneering work in insect physiology made significant contributions to the field regardless of his geographical location. His later work, primarily conducted in Latin America, included nurturing a new generation of insect physiologists and neuroscientists. This further emphasizes that scientific innovation is not confined to well funded Western institutions. Núñez's achievements demonstrate that substantial scientific contributions can emerge from contexts often considered peripheral. The sophisticated experiments he conducted in Argentina, often with homemade instruments, stress the creativity and agency of scientists working in resource-constrained environments.

His career is also consistent with recent discussions on the circulation of knowledge and the role of Latin American scientists in global networks. Núñez's move from Argentina to Germany illustrates the permeability of borders in scientific knowledge production. While he benefited from the mentorship and resources of prestigious institutions, he also contributed ideas and research cultivated in Argentina, enriching the scientific community abroad. This bidirectional flow of knowledge challenges the notion of Latin America as merely a recipient of scientific knowledge and stresses the active contributions of Latin American scientists to global science. Núñez's life and work remind us that the history of science is not solely about major discoveries made in the West but also includes significant contributions from scientists in other parts of the world. His ability to bridge local practices with global discussions illustrates that scientific knowledge is not simply transferred from the centre to the periphery but is actively constructed and negotiated across diverse contexts. This is particularly relevant today, as it reveals the importance of studying how science develops in peripheral contexts and interacts with local societies, a topic often overlooked by the mainstream science and technology studies community. Scholars emphasize that understanding these dynamics is crucial for a comprehensive view of globalized science. As science becomes increasingly global, scientists from semi-peripheral countries, like those in Latin America, are often integrated into large international research efforts. However, their roles are frequently limited to technical tasks or data collection rather than contributing to theoretical or conceptual development.[21] This pattern reflects a broader issue within the global scientific community: the underappreciation of the full range of contributions from scientists in these regions. By focusing on these overlooked aspects, we can gain a deeper understanding of how scientific knowledge is constructed and circulated across different contexts, challenging the notion that scientific innovation is solely the domain of well funded Western institutions.

21 A. Feld and P. Kreimer, 'Scientific co-operation and centre-periphery relations: attitudes and interests of European and Latin American scientists'. *Tapuya: Latin Am. Sci. Technol. Soc.* **2**, 149–175 (2019). (http://dx.doi.org/10.1080/25729861.2019.1636620)

Closing remarks

It is hard to think of a topic in biology that did not capture Núñez's curiosity. He could spend hours discussing subjects such as the role of introns or the emergence of redundancy in intracellular pathways. Yet, one area ignited his passion above all others: the intersection of evolutionary theory, biological complexity and engineering. This fascination was especially evident in his exploration of the intricate relationship between flowers and honeybees, a subject he cherished throughout his career. I have never encountered a biologist with such a profound understanding of this relationship.

Núñez shared Ernst Mayr's (1904–2005) belief that biology requires a philosophical approach integrating engineering and evolutionary perspectives.[22] He argued that this integration not only enhances our understanding of biological systems but also inspires innovative technical solutions drawn from nature. His passion for insects extended beyond individual species to their diversity, adaptations and stereotypical behaviours, which provided abundant material for developing energy-efficient criteria based on engineering principles. He was particularly captivated by the additional layer of ergonomic complexity introduced by eusociality, which fuelled his fascination with honeybees. Núñez thrived on embracing complexity. To young biologists, he recommended essential reads such as *Portraits from memory* by Richard Goldschmidt, *Cybernetics: or control and communication in the animal and the machine* by Norbert Wiener, *The growth of biological thought* by Ernst Mayr and *Symbiosis in cell evolution* by Lynn Margulis.[23]

Josué embodied a deep passion for science, paired with a great sense of humour. He was one of the most intelligent biologists I have ever met and unquestionably the humblest. Despite receiving numerous awards, he never sought recognition. His profound influence on generations of students is undeniable. I deeply miss our conversations and hope this tribute inspires young biologists, especially insect physiologists, to explore or rediscover his work, which stands as an exemplary contribution to science.

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22 E. W. Mayr, *The growth of biological thought* (Harvard University Press, Cambridge, MA, 1982), p. 73.

23 R.B. Goldschmidt, *Portraits from memory: recollections of a zoologist* (University of Washington Press, Seattle, 1956); Wiener, *op. cit.* (note A); Mayr, *op. cit.* (note B); L. Margulis, *Symbiosis in cell evolution* (Freeman, New York, 1993)', where the new references should be in the journal style, 'A' is currently '11' and 'B' currently '22'.

Data accessibility

This article has no additional data.

Declaration of AI use

I have not used AI-assisted technologies in creating this article.