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THE SOCIETY OF POPULATION ECOLOGY

IN MEMORIAM

Yosiaki Itô 1930–2015

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At Ueno Zoological Gardens on May 25, 2002. Provided by Yosiaki Itô

Introduction

Dr. Yosiaki Itô, formerly a Professor at Nagoya University, passed away on May 15, 2015 from liver failure at the age of 85. He was a leading scientist in the fields of ecology and entomology in Japan and was president of the Society of Population Ecology and the Japan Ethological Society in the 1980s and 1990s. Through his recognized contributions to Japanese science, academia, and society, Itô received numerous awards, including the Japan Prize of Agricultural Science (1972), the Yomiuri Prize (1972), and the Minakata Kumagusu Prize (2007). Because Itô's activities were so wide and diverse, this memorial paper became a collaboration of five coauthors! We would first like to briefly note our personal relationships with Itô. KT was supervised by him in Nagoya; TM and MY worked with him on the sterile insect technique (SIT) project; MS was his coauthor on the major Japanese textbook "*Animal Ecology*" (1992, 2004); and EK was his co-worker in the early development of population ecology in Japan.

Itô's professional career was quite unusual, as he himself admitted (Itô 1975, 2003). He was never a graduate student, because he was hired as an officer of the Ministry of Agriculture, Forestry, and Fisheries (MAFF) immediately after graduating from Tokyo Vocational School for Agriculture (now Tokyo University of Agriculture and Technology) in 1950. However, he was soon suspended from this job, because he was accused of involvement in the so-called May Day Incident of 1952. This suspension lasted for an astounding 17 years until a final decision of "not guilty" was reached in 1970. Itô's doctorate was awarded by Kyoto University in 1960; under the Japanese system, he was given the title of "Thesis-Only Doctor" during this job-suspension period.

Population ecology at the National Institute of Agricultural Research in Tokyo

The brilliant career of Yosiaki Itô as one of Japan's leading population ecologists started at the National Institute of Agricultural Research in Tokyo in 1950, where during his

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suspension he was not paid but was allowed to work by the head of the laboratory.

His first work was laboratory experiments on the population growth and dispersal movements of four aphid species—*Aphis glycines*, *A. maidis*, *Rhopalosiphum prunifoliae*, and *Macrosiphum granarium*—on their host plants, soybean (in the case of *A. glycines*) and barley (in the case of the other three species) (Itô 1952, 1960). His main conclusions were: (1) during early, low-density periods, the population of each species settled and grew freely on those host parts that the species preferred; (2) however, as the density rose and the preferred parts became saturated, dispersal to other, less preferred parts of the plant occurred and the population continued to grow further; and (3) when the whole plant had become saturated, the aphids began to disperse to neighboring plants and the population continued to grow until it had filled the capacity of the experimental habitat. This monumental work is now widely recognized as the first Japanese study to succeed, through simple experiments, in proving the importance of dispersal to the spatiotemporal dynamics of insect populations: such dispersal can consistently play an important role in converting the effects of intra- and inter-species crowding from negative to positive by promoting efficient resource utilization.

As is well known, Itô then continued to work with amazing passion as a young pioneer in the equally young field of population ecology in Japan. Whereas on the one hand Itô made a great contribution to the general promulgation of this field of science by publishing several textbooks and also by helping to establish our Society of Population Ecology, on the other hand he also conducted many original studies covering various themes and subjects. In those early years, his field studies of the fall webworm *Hyphantria cunea* (Itô and Miyashita 1968; Itô et al. 1969) were especially important. This moth species and forest pest had recently invaded Japan from North America and had already spread widely throughout central Japan. As a pivotal member of the group of entomologists rapidly organized to study the pest's biology, Itô took charge of the analysis of field population dynamics in fixed plots. Covering as many as 12 generations in 6 years, this has long been evaluated as the first full-scale insect population study in Japan to be based on elaborate life-table analysis. In fact, this epoch-making work characterized the species' population. It revealed that (1) larval mortality caused by the main predators (birds and *Polistes* wasps) was generally inversely dependent on larval population density, thus leading to characteristic gradation-type moth-population increases; and that (2) adult fecundity showed a clear trend toward population density dependence (i.e. it declined with increasing density), thus playing the role of regulating and stabilizing moth populations in the long run.

These studies of Itô's were performed in accordance with the world's best analytical methodology at the time; moreover, he never forgot to critically check the logic and any associated problems, and in his review articles he made many constructive proposals to improve the methodologies (e.g. Itô 1972, 1973).

It's evident that these early field studies gave Itô, as one of the most powerful leaders of population ecology in Japan, a realistic basis for promoting his wide-ranging activities. Furthermore, they demonstrated how studies at the forefront of population dynamics should be done and what problems are involved from a global perspective; thereby they continued to stimulate many young Japanese ecologists of subsequent generations to critically consider the direction of their own ongoing studies. Itô's studies thus acted as effective triggers of general interest in the further comprehensive development of population ecology by incorporating other closely related fields, such as behavioral and evolutionary ecology.

SIT project in Okinawa

In 1972, soon after the suspension from his government job was lifted, Itô moved to Okinawa on a mission: to eradicate the melon fly *Bactrocera cucurbitae*. This serious pest began invading the islands of the Ryukyus in 1919 and was expanding its distribution to the north. MAFF tasked Itô with eradicating the fly before it reached the mainland; the sterile insect technique (SIT) invented by Knipling (1955) was used. Itô directed and supervised this difficult project and contributed greatly to a general improvement of the SIT. Finally, in 1978, the melon fly was eradicated from Kume Island (the chosen pilot study site); by 1993, after Itô's departure from Okinawa, it had been eradicated from all of Japan. The heroic history of the project and its technical advances are documented in numerous papers (e.g. Itô and Iwahashi 1974; Itô and Koyama 1982; Koyama et al. 2004) and books (e.g. Itô 1980; Itô and Kakinohana 1999). The mass-rearing factory built in the city of Naha artificially reared more than 250 million melon flies each week. However, one important practice learned from this achievement was that not only the number of insects released but also the quality of the insects (e.g. their ability to compete sexually) was extremely important to the success of SIT projects. Itô (1980, 2003) stressed that the basic biology and ecology of the pest need to be studied in depth because, for example, without knowing its mating behavior in the field we can not assess the males' ability to compete. The best known of Itô's words among Japanese researchers were "The most basic study is the most useful type of applied study;" these words likely reflect his own experience.

During his 6-year stay in Okinawa, Itô also studied the ecology of other insects. Examples included phase variation of the locust *Locusta migratoria* on the Daito Islands (e.g. Itô and Yamagishi 1976), the population dynamics of the sugarcane cicada *Mogannia minuta* (e.g. Itô and Nagamine 1981), and the ecosystem effects of eradication of the oriental fruit fly *Bactrocera dorsalis* (Itô and Iwahashi 1974). Even after leaving the island, Itô continued to collaborate with researchers in Okinawa and left numerous papers, such as those on the behavioral ecology of pest flies (e.g. Itô and Yamagishi 1989, Kuba and Itô 1993) and population estimation of the West Indian sweet potato weevil *Euscepes postfasciatus* (Kinjo et al. 1995), a current target of SIT. In the course of these projects Itô mentored many young researchers—mainly employees of the Okinawa prefectural government—with heartfelt enthusiasm. As a result, Okinawa has become a center for applied entomology and animal ecology in Japan.

Sociobiological studies in Nagoya, and establishment of the Itô school of thought

Itô sometimes stated that researchers needed to change what they study over their lifetimes. After he moved to Nagoya University in 1978, he put this idea into action by starting sociobiological studies of social wasps—a research area markedly different from his previous main area of expertise. He later confessed (Itô 2003) that this was driven by his irresistible, growing interest in the evolutionary biology of animal social behavior—an interest that he had felt since writing *Comparative Ecology* (Itô 1959). In this new theme, he conducted extensive empirical investigations of wasps by using his own eyes—an approach opposite to that of *Comparative Ecology*, which was a thorough bibliographical review of literature. He initiated this project in Japanese polistine wasps, focusing mainly on *Ropalidia fasciata* in Okinawa. Eventually he extended his scope to include the Polistinae of Panama, Brazil and Australia—world centers of biodiversity of these insects. His scientific adventure produced numerous papers and finally resulted in the monograph titled "Behavior and social evolution of wasps: the communal aggregation hypothesis" (Itô 1993) and an additional book written in Japanese (Itô 1996). The take-home message of these books was that "parasocial" mutualistic association of multiple females plays a key role in the initial stage of eusocial evolution in wasps. This idea was in line with those discussed in social bees (Lin and Michener 1972) and wasps (West-Eberhard 1978). Although the findings of a recent comparative study using molecular phylogeny do not support this idea (Hughes et al. 2008), it is also true that a recent study using high-resolution DNA markers has revealed the importance of mutualism—social behavior to enhance individual direct fitness but not indirect fitness—in pleometrotic colony founding in a *Polistes* wasp (Leadbeater et al. 2011). The potential lesson from those studies is that mutualism and kin selection often operate simultaneously when hymenopteran females cooperate, but that lineages have to experience the monogamic state to evolve a sterile caste.

Surprisingly, almost all of Itô's field studies of wasps were done after he reached the age of 50. This incredible continuing enthusiasm may have come from his philosophy of empiricism: as he said in his autobiography (Itô 2003), "theories are destined to give way to the new, but facts remain." [Itô in fact wrote two autobiographies (Itô 1975, 2003); they are important to the history of science in Japan and await English translation]. As an extension of his sociobiological studies in Nagoya, Itô (1989) wrote a review of aphid soldiers. This well-cited article was the first review of these enigmatic insects to have been written in English. Itô's textbooks published in the early 1980s (e.g. Itô 1982) encouraged many young Japanese to study wasps and the behavioral ecology of other animals during this period. Furthermore, between 1980 and 1990, multiple international conferences in ecology and evolutionary biology were held in Japan. Itô always played a host organizer role, as recorded in conference proceedings (e.g. Itô et al. 1987), and he invited many leading scientists from around the world (mainly in the field of evolutionary ecology), including T. H. Clutton-Brock, R. H. Crozier, R. H. Gadagkar, D. T. Gwynne, W. D. Hamilton, P. Jaisson, J. Kikkawa, J. R. Krebs, R. Lande, R. U. Maschwitz, M. May, G. H. Orians, N. Pierce, R. Thornhill, M. J. Wade, M. J. West-Eberhard, and E.O. Wilson. Undoubtedly these opportunities gave Japanese animal ecologists the chance to share information internationally to an unprecedented extent. Not surprisingly, Itô's laboratory at Nagoya University became a center of information transmission in that era. Not only the first author of this obituary, but also many ex-students and ex-staff of Itô's laboratory at Nagoya University, including Fusao Nakasuji, Yoshikata Tsubaki, Eiiti Kasuya, Kiyoshi Nakamuta, Koichi Tanaka, Hironori Yasuda, Koji Tsuchida, Ken-ichiro Honda, Yoshinari Tanaka, Hideki Ueno (now deceased), Takatoshi Ueno, Tamito Sakurai, Michael T. Siva-Jothy, Bruno Corbara, and Christian Peeters, are now established global authorities in the fields of ecology and entomology. Moreover, in addition to the abovementioned people, a substantial portion of the current generation of Japanese ecologists who were not directly supervised by Itô but were influenced by his writings and behavior profess to belong to his school of thought.

Enthusiastic writing of textbooks and monographs

Itô enthusiastically published many important textbooks for students and young researchers. *Comparative Ecology* (in Japanese; 1959) and *Comparative Ecology* (second edition) (in Japanese, Itô 1978; English edition 1980) are representative examples. The first edition was written and published during the period when Itô was suspended from work at MAFF, for reasons already mentioned. In the preface to the first edition, Itô proposed an integrated analysis of controversial issues in population ecology and sociobiology by using the comparative method. He cited Konrad Lorenz's principle of this method, focusing on "similarities and dissimilarities" among species in a related taxon, and he analyzed the evolutionary processes of different animals from a sociobiological perspective. He paid particular attention to the evolution of social structure and the analysis of parental care. In Chapter 1 of the first edition, he focused on two opposite directions of fecundity evolution, namely the production of many or few offspring. He advocated that the production of a small number of large progeny, with parental care, should be an adaptive strategy in the oligotrophic environment, where it should bring about social evolution. This idea originated with the British ornithologist David Lack (Lack 1954). However, Itô further expanded it and developed his own, original concept relating population dynamics to animal social behavior, as shown in Chapter 1 "Reproduction and death," Chapter 2 "Population dynamics," Chapter 3 "Territoriality," Chapter 4 "Dominance hierarchy," Chapter 5 "Insect society," Chapter 6 "Integration of animal societies and the path to human evolution," and Chapter 7 "Conclusion". The first (1959) edition of *Comparative Ecology* preceded the publication of a similar seminal work published in English, namely *Sociobiology: the New Synthesis* (Wilson 1975), by 16 years.

In the preface to the 2nd edition of *Comparative Ecology*, Itô pointed out two great changes in evolutionary ecology and sociobiology that had occurred since the appearance of the first edition. First, our understanding of the social structures of mammals, including primates, had been greatly expanded, and second, *The Theory of Island Biogeography* (MacArthur and Wilson 1967) had been published and E. R. Pianka had argued an adaptive life-history strategy, largely in his textbook *Evolutionary Ecology* (Pianka 1974, second edition Pianka 1978); this strategy was based on MacArthur and Wilson's *r*/*K*-selection theory. The concept of *K* selection predicts large body size, longevity with iteroparity, and fewer and larger progeny in a fairly constant or predictable (more certain) environment, and it has some features in common with Itô's theory. However, Itô's original contribution was to connect parental care of animals to social behaviors and social evolution, whereas *K*-selection theory cannot predict this connection. In Chapter 5, although Itô certainly agreed with the importance of Hamilton's (1964) kin-selection theory of the emergence of infertile castes, he also paid attention to the increase in colony size that kin-selection theory did not explain. He pointed out two ways to increase colony size: first, quasisocial connection among sisters, and second, mother–daughter association. He particularly emphasized the importance of mother–daughter association in increasing colony size. Therefore, he rarely cited or referred to the work of Hamilton (1964) in other chapters. This style is opposite to that of Wilson's (1975) *Sociobiology: the New Synthesis*, which was structured throughout on the basis of kin-selection theory. As Itô was a naturalist all his life, he would not have liked to have sided with Hamilton (1964) and the theory-oriented stream of the late 1970s, when the evolutionary conditions for altruistic behavior, $rb > c$, had not yet been quantitatively tested. The first edition of *Comparative Ecology* (1959) would have been highly acclaimed all over the world had it been translated into English.

Itô was prolific in his writing of many other textbooks. Some examples are *What Governs the Population Abundance of Animals?* (in Japanese; Itô and Kiritani 1971); *Animal Ecology* (Itô 1975, 1976; in Japanese); *Research Methods in Animal Ecology* (in Japanese; Itô and Murai 1977); *An Introduction to Socioecology: Reproductive Strategy and Social Behaviors* (in Japanese; Itô 1982); supervision of the Japanese translation of Wilson's 1975 work *Sociobiology: the New Synthesis* (Itô 1983–1985); *Survival Strategy in Animals* (in Japanese; Itô et al. 1990); and *Animal Ecology* (in Japanese; Itô et al. 1992; 2nd edition, Shimada et al. 2005). The two editions of *Animal Ecology* (1992 and 2005) were published to provide graduate students and young researchers with a continuing, high-level integrated body of knowledge on ecology. Itô enthusiastically encouraged and prompted his co-authors to edit and finish the first edition. Thanks to his active supervision, the two editions of *Animal Ecology* have sold in total about 8000 copies and have made a strong contribution to higher education in ecology in Japan.

Back to Okinawa, and life in retirement

After retiring from Nagoya University in 1993, Itô moved back to Okinawa. His academic mission in his new position, Professor of Okinawa University, was to teach general biology to undergraduate students from non-natural-science departments such as law and economics. As well as continuing with his wasp study, he started a new project on

conservation ecology. His main concern was the threatened biodiversity of the Ryukyus—especially in the Yanbaru forest in the north of Okinawa's main island. He stressed how this fascinating landscape, with its high levels of island endemism, is endangered by human activities (e.g. Itô and Aoki 1999, Itô et al. 2000).

After retiring from Okinawa University in 1998, Itô spent the rest of life at his home in Nisshin, a suburb of Nagoya. He continued studying and writing until he died. His last book (Itô 2009) was on a fritillary butterfly that is considered to be an indicator of global warming, as its distribution has recently been expanding to the north. He delivered his last conference lecture on 27 March 2014 at the annual meeting of Applied Entomology and Zoology Japan, held in Kochi. He seemed very happy with his eventful life of dedication to science, thought, and human society. We will never forget him for his enthusiasm.

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