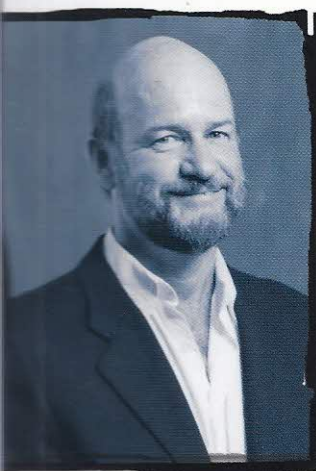


# Leaders in **Animal Behavior**

The Second Generation



**Edited by**

Lee Drickamer and  
Donald Dewsbury

CAMBRIDGE

## Living with birds and conservation

AMOTZ ZAHAVI



### Begininmgs

I don't remember myself without birds. My mother used to say that I was watching them before I could even walk or talk. I was born August 14 1928, in Petach-Tiqva, then a small town near Tel-Aviv, Israel, then Palestine, under the British mandate. Petach-Tiqva was the first Jewish village built in Israel by Jews in the nineteenth century, and my grandfather was among the early settlers there. When I was growing up there were many open fields and orchards among the houses, and I used to set out in the early mornings to watch birds before going to school. I did not know anybody who knew birds other than the most common ones, and there were no illustrated guidebooks available to me to help in their identification. I enjoyed the birds, found their nests and knew their songs, so I had my own names for them.

At the age of 12, in 1940, I met Dr Heinrich Mendelssohn. He was the director of a small zoo at the Biological-Pedagogical Institute in Tel Aviv. From then on, I could identify birds and learn their proper names at the collection of stuffed birds that was exhibited at the zoo.



and there was someone who was interested in my observations. I had the privilege of accompanying Mendelssohn in the field and I attended many of his talks.

My only sib sister died of pneumonia at the age of 15, in 1941, a few months before the sulfa drugs that could have saved her life were first available. Following her death my family left Petach-Tiqva. I studied at the Pardess Hana Agricultural Secondary School.

In 1941 the German army was advancing in North Africa towards the Middle East. The British were preparing to move their army to India. The Jewish community in Israel was facing the danger of extermination. Plans were made to make the Carmel mountain range into a stronghold and fight to the end. I remember how we, the high-school students, participated in these preparations. Soon, however, the British defeated the Nazis in the battle of El Alamein and we were saved.

I was a boy scout. At that time our goal was to establish new farming settlements. I planned to be a member of a kibbutz (a communal settlement) and a farmer. The school taught agriculture and science along with practical work. We worked on the farm two days a week in the first three years, and up to three days a week during the last two years. I got special permission to use these days to watch birds in the spring in exchange for working for a whole month during the summer vacations.

Mendelssohn persuaded me, in 1947, to study biology rather than agriculture at the Hebrew University of Jerusalem. His argument was that I could be a farmer without a university diploma, but that it would be more difficult to go into biology if I studied agriculture. He also argued that, since at that time there were hardly any other young ornithologists in Israel, being a professional ornithologist would be a greater service than adding one more farmer to the many who were already there.

1947/8 was to be my first year at the university, but within a month the War of Independence interrupted my studies for a year. I was not involved in actual fighting (I was exempt because the recent death of my sister left me as an only child). Instead, I drilled young people at the besieged city of Jerusalem. Later I was the commander of a company that was stationed in several kibbutzim in the Jordan valley, near the Sea of Galilee.

In 1949, after my military service, I attended some geology courses besides biology. One of the lecturers, Professor Ben-Tor, was conducting a geological survey of the Israeli Negev, a desert that extends over more than half of the country. Before 1948, the British authorities of Palestine did not allow Jews to travel freely in that part of the country. My knowledge of life in the desert was therefore very restricted. Ben-Tor needed helpers to carry stones and guns, cook, and guard at night. I was among the few students who felt themselves lucky to accompany the survey. During 1949–54 we spent a few hundred days in the field. I missed many lectures and much lab work, but I learned much about the desert and got to know its geology, its flora and its fauna (mainly the vertebrates). The biologists among the student-carriers included Eviatar Nevo, now a famous evolutionary biologist at Haifa University, and the late Amiram Shkolnik, who became a professor of Eco-physiology at Tel-Aviv University; we collected plants, trapped rodents and watched the birds. It was at that time that I fell in love with the open desert.



Figure 21.1. With friends in the Hula swamp 1952.

In Jerusalem I studied with Yaakov Wahrman the chromosomes of gerbils and spiny mice that we collected in the desert (Zahavi & Wahrman 1957). The study revised the systematic relationship of several of the rodents, and found polymorphism in the number of chromosomes of certain populations of one of these species, *Gerbillus pyramidum* (Wahrman & Zahavi 1958). It was good evidence for an active speciation process going on in the coastal dunes of the eastern Mediterranean.

I did not plan to be a professional ornithologist. My idea of ornithology, at that time, consisted of identifying birds, finding nests, and surveying bird populations. Hence, at the end of 1952, I started a project in biochemistry for my master's degree under Professor Reich (there was no B.Sc. degree at the Hebrew university at that time). I was planning to watch birds in my spare time. But in February the birds began to sing, and I could not resist the temptation to go out to the field. I excused myself to Professor Reich and took up a study of the birds of the Huleh swamp as my thesis, with Mendelsohn as my adviser (Zahavi 1957) (Figure 21.1). I was sure that by making this decision I was giving up all intellectual challenges, but it was a daily occupation that provided much enjoyment. Tinbergen's book *The Study of Instinct* (Tinbergen 1951) influenced my decision to learn more about the scientific study of animal behaviour. I applied to work with Niko Tinbergen for a year. A recommendation by Col. R. Meinertzhagen, whom I accompanied for a few days in the Israeli desert, helped me receive a scholarship from the British Council, and Tinbergen agreed to accept me into his group.

In spring 1954 I married Avishag Kadman, a fellow student majoring in botany, whom I courted in the Huleh swamp. Our first daughter, Naama, was born before I left for Oxford.



### Tinbergen and Oxford

This was my first visit abroad. In Israel people were dressing very informally. My parents insisted that in Europe I should present myself as a respectable person, so they fitted me with a suit and tie. When Professor Tinbergen invited me to dinner at his home, I put on the suit and struggled with the tie, only to find Niko in his shorts, inviting me to join him in peeling potatoes. I remembered that moment when, ten years later, Rami, my future technician, appeared dressed up in suit and tie for his work-interview with me.

I spent January – March 1955 with Tinbergen's group at Oxford. I attended seminars with, among others, Desmond Morris and Mike and Esthy Cullen, and became acquainted with the jargon and the way of thinking of ethologists. I visited Cambridge and met with Robert Hinde and Peter Marler. In the spring I accompanied Uli and Rita Weidman to study the black-headed gull colony at Ravenglass, and spent most of the breeding season there. I performed an experiment of my own, putting additional nests near the original ones in the territory. When I placed a partition between the two nests, both members of the pair incubated simultaneously for long periods. I concluded that they were competing over incubation, and suggested that the extra urge to incubate was a mechanism that ensured that the nest would be incubated constantly. Like all ethologists at that time, I used group-selection arguments when there was no obvious way to suggest how a certain behaviour benefited the individual directly. Years later, with the understanding of the Handicap Principle, I reinterpreted the behavior of the gulls to suggest that prolonged incubation was used by each bird as means to increase its prestige vis-à-vis its partner.

Later that year I had the privilege of attending the third meeting of the European ethologists, at Groningen (the ethologists tried to keep their conferences small and intimate by restricting attendance). At the conference I became acquainted with Konrad Lorenz, as well as the Barrends and other Dutch ethologists. I fledged from all these meetings as an ethologist.

My stay in Europe was interrupted in August 1955 by the death of my mother.

I did not have the time to write down my observations on the black-headed gulls: back in Israel I was committed to work for conservation.

### My involvement with conservation

In 1948, when Israel became an independent state, the Jewish population numbered only 600,000. By 1951, immigration had increased the population to two million. The newly formed state of Israel was concerned with settling new immigrants and with defense. Conservation was the last thing on the mind of the authorities. The Botanical and Zoological Societies formed a joint committee to do something about conservation, mainly by advising the government. Mendelssohn, my mentor, was the very active chairman of that committee.

In 1950 the government of Israel decided to reclaim and drain the Huleh Swamp and lake. I was anxious to study the bird life of the area before it vanished. Once more I asked my

teachers at the university to excuse my absence from formal lectures and laboratories, and spent many days observing the birds, observations that turned into my M.Sc. thesis in 1954. One day, I believe in 1952, Mendelssohn asked me to accompany a committee of the national planning department that came to study the feasibility of creating a small nature reserve in the area. I guided them in the swamp and lake in a boat, and realized how little they knew of the area. Together with several senior scientists (all of them my teachers), I attended the final meeting of the governmental committee that was to decide the size of the future nature reserve. Comments of members of the committee and its chairman made me realize that they were not impressed by the scientific arguments. I stood up and described the nest of the white-tailed eagle that I had found earlier that year in the area, the impressive size of the nest, the large and beautiful bird flying down daily to fish in the lake. I insisted that it needed at least 1000 acres of lake and swamp for its survival; otherwise that majestic bird would disappear from the region. Obviously this was not a fully researched scientific argument. A few weeks later I met the chairman of the committee on the street. "Come here, my boy", he called to me (he was over seventy years old); "because of you we decided to allocate 1000 acres to the nature reserve." Suddenly I realized that I could influence decisions of where a proposed nature reserve would be and what its size would be, and could save some of the area and its birds.

In 1952 my friend Azaria Alon, a biology teacher at kibbutz Beith Hashita, another of Mendelssohn's students, suggested that we form a non-governmental organization (NGO) that would act rather than just advise. We suggested that the committee for conservation should itself become that NGO: they agreed, and the Society for the Protection of Nature in Israel (SPNI) was created. Azaria and I were the only young members of the board. All the others were professors or middle-aged biology teachers. Azaria was busy teaching at Beith Hashita. Hence, I happened to be the only person free to handle the office work of the new NGO. I used to walk around with a book of receipts, asking my friends whether they happened to have on them two pounds. When they gave me the money, believing that I needed some personal help, I would give them the receipt and thank them for joining the SPNI. Most of the early members were biology teachers who were personally connected with Mendelssohn in one way or another. Other members of the SPNI were mostly kibbutz members interested in natural history. Soon after, when I went to Oxford, Avraham Toren (Bumi), another biology teacher from kibbutz Maabarot, took over the responsibility of being the secretary of the SPNI. However, as there was no money, he had to teach most of the time, in order to earn his salary.

When I returned from Oxford in August 1955, the SPNI was in a difficult state. There was no money, and membership was not increasing. Something had to be done. Although I had the opportunity to start my Ph.D. studies as an assistant at the department of zoology at the Hebrew University (the only university in Israel at that time), I decided to serve for a few years as a full-time secretary of the SPNI, trying to establish it firmly. My plan was to return to the world of academia after three years, but these stretched to be 14 years.

Tel-Aviv University was created at around that time, by the merger of several independent semi-academic institutions. The Biological Pedagogical Institute, with Mendelssohn as its



head, became the biology faculty of the new university. I suggested to Mendelssohn that he should incorporate my activities in conservation with those of the faculty. He had the courage to put me on the payroll of the department of zoology, as a demonstrator, although he knew that I spent most of my time organizing the SPNI. He also helped the SPNI by providing office space and office services within the department. I am sure that without his support, the fledgling SPNI would not have survived.

The limited funds of the SPNI were spent on employing wardens in several key areas of special importance for conservation. The SPNI also organized public events, lectures, and yearly conventions with guided tours for its members and the general public. The events provided some net income and were therefore extended to become weekly tours guided by the local wardens of the SPNI. The income from these events became a major source of funding. It was the immediate need for funds, rather than the long-term benefits of education, that started the SPNI's education system. We soon realized, though, that our work as guides and our educational efforts actually created a public that backed our endeavors for conservation.

Independently of the SPNI, Yosi Feldman was appointed as the director of a youth hostel in Ein Gedi (an oasis on the shores of the Dead Sea), where he attempted to create a Field School to guide tours of youngsters in the back country of the Israeli desert. The SPNI already had a warden at Ein Gedi, so the SPNI joined Yosi Feldman and together created the first Field Study Center (Field School). The staff consisted of several guides and volunteers, plus a technical staff of 2–3 persons. The staff provided services to the tourists that visited Ein-Gedi and kept the area clean. The ministry of education agreed to let the SPNI provide guides for school outings. This agreement provided financial support for the system of field study centers and facilitated direct contact with a large population of school children. It did not take long to enlarge the staff of the SPNI in other regions from single wardens to small groups, creating additional Field Study Centers that ran tour services to schools. The ministry of housing joined in to help and built hostels and classrooms for the centers.

Our second daughter Tirtza was born in May 1957. Avishag took care of the family besides her own research in plant physiology, and I was busy with the SPNI. In the 1960s the girls were already old enough to travel with us. We often traveled together to the various Field Study Centers. Our daughters enjoyed these travels, sitting together with our dog at the back of our old station-wagon.

In the early 1960s the SPNI played a central role in passing a bill of conservation in the Israeli Knesset (the parliament). We managed to convince the Knesset to establish two separate authorities, one for the national parks (mainly archeological and historical sites for tourism) and another for nature conservation. We said that the creation and sustaining of national parks inherently involves development and change, whereas conservation should strive to leave nature undisturbed as much as possible. We did not realize at the time that the urge to develop is inherent in any authority, no matter what its stated goal is.

I myself served for thirty years on the board of the National Parks authority, trying to take care of nature conservation within the national parks.

Once the governmental authority was established, a retired general, Avraham Yofe, was appointed as its chairman, and Uzi Paz, a former warden of the SPNI, as its director. Most of the burden of fighting for the creation of nature reserves and their management was no longer upon the SPNI. The Nature Reserve Authority increased the number and area of the nature reserves and, together with the SPNI, did a great deal to preserve the wild flowers and wildlife around the country.

The SPNI focused on enlarging the field study center system and its educational activities. It still retained a conservation department, lest the politicians, ruling over the governmental agencies, force the conservation authorities to agree with policies that conflict with conservation. There were several cases in which the SPNI indeed intervened in order to change governmental policies, something that a governmental authority cannot do. One of these cases was the conservation of the spring of the river Dan at Tel-El Kadi, one of the sources of the Jordan River. The authorities decided to capture the water of the spring at the source. The nature reserve authority decided not to fight against this decision. I also thought that there was no chance to win the fight, because of the high economic value of the project. However, our local warden, Yossi Lev-Ari, decided to fight for the spring, and I agreed to provide the support of the SPNI. He succeeded in convincing the local villagers, the ones who were to benefit from the project, to abandon the plan. The spring is still there, within a nature reserve, and a great many people enjoy its beauty every year. This fight convinced me that it was time to let younger people take the lead in fighting for conservation.

Around 1970 my relations with the Nature Reserve Authority (NRA) and General Yoffe became strained over the transfer of an overpopulation of gazelles from the lower Galilee, where they were becoming pests due to strict enforcement of the hunting law and the lack of predators, to the Golan Heights. Together with other Israeli scientists, I objected to the transfer, because the Golan had its own local population of gazelles, and we were afraid that mixing the populations would result in the loss of local adaptations. However, the NRA did not heed our objections. General Yoffe assured me that he could always find a scientist who would endorse his policy.

### *The Institute for Nature Conservation Research*

Now that the NRA had taken over the responsibility for the management of reserves and the SPNI focused on education, there was an obvious need for a scientific foundation for conservation. It seemed reasonable to me that its place should be at a university. Once more, Mendelssohn provided the solution: at that time he was the Dean of Science at Tel-Aviv University, and he agreed to form the Institute for Nature Conservation Research in 1965. I became its head, until 1982. Unfortunately, the institute did not have the hoped-for impact on nature conservation policy. The governmental authority did not like outside advice, and hired its own scientists. So did the SPNI after I left. The Institute did have some impact on the conservation of freshwater habitats (due to the work of Dr Avital Gazit), the monitoring of pesticides in the environment (Professor Al Perry), on landscape surveys (conducted by Dr Zeev Meshel) and on the development of biological control of pests (Dr Baruch Sneh).



When I started my babbler research at Hazeva, the farmers, trying to save their crops, were killing and poisoning everything. They did not know which species of birds or mammals were doing the damage. Some of the habituated babbler groups were poisoned. I recruited Zohar Zuk-Rimon, my assistant from the institute, to monitor and take care of the individual birds and mammals that caused damage to the fields. Over a few years he shot and trapped some porcupines, hares, crested larks and bulbuls that were doing damage, but the rest of the wildlife survived. After that the local municipality and the Nature Reserve Authority took upon themselves the job of controlling pests in the region, and the farmers stopped the widespread use of poisons against birds and mammals.

The Institute for Nature Conservation Research was disbanded in 2005 when the School for Environmental Sciences was established at Tel-Aviv University. The president of the university and the donors were more interested in the study of the physical environment: pollution, energy, planning and environmental laws. As a retired professor, I failed to convince the university authorities of the importance of research for the conservation of the fauna and flora and the natural environment.

At the end of 1969 Azaria Alon replaced me as the general secretary of the SPNI. By that time the SPNI had around 10,000 members and five field study centers. Some conservation research was going on at the centers and provided stimulation and relief for the guides. The society encouraged and helped its guides to study and obtain university degrees.

In 1980 the SPNI and its three former secretaries – myself, Azaria Alon and Yoav Sagi – received the Israel Prize (the highest governmental prize in Israel) in appreciation for the services the SPNI and its directors provided to the state of Israel.

### Back to science

Running the SPNI was a very tiring job. It was time to go back to research. In the late 1960s most of my colleagues in the academy were already professors, heads of departments or scientific institutes. However, I was prepared to start from the bottom. During my last few years as the secretary of the SPNI I was already doing research for my Ph.D., on the wintering behaviour of the white wagtail, watching the birds in the mornings before going to the office (Zahavi 1971a). Together with my assistant, Rami Dudai, I caught and colour-ringed a large number of wagtails. Many of them were found on municipal garbage dumps near Tel Aviv. We used to visit these dumps early in the mornings to follow the birds and do some experiments. I got to know a man who was scavenging the garbage, collecting items for his living. One day he asked me what I was doing there. When I told him that I was catching birds for the university, he nodded his head in sympathy, wondering about the strange jobs people were willing to undertake to make a living.

I found that the wintering wagtails could be found in three different social organizations: some males held permanent territories, and many of the ones that did so accepted a female into the territory, whereas the rest of the population wandered in flocks. I found that I could experimentally change the behavior of the wagtails from flocking to territorial, and vice versa, by changing the distribution of food from an even distribution, where the birds fed in

flocks, to distinct piles, around which certain individuals formed boundaries and defended territories. Females often paired with the owner of such a territory. Such pairs could be quite stable over several weeks. Although the pair-forming displays at the wintering territory were similar to those of sexual pairing, it had nothing to do with reproduction, but rather allowed the females to obtain access to food that was otherwise only available to the dominant males. The males gained by having a subordinate helper to defend the territory. Both territorial and flocking birds met at night in communal roosts. I suggested that in this way a territorial bird that lost its feeding territory might follow a flock to a good feeding ground, as suggested by Ward for *Quelea* (Ward 1965).

I returned to Oxford in 1970, this time to the Edward Grey Institute. David Lack, the head of the Institute, kindly accepted me as a visiting scientist. Our family lived in Reading, where Avishag was able to pursue her plant physiology research with Dr Daphne Vince-Prue, and I traveled daily to Oxford.

I spent much time at the excellent library of the Institute, writing my Ph.D. dissertation as well as a paper on the function of pre-roost gathering and night-roosts as information centers (Zahavi 1971b). I became interested in the general question of the relationship between a bird's ecology and its social adaptations, and was introduced to the studies of Ian Newton and the long-term tit study at Wytham Wood, supervised by Chris Perrins.

When I returned to Oxford in 1970 I was completely unaware of the big controversy between Wynne-Edwards and Lack and Maynard Smith, about group selection versus individual selection and the then new theory of kin selection. When I worked for conservation I had little time for reading. I kept some personal connection with Tinbergen's group, but it seemed that the ethologists were not involved in that controversy. The year with Lack convinced me that individual selection was the only stable selection mechanism.

At the ornithological congress in the Hague (September 1970) I met Peter Ward, a meeting that resulted in my travelling with him to East Africa and a paper we wrote together on the gatherings of birds as information centers (Ward & Zahavi 1973). That paper was well received, and was later supported by field experiments (Parker-Rabenold 1987; Heinrich, 1988).

In spite of my conviction that behavioural phenomena should be interpreted only according to individual selection, I made the mistake of interpreting the communal displays of the pre-roost gatherings as a means to increase the size of the roost and the amount of information contained in it. This is a classical case of an argument of group selection that does not explain why an individual bird spends energy and time on participating in the group's display. It is easy to fall into the trap of explaining adaptations by their contribution to the group.

Ten years after the paper was published I received a letter from *Current Contents* addressed to Peter Ward, who had passed away a few years earlier, informing us that "This paper has been cited in over 125 publications over the last ten years, making it the 3rd most cited paper ever published in this journal." I was asked to comment on developments in the field in the intervening years. I used the opportunity to correct my mistake: I suggested that participating in the communal displays enables each individual to assess and compare itself to its



neighbours and to attach itself the following day to a subgroup of ability comparable to its own, with which it can match (Zahavi 1982, 1983, 1996; Zahavi & Zahavi 1997).

At Reading I cooperated with Don Broom and some other bird ringers; we ringed wagtails at the sewage farm, and learned that British wagtails also form winter pairs on their winter territories and spend the nights in communal roosts, with all the other wagtails. My family was greatly disappointed. They often helped me watch the wagtails on the rubbish dumps in Israel; when we visited abroad, our hosts often took us first to the sewage farms and rubbish dumps, where many birds could be found. Before going to Britain we told our girls that we would spend most of our free time in forests and parks. However, on our first day at Reading, we already followed the British wagtails, which were leaving the beautiful park to roost at the sewage farm.

My stay in Europe was interrupted this time by the sudden death of my father. I became an orphan at the age of 42.

When I returned to Israel I was offered the position of a senior lecturer at the Department of Zoology of Tel-Aviv University. I think I owe this also to Mendelsohn.

### **The start of the babbler study**

My interest in the babblers had already started at Oxford. The study of the wagtails clarified for me that ecological conditions can shape the social organization of organisms: why birds flock, keep territories or pair to defend the territory. In the library of the EGI I read the papers of Skutch on helpers at the nest (Skutch 1935) and others. These papers drew my attention to group-territorial birds and the problem of helping at the nest. I knew that in Israel babblers have helpers, and decided to try to understand that system.

With the help of the late Rami Dudai, my excellent technical assistant, who worked with me in my wagtail study, we ringed a population of some 20 groups of babblers around the Hazeva field study center. Observing the babblers became more and more difficult, however. They became wary of us because we approached their nests and caught members of their group. They considered us to be super-predators, to such an extent that we could watch them only briefly from great distances with telescopes, or from hides. I was desperate and about to quit, when I was lucky enough to visit Glen Woolfenden and his tame scrub jays in Florida in 1973. Glen invited me to come and watch his birds. He carried his binoculars and a pocket full of peanuts. I wondered whether he had left his telescopes in the hides in the field. Once outside the station he whistled, and several jays came flying, one landing on his hand. He told me that jays in the neighborhood were used to people feeding them peanuts, and he managed easily to tame the population he was studying. I hoped that the babblers would be as smart as the jays, and would learn that human presence could be beneficial. We started to provide the babblers with tidbits of bread whenever we met them. It took the whole of 1974 to tame the population. My daughter Tirtza was the first person to hand-feed a free-living babbler, by the name of LZTM. By the end of the year we could stand among babblers without interfering with their behaviour, sit next to a nest without a hide, and watch their intimate copulations, which they do away from the group. We have continued to follow the



Figure 21.2. Introducing our grandchildren Oren and Kinneret Ely to the Babblers, 1998.



Figure 21.3. Babblers play like puppies.

same population ever since (Figure 21.2). In the last few years we tamed a few desert larks, bulbuls, shrikes and blackstarts. One can observe so many details of behaviour from watching a tame wild bird in its natural surroundings. We use these birds as objects for teaching students and as a means to encourage eco-tourism (Figure 21.3).

Throughout the years we were lucky enough to have with us at Hazeva a large number of volunteers and students, many of them from abroad: Kenya, Japan, New Zealand, Australia,



the USA, Canada, Britain, Germany and others – so many indeed that it is not possible to name them all here.

### The Handicap Principle

The course I taught at the University was called “Socio-Ecology”. I did not know at the time that I was a sociobiologist; Wilson’s book had not been published yet. In 1972, when I was trying to explain Fisher’s model about the evolution of the peacock’s tail to my students, Yoav Sagi raised doubts about the validity of Fisher’s model. He wondered why the females that, according to Fisher, started the process by choosing males with the longest tail because tail length was correlated with quality, should continue to choose the males by the length of their tails once, according to Fisher, the extra length of the tails reduced the quality of the males, and the correlation between tail-length and quality was lost. It took me several months to come up with the idea of the Handicap Principle (I started to use this term only in September 1973). I suggested that the burden imposed by signals of mate choice serves to test and advertise the quality of the males. Only high-quality males can carry a cumbersome tail. Therefore, females that select males with the most elaborate and cumbersome characters can be sure that they select from among the best male phenotypes available to them. I suggested that these burdens are similar to “handicaps” used in sports, where a more experienced player is disadvantaged in order to make it possible for a less experienced player to participate in the game. For example, a handicap in a horse-race means varying amounts of weight that are added to the saddles of the highest-rated horses. Winning with a handicap confers higher status on the winner. My family accepted the theory wholeheartedly without any reservations. Naama later made use of it in her human history seminars. Not so with my colleagues. Some of the problems might have been semantic: when I picked the term “the Handicap Principle” I was not aware that the term “handicapped” had become the politically correct synonym for “invalid”. In his book *The Selfish Gene* Dawkins recalls asking me whether a male should cut off a hand or a leg in order to be attractive. An American researcher was sure that the term handicap meant only “invalid” or “disabled,” and, when I tried to explain why I used the term handicap, she was offended and asked me whether I was trying to teach her English.

The following account of my attempt to introduce the Handicap Principle to my colleagues abroad is based on my letters home from that period.

In January 1973 I visited Oxford again. I discussed the idea of the Handicap Principle with Tinbergen, Ian Newton, Mike Cullen, and others. They were interested, but not convinced. As for myself, I realized that the Handicap Principle was not restricted to sexually selected signals, but explained the evolution of other signaling systems as well. It explained why the Egyptians built the Pyramids, and the purpose of the mysterious big statues of Easter Island. Many phenomena that were earlier explained by kin selection could be better explained by the Handicap Principle, which thus made kin selection redundant. I realized that I had to write a book in order to disseminate these ideas. It took us more than twenty years to write that book.

Unlike the papers on information centers, the idea of the Handicap Principle raised much opposition. During August and September 1973 I had the opportunity to discuss the Handicap Principle with many colleagues. I discussed it with Maynard Smith and Robert Selander at the International Congress of Systematic and Evolutionary Biology in Boulder, Colorado. Maynard Smith was interested but not convinced. He promised, however, to consider my paper for publication once I had written it. Selander was more agreeable. We had lengthy discussions, which continued later when I visited him in Austin, Texas. There I used the term “Handicap Principle” for the first time, in my letter home. On that same visit to the USA I presented my ideas at the Ethological congress in Washington, D.C. People were interested, but, as usual, not convinced. I think that the problem was that the idea was too basic and too simple to be “scientific”. It was received as “legitimate” only years later, when Allen Grafen made formal models of the Handicap Principle (Grafen 1990a,b). Interestingly, I found later that economists, anthropologists, and members of other disciplines that deal with humans did not have any problem in accepting the Handicap Principle. At the Smithsonian Museum in Washington I was especially impressed by the handicap represented by the huge stone slabs that were used as money in the Yap Islands in the Pacific.

During that summer I collected information about a number of studies of different cooperative breeders. Following the conference we, a group of Israeli ethologists including Mendelssohn, traveled to Costa Rica, where I spent several days with Sandy Vehrencamp in her study area and observed the anis. From Jack Bradbury I learned about social bats, and was impressed by studies of the polyandric jacanas. From there we went to Barro Colorado Island, Panama, where I learned from Yael Lubin about the social spiders. I also visited Glen Woolfenden in Florida and his tame jays.

In Austin I had lengthy conversations with Selander. We discussed how the ecological conditions shape the social and breeding organization of different organisms, including the social insects, suggesting that breeding systems should be interpreted as production lines. In particular we discussed how the ecology can explain why one sex rather than the other is dominant. ( Chapter 14 in Zahavi & Zahavi 1997). Selander tried to get me interested in some papers with formal models – but I found that, although the mathematics might be quite elaborate, the biological assumptions that were at the base of the models were usually too simplified, and often completely wrong. I still cannot understand why formal models are considered superior to a verbal logical analysis in the discussion of the evolution of social interactions. Social interactions are too complex for formal mathematical models. However, the logic of the evolution of social interactions can be discussed and resolved verbally. In Austin I also realized that the Handicap Principle can explain altruism: altruism could be interpreted as a signal that displays the social status of the altruist, and the investment in the altruistic act could be interpreted as the “handicap” that attests to the honesty of that signal (Zahavi 1977a). Altruism was thus explained by individual selection. I also became aware of the weakness in models of kin selection and reciprocity, a weakness shared by all models of indirect selection: all of them are vulnerable to social parasites, which can destroy any system based on indirect selection (Zahavi 2003).



Robert Trivers told me that when I visited him at Harvard later that month, he was tempted to throw me out of the room because of that heresy – but remembered in time that Selander, in a telephone call, told him that he should try and listen to me, because although I was not using the conventional terminology, I was saying something important. At Harvard I spent most of my time trying to convince Trivers, to no avail. I also met with E. Mayr, E. O. Wilson and others. I returned home on the eve of Yom-Kippur, 1973. The next morning the war broke out.

### *The Yom-Kippur war*

In October 1973 Israel was attacked by Egypt and Syria. During the war I volunteered to serve as an ambulance driver. Our regiment was used as a reserve and we were not involved in fighting. I had ample time to read Darwin's book on sexual selection. During the long dark evenings in the desert I was listening to the jokes and chatter of the young soldiers and realized that, although I knew the lexical meaning of all the words, I was often at a loss to understand the jokes, the meaning of sentences and other subtleties of their conversations. There was a gap of only 20 years between us, and there were already so many changes in the use of idioms.

In the summer of 1974 I visited Britain again, on my way to the 16th International Ornithological congress at Canberra, Australia. I often stayed with friends and colleagues, learning about their research and discussing new ideas. I apologize for not being able to thank each of them individually here.

In Oxford I gave a seminar arguing against the idea of kin selection and tried to explain the logic of the Handicap Principle. Several years later I had a lengthy discussion with Allen Grafen. It took ten more years and two more lectures to convince him, and subsequently the sociobiology community, about the validity and importance of the Handicap Principle.

On my way back from Australia I visited John Maynard Smith at his home in Sussex. We discussed the idea of the Handicap Principle while walking in the open fields around the house. He admitted that the Handicap Principle was an attractive idea. However, he insisted that unless a formal model was made to test the idea, he was not convinced that it could work. My argument was that the logic of the handicap can be assessed with a verbal model. I am grateful to Maynard-Smith for accepting my paper in the *Journal of Theoretical Biology* (of which he was the editor) without a formal model. Moreover, his paper opposing the Handicap Principle (Maynard-Smith 1976) stimulated others to pay attention to my paper. I am much in debt to him for advertising the principle that otherwise might have been ignored, like some of my later papers dealing with basic problems in evolution such as "The Testing of the Bond" (Zahavi 1977c).

My paper "Mate Selection: a Selection for a Handicap" was finally published in 1975. Right away, I found myself debating the logic of the Handicap Principle with theoreticians (Davis & O'Donald 1976; Kirkpatrick 1986). Like Maynard Smith, they rejected the Handicap Principle using genetic models, even though I explicitly discussed its use in phenotypic interactions, especially after 1977 (Zahavi 1977a,b). The simple argument of the

Handicap Principle was considered by theoreticians to be “intuitive”, despite the fact that it was based on a sound logical argument. For some reason that I cannot understand, logical models expressed verbally are often rejected as being “intuitive” and only mathematical models are considered by theoreticians even when their basic assumptions are unrealistically simplistic.

However, there were exceptions. Hamilton and Zuk (1982) used the Handicap Principle to suggest that bright-coloured plumage can advertise health and the absence of parasite infections. Diamond (1990) used the Handicap Principle to explain why people drink alcohol and use drugs. When I asked him how it was that he used the Principle that everyone else rejected, he answered that it “simply made sense.”

In a talk at the Ethological Conference in Parma, Italy, in September 1975, I presented the Handicap Principle and pointed out that it can explain the evolution of altruism. Lorenz was greatly impressed. I think that he felt relieved, because he did not like the use of formal modeling that seemed to be taking over sociobiology.

At about that time I was greatly impressed by Schelling's book *The Strategy of Conflict* (Schelling 1960), especially with his suggestion that often conflicts are not just a matter of interaction between two parties: third parties are frequently involved as witnesses. I used his ideas to suggest that in addition to a signaler and a receiver, third parties are involved, and they play a role in shaping the pattern of some signals (Zahavi & Zahavi 1997). In my short paper “Why Shouting” (Zahavi 1978a) I suggested that the loud begging calls of fledglings of babblers are also directed to the attention of predators, in order to force their parents to take care of them.

In autumn 1976, when I visited Harvard again, I met with T. Schelling and his student, Michael Spence, who suggested an idea similar to the Handicap Principle, explaining the importance of the burden imposed on students to obtain university degrees as a test for their quality (Spence 1973). I found I could easily explain the Handicap Principle to them (both received the Nobel Prize several years later).

Hamilton was among the visitors to the babbler study area. I am not sure whether this visit convinced him of the validity of the Handicap Principle, but I certainly failed to draw his attention to the weakness of kin selection theory. Upon my suggestion, Hamilton kindly invited me in 1989 to present a series of talks in Oxford. I was hoping that by a series of consecutive talks I would be able to convert at least a few Oxfordians to the Handicap Principle. This time I succeeded. At the end of my second talk, Grafen declared that I was right, and that he believed he found a way to create a formal model of the Handicap Principle. Consequently he published two formal models (Grafen 1990a,b) and thus vindicated the Handicap Principle to people who insisted on mathematical models. In his papers Grafen also stated that the “main biological conclusions” of his models were “the same as those of Zahavi's original papers on the Handicap Principle” and that “the Handicap Principle is a strategic principle, properly elucidated by game theory, but actually simple enough that no formal elucidation is really required.” At last the Sociobiology community accepted it. Although many prefer the terms “costly signaling,” “honest advertisement” or similar synonyms rather than the term “Handicap,” the main idea that signals require



a special investment to ensure their reliability is now generally accepted. At a conference in August 1990, Maynard Smith strongly endorsed the Handicap Principle. Still, both Maynard Smith and Grafen, as well as many other sociobiologists, did not accept my opinion that all signals are loaded with handicaps (Maynard Smith & Harper 2003).

Many of my colleagues claim that I present new ideas because of an urge "to be different." In fact, the logic of the Handicap Principle, together with a very stubborn belief that selection works only directly on the individual, made it necessary for me to reconsider many of the interpretations of social behaviour presently accepted by sociobiologists. In the second edition of *The Selfish Gene* (p. 313), Dawkins remarks that if the Handicap Principle is correct "it might necessitate a radical change in our entire outlook". Unfortunately these implications of the Handicap Principle have not been discussed by the scientific community. Many of these interpretations are presented and discussed in our joint book *The Handicap Principle* (Zahavi & Zahavi 1997). Nearly every one of the 18 chapters of the book reconsiders some social phenomena in a new way. In a recent paper "Indirect Selection and Individual Selection in Sociobiology: My Personal Views on Theories of Social Behaviour" (Zahavi 2003), I comment that

being on the periphery has its benefits: if I were dependent on my colleagues for the advancement of my scientific career or my social status, I would not have been able to continue developing the Handicap Principle over the many years when it was nearly unanimously rejected. Luckily I was living in a distant corner of the world, and usually interacted with other sociobiologists only once a year, at conferences. At home, my social status and my scientific career were well secured because of my previous "altruistic" work in conservation.

### **Some implications of the Handicap Principle**

Although much of the following is described in our book and my papers, I believe it may interest readers to follow the lines of thought that led to the development of some of the implications of the Handicap Principle. My wife Avishag helped me define and describe ideas in better form in my book and in many papers, and often had a significant part in the shaping and the clarification of ideas.

#### ***The inflation of signals as a test for the Handicap Principle***

For many years I was troubled by a nagging question: how can I verify my hypothesis that in signals, investment is obligatory, rather than being a side effect as is the case with any other trait? In order to answer this question, I had to define the difference between the selection of signals and that of other traits. The distinction between the selection mechanism of signals and that of all other traits became clearer to me when my daughter Naama studied the history of the use of lace. Naama, by that time a student of history at the Hebrew University of Jerusalem, became interested in the use of lace for decorations in Europe in the sixteenth and seventeenth centuries. Lace was very expensive because of the large amount of skilled labor

that was needed to produce it. Its value was above that of its weight in gold, and as such it served to advertise people's wealth. Soon after lace-making machines were invented, the price of lace dropped drastically (Pond 1973). At first everyone used large amounts of lace – but very soon it went out of fashion, as it could no longer serve to distinguish the very rich from the moderately well-to-do.

I realized that Naama's description of the use of lace could be the solution to my problem. Signals can function to differentiate between signalers only when the investment in the signal is differential: easier to high-quality signalers and more difficult to low-quality signalers. If the investment is reduced to the extent that all individuals can signal alike, the signal can no longer function to highlight differences between signalers, and is selected out by a process similar to inflation in money – unlike non-signal traits, the benefit of which increases when the investment required to develop them is reduced. I therefore suggested that natural selection includes two selection mechanisms: a selection for efficiency, by which most traits are selected; and signal-selection, which encompasses the signaling components of Darwin's sexual selection, by which all signals are selected. The process of inflation can test and support the theory that signals are selected by a different mechanism from that of all other traits (Zahavi 1981a,b.; Zahavi & Zahavi, 1997). However, the evolutionary process of inflation cannot be tested in multicellular organisms by short-time experiments. I therefore became interested in the social behaviour of microorganisms, thinking that their brief generation-period might enable one to test the idea experimentally (see below). I have not yet managed to find a laboratory that would conduct the experiment.

### *Providing clear and precise information as a handicap*

When I tried to define the borderline dividing signals with and without handicaps, I focused on a set of markers that were considered as markers of belonging to a certain set, such as species, gender or age group. Markers that are considered set-specific, such as a dot, or a line across the tail, are often very small and seem to require only minute investment. The question was whether these signals entailed handicaps. I resolved this question by pointing out that these patterns do not carry messages in their own right, but rather they are standards by which information on body shape, size, movements, etc. is better shown. A dot on the forehead can help to evaluate the shape of the forehead. Other ornaments, such as lines, stripes, and colour patches, can serve as reference points to the size or shape of the individual or its body parts, or to the quality of its movements (Zahavi 1978b). Like all other signals, these set specific signals have evolved through competition among individuals to advertise their advantages over other members of their own set, rather than to advertise their belonging to the set (Zahavi 1978b; Zahavi & Zahavi 1997). Obviously, once these markings were present, they could be used to infer that an individual belonged to a certain set. However, this was not the primary reason these signals were selected for and maintained by natural selection.

Hasson (1991) and Maynard Smith and Harper (2003) suggest that such set-specific characters provide information without imposing a cost on the signaler. They term them



“Amplifiers” and “Indices”, respectively. I suggest that providing clear and honest information about the exact quality of a signaler is in itself a handicap. The gains and losses of such displays are differential: the better individual usually gains, because its superiority becomes more obvious. The lesser one loses, because its defects become more noticeable, and it can no longer exploit the margin of doubt as to its qualities. However, even the best individual in a group may lose – when a still better one joins the competition; and the lowest-quality one may gain when someone of a still lower quality joins in.

### *Ritualization*

This is the process by which signals evolve out of traits that were not signals to begin with (Huxley 1914). Huxley suggested that the process of ritualization evolves due to the common interest of partners to communicate clearly. However, the idea that standard patterns evolve through competition enabled me to suggest that ritualization also evolves as the result of competition among individuals to advertise their qualities. Observers can judge small differences between competitors better if the competitors display their abilities in a standard way. This is the reason that strict standards are imposed at the highest levels of human contests in areas such as sport, beauty, or music. Ritualization is the process by which such competitive standards evolve (Zahavi 1980; Zahavi & Zahavi, 1997).

### *Cheating*

I use the following definition for a signal: a trait that has evolved, in the signaler, in order to transfer information to receivers to affect the behaviour of the receivers in a manner that is beneficial to the signaler. The receiver should respond only to reliable signals, to ensure that the change in its behaviour suits its own interests as well. Hence receivers select signals to be reliable. With the HP I was able to reinterpret, as honest signals, many interactions that were considered as cheating or manipulations (e.g. Dawkins & Krebs 1978).

### *Threat signals*

The phenomenon most often interpreted as cheating is threat displays, in which the signaler is described as trying to display its size as bigger than it really is, by growing manes, extending crests and spreading fins. For example, the manes of monkeys and lions are supposed to increase the apparent size of the head. However, if that is the reason, why are the manes coloured differently from the rest of the head? I suggested that the coloration of the mane displays it clearly as an appendix. In fact, manes impose additional handicaps, since by forming a frame around the head they reduce somewhat the apparent size of the head. This is a handicap that a mature lion or monkey can afford, but a young one that wishes to display its skull as big as it is cannot afford (Zahavi & Zahavi 1997; Zahavi 2006).

### *Cuckoos*

Cheating is also supposed to explain the relationship of some cuckoos and their hosts. In 1975 I stayed with Karl Vernon at his study site of the helmet shrikes in Zimbabwe. In the evenings, sitting outside the bungalow, I was listening to his stories about his studies of social parasites among the South African birds. One of the stories was about a cuckoo that pushed the host out of its nest, laying its egg while the host perched on the rim of the nest. After the cuckoo departed, the host resumed its incubation, not bothering to evict the parasite's egg, which was very different in colour and size from its own. This story did not fit the prevalent idea that a social parasite cheats its host by mimicking the host's egg. Also, it was not reasonable to assume that natural selection has "not yet" had the time to select for a cleverer host. During one of these long nights I figured out the "Mafia model." In my paper (Zahavi 1978c) I did not use the term "Mafia," but I described a strategy similar to the one used by the Mafia to explain the logic of the model: I suggested that the cuckoo should revisit the nest and predate on the offspring of a host that rejected its eggs, but not predate if a cuckoo nestling was present in the nest. It is important to note that the benefit to the cuckoo is not in punishing of the host, but in the food it gets, or in forcing the host to re-lay in a territory governed by the individual parasite. The term "Mafia model" was coined by Soler in his paper on the great crested cuckoo (Soler *et al.* 1995). Avishag and I visited Soler and stayed with his team in their residential caves, and enjoyed watching the interactions of the magpies and the crested cuckoos. (Zahavi & Zahavi 1997, p. 189).

The story of the European cuckoo and its reed warbler host is quite different. The European cuckoo is a successful nest parasite. When its egg is accepted, the parasite's nestling kills all of the host's offspring. Still, in the same host population, some individuals evict the cuckoo's egg, whereas others do not evict it. Such mixed populations are found across Eurasia from Britain to Japan. I could not believe that over all that area selection has not "yet" eliminated the reed warblers that cannot recognize a cuckoo egg. I speculated that the coexistence of rejecters and acceptors was the result of some equilibrium. Obviously I did not know what that equilibrium was. My student Arnon Lotem decided to study why some reed warblers do not reject the eggs of the European cuckoo. Nick Davies could not accommodate him at Oxford, so Arnon decided to study the interactions of cuckoos and reed warblers in Japan, in collaboration with Hiroshi Nakamura. We met Hiroshi and his family a year earlier, on our visit to Japan, and enjoyed their hospitality, including a visit to a potential study site and to the mountains. The conclusion from Arnon's study was that the difference between acceptors and rejecters was not a consequence of genetic polymorphism, but rather of age. Arnon found that the acceptors were first-year breeders, whereas older birds usually rejected the cuckoo eggs. He suggested that at its first breeding, the warbler was not yet familiar with the coloration of its own eggs – there was therefore a danger that it would eject its own egg instead of that of the cuckoo (Lotem *et al.* 1995). It is important to note that, although selection can develop cuckoos that mimic the eggs of reed warblers in general, they cannot match the pattern of the eggs of the particular individual they parasitize.



Arnon's study did not provide an answer to the question of why hosts continue to feed their parasite's nestling and fledgling, even though the shape and size of the cuckoo nestling is so different from that of their own offspring. My present hypothesis is that, once the host loses the chance to breed that year, tending to an alien nestling provides the host with higher social prestige than the alternative of not having anyone to feed at all. Such prestige helps it breed successfully in the following years. This answer is similar to my interpretation of helpers at the nest in cooperative breeders: they feed offspring that are not their own and are often not related to them.

### Babblers and altruism

When I started to study the babblers in 1971, I did not believe in interpretations based on group selection, but I was willing to explain social adaptations by kin selection or reciprocity, as most people still do today. However, data collected during the first years of the study revealed that large groups of babblers did not reproduce better than groups of average size (Zahavi 1974, 1989). Hence, I was faced with the problem of why all individuals in large groups invest in helping when their help is not needed. Furthermore, detailed observations revealed that individuals compete with one another to help, and sometimes are even aggressive towards other group members that try to help. The first indication that babblers compete to act as altruists came from the observations of my daughter Tirtza, who collected data on sentinel activity. The data revealed that dominants replaced subordinates as sentinels, but subordinates did not replace dominants directly. Allofeeding in adult birds is also nearly always unidirectional: in almost all cases, higher-ranking individuals feed lower-ranking ones. Subordinates that are not ready to give up their post as sentinels, or ones that do not accept a feeding, are sometimes attacked by the dominant. Most allofeedings are carried out in the open, and the donors usually advertise their donations by loud purrs, calling the attention of the rest of the group: we often see group members raising their heads and watching allofeeding interactions. Sometimes they come to intervene (Kalishov *et al.* 2005) (figure 21.4).

Since I developed the Handicap Principle at the same time that I started my study of the babblers, I was able to suggest that in babblers, and in many other group-living animals, altruism could replace overt aggression as means of advertising claims for social prestige. Furthermore, the investment in altruism could be interpreted as a handicap that attests to the reliability of the claim (Zahavi 1977a,b.). Data collected by my students and collaborators further support the theory that altruism in babblers can best be interpreted as an investment in claiming social prestige. (A partial list of these studies is given in our book, several of these are in Hebrew with brief English summaries only, as some of these students chose not to pursue an academic career, and thus were not pressed to publish their work in English.)

In 1981 Tamsie Carlisle joined our team. Tamsie came to Hazeva after conducting a B.Sc. study with Dawkins and a Ph. D. with Trivers – that is, she came from the hard-core of kin selection and reciprocity theories. She studied the helping at the nest by yearling

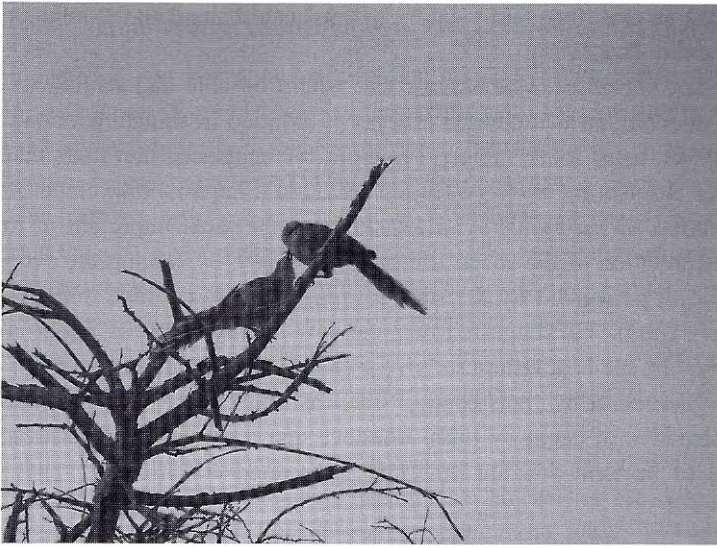


Figure 21.4. A dominant babbler feeds and exchanges a subordinate sentinel.

babblers. Her results convinced her that the only way to interpret her data was to assume that the babblers compete to help, an assumption that could not be accounted for by kin selection or reciprocal altruism (Carlisle & Zahavi 1986). Also, babblers often help non-relatives that join their group, although they know that they are not related (as shown by the patterns of avoidance of incest). Competitive altruism in babblers represents a constant quest for prestige among these group-living birds (Zahavi 1990). The idea that social prestige has an important role in all social interactions, including those of the mating pair, resolved my observations at Ravenglass years ago, when I noticed the competition between the male and female black-headed gulls. Instead of trying to exploit one another, letting their partner invest in incubation, they compete to incubate. I was now able to suggest that each one invested to increase its prestige in the eyes of its partner.

Not everyone who studied our population of babblers at Hazeva agreed with my conclusions. John Wright, who spent several seasons studying the feeding at the nest and collected data on sentinel activity, did not notice evidence for competition to serve the group, and interpreted his results with a model of group-augmentation, which is in fact a model of group selection (Wright 1997). I believe he underestimated or probably missed behaviours that we interpret as competition.

### **Signals among microorganisms**

I became interested in studying signaling and social behaviour of microorganisms for two reasons: I could not believe that even an individual bacterium or amoeba would kill itself for the sake of other individuals, and I hoped that the study of the signaling of microorganisms



would suggest an experimental model by which I could simulate the inflation process of signals (Zahavi & Ralt 1984).

We have not yet found a laboratory that would be able and willing to conduct an experiment in evolution to study the process of inflation in signaling among microorganisms. However, using the Handicap Principle, we suggested that traits that used to be interpreted as altruism by models of group selection (Shapiro 1998) could be interpreted better by models of individual selection. Perhaps the most important of these studies was our interpretation of the social life of slime molds, explaining the evolution of the active cell death performed by the stalk-forming cells as a selfish trait (Atzmoni *et al* 1997; Zahavi 2005). We suggested that, for low-quality amoebas under stress, active cell death may be the best option to have a chance to pass at least some of their genes to the next generation by transfection. Small as that chance may be, it is still better than the alternative of death by lysis. I believe that a similar interpretation may apply to bio-films of bacteria that are presently interpreted according to models of group selection.

### *The production of antibiotics as a selfish trait*

Bruce Levin, then at Amherst, directed my attention to the problem of explaining the evolution of antibiotics by a model of individual selection. Microbiologists interpret the production of antibiotics by bacteria as weapons by which populations of bacteria fight each other. This interpretation begs the question: why should every individual bacterium invest in producing the antibiotics? There are millions of bacteria in a population. Any individual that refrains from investing in the production of antibiotics would have an advantage over those that invest for the sake of the population. Trivers (1971) already pointed out that when an individual has the chance to exploit another and does not do so, that individual is an altruist. Bruce told me about his studies of bacteria in sewage. He expected that the fierce competition among the many bacteria species would result in a high secretion of antibiotics in sewage. However, he found the opposite: the amount of antibiotic secretion was very low, too low to eliminate stocks of susceptible bacteria. This suggested that in sewage bacteria were not using antibiotics as a weapon against other populations. At about that time, I saw in Jim Shapiro's lab in Chicago how individual bacteria space themselves: each is surrounded by a tiny space, like the individual space around a bird within a flock. I suggest that the antibiotic serves to protect the tiny space surrounding an individual bacterium against encroachment by its neighbors. This suggestion is supported by the well-known fact that the antibiotic industry has to select special bacterial lines in order to produce large quantities of antibiotics. The evolution of antibiotics can be compared to the development of the longbow in Britain. It is reasonable to assume that the longbow was used by British people to fight their fellow British. King Henry V used the British bowmen to fight the French. The battle of Agincourt was won by the longbow – however, the longbow was not developed for that purpose.

### **Our dog Namir and his contribution to the theory of testing the bond**

My first and only dog was Namir, a beautiful and lovely German pointer (Figure 21.5). I intended to use him to locate the nests of the red-legged partridge that I was planning to study once I finished with the babblers. All through his ten years with us Namir was frustrated, because he was not allowed to run after the partridges in the study area. He was not interested in babblers, however, and readily stayed in the jeep when we were in the field. As soon as I left the jeep, he would move to the front to take over the driver's seat, which he probably considered to be the most prestigious. Later he would relax and lie down across the back, completely ignoring the babblers that would often hop around him, looking for tidbits. But although I was able to command him not to run after partridges, I could not stop him when a hare ran in front of the car. He kept pursuing them, although he never managed to overtake any of them.

Namir's main contribution to science was his habit of jumping on me when I came home tired from work, just as my little daughters used to do years earlier. His favourite place at home was the passage between the kitchen and the dining room, where we had to push him to pass by, or on the doorstep when he realized that I was getting ready to leave the house. At that time I was observing daily the clumping and allopreening of babblers, and especially their morning dances, in which they jump over one another, push one another, and interfere



Figure 21.5. Our dog Namir.





Figure 21.6. Allopreening (photo by Oded Keinan).



Figure 21.7. "Water dance". When these desert birds find water they often cannot resist getting wet – followed by the water dance.

with the movements of their group members (Figures 21.6 – Figures 21.8). I could not avoid noticing the common elements in the behaviour of the dog, the babblers, and my daughters when they were young. I concluded that by imposing a burden, individuals are testing the social bond between them. The reaction to the interference provides a clue and a measuring



Figure 21.8. Babblers in a night roost.

stick to the motivation of the social partner to bond. Indeed, why would one who is not interested in a social bond accept the burden of an interfering partner? In my short, but I believe very important paper: "The testing of the bond" (Zahavi 1977c), I acknowledged and expressed my thanks to Namir.

### **Faithful bees**

During our long drives, whether abroad or during the weekly shuttle between our study area at Hazeva and our home in Tel-Aviv, we discuss (and often argue over) interpretations of our own observations or those of colleagues. One such endeavor was to understand why bees stay faithful to the flowers they pollinate. The stimulus to ask the question came one day when we were standing with our friend and colleague Professor. Danny Cohen in front of the botany department at the Hebrew University of Jerusalem. The flowers in the bed resembled those of a legume. However, we learned from Danny that they were in fact not a legume. Danny suggested off-hand that these flowers resemble the legumes in order to cheat the bees and lure them to visit them. On our way to Hazeva, we started to ponder about the system of plant-bee interactions. We knew that when collecting pollen, honey bees and some other bees are faithful to a single plant species on each collecting trip. Obviously it is in the interest of the plant to be pollinated by, and send its pollen to, flowers of its own species only. However, we could not see why the bee should care to be faithful, instead of collecting pollen from the nearest flower of whatever kind. We also knew that when honey bees collect nectar, they are not necessarily faithful to the species, often moving between flowers of very different structures. We therefore decided that somehow the plants must be manipulating



bees to stay faithful to them when collecting pollen. The logical conclusion was to look for the answer in the grains of pollen.

We knew that pollen grains vary greatly in shape, size, and structure even among closely related species. We hypothesized that perhaps the pollen of a single species sticks together to form a neat pollen pack, but that trying to pack together pollen of different species could cause the bee to lose its load of pollen. If pollen from a different species would cause the bee to lose the load, it would be worth while for the bee to spend time on searching for flowers of a single species. In cooperation with Dr Avner Cohen from the Volcani center and Professor Dini Eisikowitch from Tel-Aviv University, an expert on pollination, we examined loads of pollen under light electron microscopes. Indeed, loads composed of pollen of a single species were packed neatly, the grains fitted tightly to each other. However, even a single foreign grain disrupted the packing and often caused the loads to crack (Zahavi *et al.* 1984). Subsequently Dini and his students extended and verified these observations.

### Colour

Wherever we traveled – in the deserts of the Namib or the Kalahari, in Peru or in Australia, in the tropical forests of the Old and the New World, in the swamps or on the sea shore – we tried to observe and make sense of the choice of colour for display in birds' plumage. Avishag's expertise in the effects of light spectra on plant development was of help. Our general conclusions about the factors that select for the use of a particular colour in advertising are described in our book (Zahavi and Zahavi 1997).

In our travels we met many fellow researchers. We visited their research areas, discussed their observations with them, and often enjoyed their hospitality at their homes. I apologize for not being able to thank most of them by name in this chapter.

### The Hazeva Field Study Center

The center was established in 1969 by the SPNI when I was still its general secretary. From 1971 it was the base for our babbler study, housing our volunteers and students. I usually spend 2–3 days there every week. The center also forms a base for conservation, education and research for the Rift Valley and the central Negev. The activities of the center facilitated the formation of two small but beautiful Nature reserves, the Shezaf and the Gidron, adjacent to the Jordanian border. The babbler research in these areas played a role in convincing the authorities to establish the reserves.

In 1997 the SPNI decided to close its activities at the Hazeva Field Study Center. The Center's buildings were derelict houses of a former army camp and a set of badly designed buildings that presented difficult maintenance problems. Maintenance was very costly, and it was not balanced by the income provided by visitors. Closing the center was also in line with a new policy of the SPNI, to concentrate on activities in city communities rather than in the field. I opposed that trend. Hence, I suggested to the SPNI that I should take upon myself

the responsibility for the operations and financing of the center. The burden was much greater than I had expected. Much of my time and efforts over the following ten years were invested in maintenance, looking for financial support, finding the staff to operate the center, and renovating the derelict hostel, dining room, kitchen, and classrooms. Still, I succeeded. I did not do it alone: several guides and technical staff, and a good number of young volunteers who came to help for one year or more, carried out the day-to-day operations. I would not have been able to succeed without their help. Not least, I am obliged to several donors including my family, who provided financial support. In 2006 the center was maintaining itself financially and I handed it back to the SPNI, whose new director promised to keep it going.

Obviously, I was doing less scientific research during these years, but I continued to observe the babbler with my students, and had the satisfaction of having around me young people who felt responsible for conservation and education with the same spirit that was found in the SPNI when I headed it. I am especially grateful to my former student Roni Ostreicher, who has been living at the center with his family since 1989 and continues to participate in the babbler study.

### **The evolution of pheromones and hormones**

Over the past few years, and especially since 2006, my main scientific challenge has been trying to understand the evolution of chemical signals. I suggest that, like other signals, pheromones are shaped by the Handicap Principle – that is, there is a relationship between their chemical structure and the messages encoded in them. The similarity between the structure of many pheromones and hormones led me to conclude that the Handicap Principle is effective even among cells of the multicellular organism. In the multicellular organism, handicaps prevent hormone production by cell phenotypes that have not developed properly. This means that the patterns of hormones – their chemical properties – should also bear a relationship to the messages encoded in them. (Zahavi 1993, 2006, 2008). With my students, we read literature on microbiology, chemistry, endocrinology and histology, and discuss what we find with professional colleagues. Preliminary results of the study of the sex steroid hormones already helped to suggest what is the message in testosterone and in estrogen and why testosterone is secreted by one type of cells and estrogen by another (Zahavi & Fuks, in preparation.)

### **Group selection vs. individual selection**

I am convinced that natural selection works only through the individual. It troubles me very much to find that models of group selection are again often used to explain evolutionary phenomena (Wilson & Holldobler 2005; Wilson & Wilson 2007). I am also concerned about the use of models of indirect selection such as kin selection and reciprocity by mainstream researchers. I am concerned because these theoretical approaches affect the definition of



objectives, the planning of research, the set of facts to be collected by observations or experiments, and, of course, the interpretation of results. When a certain trait helps the group but seems to harm individuals possessing it, researchers often follow the easy way out to explain the observations with a model of indirect selection. They stop searching for the possibility that the individual within the group is doing the best it could do to serve its own interests. Interpretations based on individual selection may require more data and may not be easy to develop. In the past I was able to suggest interpretations based on individual selection for data that were interpreted by indirect selection by other researchers. What I consider as major successes in that effort are my re-interpretations of altruism in babblers and in slime molds.

It took 15 years to “vindicate” the Handicap Principle as a means by which signals evolve to be reliable. It may take longer to appreciate its use in signaling within the body and its importance in explaining signaling in microorganisms and in the social insects with models of individual selection. This is one of the reasons why I continue to teach undergraduates, in the hope that sooner or later they will look for the facts and find the means for such interpretations.

### Epilogue

I am still deeply involved with conservation, trying to preserve as much as possible of the natural landscape and wildlife of Israel, especially the desert. I advise the SPNI and governmental agencies, and educate young volunteers and visitors at the field study center at Hazeva to appreciate nature and to fight for its conservation.



Figure 21.9. From right to left: Naama, Kinneret, Tirtza, Amotz. Avishag is behind the camera. (2007).



Figure 21.10. Avishag, 2008.

With my wife Avishag, both of us now retired, we continue to watch the babblers in the early mornings several days a week. We know each babbler personally, by a name coined from the initials of its four rings. We have followed most of them since they fledged from the nest. We watch how they compete to establish their prestige in their own group. We follow their fate when they disperse to join other groups, or become refugees. A few individuals eventually succeed in breeding for a short, or sometimes even a very long period. We mourn when they die. We collect their stories and hope that eventually we shall find the time to write them down (Figures 21.9 and 21.10).

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