The Sunning Behaviour of Birds

A Guide for Ornithologists

K.E.L. Simmons

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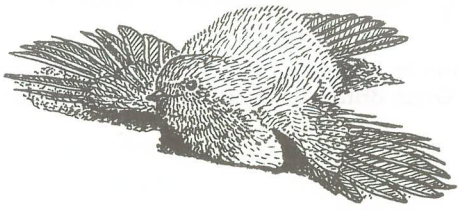

Illustrated by
ROBIN PRYTHERCH

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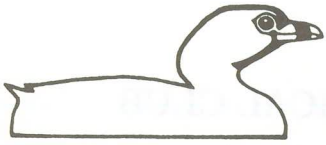

Dedicated to my dear friends
Bernard and Marjorie King

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List of Birds Illustrated

NOTE ON THE ILLUSTRATIONS

All the illustrations were traced from photographs, drawings, and one painting or, in the case of films, off the screens of viewing monitors. Where necessary, the traced outlines were then reduced or enlarged so that figures in groups appear at roughly the same scale. The stylized form adopted is designed to show the posture of the bird, the state of its body plumage (i.e. fluffed, ruffled, or sleeked), and the positioning of the wing and tail feathers; the state of moult is therefore revealed with maximum clarity. As shadows help to indicate the direction of the sun rays, they are shown fully except in some cases where the detail was unclear.

The following list gives the illustration sources, which were photographs unless otherwise indicated.

1. Black Skimmer *(Michael L. Smith)*
2. Cape Cormorant *(S. Pringle)*
3. Masked Booby *(George A. Bartholomew)*
4. Double-banded Courser *(G.L. Maclean)*
5. Egyptian Plover *(Thomas R. Howell)*
6. Gray Gull *(Thomas R. Howell and others)*
7–8. Jackdaw *(Noble Rollin)*
9. Chaffinch *(Noble Rollin)*
10. Lesser Black-backed Gull *(Noble Rollin)*
11. Reed Warbler *(Ernest Mytum)*
12. Reed Warbler *(H.A. Thompson)*
13. House Martin *(drawings R.J. Prytherch)*
14–16. Galapagos Dove *(J. Nicolai)*
17. Dunnock *(C.W. Teager)*
18. Starling *(C.W. Teager)*
19. Blackbird *(C.W. Teager)*
20. Eleonora's Falcon *(Richard Vaughan)*
21. Middle Spotted Woodpecker *(O. Heinroth)*
22. Bee-eater *(L. Koenig)*
23. Little Grebe *(E. Thimm)*
24–25. Bluethroat *(O. Heinroth)*

Editors' Foreword

For several years the Editorial Committee of *Bristol Ornithology* has been hoping that it may have the opportunity of publishing an occasional series of papers issued separately as supplements to the journal. These papers would be detailed, lengthy studies that would not fit easily into the pages of the journal without being sub-divided into parts spread over several issues. As with the contributions to the journal the work would be by a member of the Club.

We are fortunate and delighted to initiate the series now with this important book on the sunning behaviour of birds by Dr K.E.L. Simmons. A founder committee member of the Club, he has an international reputation as an ornithologist, ethologist, and behavioural ecologist with a bibliography of well over a hundred publications. His interests in ornithology are exceptionally wide, earning him the Union Medal of the British Ornithologists' Union in 1979, but it is for his studies on the Great Crested Grebe (still continuing) and on topics such as the comfort behaviour and parental anti-predator strategies of birds that he is best known. He has been an editor of *The Birds of the Western Palaearctic* since 1971, co-Editor with Stanley Cramp for Volumes 1–3 (for which he wrote many of the 'Social pattern and behaviour' and 'Voice' accounts) until infirmity caused his early retirement in 1980, though he still remains responsible for the taxonomic summaries for the remaining (passerine) volumes of that work. Otherwise, he has kept busy in recent years with a number of projects of his own and at present is collecting material for a biography of Edmund Selous and is working on a big review paper on brood-division in grebes and other birds, as well as engaging (with his wife) in historical research outside his main field on the composer Elgar. Since retiring he has held an Honorary Visiting Fellowship at the University of Leicester where he worked for several years in the Department of Psychology.

The author's extraordinary ability to observe and analyse some of the complex behaviours of birds is formidable. His enthusiasm is paramount in the field (which often means his garden!) when every movement or change of posture of the bird under observation is commented on with infectious enthusiasm allied to a keen grasp of the subject – enthusiasm which is manifested differently in written form where his concern for clarity and disciplined presentation of the material is evident. A certain degree of concentration may be required to gain a full understanding of the various behaviours described here, but readers are referred to the final chapter where the main conclusions are briefly summarized and a brief résumé given of the

content of each chapter. *The Sunning Behaviour of Birds* is an important contribution to the ornithological literature and the Bristol Ornithological Club is proud to be responsible for its publication. The Editors would like to acknowledge the assistance of the Royal Society for a contribution towards funding this book.

K.J. Hall K. Howard
C.J. Newman R.J. Prytherch

Author's Preface

A well-known ornithologist and birder once told me that he was interested in everything about birds except their 'behaviour'. If one accepts as a definition of bird behaviour 'everything that birds do', then his statement was a particularly strange one, perhaps indicative of the swing in modern birding, birdwatching, and ornithology to treating the bird as a unit to be spotted, identified, listed, conserved, counted, and plotted rather than *watched* in the true sense.

I suspect, however, that what he meant was 'Behaviour' with a capital 'b' and what he had really set his mind against was the *interpretative* study of bird behaviour, especially the analysis of displays and other complex social interactions. Be that as it may, I would go so far as to say that anyone who considers himself to be a serious birdwatcher, even an ornithologist (i.e. a student of birds who aims to make scientific contributions to our knowledge of birds and bird-life), cannot but be interested in and want to understand 'what birds do' in all its manifestations, especially if he be also intent on self-education and has an open mind.

It is for such a person, especially, that I have written this review, my subject being the 'sunning' behaviour of birds — 'something that birds do' that can be seen, studied, and pondered over even in one's own garden. This is true also of many of the everyday habits of birds, about which, alas, even those with a lifetime of birdwatching behind them may sometimes remain woefully ignorant.

The book was mostly drafted in 1981–82, completed in 1983, and revised for publication in 1984. Supplementary facts and comments, including details of important additions to the literature published in 1983–84, have been placed in the Notes section (Appendix). The line drawings by Robin Prytherch were prepared after the text had been completed so any cross-reference is from the captions to the text.

The scientific names of bird species mentioned in the text, captions, and reference appear in the Index of Birds at the end of the book. Particular attention is given to the birds of the northern hemisphere for which I have followed, in the main, the scientific nomenclature and order of K.H. Voous's *List of Recent Holarctic Bird Species* (British Ornithologists' Union, 1977), though the names of North American species are, again with a few exceptions, those of the American Ornithologists' Union Committee on Classification and Nomenclature (see *Auk* 99, supplement, 1982). Throughout, however, I have mostly indulged my own preferences for the English names of birds used.

Though I prefer to employ the term 'sunning' exclusively as the generic name for the main phenomena under discussion here, confining 'bathing' to true bathing in water, the name 'sun-bathing' is also of such wide currency that I have not tried to avoid its use entirely.

ACKNOWLEDGEMENTS

My special thanks are due to the Bristol Ornithological Club, for undertaking the publication of this book, and to the Editorial Committee of the Club, for help and encouragement during its creation. In particular, I must mention Ken Hall and Robin Prytherch who were responsible for its design and production. Robin Prytherch also compiled the index and undertook to prepare the many illustrations which so enhance the appearance and scientific value of the book, taking almost unbelievable pains over them. He also contributed observations and helped in many practical ways, as did my wife Marion Simmons (of the University of Leicester Library).

I am also most grateful to the following for their help: Prof. T.J. Cade, for correspondence on falcons and other birds-of-prey; Dr C.H. Fry, for correspondence on bee-eaters; Robert Gillmor, for lending me his volumes of Heinroth and Heinroth (1924–33) and for his observation on the Wren; Derek Goodwin, for translating Wennrich (1980) and parts of Nicolai (1962) and Prinzinger (1983); Bernard King, for sending me his sunning records (the cream of which are used in this paper); D.E. Ladhams, for the four interesting sunning records used here; Chris Measures, for the observation on the Giant Kingfisher; A.T. Moffett, for answering my queries and for observations; the Royal Society, for supplying a computer, floppy disk unit, and printer for word-processing (without which the composition and detailed revision of this paper would not have been possible); Dr. R.W. Storer, for correspondence on grebes; and M.G. Wilson, for supplying certain key references, photocopies, and translations (and, in particular, for painstakingly checking through the Heinroths' book for me before I had access to a set).

K.E.L. Simmons
Leicester, England
October 1986

CHAPTER ONE

Introduction

Sunning may be described for practical purposes as behaviour by which a bird deliberately positions itself in the rays of the sun (electromagnetic radiation, solar radiation, solar energy, insolation), often adopting a special posture. This phenomenon has proved to be an even more puzzling and enigmatic habit than anting and dusting, with which it is often associated (in many people's minds at least). As with anting and dusting, we first have the problem of distinguishing between motivational and adaptive features of the behaviour (cause and effect). However, whereas the function of anting has clearly to do with the biochemical properties of the ants (Simmons 1966) and that of dusting with the abrasive and absorbent properties of the fine dry earth or sand (Healy and Thomas 1973, Borchelt and Duncan 1974), it is by no means generally agreed yet which type of solar energy is important in the achievement of the main biological effects of sunning, i.e. invisible short-wave radiation (especially the ultra-violet), visible medium-wave radiation (light), or invisible, infra-red long-wave radiation (heat). There is also the question of whether sunning birds react primarily to the sun as a source of heat or as a source of light, either as an unconditioned (innate) or conditioned (learned) response.

I have been making observations on the sunning behaviour of birds for many years now and have just brought up to date my entry on this topic in *A New Dictionary of Birds* (Simmons 1964) for the recent *A Dictionary of Birds* (Simmons 1985). The main object of the present paper is to examine sunning behaviour afresh in more detail than was possible in the two dictionary articles, drawing on my own extensive field-work (see Note 1, Appendix) as well as on the sunning literature (see Chapter 3).

In my first account of sunning (Simmons 1964), I considered the behaviour to be, like anting and dusting, a subsidiary form of feather maintenance, of which bathing, drying, oiling, preening, and head-scratching are the major forms. Though the exact role of sunning in feather- and skin-care is obscure, it could serve, I suggested, to expose the feathers and the organic fluids on the plumage to the sun's rays, especially in the ultra-violet wavelength, and do the feathers 'good' by affecting the properties of the preen-oil in some way; it could also provide a source of Vitamin-D from the irradiated preen-oil, which is ingested during preening, and benefit the feathers in other (unspecified) ways. Further, the warmth of the sun could cause ectoparasites to become active in

the plumage and thus be more accessible to the bird when it engages in the preening and head-scratching that commonly occur during and after sunning spells. Sunning is performed in all types of sun conditions, and even under artificial light in the case of captive birds, the form of the postures adopted being partly dependent on the position of the sun in the sky and on the 'mood' of the sunning bird. A bird may resort deliberately to a favoured place to sun itself, or start sunning suddenly during other activities, in response to strong stimuli when the sun comes out. In discussing the conflicting ideas on the nature of the motivation of sunning behaviour, I pointed out that, though inexperienced individuals seem to react automatically ('purely instinctively') to some quality of the sun, probably its warmth and brilliance, experienced birds seem to learn to react to the sun more as an entity, especially the sight of it (even on cool windy days). I felt it unlikely that sunning is 'primarily nothing more than a simple temperature response' to overheating, as some ethologists have considered it to be (see, e.g., Morris 1956), though birds may gape and often appear to collapse in distress when adopting extreme sunning postures in the full heat of the sun.

Subsequently, I came strongly to the opinion that a number of different phenomena had been lumped together under the terms 'sunning' or 'sun-bathing' (see also, e.g., Mueller 1972) and that I had taken a much too restricted view of the possible functions of the behaviour; in particular, the thermo-regulatory aspects of sunning needed reassessment. What is widely accepted as sunning behaviour is probably a product of two systems working separately or simultaneously (and sometimes clashing); one of these is concerned with temperature control (thermoregulation), the other with feather maintenance. In my recent summary of the topic (Simmons 1985), I therefore recognized two adaptive types of sunning, each being a reaction to the sun as a precisely identified source of heat:

> (i) *'sun-basking'*, which together with other forms of heat-basking, such as 'smoke-bathing', is a means of absorbing heat and hence a form of thermoregulation (see Chapter 7); and
> (ii) *'sun-exposure'* (or sunning proper), which probably functions in feather maintenance and related ways, and hence is a form of comfort behaviour (see Chapter 8).

Though basically quite distinct in function, the two types of sunning share certain causal factors and postures and are likely to overlap at times.

I want to expand these ideas in the present review. The subject is extremely complex, especially when motivational and developmental factors are considered, and doubtfully able of full elucidation at the present stage of knowledge; nevertheless, some progress is possible, especially with the application of traditional ethological concepts on motivation (see Chapter 9) as well as those of the more modern approach of behavioural ecology. Besides any maintenance benefit they might obtain from the irradiation of their plumage

and skin by solar rays, and any energy-saving benefit from maintaining or raising their body temperatures in cold conditions, birds may sun at times, it has been suggested, also in order to lower their body temperatures in hot conditions. Whether sunning postures are used as deliberate heat-stress postures in this last way and, if so, should such behaviour be termed sunning, requires careful assessment.

With these points in mind, it seems best first to examine in general terms the various forms of response that birds show when exposed to strong sunshine, reviewing at the same time the general features of their thermoregulation (for literature, see Calder and King 1974).

CHAPTER TWO

Thermoregulation

It should be remembered that birds, being warm-blooded (homoiothermal), typically maintain a constant and optimum body temperature about which they operate most efficiently; in most species, this is around 40°C (somewhat lower at night than during the day and when resting than when active) and is achieved through the process of metabolizing stored nutrients. They must call heavily upon these energy resources in order to thermoregulate except when the ambient temperature lies within their zone of thermoneutrality, metabolism then being at a minimum. This zone is defined by a lower and an upper critical temperature and varies adaptively in different climatic regimes. In passerines, the lower critical temperature is about 18°C in species living in temperate regions but lower (at about 9°C) in cold-adapted species and higher (at about 30°C) in heat-adapted ones; the upper critical temperature is more difficult to determine but ranges between 30 and 38°C.

When the ambient temperature is lower than the bird's zone of thermoneutrality, the net heat-flow is out from the bird into the environment causing cold stress and bringing with it the dangers of enforced hypothermia. The rate of heat loss depends, for example, on the particular species' metabolic rate and on the efficiency of its insulation (achieved mainly through the plumage) which determines whether its thermal conductance (heat-transfer coefficient) is low (as in cold-adapted birds) or high (as in heat-adapted ones). In order to reduce the drain on its metabolic reserves, the bird may become inactive and lower its body temperature, even to the extent of becoming temporarily torpid (adaptive hypothermia) in extreme cases, especially overnight. When active, however, the bird needs to show positive thermoregulatory behaviour to increase its metabolic rate. It may, for instance, shiver to raise its temperature, but the most common reaction to the cold is the ptilomotory one of 'fluffing' the plumage, i.e. erecting the contour feathers just enough to trap a layer of warm air next to the skin (see Morris 1956) – typically with all but the distal ends of the wings encased in the flank feathers – thereby enhancing the insulating properties of the plumage and reducing the gradient of heat loss. The bird may also reduce the amount of heat radiating from its extremities by tucking the bill and one or both feet away among the feathers, such 'foot-stowing' being a special feature of aquatic species such as the grebes (Podicipedidae) and waterfowl (Anatidae). Clearly, any warmth that a bird might obtain from the

heat of the sun or other source in such circumstances would be greatly beneficial.

BIRDS IN THE SUN

In conditions of strong sunshine (intense solar radiation) with the air temperature also high and the ground surface hot, the ambient temperature may rise above the bird's zone of thermoneutrality; then the net heat-flow will be from the environment into the bird causing heat stress and the danger of enforced hyperthermia. It can, of course, react passively by avoiding the sun or its full over-heating effects (seeking a cooling micro-climate such as a shaded or windy spot) and by restricting its activity to the cooler hours of the day; but if it remains in the heat of the sun through necessity (because of the nature of the habitat, because it needs to feed, because it is concealing itself in the open, because it has to attend eggs or young, and so on), then it must perform positive thermoregulation, attempting to rid itself of excess heat or at least to reduce the gradient of heat gain through cooling behaviour of various types (heat-dumping). Depending on local conditions, this may involve one or more of the four modes of heat-transfer: convection, conduction, radiation, and evaporation. In convective cooling, dry heat is lost to the air either freely or through the action of the wind (forced convection); in conductive cooling, dry heat is lost to the ground or other external object if these are colder than the bird; in radiative cooling, dry heat is lost by energy transfer to the environment; finally in evaporative cooling, heat is lost through water loss. Both active and inactive birds reacting to heat stress also show a rise in body temperature to combat it (adaptive hyperthermia), thus reducing the gradient between their own and the environmental temperature.

When attempting to cool itself, a bird often adopts special heat-stress postures. The simplest of these involve the ptilomotory responses of either 'sleeking' the plumage (i.e. pressing the contour feathers down), especially when active, or 'ruffling' it (i.e. erecting some or all of the contour feathers fully), especially when inactive (Morris 1956; see also Dawson 1954); in both cases, any warm air trapped between plumage and skin is expelled or liberated, thus reducing the insulating properties of the feathers. Plumage ruffling also helps to dissipate body heat through radiation, and through forced convection by facilitating the passage of air through the feathers and on to any exposed skin. In severe conditions, the bird may also spread the wings and tail; then, the heat-stress (cooling) posture adopted can strongly resemble a true sunning one. The heat-stress posture, however, is often distinctive. Passerines, for example, sleek the plumage, hold out the closed wings from the body, thus exposing the thinly feathered sides of the thorax (Dawson 1954), and gape. In experiments on captive emberizine buntings (the Corn, Reed, and Yellow), Andrews (1956a) exposed the birds to heated air and induced – as well as gaping and

panting – progressive sleeking of the body feathers (especially those of the belly) and the lifting of the closed wings (which were moved up and down slightly every 1–2 seconds by the Corn Bunting). Essentially similar results were obtained by Ligon (1968) with captive Elf Owls, with the addition of gular-fluttering (see below). Cooling may also be achieved by keeping bare areas, such as the legs and feet, in the shade of the rest of the body (heat lost through conduction) or off the hot substrate; also by submerging the legs in water or by bathing (enforced convection). Though flight itself is heat producing through the muscular activity involved, birds can cool themselves by rising high in the sky and soaring, especially in hot climates. African passerines have been reported to fly with their legs extended at the hottest time of the day (Frost and Siegfried 1975); like the soaring birds, they achieve heat loss through forced convection (see also Butler 1982, Bryant 1983).

The most effective way of losing excess heat (both metabolic and environmental), especially when the ambient temperature rises above body temperature, is through the evaporation of water. Some heat is lost via water evaporated through the skin, and from the plumage (e.g. after bathing), while birds of a few groups such as storks (Ciconiidae) and New World vultures (Cathartidae) lose heat through urohidrosis, the evaporation of faecal fluids deliberately excreted on to their legs (Kahl 1963, 1971; Hatch 1970). However, evaporative cooling is achieved mainly via the respiratory tract: by simple gaping (exposing the moist buchal cavity), by panting (the exaggeration of the

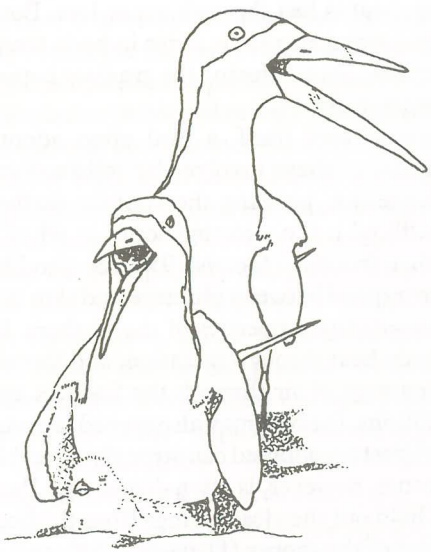
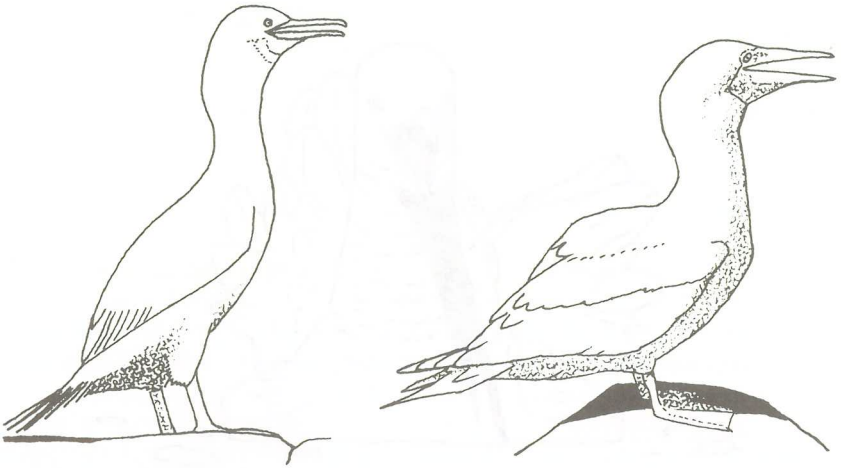


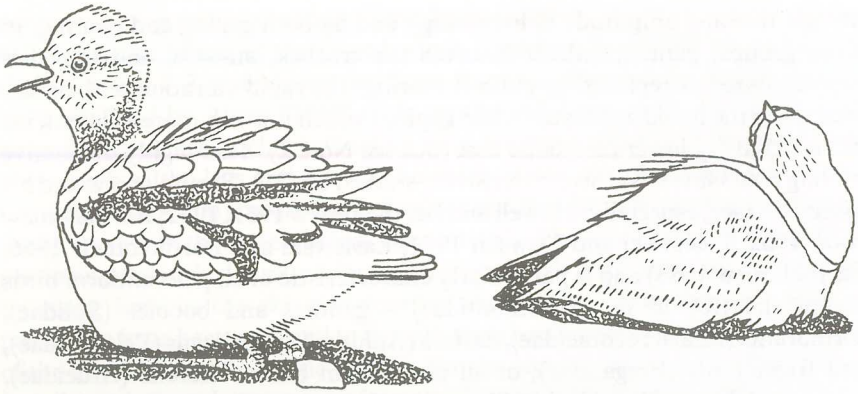
Fig. 1 *Cooling posture of Black Skimmer at nest, brooding bird and adjacent adult; note drooped wings, and open bill for panting.*

normal rate and amplitude of breathing), and by both gaping and panting. In some groups, panting (which involves the trachea, air-sacs, and lungs) is supplemented or replaced by gular-fluttering (the rapid vibration of the gular area using the hyoid apparatus while gaping) which is much more efficient, i.e. has a strikingly lower metabolic cost (but see Note 2). This highly distinctive cooling mechanism has been extensively studied by G.A. Bartholomew and his associates (see, especially: Howell and Bartholomew 1961, 1962; Bartholomew *et al.* 1962, Lasiewski and Dawson 1964, Lasiewski and Bartholomew 1966, Bartholomew 1966) and is particularly characteristic of all pelecaniform birds except the tropicbirds (Phaethontidae) – gannets and boobies (Sulidae), cormorants (Phalacrocoracidae), darters (Anhingidae), pelicans (Pelecanidae), and frigatebirds (Fregatidae); of all ciconiiform birds – herons (Ardeidae), storks, and ibises (Threskiornithidae); and of nightjars (Caprimulgidae). It has also been reported, for example, from lapwings (Vanellinae), sandgrouse (Pteroclididae), certain doves and pigeons (Columbidae), cuckoos (Cuculidae), and owls (Strigidae), but not from any passerine.

Ground-nesting birds in particular are often subjected to severe heat stress, including such groups as the sulids (Howell and Bartholomew 1962, Bartholomew 1966, Cooper and Siegfried 1976; see also Chapter 5), coursers (Cursoriinae) (e.g. Maclean 1967, Howell 1979), *Hoplopterus* lapwings (e.g. Naik *et al.* 1961, Jayaker and Spurway 1965), and gulls (Laridae). As well as direct solar radiation, they are exposed to diffuse, atmospheric, ground, and reflected solar radiation. Such problems have also been discussed by Reynolds (1977): see Note 3.



Figs 2–3 *Cooling postures of Cape Cormorant (left) and Masked Booby; note open bill for gular-fluttering, and shade cast by birds over own feet.*



Figs 4–5 *Cooling postures of Double-banded Courser (left) and Egyptian Plover on nest; note (e.g.) raised dorsal plumage of both birds and squatting stance of the courser.*

The Gray Gull, which is unique in nesting inland in the barren deserts of northern Chile, is subjected to extreme thermal stress when incubating (Howell *et al.* 1974). As the solar heat increases during the morning, these gulls first begin to ruffle their back and scapular feathers but remain sitting; by midday, they rise, panting, over the nest to shade the eggs with the plumage fully ruffled (even the short feathers on head and neck) and the wings slightly open and drooped. When the inevitable strong wind rises in the early afternoon, they face into the wind still fully ruffled and can eventually settle down on the eggs again as the surface temperature cools.

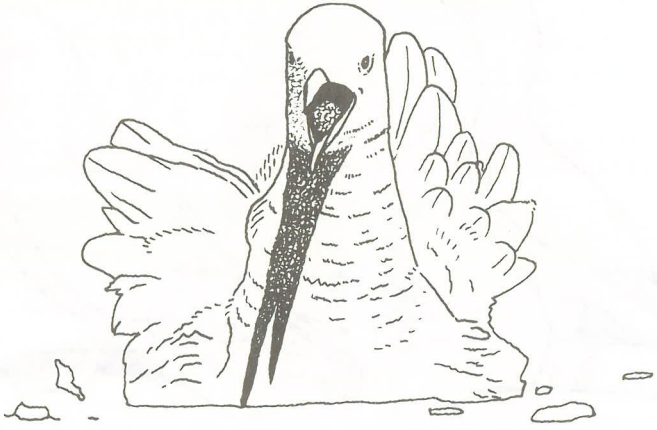


Fig 6 *Cooling posture of Gray Gull on nest. The bird is facing the sun, its plumage additionally ruffled by the strong wind blowing from behind.*

The authors suggested that the dark plumage of the Gray Gull 'may aid in avoiding excessive heat loading from solar radiation by allowing the outer surface to absorb heat and then lose it by convection, thus preventing deep penetration of heat to the body proper'. The same cooling mechanism had also been suggested by Marder (1973b) for the all-black, desert-living Raven. In their study of incubating Herring Gulls, Lustick *et al.* (1978) showed that orientation is just as important as posture, etc. In sunny conditions with little or no wind during April and May, the birds would face the sun all day, rotating through 180 degrees; they thus reduced the surface area exposed to direct sunshine and absorbed less radiation through their white frontal plumage than through their dark dorsal plumage (see further in Chapter 7).

CHAPTER THREE

Some General Aspects of Sunning: The Literature

Following the brief and necessarily oversimplified survey of thermoregulation in the last section, we can procede to an examination of sunning itself, first by way of the sunning literature which I have used to try to give an historical perspective of the subject while bringing out a number of general points. More detailed treatment of topics such as sunning postures will be presented in following chapters.

SOME EARLIER CONTRIBUTIONS

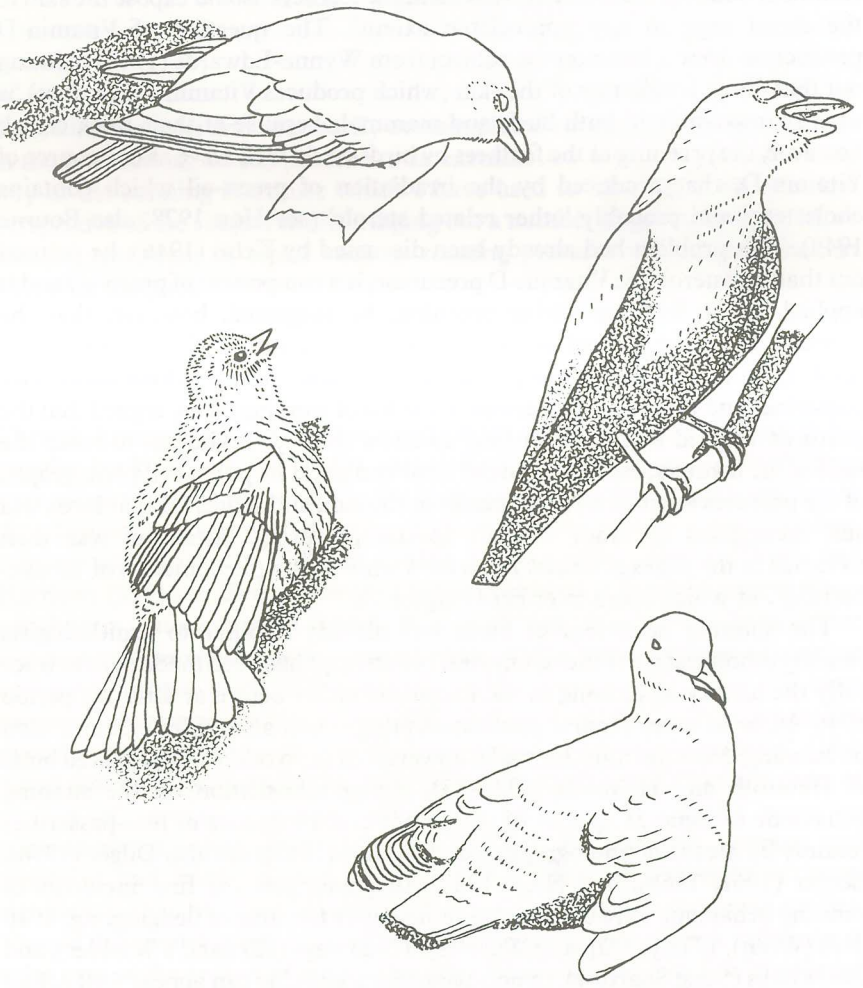
Though Armstrong had included a section on the topic of sun-bathing in his popular book on bird life (1943), mentioning some seven species, and there were other scattered references in the bird literature earlier, serious interest in the phenomenon amongst British ornithologists was mainly a post-war one, starting with notes by Williams (1946), Colyer (1946), Beven (1946), and Harrison (1946) in *British Birds*. These stimulated a flood of observations which were summarised by Gibb (1947). In all, some 25 species – 20 passerine and nine non-passerine – were covered. Most of the reported records of sunning (occurring in the period May–August) clearly covered what I now call 'sun-exposure' behaviour (typical sunning); however, others (occurring in the period September–December) could possibly have been of 'sun-basking'. Gibb noted that juveniles seem particularly prone to sun-bathe and that the dates of records of sunning generally showed 'a tendency, if nothing more, to concentrate at times of moult'. This possible link between sunning and moulting had been stressed by Harrison (1946) who thought it 'most significant' that his tame Tawny Owl, a crepuscular and nocturnal species, 'should deliberately seek out perches directly exposed to the full influence of solar rays at the season of moult' (see also Harrison 1942); he felt 'convinced that sun irradiation plays an important role in the process of the moult' through 'its local effect in stimulating the feather papillae to develop' and 'through the central and endocrine systems'. Sun-bathing in the Black Kite, studied in the Middle East, also appeared to be correlated with moult, with its spring

beginning and autumn ending at least, the birds probably receiving 'adequate irradiation from the blaze of the summer sun without special effort' in the time between (P.H.T. Hartley, in Gibb). Gibb also discussed the possibility, raised by one of his contributors (Dr L. Lloyd-Evans), that sun-bathing may 'be linked with the metabolism of vitamin D', especially in juveniles, achieved through the 'irradiation of the substance ergosterol in the skin, as happens in mammals', by exposing the skin to direct sunlight. This would account for 'the fluffing out of the feathers' that accompanies sun-bathing, but an editorial comment doubted that such movement of the feathers '*would* expose the skin to the direct rays to any appreciable extent'. The question of Vitamin-D production drew a letter on the subject from Wynne-Edwards (1947) pointing out that direct irradiation of the skin (which produces Vitamin-D3 in man) 'is usually impossible in both birds and mammals because of their thick coats'; however, the preening of the feathers by birds could well serve as one source of Vitamin-D, that produced by the irradiation of preen-oil which contains cholesterol and probably 'other related sterols' (see Hou 1928, also Bourne 1949). This problem had already been discussed by Kelso (1946): he pointed out that ergosterol, the Vitamin-D precursor, is a component of preen-oil and is applied to the feathers during preening; he suggested, however, that the vitamin or the ergosterol is swallowed during anting (which seems most unlikely to me). Rollin (1948), in a valuable contribution which added two passerines and three non-passerines to the list of sunning birds, argued that the postures adopted when sun-bathing *do* allow the rays of the sun to reach the base of the feathers, especially on the head and neck; he published photographs of the postures adopted by four species in the sun, and indicated that birds will sun themselves at times without special posturing. Attention was then switched in the pages of *British Birds* for a while to the phenomenon of 'smoke-bathing', of which more later (in Chapter 7).

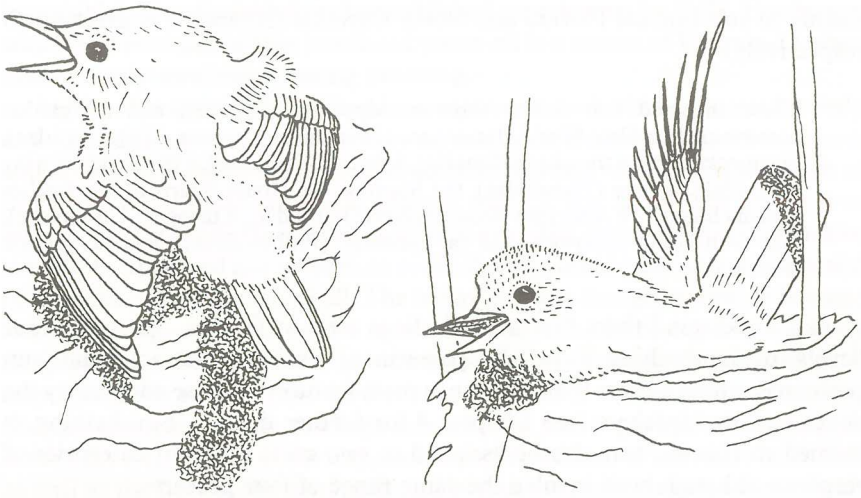
The sunning behaviour of birds was already familiar to ornithologists (mainly ethologists) in other countries. No attempt has been made here to trace fully the history of sunning in the literature, either before or after the period 1946–48, or to cover general publications that might also include information on sunning. Mention must be made, however, of the work on hand-reared birds of Heinroth and Heinroth (1924–33), giving information on the sunning behaviour of some 21 species of passerines and 19 species of non-passerines (mainly by means of photographs), and of Nice (1943); see also Dilger (1956), Berger (1961, 1968), and Nice (1962). In passerines, the first incidents of sunning behaviour were observed at or just after the time of fledging, e.g. at 16 days (Wren), 17 days (Aquatic Warbler), 17–23 days (Kirtland's Warbler), and 29–38 days (Song Sparrow); in non-passerines, sunning can appear well before fledging, especially in groups with precocial young such as gamebirds (Galliformes) and rails (Rallidae), from as early as 10 days from chicks in down (see also Goodwin 1953). In his contribution, based on a study of the ontogeny of the behaviour of North American thrushes in captivity, Dilger (1956)

thought that 'heat seems to be a more important stimulus than light' in eliciting the sunning behaviour of the young birds 'although light must be present (they will not sunbathe to a hot iron nor to an ultra-violet lamp which gives off little heat)'; an 'infra-red lamp, however, stimulates a response quite readily'.

In this country, notes on sunning by one further passerine (Buxton 1950, Pritchard 1950) and three non-passerines (Rogers 1950, Mason 1950a,b) followed Rollin's paper (see above). It was the topic of sunning by herons in



Figs 7–10 *Birds observed sunning by Noble Rollin: Jackdaw (two upper birds); female Chaffinch (left) in typical 'lateral' posture; and juvenile Lesser Black-backed Gull in 'wings-down' posture (this and other sunning postures are described in Chapter 4).*



Figs 11–12 *Behaviour in sun of Reed Warbler on nest: cooling posture while shading young (left) and 'collapsing' — probably an induced 'raised-wing' sunning posture.*

particular that most engaged interest at this time, however (Boyd 1950, Tully 1950, Rooke 1950 and others, Gush 1951); most of these records seem referable to typical sunning but others indicated that herons will sun-bask at times early in the day, though this drew no comment at the time. Mention must also be made at this point of an important observation by Brown and Davies (1949) on nesting Reed Warblers: when shading the young from the sun, the adult would sometimes 'collapse', apparently from heat stress, lying on one side away from the sun perhaps for several minutes at a time with the exposed wing stretched up vertically, feathers ruffled, panting. The similarity of this posture to certain sunning ones raises the possibility that the birds were really sunning (see below, and later chapters). Finally in this period, Goodwin (1956) briefly described the main sunning postures as part of a general review of behaviour connected with the care of the body surface; see also Goodwin (1961) and below.

HAUSER AND OTHERS

A key paper (Hauser 1957) then appeared in America; though written without any reference to work done on sunning abroad, this must be considered the single most influential contribution on the subject (albeit a rather confusing one), and merits consideration in some detail at this point. Hauser studied the sunning and sunning-like behaviour of 33 species of North American birds,

mainly in sub-tropical Florida and North Carolina (30 and 35 degrees north respectively).

> These included two doves, three woodpeckers (Picidae), and 26 garden passerines: two New World flycatchers (Tyrannidae), a wren (Troglodytidae), two mockers and a thrasher (Mimidae), a thrush (Turdidae), a tit (Paridae), a jay (Corvidae), a vireo (Vireonidae), the Starling, the House Sparrow, two finches (Carduelinae), five American wood-warblers (Parulidae), a tanager (Thraupidae), four American sparrows and a cardinal (Emberizinae), and a grackle (Icteridae).

As I understand them, her main findings were as follows. There are four 'levels' of sun-bathing shown by passerines, involving characteristic 'sun positions', which appear to be similar in most features to those adopted by the doves and woodpeckers (see Chapter 4 for further details). Sun-bathing, it seemed to Hauser, can also be assigned to two quite different categories of response although both involve the same range of four postures:

> (i) the *'voluntary'* (normal sun-bathing), performed deliberately, 'apparently for reasons of health and well-being' and associated with preening; and
> (ii) the *'compulsory'*, assumed involuntarily 'when the bird is suddenly and apparently unexpectedly exposed to direct sunlight, under more or less extreme conditions of humidity and heat', the response appearing 'to be unpremeditated and irresistable' with the bird departing for the shade as soon as it has 'recovered'.

As well as her own examples, Hauser interpreted the behaviour of the Reed Warbler described above as a case of compulsory sunning.

Spells of *voluntary* sun-bathing, she found, often alternated with brief spells of preening, head-scratching, and feeding, though when it was very hot the birds did not preen at the sunning place and probably bathed afterwards. Sunning sessions also sometimes followed bathing and preening; and three species (Carolina Wren, Brown Thrasher, House Sparrow) were noted to combine dusting and sunning. Normal sunning occurred, often sociably, at certain sites 'day after day and month after month'; however, though there were also many incidents during hot dry periods, it was most frequent on days of strong sunlight following a spell of rainy or dull weather (as if the birds are deprived of 'necessary irradiation' by continuous days without sun and have to make up for it afterwards). Juveniles were seen sunning more often than adults except during the period of the latter's post-breeding moult (see further, below). While admitting that the function of normal sunning is not known, she wondered if the behaviour might result in the absorption of ultra-violet rays through the eye (see Chapter 8), stimulate the production of preen-gland oil for the dressing of the plumage, or help to remove external parasites (which might increase in numbers during the times when damp, cool weather made sunning

impossible). She also mentioned unpublished experiments by Dr H. Friedmann which had established that irradiated preen-oil is a source of Vitamin-D when inadvertently swallowed during preening.

At Mrs Hauser's home in Florida, *compulsory* sun-bathing occurred mainly at a south-facing window feeder-tray especially on cloudless, humid days with still air and intense sun. The temperature at this site was particularly high at times and some birds avoided it entirely while it was in the sun (about four hours a day) or made their visits as brief as possible; juvenile Blue Jays, unlike the adults, appeared not to learn to avoid the tray during the sunny hours and reacted the most intensely of all. The behaviour was thought at first to be some form of heat prostration, later a means by which the birds regulate the body temperature when exposed to strong sunshine through 'a physiological response generated by the bird's heat-dissipating mechanism'. However, because the temperature readings taken at the feeder probably included the heat of the air, the heat of the tray, and the reflected heat of the white brick wall as well as the heat of the sun itself, and because sunning can also occur in air temperatures as low as 13–16 °C, Hauser also concluded 'that heat, alone, is not the motivating factor' and 'that the rays of the sun, rather than heat alone, caused the response'. As evidence for this last conclusion – which was, presumably, that it was the light of the sun (or some other non-thermal quality of sunshine) to which the birds were reacting as well as to its heat – she described how a female Northern Cardinal on the feeder during conditions of intermittent sun and cloud assumed one of the sunning postures each time the sun came out and abandoned it each time the sun went in, evidently assuming (incorrectly in my opinion) that little or no heat was involved. She also thought that humidity was more important than high air temperatures in eliciting compulsory sun-bathing.

It is difficult to reconcile all Hauser's conclusions with one another, or to get a complete idea of the seasonality of the sunning behaviour she observed (but see below). Her category of compulsory sun-bathing would seem to include heat-stress behaviour involved in cooling (and hence not strictly sunning at all) as well as true sunning induced by very strong external stimulation. The allocation of sunning episodes to the voluntary or to the compulsory, especially away from the feeder, seemed arbitrary and indicate an ignorance of the true nature of instinctive behaviour of this type (discussed further in Chapter 9). As to the role of heat in the elicitation of sunning behaviour (see also Dilger 1956, mentioned earlier), the observations of another American (Lanyon 1958) on hand-reared birds (a Western Meadowlark and a Starling) established the importance of 'a sudden warming of the bird's immediate environment' in the external motivation of sunning; his birds had first performed naturally in sunshine and later learned to do so in the heat of a convector heater under artificial light, continuing even when the light was switched off. Whitaker (1957; see also below), in her review of anting, queried Hauser's conclusion about the role of light in eliciting compulsory sunning and saw parallels

between sunning and anting, both of which she regarded as reactions to 'heat', i.e. sources of 'thermogenic' stimuli (but see Simmons 1958, 1966, for a different interpretation for anting); she also thought that certain sunning postures are 'very much like some of the attitudes described for anting', recalling the assertion by Rothschild and Clay (1952) that 'many birds when sunning themselves take up the passive anting position'.

In a later paper, published posthumously, Hauser (1973) stated that sunning at the North Carolina locality occurred among resident species from March to October, but mostly in June and July, though some winter visitors sun-bathed in the autumn and again from February until departure in April or May. She thought that the residents prefer sunning to anting during the period April to July, and anting to sunning during the period August to September (when they are also at the peak of the post-breeding and post-juvenile moult). The supposed link between anting and the moult had already been pointed out by Potter (1970); see further in Chapter 6.

Potter returned to the problem later (Potter and Hauser 1974), combining her observations on anting and sunning (also made in North Carolina) with those of the late Mrs Hauser. She now suggested, making no reference to earlier comments in the literature on this possibility (see above), that sunning and moulting are correlated as well as are anting and moulting. Most sunning occurs, in her opinion, when the moult affects the head, back, and breast (the feather tracts most easily exposed to sunshine but difficult of access with an ant held in the bill), most anting when the moult moves later to the wings, tail, and their coverts (those most easily reached with an ant in the bill). Thus, sunning and anting are complementary 'comfort-motivated' forms of behaviour used 'as means of applying heat to the skin' in order to soothe it during moult, the 'impulses to ant and to sunbathe' having a common origin. Understandably with this change in the interpretation of sunning behaviour, which appears to me to be made against many of the established facts (see later chapters, below), no distinction was made between voluntary and compulsory incidents of sunning (in Hauser's original sense); further, the importance of heat in the elicitation of sunning was belatedly recognized.

FURTHER CONTRIBUTIONS

Burton (1959), in his book on possible natural phenomena that might explain the phoenix myth, included some comments on the 'sunbathing or basking' behaviour of birds (and on their bathing, preening, and anting), covering reptiles and insects too. As well as providing descriptions and photographs of sunning postures in corvids and the Tawny Owl, he stressed the 'trance-like appearance' of sunning birds and the almost ritualistic use of certain sunning spots, possibly at particular times of the day. Though pointing out that sunning probably did have an anti-rachitic function, through the irradiation of preen-oil

'with the consequent formation of a vitamin', he appeared eventually to class the behaviour with other so-called animal addictions such as self-annointing, anting, and (in man) tobacco smoking. He recognized 'three phases in exposure to the sun':

> (i) 'sunbathing at ordinary intensity' (normal sunning);
> (ii) 'high-intensity sunbathing . . . the exaggerated, and often fantastic, postures, accompanied by an appearance of a trance'; and
> (iii) 'prostration from heat' (though 'this is hardly to be classed as sunbathing').

Among the second category, Burton included behaviour like that observed by Brown and Davies in the Reed Warbler and most of what Hauser described as compulsory sunning, though he rejected her category of voluntary sunning. His opinion, much like that of Hauser, was that 'Sunning seems to be the result of an innate response to bright light, accompanied or not by warmth . . . more dependent upon the brightness of the sun than on the temperature of the air'. As he believed that anting is the behaviour pattern that is basically a response to heat or the impression of heat (see Whitaker 1957), Burton seemed forced into seeking a different stimulus for sunning, even in lizards and other cold-blooded animals, which, as it is well known, *must* sun-bask at times in order to gain heat. Though, unlike Whitaker, he saw little similarity between the sunning and anting postures themselves, he thought that sunning, anting, preening, and bathing are all inter-linked, with 'the possibility of one set of behaviour overflowing into another', and 'that sunbathing, the most primal of all, may have furnished the origins of anting'.

Similar ideas were advanced by Conway (1959), a zoo curator familiar with sunning and other behaviour in a diversity of bird species; he, however, recognized heat as the main factor involved in sunning. He too thought that 'the limits of behaviour termed anting, bathing, dusting or sunning are arbitrary at best' and that such behaviour might be 'points on a continuum'. Sunning and anting, in his view, are closely connected: perhaps 'the same basic response varied by position and focus of stimulus'; 'active' anting is a response to an extremely localized, or focused, 'thermogenic' stimulus (see Whitaker 1957) and sunning a more general reaction to a more diffuse heat source (see Lanyon, outlined above), with 'passive' anting intermediate, perhaps depending on the moderately localized stimuli of numbers of ants (see Chapter 6 for brief descriptions of active and passive anting). Whitaker (1960) took up this idea again, claiming that 'It is well known that certain parallelisms of posture and movement may occur in the sunning, bathing, dusting, and anting activities of birds', which are 'not separate and distinct habits but a behavioral complex', as indicated by the likelihood 'that the sensation of heat can be a common factor'. Her evidence, however, was far from convincing, the given cases being referable to sunning (Western Kingbird, Blue Jay) and probably to incipient dusting (young Brown Thrasher); in all cases, background warmth as well as

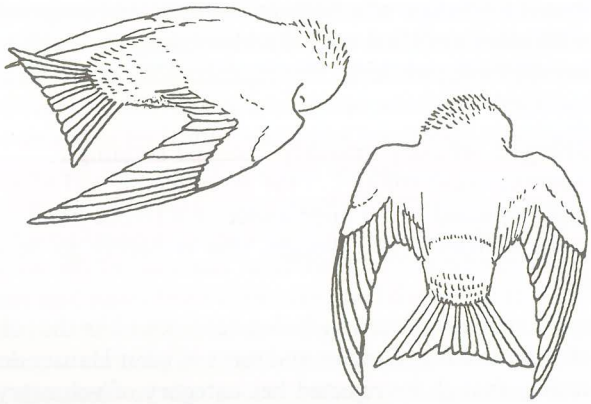
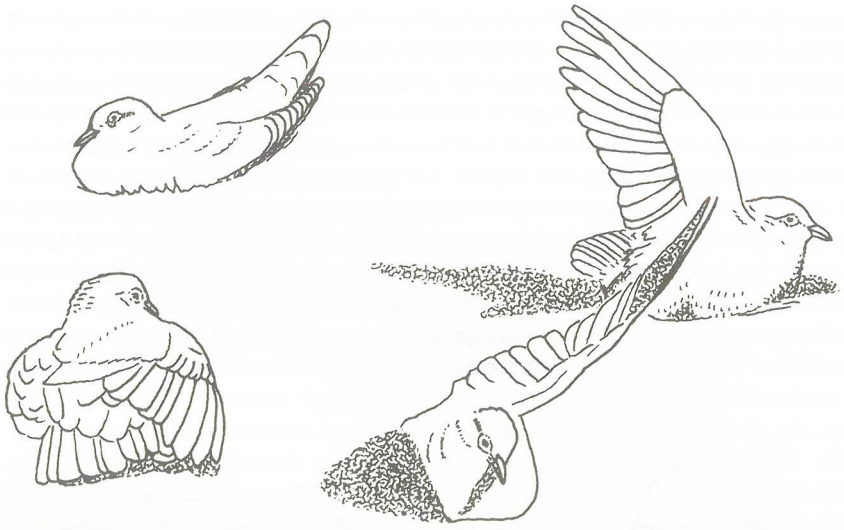


Fig. 13 *'Spreadeagle' postures of sunning House Martins as recorded by R.J. Prytherch.*

direct solar heat seemed clearly involved (see also below, and Chapter 8).

The sunning behaviour of martins and swallows (Hirundinidae) next drew attention in America (Johnston and Hardy 1962, Whitaker 1963, and Barlow *et al.* 1963), adding to the earlier observations made in the Old World by Heinroth and Heinroth (1924–33), P.H.T. Hartley (in Gibb 1947), and Rollin (1948), though these were not mentioned by any of the American contributors; for later notes on hirundines, see King (1970), Prytherch (1981), and Butler (1982). Most of these records seem to be referable to sun-basking in hot places on otherwise cool or windy days, as also may those cited by Whitaker (1960) of thousands of immature Sand Martins (Bank Swallows) gathering on a tarmac surface and some 40 immature (Barn) Swallows gathering on warm sand. However, the Sand Martins and Cliff Swallows watched by Barlow and others sun-bathed in conditions of high air temperature and humidity, though here too it was suggested that some of these birds, having alighted for other purposes, were stimulated to sun-bathe on being warmed suddenly on the hot surfaces (asphalt road, etc.) that they encountered.

Meanwhile, a study on sunning and other forms of 'bathing' in captive pigeons and doves of 19 species had been published in Germany (Nicolai 1962); see also Heinroth and Heinroth (1949) and Goodwin (1967b). Nicolai, too, found that a hot surface can be important in inducing high-intensity sunning at times (see further in Chapter 4). Almost all his columbids were keen sun-bathers but the frequency of the behaviour varied according to the type of habitat to which each species is adapted. In captivity at least, individuals of species that inhabit open country in the wild, including scrubland and open woodland, sunned themselves frequently and regularly, usually in the middle of the day (his Galapagos Doves, housed indoors, would gather habitually at



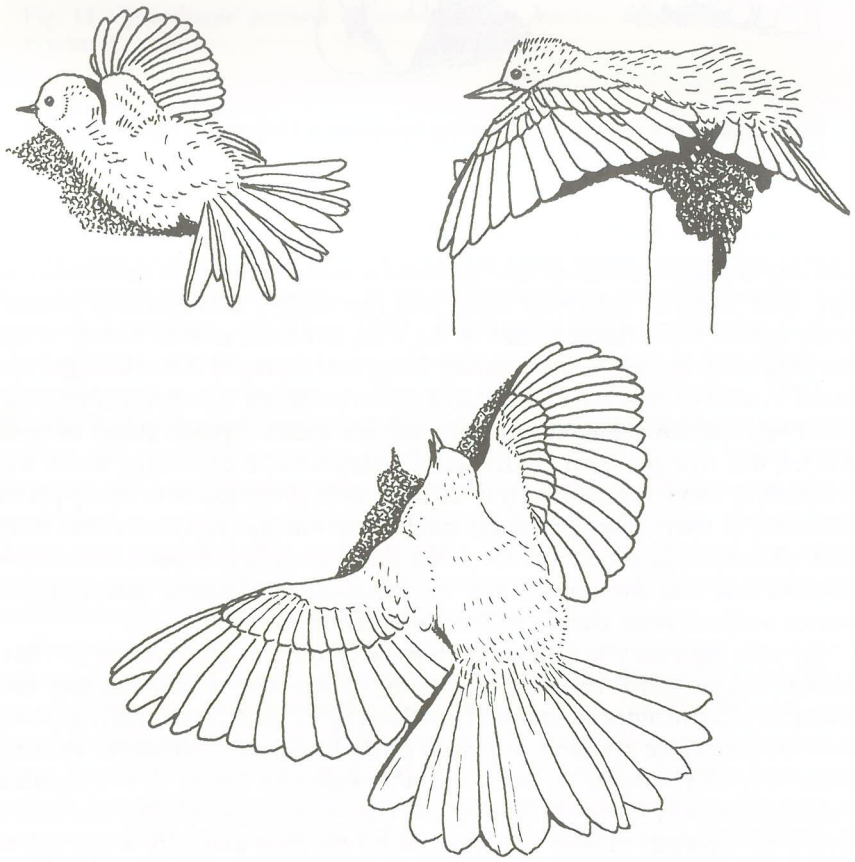
Figs 14–16 *Intensity-sequence of sunning behaviour in Galapagos Dove as recorded by J. Nicolai: 'wings-down' (upper left), 'lateral' (lower left), and 'raised-wing' posture (two birds).*

mid-day in winter and adopt low-intensity sunning postures in the absence of sun, such *'in vacuo'* behaviour being seen repeatedly). Individuals of ground-living species that inhabit forests in the wild, however, sunned mainly in the morning when the sun was less strong. Long deprivation of direct sunlight was found to have serious physical consequences, evidently through lack of ultra-violet light (which is filtered out when the sun shines through glass): in some species, this took the form of increasing melanism of the plumage which was reversed, at the next moult, only if the birds were given access to sunny places outdoors; in some other (tropical) species, the vitamin reserves in the body were affected to the extent that the young raised from early broods, before their mothers had had the opportunity for intensive sun-bathing following the winter, suffered from rickets unlike those of later broods.

My own summary in *A New Dictionary of Birds* was published in 1964, though written much earlier. Later in the 1960s, after a long lull that had produced but two notes on sunning (Bentham 1957, 1962), a series of important contributions again appeared in *British Birds*: firstly observations on sunning postures (with photographs), sites, and other topics by Teager (1967), together with comments by Goodwin (1967a) and later by Kennedy (1968); and then a review by Kennedy (1969) which contained the first and only world list of species known to sun-bathe (see further, below). These were supplemented by a note on sunning in the Mute Swan by Hiley (1969), accompanied by a comment by me (see Chapter 4), and a note by King (1970) giving details of the

sunning of three of the species that had been listed by Kennedy. Subsequently, nothing further on the topic of sunning appeared in the journal for a number of years. In 1969 also, sunning was one of the topics briefly treated in a chapter entitled 'Care of the plumage' in The Reader's Digest/A.A. *Book of British Birds* (pp. 300–303) for which I had contributed the original text and Robert Gillmor the illustrations.

In his summary, Goodwin (1967a) pointed out that most sun-bathing is voluntary, with the bird seeking or revisiting suitable spots for the purpose; though the functions of such sunning are 'still somewhat obscure', he thought one could be the control of ectoparasites. He too doubted that typical sun-bathing is a simple temperature response (i.e. merely a heat-stress posture) but conceded that birds may sometimes show typical sunning behaviour when



Figs 17–19 *Sunning birds observed by C.W. Teager: Dunnock (left) in 'raised-wing' posture; Starling in 'spreadeagle'; and Blackbird (lower) in 'spreadeagle'.*

forced to endure high temperatures, or when suddenly subjected to them, and when brooding or incubating in comparable conditions; included in this category were the postures that certain birds adopt when shielding young (see Chapter 4). He also mentioned that many birds will expose themselves to the sun simply to get warm at times, usually without resorting to typical sunning postures, such 'simple sun-bathing' (i.e. simple sun-basking) occurring mostly on sunny mornings, just after sunrise following a cold night; in hot climates, the birds showing this behaviour prefer to rest in the shade when the temperature has risen.

Goodwin also mentioned the possible relation between sunning and the production of Vitamin-D and this topic was discussed in some detail by Kennedy (1968) who concluded that 'the balance of the evidence . . . seems not to favour the vitamin hypothesis, and other, simpler explanations of sunbathing in birds should be sought' (see further in Chapter 8). In his main review, Kennedy (1969) suggested that sunning behaviour could serve variously:

> (i) to lose heat, as a simple temperature response (as suggested by Morris 1956, but not by me as Kennedy stated), this being the 'most probable explanation for compulsory sunning';
> (ii) to gain heat, this being the purpose of voluntary sunning 'in some circumstances';
> (iii) to dry the plumage;
> (iv) to assist the moult, as suggested by Harrison (1946); and
> (v) to play a role in feather-care by increasing the flow of the preen-gland secretion, though he was not convinced that sunning served any function in feather maintenance generally, especially the control of ectoparasites.

Surprisingly, he accepted Hauser's two types of sun-bathing (voluntary and compulsory) as quite distinctive.

Also during the 1960s, and in the 1970s, physiologists started to get interested in the question of energy conservation through insolation (e.g. Heath 1962, Morton 1967, Hamilton and Heppner 1967a,b; Lustick 1969, 1971, Lustick *et al.* 1970, Heppner 1970, Ohmart and Lasiewski 1971, Calder and King 1974, De Jong 1976). See also Kahl (1971) for storks and Storer *et al.* (1975) for grebes. This topic will be discussed in detail in the chapter on sun-basking. A cautionary note was struck by Cade (1973), however. While confirming, from his own observations on mousebirds (Coliidae) and the Pygmy Falcon in the Kalahari Desert, that sunning behaviour can have a heating function, he had also observed how his tame Bateleur Eagles would sun-bathe long after they had become hyperthermic and had to pant heavily to cool themselves. Similar behaviour had been seen from many birds that engaged in a 'sudden explosion of sun-bathing activity' at the Los Angeles Zoo one day when the rays of the afternoon sun began to penetrate their aviaries: 'a stimulus situation . . . similar to the natural occurrence of a sudden change from

shade to bright sunlight, as when an obscuring cloud moves out of the sun's path or when the sun first appears above the horizon in the morning . . . situations associated with spates of sunning by birds in nature (Kennedy 1969, Kahl 1971, Cade, unpublished notes)'. Most of these birds, he suggested, must have been well within their zones of thermoneutrality or approaching the upper critical limit at the time. He thought that such behaviour is 'inconsistent with a heat-absorbing function for sun-bathing'; neither can it 'have a cooling function when birds face the sun', so 'it would be a mistake to conclude that sun-bathing is mainly or only a thermoregulatory mechanism'. Among several unexplained aspects that did not fit this last assumption, 'the compulsive or reflexive character of the response under strongly stimulating conditions even when the bird is overheated' should be noted. Thus, once again, the evident dichotomy of the phenomena, involving sun-basking (on the one hand) and 'something else' (on the other), was being probed.

This and other problems of interpretation had already been covered in a short review by Mueller (1972) though the experiments that stimulated it seem to have been inconclusive. He had subjected captive Broad-winged Hawks to sources of white and red light with different intensities of brightness but approximately equal intensities of total radiant energy. From their reactions, he concluded that his buzzards were 'responding to an increase in illumination, not heat' and that it seemed 'unlikely that the sunbathing was a conditioned response to light with the unconditioned stimulus being heat'; however, as the birds had not been taken from the nest until three weeks old, it seems likely to me that they had already gained enough experience of the sun in the wild to identify a bright, localized light as a potential source of heat (see further in Chapter 9). In his introduction, Mueller had suggested that 'there are at least several kinds of sunbathing behaviour and perhaps several functions as well' but he later recognized just two:

> (i) 'sunbathing' proper, 'involving exaggerated stereotyped postures held for a relatively prolonged time', the function of which 'remains obscure'; and
> (ii) 'basking', forms of sunning-like behaviour 'without any extraordinary postures' which, together with other forms of 'heat-bathing' (such as 'smoke-bathing'), 'appear to function in the conservation of body heat'.

In his introduction, Mueller had also concluded 'Of the several hypotheses concerning the function of sunbathing behaviour (see e.g., Simmons 1964, Kennedy 1969), the conservation of body heat seems to be gaining acceptance'; in fact, no such function of sunning had been suggested by me, and now Mueller himself was excluding such behaviour from the category of true sun-bathing, presumably because his experiments had overstressed the importance of light as a factor in eliciting exaggerated sunning postures.

A brief review by Haensel (1972), accompanying photographs of a number of ciconiiform and accipitrid birds (taken in captivity by G. Budich), was

confined to a few European sources (mainly Nicolai 1962). Sun-bathing generally, Haensel concluded, airs and warms the body, builds up the powers of resistance by affecting the vitamin budget (stabilizing Vitamins-A, -B2, -C, and -E, and regulating Vitamin-D), improves the circulation of the blood, generally promotes health and efficiency, and discourages feather-lice (Mallophaga), which were said, on the authority of Dathe (1964), not to be able to tolerate solar radiation. A note on the sunning of a hand-reared Starling (which was especially fond of sunning after a cool night or a bathe) followed in the same journal (Langfeld 1973).

The question of the synthesis of Vitamin-D by sunning had also been raised by Weisbrod (1971) in his study of the 'toilet behavior' of the Blue Jay. Unlike other reviewers, however, he thought that the vitamin is produced *after* the ingestion of the preen-oil, or of the feathers themselves, through the later exposure of the skin to sunlight. Otherwise, it seemed to him that sunning 'may be important in the maintenance of the feathers or the integument', judging from the feather and limb postures ('suggestive of toilet behaviors') adopted by his jays when performing. The feather ruffling and gaping that occur during sunning, he suggested, 'may also be partly a response for regulating body temperature' due to the heat, though such a possibility, 'if true, does not necessarily mean that heat regulation is the sole function of sunning (if a function at all)'. Also in America, as we have seen, Hauser (1973) and especially Potter and Hauser (1974) had returned to the topic of the possible relationship between sunning (and anting) and moulting.

Finally for the 1970s, mention must be made of a short review by another zoo curator (Poulson 1974) based on his own observations of sunning by some half dozen species in the Copenhagen Zoo and two (Blackbird, Song Thrush) in the wild and upon a selection of the literature (including Heinroth and Heinroth 1924–33, Hauser 1957, Teager 1967, Kennedy 1969, and Mueller 1972). He found that sunning occurred mostly at the warmest time of the day at the warmest time of the year, especially after a spell of cloudy weather, either when the birds 'deliberately went into a sunny place or by accident were suddenly caught by the sunbeams'. Captive birds also sunned indoors under 'light from spotlights' but not under 'the diffuse light from neon tubes'. As sunning also occurred 'at other times of the year, when it was cold', he concluded (while conceding that it could possibly be 'released by radiant heat') that 'sunning is not caused by warmth as such' but is a reaction to bright light. After reviewing theories on the possible function of sunning, he suggested that the behaviour (which is accompanied by feather erection, followed or interspersed with preening, and seems to increase in frequency at the time of moulting) is performed 'to accumulate warmth' and 'belongs to comfort behaviour and in some way is good for the feathers', while possibly at the same time providing 'pleasurable stimuli'.

RECENT CONTRIBUTIONS

So far in the early 1980s, additions to the sunning literature have included: a key note on the function of sunning, based on observations mainly on the Indian White-backed Vulture (Houston 1980); a paper giving extensive field observations on the timing of bathing, dusting, and sunning (Stainton 1982); a paper on the wing-drying and sun-basking behaviour of the American Darter (Hennemann 1982); short papers on the sunning postures of captive pheasants and ibises (Wennrich 1980, 1982); the notes by Prytherch (1981) and Butler (1982) on hirundines already mentioned; and notes by King (1981b) on the Caspian Tern and Simmons (1982b, 1983) on the Mistle Thrush and Wren. Some 1983–84 additions are given in Note 4. American birdwatchers have had the subject reviewed for them quite adequately by Terres (1980), though his implication that sunning is *only* a reaction to sudden exposure to strong sunshine is misleading. For earlier summaries, see for example Berger (1961), Welty (1964), and Yapp (1970); like Terres, these authors treated sunning in the general context of 'bathing' (Yapp under the unexplained heading of 'Self-stimulation'). Generally, however, the topic of sunning has been neglected in general works on ornithology and bird behaviour, but there is a short entry on 'sun bathing' in McFarland (1981) where it was reported that sunning in pigeons 'is a response to light' as 'demonstrated by experiments using a bright directional light in a temperature-controlled cage'. Unfortunately, this statement was undocumented and I have not traced its origin; it led to the conclusion that sunning in birds, unlike that of many, predominantly cold-blooded, animals, 'is not primarily thermoregulatory, but is designed to allow sun-light to reach the skin' probably to encourage 'the synthesis of vitamin D in the skin', a surprising gloss which overlooked most of the pertinent literature.

After a brief review of suggested functions for sunning, Houston concentrated on the possible function of those forms of the behaviour that are evidently not concerned with thermoregulation. He described how his vultures would sun themselves only under certain conditions, not at the communal night roost in the morning sun but when resting in trees or on the ground later in the day after flying in to a source of food; then they postured only in strong sunshine, reacting within five seconds if it had been overcast previously, each bird for a standard spell of four to five minutes only, even if the sun remained strong. He suggested, and proved experimentally, that exposure to heat for just this period rapidly restores the flight-feathers to their original shape after they have become deformed by the stresses of flight (this process otherwise requiring several hours of rest); such an explanation of sunning, he suggested, could well apply to other large species that soar or flap for long periods, though perhaps not to small birds, the behaviour in that case 'probably serving a number of functions which may or may not include feather maintenance'.

Stainton's work was carried out in south-east England over several years, that on sunning mainly involving the Blackbird, Song Thrush, and Starling.

These species were found to sun mostly and at highest intensity during the twelve mid-summer weeks (11 May to 2 August), during those hours of the day (as well as seasonally) when the sun is high in the sky; unlike the birds observed by Potter and Hauser (1974) in America, the English ones sunned most during settled spells of sunny, dry weather and seldom directly after rain, though outbursts of sunning occurred at times on the next sunny day after a sequence of sunny days had been interrupted by a rain shower or a day or more of overcast. The birds would usually perform in bright sunshine, when air temperatures were in the range 18–30°C, but also in rather hazy conditions when they (and Robins and Dunnocks) 'sometimes switched out of, and back into, sunning postures with minor gains and losses of light'. Fluctuations in heat in such circumstances were, however, not considered by Stainton who (like Hauser, Burton, Mueller, and Poulsen) seemed to attach primary importance to light in the causation and function of sunning; in her opinion, heat is more of a deterrent, though less so than in the case of bathing and dusting. Thus, she argued, sunning could well 'represent a supplementary or alternative way of using sunshine' to bathing or dusting, all three commonly occurring 'when and where it is sunny'. The two thrushes and the Starling usually adopted postures of the type recognized by Mueller as true sun-bathing ones (though descriptions of the postures involved, and of sunning sites, were outside the scope of the paper). She found it difficult, however, to define the sunning behaviour of the House Sparrow (spells of which tended to be brief and casual), Wood Pigeon and Feral Pigeon. The two pigeons were often observed lying down in sunny places where they would bask (in the restricted sense of Mueller) most of the time, with individuals changing into and out of sunning postures quickly and frequently. The sparrows behaved rather similarly while loafing at their dusting sites in summer, some perhaps sunning briefly when the sun came out but most beginning to dust and preen; in winter too, an onset of sunlight was more likely to be followed by bathing or dusting than by sunning. Heinroth and Heinroth (1924–33), incidentally, had already pointed out that gamebirds are particularly likely to dust when the sun is shining; Conway (1959), too, recorded that captive gamebirds are prone to dust in the sunny parts of their cages, relating this to the heat factor involved. Summers-Smith (1963), however, found that House Sparrows sun mainly on roofs away from their dusting sites (see further in Chapter 4).

A LIST OF SUNNING BIRDS

Sunning behaviour has now been reported in numerous species of birds of many taxonomic groups. Kennedy (1969) listed some 85 species of 25 non-passerine families and 85 species of 23 passerine ones, of which 25 species had been included from the unpublished notes of I.J. Ferguson-Lees, a further three from those of Bernard King (see also King 1970) and one from those of J.C.

Rolls, and the rest from the literature, though a number of records from sources cited were overlooked and have been added to the totals below, plus a few more from other earlier sources that I happen to have noted.

Some of the omissions were from Heinroth and Heinroth (1924–33), surprisingly as that work was cited by Kennedy for other records, and included the Glossy Ibis, Honey Buzzard, Red Kite, Hobby, Grey Partridge, Great Bustard, Oystercatcher, Stone Curlew, Short-eared Owl, Middle Spotted Woodpecker, Whinchat, Blue Rock-thrush, Aquatic Warbler, Great Reed Warbler, Barred Warbler, Marsh Tit, Blue Tit, Penduline Tit, and Rock Sparrow. Further, priority of records for the following species should also have been given to the same authors: the Grey Heron, Rock Dove/ Feral Pigeon/ Domestic Pigeon (see also Heinroth and Heinroth 1949), Turtle Dove, Nightjar (see also Heinroth 1909, Turner 1914, Lack 1932), Bee-eater (see also Koenig 1951), Hoopoe, Wren, Blackbird, Great Tit, and Tree Creeper.

The families represented in Kennedy's list, as supplemented, were as follows (plus the four families from Heinroth and Heinroth he omitted).

NON-PASSERINES: the Podicipedidae (grebes), one; Procellariidae (petrels and allies), one; Sulidae (boobies, gannets), four; Ardeidae (bitterns, herons), 11 – see also Meyerriecks (1960) for the Green-backed Heron, Tricolored Heron, Reddish Egret, Snowy Egret, and Great Blue Heron; Ciconiidae (storks), one; Threskiornithidae (ibises), two; Anatidae (wildfowl), two; Cathartidae (New World vultures), five – see also Armstrong (1943) for the King Vulture, Poulsen (1963) for the Andean Condor; Accipitridae (Old World vultures, hawks, and allies), eight – see also Owen (1916, 1919) for the Sparrowhawk; Falconidae (falcons and allies), four; Tetraonidae (grouse), two – see also Kratzig (1940) for the Willow Grouse; Phasianidae (partridges, pheasants, and allies), four; Rallidae (rails and allies), nine; Otididae (bustards), one; Haematopodidae (oystercatchers), one; Burhinidae (thick-knees), one; Charadriidae (plovers), one; Scolopacidae (sandpipers and allies), one; Sternidae (terns, noddies), four; Columbidae (doves, pigeons), 24; Cuculidae (cuckoos), two; Tytonidae (barn owls), one; Strigidae (typical owls), four; Caprimulgidae (nighjars, etc.), one; Colliidae (mousebirds), three; Meropidae (bee-eaters), three; Upupidae (hoopoes), one; and the Picidae (woodpeckers), three.

PASSERINES: the Tyrannidae (American flycatchers and allies), three – see also Whitaker (1960) for the Western Kingbird; Alaudidae (larks), 10; Hirundinidae (swallows, martins), five; Troglodytidae (wrens), two; Mimidae (thrashers), three; Prunellidae (accentors), one; Turdidae (chats, thrushes), 19 – see also Nice (1943) for the Redstart; Sylviidae (warblers and allies), ten; Muscicapidae (flycatchers), one; Aegithalidae (long-tailed tits and allies), one; Paridae (true tits), four; Certhiidae (creepers), one; Remizidae (penduline tits and allies), one; Laniidae (shrikes), two; Corvidae (crows, jays, and allies), five – see also Burton (1959) for the Jay, Magpie, and Rook; Sturnidae (starlings), one; Passeridae (Old World sparrows), three; Estrildidae (waxbills, etc.), one; Vireonidae (vireos), one; Fringillidae (finches), 11; Parulidae (American wood-warblers), six – see also Berger (1961, 1968) for Kirtland's Warbler; Thraupidae (tanagers), one; Emberizidae (buntings and allies), nine – see also Nice (1943) for the Song Sparrow; and the Icteridae (troupials, etc.), two – see also Lanyon (1958) for the Western Meadowlark.

At least three other families (all non-passerine) should also have been added to the list:

> the Laridae (gulls), three species – the Black-headed Gull, Lesser Black-backed Gull, and Herring Gull (seen by Rollin 1948 to sun themselves in captivity without going into 'normal sun-bathing postures'); Psittacidae (parrots), a 'number of species' observed in captivity by E.N.T. Vane (see Harrison 1961); and the Bucerotidae (hornbills), two species – the Casqued Hornbill and the Crowned Hornbill (see Kilham 1956).

These records give a good idea of the variety of birds concerned, though some were inadequately substantiated and others probably misinterpreted. Sunning behaviour is evidently widespread in the kingdom Aves, unlike dusting and anting for instance, though the task of making a really comprehensive list of sunning species is a daunting and perhaps rather pointless one, rather like listing the birds that bathe. However, as with bathing (see Simmons 1985, under 'Comfort Behaviour'), an analysis of the method of sunning shown by different species and higher taxa would be valuable and that cannot be adequately done from unannotated lists and records, especially those that have not been compiled critically enough.

In particular, it seems dubious to met to classify species as sunning ones solely on the basis of the *assumed* sunning of the unfledged young (which may not yet be able fully to control their own temperatures) when the postures adopted are not shown by the adults and the adults themselves have not been recorded as sunning. At least three species found their way on to Kennedy's (1969) list thus: the Great Crested Grebe, the Australasian Gannet, and the Killdeer.

The grebe was included solely on the basis of Rankin's (1947) casual comment that two recently hatched chicks that he was photographing sunned themselves when hot sunshine fell upon the carrying adult's back at the nest. Though B.W. Tucker stated that adult Great Crested Grebes in spring 'when undisturbed, will sometimes land and sun . . . close to water's edge' (Witherby 1940), I have never seen any individual of this species, adult or young, show true sunning behaviour in thousands of hours watching since 1948. That adults of some, mostly small, grebe species will sun-bathe in a quite characteristic manner has been shown by the later observations of Storer *et al.* (1975; see Chapters 4 and 7), but such behaviour seems not to occur in larger species of temperate climates. Those chicks of the Great Crested Grebe may have been basking as supposed but they may just as well have been attempting to cool themselves by leaving the heat trap under the adult's wings; we just do not know as the observation has never been repeated and Rankin's photograph was unhelpful. Similarly, the Killdeer was included solely on the alleged sunning of the chicks in a posture that is adopted when resting, whether in the sun or not: the birds 'sit back on their heels, holding the body up at right angles to the long outstretched tarsi', a posture that the adults were never observed to take (see

Fig. 20 *Cooling posture of Eleonora's Falcon at nest; note ruffled dorsal plumage and drooped wings.*

Davis 1943). The posture also differs both from the more common one adopted by young Killdeers in the sun (see Nice 1962) and the simple sunning posture that adult waders and gulls assume at times (see Chapter 4). Finally, the gannet was listed as a sunning species on the authority of Warham (1958) who, however, categorically stated that the adults were never seen to sun themselves although the downy nestlings 'appeared to sun-bathe' at times. In fact, none of the three species of gannet is known to show sunning behaviour (see Nelson 1978) though the six species of booby do; all sulids, however, show elaborate cooling behaviour and the situation is most complex (see Chapter 5).

A number of other sunning records included by Kennedy seem suspect, but I will comment only on one more here. Though later known to show true sunning behaviour (see Ristow *et al.* 1980), Eleonora's Falcon seems to be on the list solely on the basis of a photograph in Vaughan (1961) of a female adopting a heat-stress posture in order to cool herself on the nest, as the caption made clear. As Kennedy had accepted Hauser's category of 'compulsory' sunning behaviour, he presumably included species like Eleonora's Falcon on that basis, unwisely in my estimation (see further in Chapter 4); he was not consistent, however, and omitted the Reed Warbler (see above).

CHAPTER FOUR

Sunning Behaviour Described

I believe that our better understanding of sunning behaviour has been hindered by those who consider it merely one aspect of a general 'bathing' phenomenon (such is the misleading effect of blanket terms of this kind). Much misunderstanding has arisen because of the lack of a comprehensive general classification of sunning postures and of detailed descriptions. While most observant birdwatchers would recognize a bird sunning typically – that is, one adopting a characteristic posture, usually on the ground, in strong sunshine – it is by no means generally agreed, as we have seen, what constitutes the full range of sunning behaviour. Many accounts of sunning in the literature describe only a few, often single occurrences (and those not always accurately) and deal only with the more striking postures. Kennedy (1969), for example, included in his category of 'sunbathing' mainly the 'typical attitude . . . spread-eagled with tail and wings spread, contour feathers ruffled, mandibles parted and the eye facing the sun wide open', though he also mentioned that some birds (pigeons, hirundines, Tree Creeper, Dunnock) expose the underwing. Similarly, Mueller (1972) would restrict true 'sunbathing' to 'those behaviour sequences involving exaggerated, stereotyped postures held for a relatively prolonged time', such postures consisting of 'spread wings or one upraised wing'. Both these reviews, therefore, failed to identify the sunning posture that is the most commonly seen, especially in passerines, near-passerines, and pigeons; this had been described succinctly by Goodwin (1956, etc.) as 'leaning sideways with feathers erected and the near wing and near half of the tail spread'.

Hauser (1957) recognized four 'levels' of sun-bathing in passerines, involving characteristic 'sun positions' (which appear to be similar in most features to those adopted by the doves and woodpeckers she observed).

> In Level I, the bird elevates the crown feathers, droops both wings so that the tips of the primaries touch the ground, and spreads the tail.
> In Level II, it also has the body plumage 'fluffed fully' (i.e. ruffled).
> In Level III ('full' sun position which usually lasts from 15 seconds to two minutes or more at a time), it also leans to one side, settles, opens its bill, and stares at the sun with the upper eye, remaining immobile.
> In Level IV ('exaggerated' sun position), it lies flat with feathers ruffled,

both wings outstretched, tail fanned, and head often inclined far to one side; when the back is to the sun, the rump feathers are erected so much that the naked oil-gland is fully exposed.

Though the distinctions need not concern us at this point, the postures of Level III (especially) and Level IV seem to be the ones most closely associated by Hauser with her category of voluntary sun-bathing, while the postures of all four levels were involved in those incidents interpreted by her as compulsory sunning (see Chapter 3). However, as suggested by Weisbrod (1971), Level I may well represent a simple heat-stress response and not sunning at all; I think this could well be true of Level II also, especially as the birds adopting both these postures at Hauser's feeder usually did so for only brief moments before departing for the shade.

Using my own observations (particularly those on passerines) as a basis, a preliminary attempt at a more comprehensive classification of sunning behaviour is presented below. I have (like Hauser) recognized different intensity levels of sunning, though these are still rather arbitrary and it has not always been easy to allocate published descriptions to them, especially among non-passerines. My five categories are:

(1) simple sunning behaviour,
(2) the 'wings-down' posture,
(3) 'lateral' postures,
(4) 'raised-wing' postures,
(5) 'spread-wing' postures.

The postures of level-2 to level-5 comprise the behaviour that most people would consider to be true sunning, particularly those of level-3 and level-4 (in which the bird exposes one side at a time to the sun) and of level-5 (in which it mainly faces the sun or turns the back to it). These are described below, drawing on published accounts as well as on my own information; additionally, some observations kindly supplied by D.E. Ladhams, Bernard King, and others have been included or appended. It should be remembered that at this stage we are concerned largely with the postures that birds adopt when they deliberately seek or remain in a place in the sun. The same behaviour may also be induced 'unwillingly' in certain instances, but that is another problem that will be dealt with mostly later (in Chapter 9). However, I have included those sunning-like postures which many birds (especially large non-passerines) adopt at the nest when caught in the sun and when shading their young, also those used for wing-drying, and will comment on them later in this chapter.

LEVEL-1: SIMPLE SUNNING BEHAVIOUR

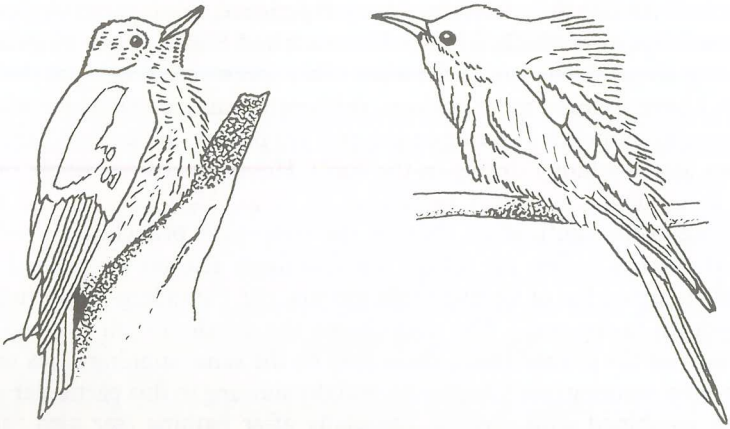
As also noted by Rollin, Goodwin, and others (see Chapter 3), passerines and other birds will sun themselves without adopting any of the more specialized sunning postures. Such basic sunning is probably widespread but generally

overlooked. Among the passerines, in my experience, this is particularly true of the House Sparrow which, like the Dunnock and Starling, can often be seen 'pottering-about-in-the-sun', even when other species are keeping to the shade, though I have in mind more obvious, deliberate sunning behaviour while the bird remains immobile ('loafing-in-the-sun') or preens ('preening-in-the-sun'), at times after bathing ('drying-in-the-sun'). House Sparrows, singly or more often in groups, show such behaviour in trees, high hedges, and bushes ('perching-in-the-sun'), often chosing the outermost branches, though sun-dappled perches within the foliage are also used; also on the ground or the equivalent, up on flat or sloping roofs, gutters, etc. ('standing-, squatting-, and sitting-down-in-the-sun'). The sites chosen are usually in full sun and out of any wind: on the ground (etc.), these may be the same sunning spots used for higher-level sunning (see Chapter 8), and the sunning in this particular species is often combined with dusting, especially after bathing (see also Stainton 1982).

I have seen similar simple sunning behaviour from other passerines (both on and off the ground unless otherwise stated), including a Wren (flat roof), Dunnocks (mainly on the ground, but also in a hedge and on a flat roof), Blackbirds, Song Thrushes (ground only), a Blue Tit (hedge), a Magpie (top of hedge), Starlings, Bullfinches (hedge, bush), and Reed Buntings; also from a Collared Dove (hedge) and a Turtle Dove (tall tree). It has also been observed in Skylarks, Meadow Pipits, Yellow Wagtails, and a Pied Flycatcher (all on the ground); and from a Short-toed Lark (roof) (B. King). Sitting-down-in-the-sun, with or without preening, is particularly characteristic of the Dunnock, both after a bathe (when it is accompanied by drying movements, particularly on short grass where the bird may first creep about mouselike when wet, drying itself against the grass stems) and at other times (when the behaviour often leads to, follows, or intersperses more elaborate, level-2 to level-4 sunning); see further in Note 5, and also under Level-2 (below).

Birds sunning in the level-1 manner often face or turn the back to the sun but may position themselves at any angle to it, usually without gaping (see also Barnes 1975); as described by Goodwin (1967a), who has seen simple sunning in a number of passerines (and pigeons), they usually just fluff the plumage to some extent at most, though they may alternate between simple sunning and more characteristic sunning postures (see also Stainton 1982). In my experience, the 'pure' basic sunning of passerines (i.e. excluding that occurring during lulls in fuller sunning, as also often happens) may involve no obvious feather posturing at all or a general fluffing or even ruffling of the body plumage, often with the wings covered by the flank feathers and sometimes also the legs by those of the belly; the head and neck feathers may also be erected and the head positioned, with bill raised, at various angles to the incidence of the sun's rays, as in fuller sunning.

Among near-passerines, level-1 sunning has been described in the woodpeckers and bee-eaters (at least). Posturing with just the body feathers



Figs 21–22 *Simple (level-1) sunning postures of two near-passerines: Middle Spotted Woodpecker (left) and Bee-eater.*

erected may be the most common manner of sunning in the Picidae (Poulsen 1974), though more elaborate postures occur (see under Level-3 and Level-5, below). Among the Meropidae, the Bee-eater (for example) will posture in the sun at various angles to the incident radiation with its feathers ruffled, either those of the breast and belly (radiation from the front) or those of the upper mantle, which are raised almost vertically so that the bare skin is exposed (radiation from the rear) (Koenig 1951). Such perching in the full sun with the back turned to the sun and the mantle feathers erected like a fan is the most common sunning posture among African bee-eaters generally, occurring at any time of the day (Fry 1972, C.H. Fry); however, this behaviour is also the low-intensity stage in more elaborate sunning (see under Level-3 and Level-5). African bee-eaters will also adopt a 'broken-neck' posture with the feathers of the side of the neck and throat to the sun, 'obviously exposing flesh to direct rays' (see further in Note 6).

Of the African mousebirds, three species (the Speckled, White-backed, and Red-faced) are known to sun in groups – singly or in clusters – with 'legs spread-eagled and bellies turned towards the warmth' (Rowan 1967). They do so mostly in the early morning, especially after precipitation (rain or heavy dew) which tends to drench the birds' lax body feathers with moisture; see also under Level-5.

Owls will at times huddle against the trunk of a tree in the sun with feathers ruffled and the wings held slightly away from the body, though this may represent level-2 or low-intensity level-5 behaviour. Such posturing has been recorded from the Little Owl (B.A.M. Chappell in Gibb 1947) and Tengmalm's Owl (see Glutz and Bauer 1980), while an eight-week old captive Barn Owl was reported sunning on a fence facing the sun with eyes closed (T.R. Evans in

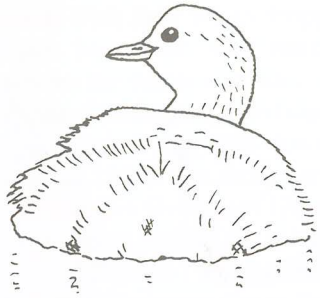


Fig. 23 *Sunning posture of Little Grebe (level-1 or level-2).*

Gibb); like most sunning birds, however, owls often stare into the sun while sunning (Heinroth and Heinroth 1924–33).

The Black Skimmer (Rynchopidae) has a simple but highly characteristic manner of sunning best described here. Bernard King watched a number of parties (each of some 20 or less) at Cape Canaveral, Florida, on 12 March 1972:

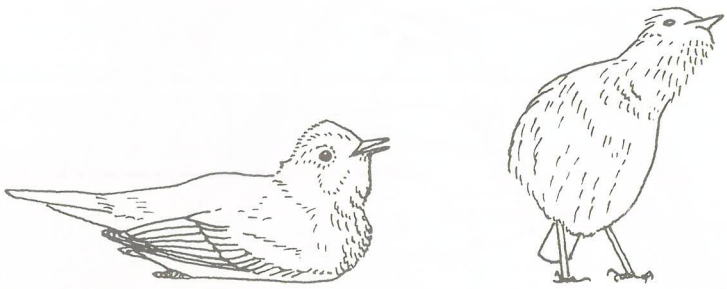
> Each bird lay prostrate on very hot sand, fully exposed in intensely hot sun for about three quarters of an hour. Stretched out with head and neck fully extended in front and legs behind, the whole of the body was rather elongated in appearance, so that, when viewed from a height or long distance, the birds looked like pieces of driftwood (for which they were first mistaken).

He subsequently saw the skimmers resting like this on many occasions, including a party of six well inland at Lake Fairview (Orlando) on a sloping concrete jetty, and remarked that 'they seem wilfully to seek the very hottest places to sun-bathe'.

Among other non-passerines, the sunning behaviour of certain grebes (see Storer *et al.* 1975, and further in Chapter 7) may for convenience be classified as belonging to level-1, though it may perhaps better be assigned to level-2: facing away from the sun, they float on the water with the closed wings uptilted, the feathers on the lower back raised, and the skin beneath exposed. Simple sunning of this sort has also been recorded from the Turkey Vulture (Heath 1962) which will spend 15–30 minutes sitting quietly facing away from the morning sun, back feathers raised, and the bare skin there exposed to the sun's rays. Among the accipitrid birds-of-prey, the Sparrowhawk habitually perches and preens in the sun (see Owen 1919); a Bald Eagle was observed facing the sun with neck and breast feathers fully ruffled (B. King).

LEVEL-2: THE WINGS-DOWN POSTURE

Passerines sitting-down-in-the-sun during level-1 sunning often fluff up the flank feathers over the wings, such a posture being especially characteristic of



Figs 24–25 *Sunning postures of Bluethroat: 'wings-down' (level-2) and 'lateral' (level-3).*

the Dunnock when settled immobile in the sun on the short grass of a lawn or the bare earth of a flower border. The Dunnock and many other passerines, however, usually while facing the sun or with the back to it, will also often adopt another simple posture when sitting-down-in-the-sun: the wings, free of the flank feathers, are merely lowered, still folded, to the ground (Simmons 1964). A photograph of a Bluethroat sitting down in such a posture appeared in Heinroth and Heinroth (1924–33). I count this wings-down posture as the first of the more definite sunning postures and its 'aim' appears to be to allow the sun's rays to fall on the bird's back and rump. It may be equivalent to Hauser's Level-I and -II sun positions, but I doubt it (see above); in any case, except during lulls in more elaborate sunning, it usually seems to be accompanied by little if any feather erection or other posturing (the tail may be somewhat spread), and the bird shows no obvious signs of heat stress.

I have seen the following garden passerines sunning themselves in the wings-down posture (while sitting down on the ground unless otherwise indicated): Blackbird, Song Thrush, Dunnock, Starling, and House Sparrow (also on roofs, etc.), all frequently: and a Wren, a Blue Tit, and a Jackdaw (standing on a post), all once each. Among these species, only the House Sparrow seems to have the wings-down posture as its main sunning posture (see further, below); in this case, there can also be considerable feather ruffling as well while the head may be raised or held towards or away from the sun. The wings-down posture is also particularly characteristic of the Starling, some birds adopting it even when others of a sunning group are in more elaborate postures; they often then erect only the head and neck feathers, while extending the neck and holding the head at an angle in various positions, looking more like a study-skin placed on the ground than a live bird. Among other passerines, what appears to be this posture has been recorded from winter flocks of White-crowned Sparrows (Morton 1967), most noticeably in the early morning hours, though it also occurred throughout the day until sunset: while they sometimes sunned on the ground between bouts of foraging, 'the birds often chose an

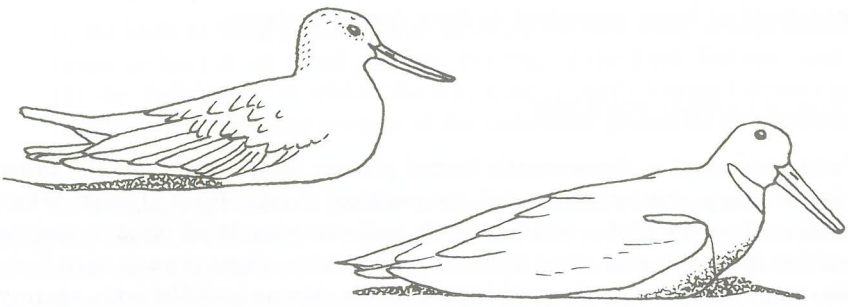
exposed perch and sat quietly with their wings dropped and contour feathers slightly fluffed'. Rock Pipits have been seen sunning with wings slightly lowered while sitting down on the warm roof tiles of tall houses (B. King).

Gamebirds, including the Red-legged Partridge, in addition to more elaborate sunning postures, will adopt the wings-down posture with the back to the sun at times (Goodwin 1953, 1956). The same is true of the pigeons: Nicolai (1962) has a photograph of a captive Galapagos Dove sunning thus (which he characterized as the lowest intensity form of the behaviour in this species); and some of the Domestic and Feral Pigeons I watched sunning at Burghley House in July 1983 (see under Level-3, below) were also in this posture, as were several of a flock of Feral Pigeons sun-basking on the sloping roof of a tall building in Leicester on 26 October the same year. (See also Note 7.)

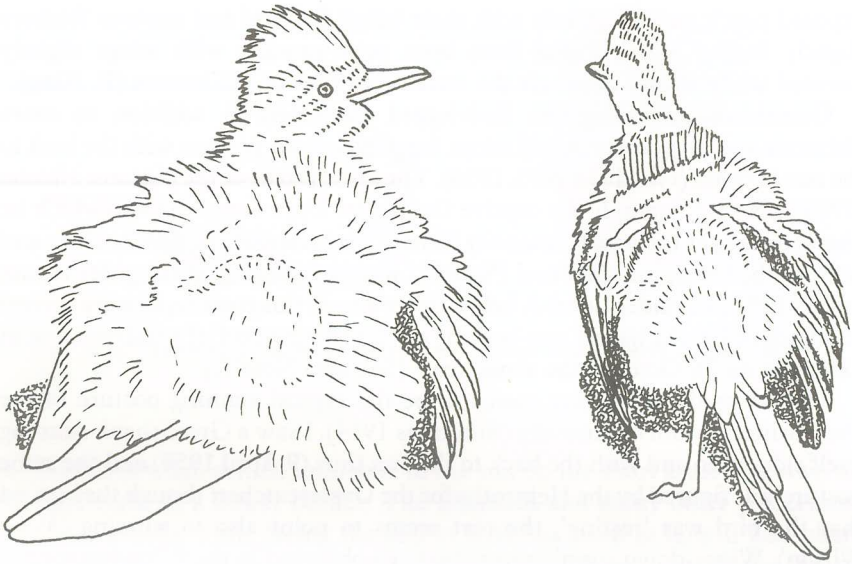
The wings-down posture seems to be the typical sunning posture of the charadriiform waders generally (Simmons 1964). I saw a Greenshank sunning itself side-on to and with the back to the sun thus (9 April 1950) and the same posture was figured by the Heinroths for the Oystercatcher: though they stated that the bird was 'resting', the text seems to point also to sunning (M.G. Wilson). Wings-down sunning has also been observed in the following species of charadriid and scolopacid waders by Bernard King:

> Oystercatcher, American Oystercatcher, Black-necked Stilt, Killdeer, Dotterel, Lesser Golden Plover, Golden Plover, and Grey Plover; Least Sandpiper, Baird's Sandpiper, Dunlin, Stilt Sandpiper, Buff-breasted Sandpiper, Common Snipe, Dowitcher (probably Short-billed), Bar-tailed Godwit, Marbled Godwit, Whimbrel, Curlew, Willet, Turnstone.

The wings-down posture also appears to be the typical sunning posture of wildfowl and gulls (Goodwin 1956, Simmons 1964) though, as the Heinroths noted, it is adopted at other times too when the birds are loafing in the shade or when the sky is overcast. See Rollin (1948) for a photograph of a juvenile Lesser



Figs 26–27 *'Wings-down' sunning posture of two waders (shorebirds): Greenshank (left) and Oystercatcher.*



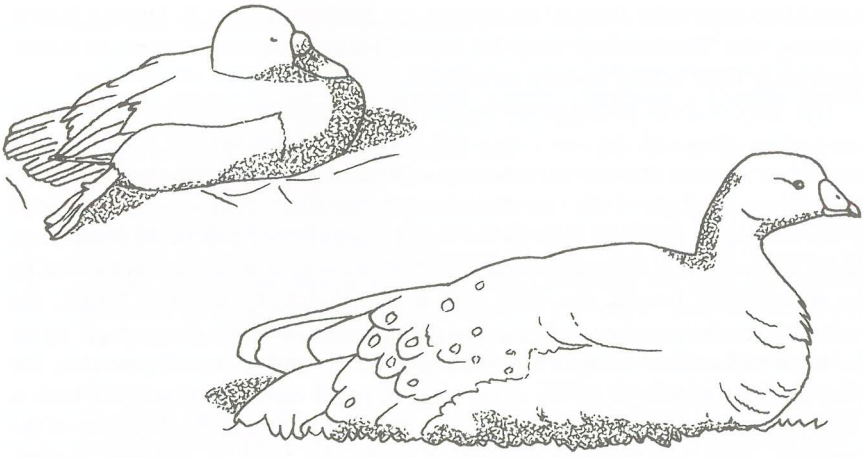
Figs 28–29 *Greater Roadrunner sunning.*

Black-backed Gull in this posture, which has also been described by King (1981b) for the Caspian Tern.

The sunning posture adopted by the Greater Roadrunner (see Ohmart and Lasiewsky 1971, Poulson 1974) seems also best allocated here: with its back orientated perpendicularly to the incoming rays of the sun, the bird droops the wings slightly, holding them away from the body, and erects the feathers of the upper back and neck to expose the bare skin there (see further in Chapter 7). Although it does not involve wing lowering, the rather similar behaviour of the grebes (which expose the back feathers by *lifting* the wings), bee-eaters, and Turkey Vulture described under Level-1 (above) should perhaps be better considered as being equivalent to these level-2 postures.

LEVEL-3: LATERAL POSTURES

Passerines adopt a characteristic lateral posture more often than any other when sunning, this being the 'full sun position' (Level III) of Hauser. When sunning thus, the bird – typically while half-squatting in an oblique-upright position (though it may stand up more or lie down) – aligns the axis of its body side-on to the direction from which the sun is shining (parallel with, slightly turned away from, or slightly turned towards it). The neck is usually extended, some or all the contour feathers are usually well ruffled (particularly those of the flanks and belly and of the head and neck), and the feet are usually hidden;



Figs 30–31 *Two species of wildfowl observed sunning by R.J. Prytherch (level-1 or level-2): Rosy-bill (upper) and Cape Barren Goose; note extended leg of first bird, presumably for cooling.*

the pattern of feather erection is variable, however, some areas (e.g. the breast, rump, and mantle) being raised at one time and not at another. Positioned thus, the bird usually leans away from the sun to a greater or lesser extent and, when sunning persistently, it will change position so that each side is orientated in turn thus. It often has the bill open and may pant heavily. Most species also keep the 'sun-eye' wide open, though with regular use of the nictitating membrane, and appear to be staring at the sun more or less throughout. On occasion, the oil-gland may be bared by erection of the rump feathers, but this is more a feature of spreadeagle sunning (see under Level-5, below).

While intermediates are common (as with all sunning postures), there appear to be only two main versions of the lateral posture:

> (i) the basic or *'wing-folded lateral'* in which the 'sun-wing' is kept folded (more or less) in its usual position, but free of the flank feathers; and
> (ii) the *'full-lateral'* in which the sun-wing is partly lowered down the flank, so that the distal portion of the individual primaries are exposed ('wing-fan').

The tail is usually spread to a greater or lesser extent in both versions: out on the ground behind the bird, or raised, or raised and twisted to the 'sun-side', sometimes exposing the underside. In the full-lateral, however, the 'sun-half' of the tail is mostly brought round to meet the down-postured wing, either one often overlying the other partly (typical 'wing/tail-fan'). At times, the full-lateral sunning posture is so exaggerated that the wing is stretched right down, half or even more fully opened, over or clear of the fanned tail ('expanded full-

lateral', or *'expanded-lateral'* for short); see further in Note 8. During lateral sunning, the 'shade-wing' may be kept folded but it is lowered at times, apparently then acting mainly as a prop.

The 'aim' of these lateral postures is evidently to position the bird so that the angle of incidence of the sun's rays fall perpendicularly on one side of it at a time; the extent of the coverage during a particular spell of sunning, however, depends on the angle of the axis of the body to the sun (i.e. on whether the head or the tail end is turned a little to the sun, or not), how far the bird leans over, which feather tracts are erected most, and on the height of the sun in the sky. In the wing-folded lateral, the flank and belly seem to be a major target, the feathers there being often fully erected and the wing at times drawn high up on the back to facilitate this; in the full- and the expanded-lateral postures, the wing and tail appear to be the main targets. In all cases, however, the bird is clearly also trying to position its head and neck in relation to the direction of the sunshine: with the feathers erected, it turns the head at different angles, exposing (e.g.) now the cheek, now the chin and throat, now the back of the head, but remaining fixed in one position at a time, often with the bill elevated.

Passerines of the following groups and species are among those known to sun laterally:

> the larks, including the Skylark (Delius 1969); the hirundines, including the Swallow (Hartley in Gibb 1947), Purple Martin (Johnston and Hardy 1962), Peruvian Martin (Whitaker 1963), and Cliff Swallow (Barlow *et al.* 1963); the wrens, including the Carolina Wren (Hauser 1957) and Wren (Simmons 1983); the waxwings (Bombycillidae) – the Cedar Waxwing (Nice 1943); the mockers,

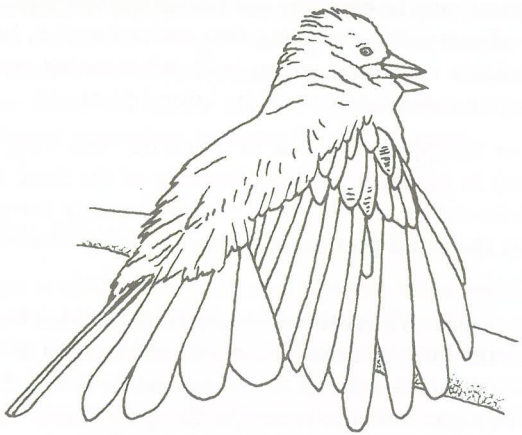
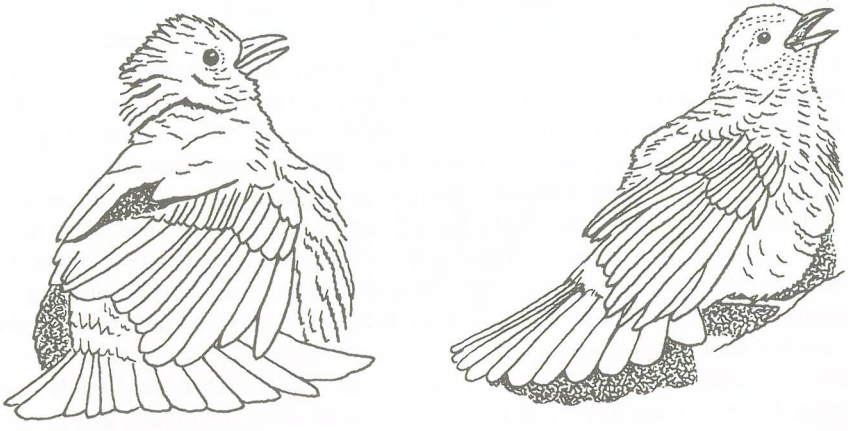


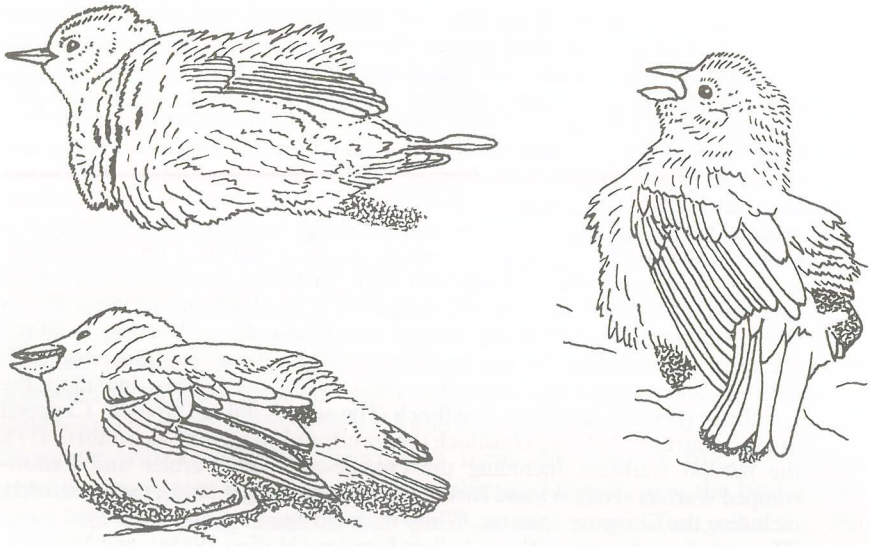
Fig. 32 *Jay in full 'lateral' sunning posture (level-3); note gaping bill in this and a number of the following figures.*

including the Gray Catbird, Northern Mockingbird, and Brown Thrasher (Hauser); the accentors – the Dunnock (Beven 1946, Teager 1967); the thrushes, including the Robin (see below), Bluethroat (Heinroth and Heinroth 1924–33), Redstart (Nice), Veery, Gray-cheeked Thrush, Swainson's Thrush, Hermit Thrush, and Wood Thrush (Dilger 1956), Blackbird (Heinroth and Heinroth), Song Thrush (J.C. Jackman in Gibb), Mistle Thrush (Simmons 1982b), and American Robin (Bent 1949, Hauser); the warblers, including the Barred Warbler (Heinroth and Heinroth); the babblers – the Pekin Robin and Rufous-chinned Jay-thrush (see below); the tits, including the Marsh Tit (Heinroth and Heinroth, Barnes 1975), Tufted Titmouse (Hauser), and Blue Tit (Barnes); the corvids, all or most species (Goodwin 1976) including the Blue Jay (Hauser, Weisbrod 1971), Jay (Burton 1959), Magpie (A.T. Moffett), and Jackdaw (Rollin 1948); the starlings – the Starling (Hauser) and Rose-coloured Starling (B. King); the sparrows, including the House Sparrow (Hauser) and Tree Sparrow (A.T. Moffett); the waxbills and allies (Goodwin 1982); the finches, including the Chaffinch (Rollin), American Goldfinch (Hauser), Bullfinch (B.M.A. Chappell in Gibb, Burton 1959) and Hawfinch (Heinroth and Heinroth, Mountfort 1957); the parulid warblers, including the Orange-crowned Warbler and Yellow-rumped Warbler (Hauser), and Kirtland's Warbler (Berger 1961); the emberizids, including the Chipping Sparrow, White-throated Sparrow, and Dark-eyed Junco (Hauser), Song Sparrow (Nice), Yellow Bunting (Moffett 1983a), and Northern Cardinal (Hauser); and the icterids, including the Common Grackle (Hauser).

Of the garden passerines that I have studied, the Blackbird will adopt the full range of lateral postures described above, as probably will most other thrushes. Though I have not yet seen the expanded-lateral from any other thrush for certain, I have recorded both the wing-folded and full versions from the Song Thrush and the full version from the Mistle Thrush and the Robin. Other passerines that I have recorded sunning laterally (in the full version unless otherwise indicated) are:



Figs 33–34 *'Lateral' sunning posture of Blackbird (two views).*



Figs 35–37 *'Lateral' sunning posture of three more passerines: Dunnock (upper left, bird in moult), House Sparrow (lower left), and Yellow Bunting. Only in the Dunnock does this posture develop at times into the level-4 'raised-wing' one (see Figs 17 and 47).*

Dunnock (both versions); Wren (wing-folded version); Pekin Robin and Rufous-chinned Jay-thrush; Blue Tit; Starling (both versions, including the expanded); Rook; House Sparrow (both versions); and Bullfinch.

Of these other species, I am most familiar with the Dunnock, Starling, and House Sparrow, all of which have certain peculiarities.

The Dunnock when sunning laterally (mostly in the wing-folded version, and with the tail fully fanned) often lies right down and keels well over on to its side, so much so at times that the head, which may be canted at various angles, is near the ground on the side away from the sun. Unlike the other species mentioned here, it may close the sun-eye while performing thus and frequently raises the sun-wing (see further under Level-4). Particularly while alternating ordinary lateral with wing-raised lateral sunning, it will at times adopt some most contorted postures, for instance with the body twisted one way and the tail the other, while exposing the oil-gland and the fully ruffled plumage of flank, rump, and belly. The sunning behaviour of the Starling is highly variable: though it will often adopt the classic full-lateral with typical wing/tail-fan in an oblique-upright posture, this species (like the Dunnock) tends to lie right down, or sometimes just to squat forwards on to the breast, legs in view ('forward-lateral'); the head is canted or stretched forward close to the ground and there is often little ruffling apart from the feathers on head, chin, and throat

(at times, it seems to be mainly exposing the bare face to the sun). While most of the sunning I have seen in the House Sparrow is of level-1 and level-2 (see above), this species will sun laterally at times, though this posture was not mentioned in the monograph by Summers-Smith (1963). Like the Dunnock, it mostly adopts the wing-folded version while settled well down; however, though it will cant the head to one side, it seems usually then to lean the body away from the sun only slightly and erect the feathers only a little at most, adopting more intense postures less frequently. Neither have I yet observed a House Sparrow in the classic full-lateral, only in a version with one wing lowered but not unfolded; but it will adopt its own version of the forward-lateral at times, crouching on to the breast with all feathers ruffled (especially those of the rump) and the tail spread, and may hold the wings in the wings-down position thus (see above; also further under Level-5). The Tree Sparrow has been observed sunning by A.T. Moffett in a similar way to the House Sparrow, leaning over with one wing lowered but not spread. Like its congener, the Tree Sparrow often combines sunning and dusting (see under Level-1, above) but the extent to which either species adopt lateral and other higher-level sunning postures then remains to be elucidated.

The photograph in Moffett (1983a) shows a Yellow Bunting in the classic full-lateral. Of the other groups listed above, the corvids, estrildids, and most of the rest also adopt the typical full-lateral posture at least. The hirundines, however, appear to assume a simpler version, rolling sideways with breast and

Fig. 38 *'Lateral' sunning posture of Green Woodpecker (a juvenile in this case).*

belly feathers erected or with drooped wings, though this seems usually to lead to or follow more complex posturing with one wing raised or with wings and tail outspread (see below under Level-4 and Level-5), while a 'lean-forward' posture also occurs (see Barlow *et al.* 1963).

Among the near-passerine and adjacent families, lateral sunning has been recorded from, for example:

> the woodpeckers, including the Green (see photograph by A.T. Moffett in Hosking *et al.* 1982), Red-bellied (Hauser), Great Spotted (A.T. Moffett), and Middle Spotted (Heinroth and Heinroth 1924–33, F. Weick in Glutz and Bauer 1980); the bee-eaters, including the Bee-eater (Heinroth and Heinroth, Koenig 1951) and many other species (Fry 1972, 1984); the cuckoos, including the Yellow-billed (Cracraft 1964, Potter and Hauser 1974); the parrots (see Harrison 1961); and the pigeons (Heinroth and Heinroth 1949, Hauser, Nicolai 1962, Goodwin 1967b).

The full-lateral posture of the cuckoos, woodpeckers, parrots, and pigeons appears to be closely similar to that of the passerines. In the Green Woodpecker, lateral sunning may alternate with frontal and rearward positioning (see Note 9). Moffett's Green Woodpecker photograph shows a juvenile sunning laterally on a dead stump, leaning over with the wing in the expanded position; the Great Spotted Woodpecker has been seen sunning in much the same manner (A.T. Moffett). Both the parrots and pigeons also adopt the expanded-lateral at times but, unlike the cuckoos and woodpeckers, will also raise one wing (see further under Level-4). In the pigeons, the expanded version may well be the normal lateral posture, as indicated by photographs in Nicolai (1962) for the Galapagos Dove (in which it was designated as the

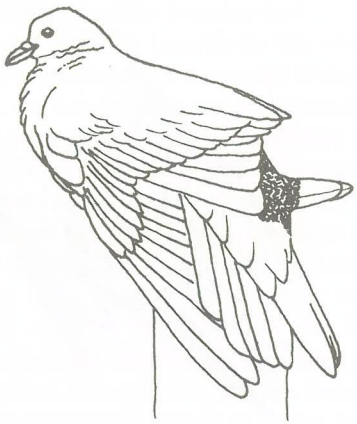
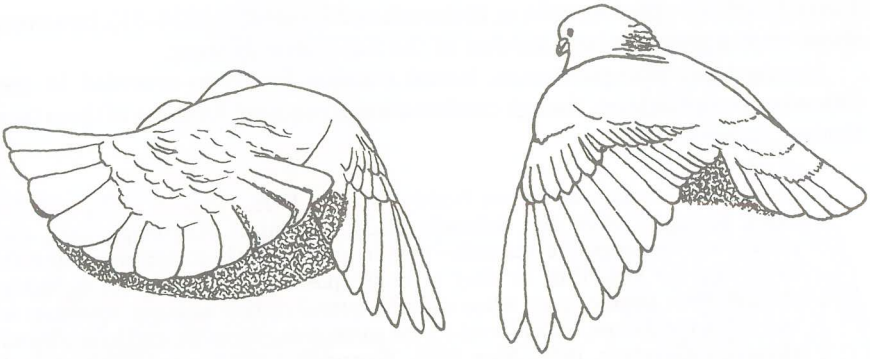


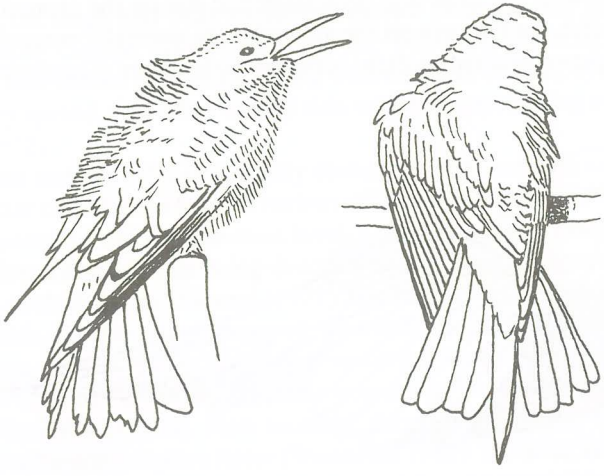
Fig. 39 *'Lateral' sunning posture of Turtle Dove.*



Figs 40–41 *Two views of 'expanded-lateral' sunning posture of Domestic Pigeon (see also Fig. 15).*

middle-intensity sunning posture) and in Heinroth and Heinroth (1949) for the Domestic Pigeon (see also Note 10).

The bee-eaters seem often to adopt simpler postures: for example, they will crouch against the soil with wings folded and roll sideways to expose the flank to direct sunshine (C.H. Fry; see also Note 11). The Bee-eater itself, though it seems as likely to sun with the incident radiation coming from the back or front (see under Level-1, above), will also sun side-on to the sun at times; then it seems the most likely to lean the head away from the sun, with the feathers of the face, neck, and upper breast ruffled (see Koenig 1951 and further under



Figs 42–43 *Two views of 'lateral' sunning posture of Bee-eater.*

Level-5, below) – photographs in Heinroth and Heinroth (1924–33), however, show what appears to be a version of the full-lateral posture.

Among other non-passerines, lateral sunning has been recorded in the following groups at least, though confirmation is required for some of them (see further, below):

> the terns, including the Brown Noddy (Watson 1908, Houston 1980) and the Black Noddy (Cullen and Ashmole 1963); the snipes (Gallinagininae); the plovers and lapwings; the bustards – the Great Bustard (Heinroth and Heinroth 1924–33); the rails (but as they typically posture both wings in a highly characteristic manner even when sunning laterally, their sunning behaviour is treated further below, under Level-5); the gamebirds generally (see Heinroth and Heinroth, Goodwin 1953, Nice 1962, Wennrich 1980), including the Hazel Grouse, Willow Grouse, Red Grouse, and Ptarmigan (Tetraonidae), and the Himalayan Snowcock, Red-legged Partridge, Grey Partridge, Common Quail, Domestic Fowl, Reeves' Pheasant, and Elliot's Pheasant (Phasianidae); the wildfowl; the ibises; the herons; and the petrels (Procellariidae).

At Ascension, I frequently saw Brown Noddies sunning laterally: with mantle feathers ruffled, bill open, and tongue raised, they would stretch the partly open sun-wing downwards and backwards so that the primaries rested over the fanned tail, which was twisted sideways. A similar expanded-lateral posture occurs also in the Black Noddy (which, however, also sometimes extends the leg on the sun-side, a detail I failed to note in the Brown Noddy).

The Great Bustard was figured by the Heinroths while preening in a lateral posture in the sun with the tail fanned and fully turned to the sun-side (see further in Note 12). Among the gamebirds, which often combine sunning with dusting, the partridges and their allies lie over on one side (or even on to the back), often with the head and neck stretched flat on the ground and the legs fully extended; the feathers on the sun-side 'are normally erected to allow the maximum penetration of sunlight between the feathers' (Goodwin: Red-legged

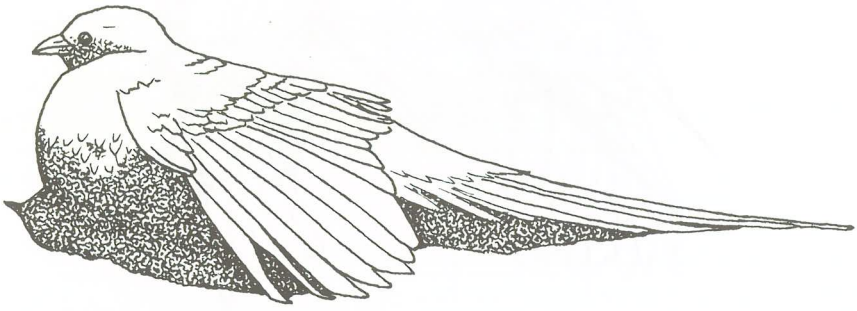
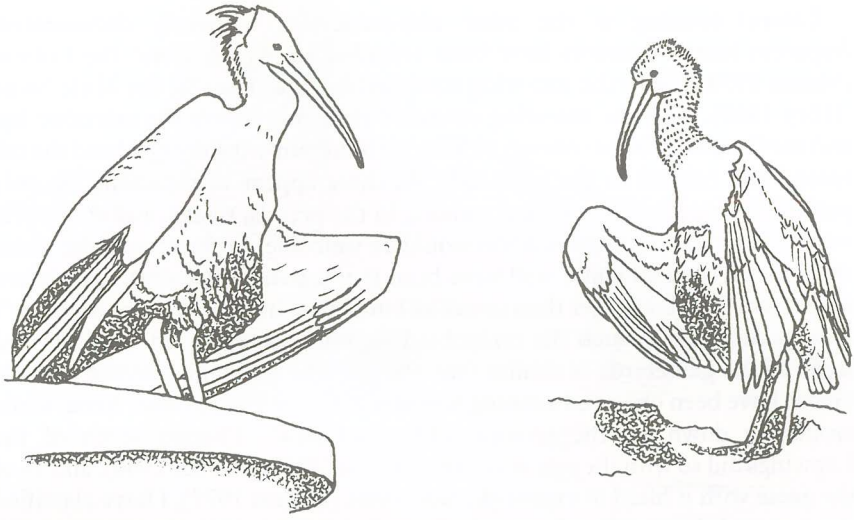


Fig. 44 *Female Elliot's Pheasant sunning on ground in 'lateral' posture.*



Figs 45–46 *Two ibises in 'wing-drooped lateral' sunning posture: Bald Ibis (left) and Glossy Ibis. See also Figs 50–51, 74–76.*

Partridge), and the wings may also be stretched down, presumably mostly (or only) on the sun-side. Photographs of captive Reeves' and Elliot's Pheasants sunning while lying on the ground (Wennrich 1980) show typical full-lateral postures; see also Note 13. The Hazel Grouse would also appear to adopt the full-lateral posture, stretching out a leg as well as the wing and tail (Bergmann *et al.* 1978). The Red Grouse when sunning, which it does at all times of the year, lies 'on one side with the opposite leg stretched out, puffing out the feathers on the thigh and belly to the full extent' (Watson and Jenkins 1964). Young Willow Grouse also stretch out the sun-wing (Kratzig 1940). The Ptarmigan sun-bathes frequently, 'lying with feathers ruffled, eyes closed and wings partly spread, and often on one side with the opposite leg stretched out' (Watson 1972).

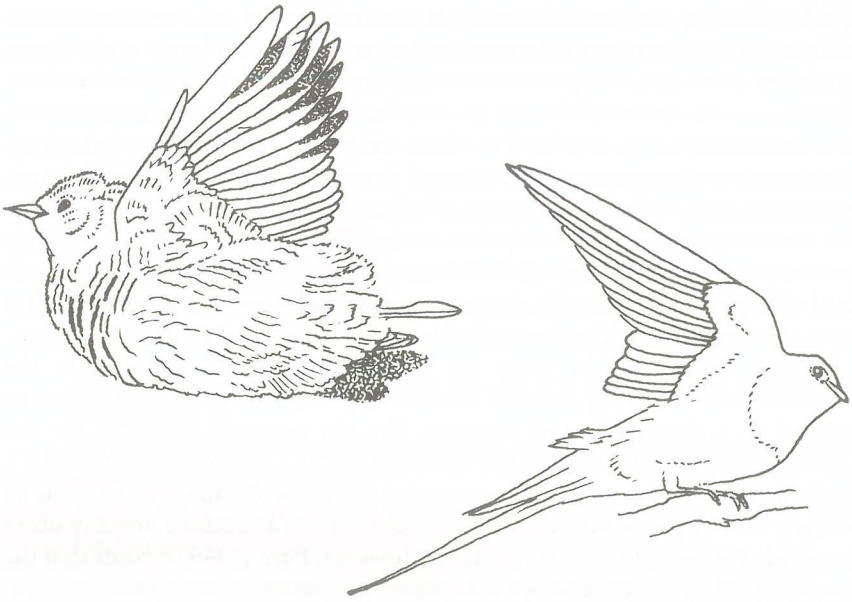
The ibises sun laterally in a highly distinctive manner that could perhaps even be better classified as being a variant of level-4 (as the undersurface of one wing is exposed to the sun) or even level-5 (as one wing is more or less well spread). I first identified this 'wing-drooped lateral' posture from a photograph of a Straw-necked Ibis in Haensel (1972): the bird was positioned obliquely to the sun with the far wing drooped forward, so that the sun fell on its undersurface, as well as on the closed sun-wing itself, etc. A photograph of young Sacred Ibises adopting the same posture in the mid-day sun was later published by Urban (1974). Now recently, the same or similar behaviour has been observed among captive ibises (Wennrich 1982): the Bald, Black, Hadada, Puna, and Glossy, the last two species also raising the sun-wing at times (see below, Level-4).

Lateral sunning in the other non-passerines is poorly documented. Apparent lateral postures have been recorded once each from: the Fulmar (Mason 1950a), with the sun-wing stretched fully backwards; the Mute Swan (Hiley 1969), with the sun-wing extended right down over the extended leg; and the Common Snipe (Mason 1950b), with the sun-wing drooped and the tail spread and twisted to the same side. As these appear to represent the only published records of specialized sunning in the petrels, swans, and scolopacid waders respectively, confirmation would be welcome. In the case of the swan, the posture adopted could well have been the 'leg-and-wing stretch' comfort-movement held for longer than usual, as I indicated in my comment on Hiley's note at the time, though the undoubted sunning posture of the noddies and some of the gamebirds is similar (see above). The Lapwing and the Canada Goose have been observed sunning laterally at Chew Valley Lake, Avon, while crouching down on the ground (D.E. Ladhams). Though seven of the Lapwings did so with the sun-wing lifted a little (30 September 1980), and 16 of the geese with it lifted to expose the underside (August 1977), I have classified these records here rather than under level-4 sunning as the wing action seems not to have involved the full wing-raising characteristic of that behaviour. Mention should be made here, too, of Nice's (1962) record of a hand-reared Killdeer chick which 'often sat or stood in the sun, slightly drooping the wing towards the sun'; such behaviour, however, has not been observed in adults (see Chapter 3). Finally, Haensel's (1972) article included a photograph of a Yellow-crowned Night Heron apparently in a type of lateral sunning posture, with the sun-wing drooped and head and neck inverted; caution is necessary, however, as this may have been a transitional attitude caught by the camera in a species which more typically postures both wings (see under Level-5). For further comments on transitional postures, see Notes 8, 15 and 16.

LEVEL-4: RAISED-WING POSTURES

A minority of passerines raise the sun-wing at times when sunning laterally. Among European species, such raised-wing postures have been recorded from: the Swallow (Heinroth and Heinroth 1924–33, Hartley in Gibb 1947); the Sand Martin (King 1970); the Dunnock (Beven 1946, Teager 1967), and presumably occurs in other accentors as well; the Reed Warbler (Brown and Davies 1949); and the Tree Creeper (Buxton 1950).

Of the passerines that I have studied, only the Dunnock adopts such a posture regularly. Unlike all the other species (including the hirundines and creeper), it never goes further to adopt a sunning posture with both wings spread (see under Level-5). Thus, the highest level of sunning in the Dunnock is the *'raised-wing lateral'* which is very common, relatively few spells of lateral sunning by individuals of this species lacking at least an occasional brief raising of the sun-wing as the bird keels right over on its side with feathers ruffled,



Figs 47–48 *Two passerines in 'raised-wing' sunning posture (level-4): Dunnock (left) and Swallow, both birds in tail-moult.*

often while gaping and panting. It most frequently orientates itself sideways to the sun but will also take up other positions with the axis of the body more obliquely aligned, either head or tail leading, flipping the raised wing up vertically, either still partly folded or more or less fully extended. Whatever the orientation of the body, however, the raised wing is always positioned so that its pale undersurface faces the sun directly – that is, so that the sun's rays fall perpendicularly upon it. The wing is typically held up only briefly, for only a few seconds at a time (if that), sometimes longer: in my experience, usually only for a maxumum of about eight seconds and seldom for very much longer (see also Note 14) though a lift of about 30 is normal according to Teager. However, the bird may raise the wing several times during a single spell of sunning and, of course, may alternate wings by positioning itself with the other side of the body turned to the sun. As well as the undersurface of the sun-wing, the areas exposed to the sun are those hidden by the wing when held in its normal position: the axillaries, the skin of the arm-pit, the feathers of the upper flank, and, often (as the fanned tail is twisted towards the sun), the feathers of the lower back, upper tail-coverts, and base of the tail, as well as the naked nipple of the oil-gland, which is deliberately exposed at times by the maximum erection of the rump feathers around it. As in the ordinary lateral sunning posture which alternates with the wing-raising, the ruffling of the flank and adjacent feathers also exposes their dark bases.

Wing-lifting during lateral sunning is characteristic of the Sand Martin also though Cliff Swallows tend 'to cross their wings above their backs while tilting, instead of raising the upper-most wing (Barlow *et al.* 1963); the Swallow, however, seems more inclined to go into the full raised-wing posture. As we have seen (Chapter 3), the Reed Warbler will sometimes assume a full raised-wing posture when apparently suffering from acute heat stress on the nest, holding the wing up for several minutes before 'recovering'. Such a posture has not been recorded under conditions obviously referable to sunning in this species; however, a photograph in Heinroth and Heinroth of a young Great Reed Warbler sunning with the sun-wing lifted somewhat, undersurface exposed, suggests that the Reed Warber could also sun thus at times.

Though I once saw a Wren lift the partly extended sun-wing to the horizontal while sunning laterally (Simmons 1983), this may perhaps best be counted as a form of level-3 sunning, like the postures described for the Lapwing and Canada Goose above. According to R.C. Jackman (in Gibb 1947), the Song Thrush also may lift the sun-wing to expose the flank while sunning laterally but I have never seen this species (nor the Blackbird nor any other thrush or chat) adopting such a posture. However, Bent (1949) records that the American Robin lies 'over on one side, with the wing on the sunny side uplifted, so that the sun penetrates under the fluffed-out feathers of the body'. Further observations are required to determine whether or not this represents true raised-wing sunning (see further in Note 15, however).

Among non-passerines, the raised-wing posture occurs in the parrots, which sun by 'lying over to one side and extending only one wing at a time, fully spread, either to one side or up above the body' (Harrison 1961), and possibly in the owls. A Barn Owl observed by Bentham (1962) lay in a small sunny patch on the ground beneath a tree: 'One wing was raised, fully exposing that side of the body to the warmth of the sunshine'. D. Scott (see Bunn *et al.* 1982) 'saw

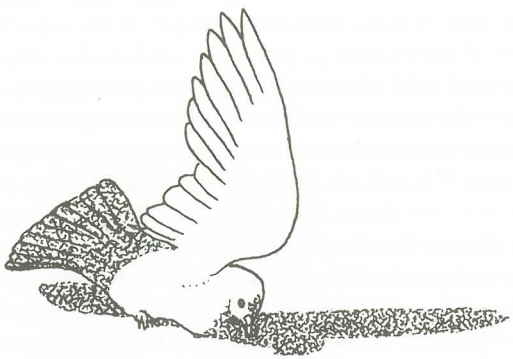


Fig. 49 *Domestic Pigeon in 'raised-wing' posture (see also Fig. 16). In pigeons generally, this posture is also used for rain-bathing.*

similar behaviour on a small number of occasions' over many years from Long-eared Owls. Once again, however, the extent of the wing-lifting is not clear.

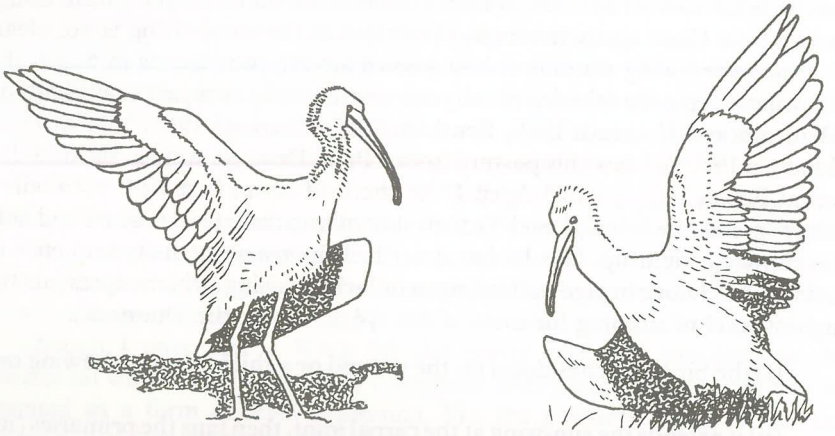
True raised-wing sunning is best known among the pigeons in which the sun-wing is typically raised vertically more or less fully open, as in rain-bathing (Heinroth and Heinroth 1949, Bentham 1957, Harrison 1961, Nicolai 1962, Goodwin 1967b). I saw this posture from a Palm Dove sunning in the mid-day sun at Fayid, Egypt, on 23 April 1950: the bird lay at first with both wings partly spread (see below, Level-5), then shifted into the lateral posture and held the sun-wing right up. Nicolai has described the usual intensity sequence of sunning behaviour in pigeons leading to full wing-raising (which represents the highest level of sunning for most of the species, as in the Dunnock):

> (i) the bird crouches down on the ground or a thick branch, drawing one wing under it;
> (ii) it extends the sun-wing at the carpal joint, then fans the primaries (my expanded-lateral posture);
> (iii) finally, if the sun is strong and it feels fully safe and relaxed, it raises the wing.

Thus, as in rain-bathing, the posture exposes the areas that are usually covered by the wing (flanks, etc., where the feathering is sparse); the feathers in these areas, together with those of the rump, are fully ruffled, thereby allowing the sun's rays to penetrate to the skin.

Nicolai found that the threshold for full-intensity raised-wing suning was very high in his captive pigeons, especially Diamond Doves. The latter, though extraordinarily 'sun-hungry' (taking every opportunity to sun), never sunned thus except in one aviary where the window-sills were covered with sheet-metal, some doing so there as soon as the sun had heated the plating, while other individuals on the floor below remained in the simpler postures; thus, the Diamond Dove, which belongs to that group of pigeons which sun most often during the middle of the day, suns at fullest intensity only when the substrate temperatures are also high (see also Chapters 3 and 8). Immelmann (1960) had recorded wild birds of this species sunning in the raised-wing posture under extreme conditions on very hot sand where the temperature was almost 70°C; the air temperature was at 45 degrees in the shade and all the other local species showed signs of heat stress (with bills open and wings lifted) and sought the shade. Very high substrate temperatures, however, do not always elicit raised-wing sunning in this species which suns thus in the wild much less frequently than its congener the Zebra Dove; when the two species sun together, only the Zebra Doves constantly have the wing up (K. Immelmann, footnote in Nicolai 1962). This suggests the possibility that the raised-wing component of such sunning in pigeons may be essentially a heat-stress (cooling) one at times or in origin, as it may be in the Reed Warbler and some other species (see Chapter 8 for further discussion).

Raised-wing sunning is performed also by the ibises. Captive Puna Ibises

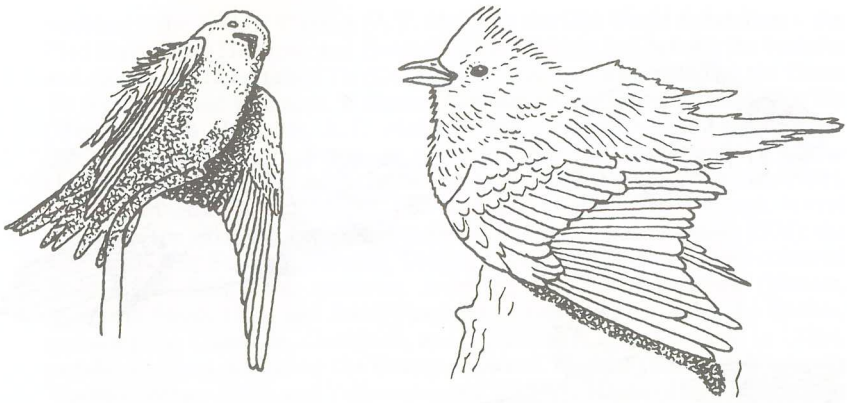


Figs 50–51 *Two ibises in 'raised-wing' sunning posture: Glossy Ibis (left) and Puna Ibis.*

would lean away from the sun, ruffle the neck feathers, and raise the sun-wing fully upwards, thus exposing one side of the head, the neck, chin, throat, breast, and belly as well as the underside of the sun-wing and part of the under wing-coverts of the far wing (which is postured much as in the ordinary wing-drooped lateral); the raised-wing posture was adopted for spells of 1–2 minutes at a time, the bird often continuing to sun laterally afterwards, perhaps raising a wing again later, sometimes repeatedly (Wennrich 1982). Similar behaviour occurred also in captive Glossy Ibises.

LEVEL-5: SPREAD-WING POSTURES

Most passerines that have been recorded sunning are known to adopt spread-wing sunning postures at times, especially during the middle part of the day when the sun is high in the sky, and often near its zenith, aligning themselves either facing towards or turned away from the sun, less often side-on or at some intermediate angle to it. When sunning thus in the *'full-spreadeagle'* (which is equivalent to the Level-IV 'exaggerated sun posture' of Hauser 1957), the bird typically squats or lies right down in a horizontal position on the ground or other flat surface with the wings fully outstretched more or less at right angles to the body, the tail fully fanned behind, and the head somewhat raised. All the contour feathers are usually ruffled, making the bird look like a ball of feathers at times, but often those of the mid-back and rump are erected most, exposing the naked external nipple of the oil-gland and the skin about it. As during lateral sunning, the bird often gapes and pants; it may tilt the head one way to



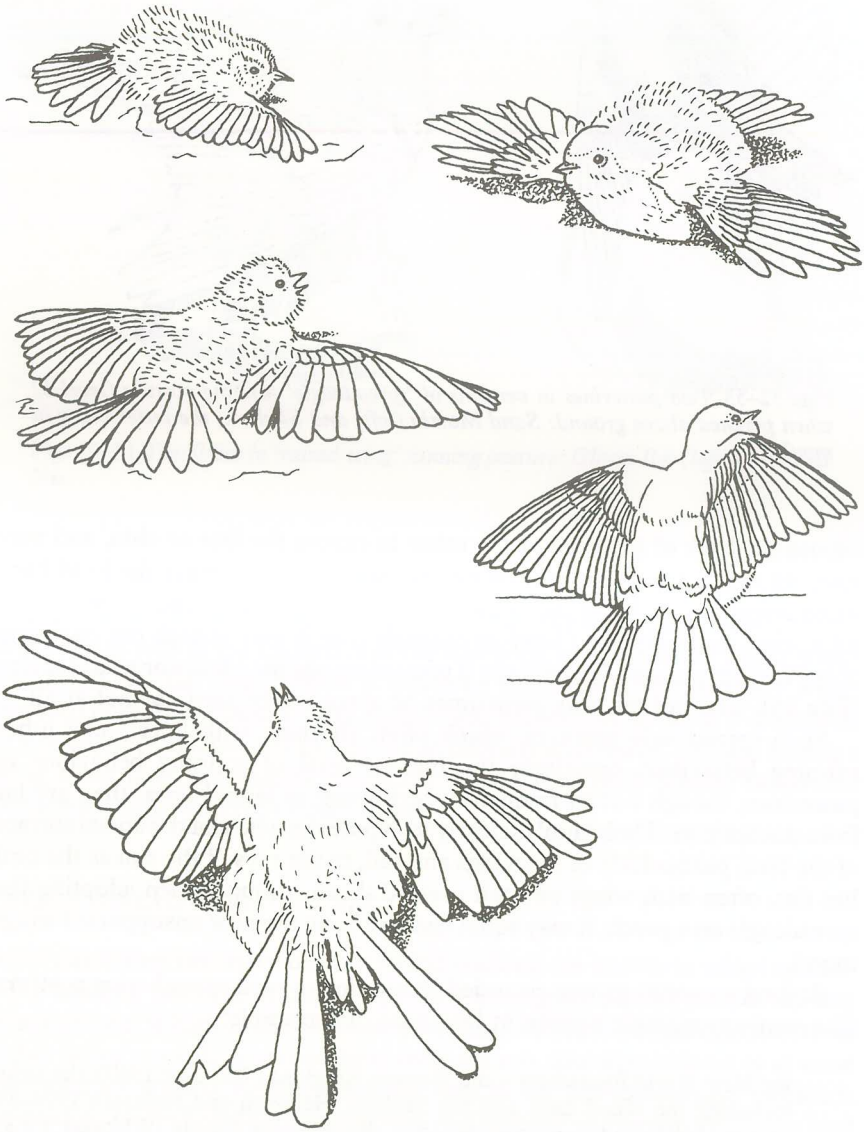
Figs 52–53 *Two passerines in versions of 'spreadeagle' sunning posture (level-5) when perched above ground: Sand Martin (left) and Skylark, the latter being in moult.*

expose the back of the head or the other to expose the face or chin, and may stare up at the sun (both eyes being kept wide open), turning the head back when orientated with the tail to the sun. At times, it will spread the wings less fully, even asymetrically (*'semi-spreadeagle'*); or it may stretch out one wing only (*'half-spreadeagle'*), especially if pressed up against a fence or wall (see also Note 16). The tail too may sometimes be spread only partly or not at all.

Such spreadeagle postures, which often alternate with lateral and other sunning behaviour, constitute the highest level of sunning behaviour in passerines; though not so frequently performed as lateral ones, they are far from uncommon. Their 'aim' is clearly to expose the whole of the dorsal surface of the bird, particularly of the wings and tail, to the rays of the sun as the bird lies flat, often with wings and tail pressed down (though when adopting the spreadeagle on a perch, it may squat less and hang the now unsupported wings more).

Among passerine groups recorded as sunning in such spread-wing postures (the semi-spreadeagle version at least) are, for example:

> the New World flycatchers – the Western Kingbird (Whitaker 1960); the larks, including the Wood Lark and the Skylark (Heinroth and Heinroth 1924–33, Delius 1969); the hirundines, including the Peruvian Martin (Whitaker 1963), Sand Martin (Heinroth and Heinroth, Barlow *et al.* 1963), and House Martin (Prytherch 1981); the wrens, including the Wren (Harrisson and Buchan 1936, R.C. Jackman in Gibb 1947, J.E.M. Mellor in Armstrong 1955, Moffett 1983a); the mockers, including the Northern Mockingbird and Brown Thrasher (Hauser); the chats and thrushes, including the Robin (Gibb 1947, Teager 1967, Moffett), Redstart (A.T. Moffett), Stonechat (B. King), Desert Wheatear (King 1970), Blackbird (Burton 1959, Teager), Song Thrush (Teager), Mistle Thrush (Simmons 1982b), and American Robin (Bent 1949, Hauser); the Old World



Figs 54–58 *Five passerines in 'full-spreadeagle' sunning posture: Wren (upper left), Robin (upper right), Great Tit, Pied Flycatcher (on perch), and Blackbird, the last being in heavy moult.*

warblers – the Willow Warbler (A.T. Moffett); the Old World flycatchers – the Pied Flycatcher (Heinroth and Heinroth); the babblers (see below); the bushtits and allies – the Long-tailed Tit (Colyer 1946); the true tits, including the Great Tit (Heinroth and Heinroth, Williams 1946, Barnes 1975, Moffett) and Blue Tit (Heinroth and Heinroth, A.T. Moffett); the creepers – the Tree Creeper (Heinroth and Heinroth, Pritchard 1950); the shrikes – the Red-backed Shrike (J.H. Owen in Gibb); the crows, including the Blue Jay (Hauser, Whitaker 1960), Jay and Magpie (A.T. Moffett), and Jackdaw (B.B.C. film), though lateral sunning is the more usual sunning posture in this family (see Goodwin 1976); the starlings – the Starling (Hauser, Teager, Langfeld 1973) and Rose-coloured Starling (B. King); the sparrows, including the House Sparrow (Hauser, Summers-Smith 1963) and Snow Finch (Heinroth and Heinroth); the finches, including the Chaffinch, Goldfinch, and Bullfinch (B.M.A. Chappell in Gibb); parulid warblers, including the Orange-crowned Warbler (Hauser), Kirtland's Warbler (Berger 1961), and Yellow-rumped Warbler (Hauser); and the buntings and allies – the Northern Cardinal (Hauser) and probably the *Emberiza* and *Miliaria* buntings (though the descriptions in Andrew 1956b are too imprecise for me to make a certain allocation). (See also Note 17.)

All the wild passerines that I have seen sunning laterally, with the exception of the Dunnock (see above, Level-4) and the House Sparrow, readily adopt full-spreadeagle postures on the ground: the Wren, Robin, Blackbird, Song Thrush, Mistle Thrush, and Starling. One of my captive Rufous-chinned Jay-thrushes was once seen in a semi-spreadeagle posture, also on the ground (25 June 1961).

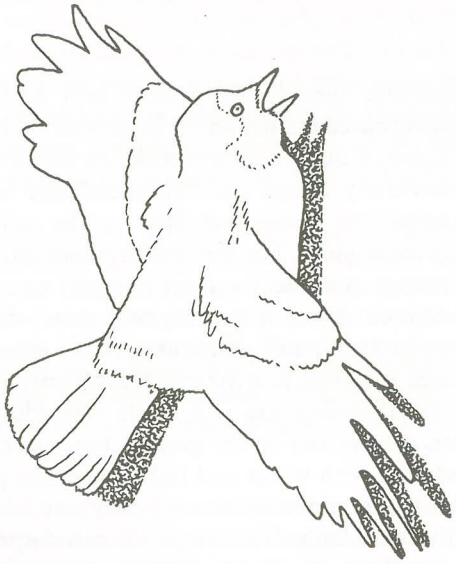


Fig. 59 *Jackdaw in 'full-spreadeagle' sunning posture on cliff slope.*

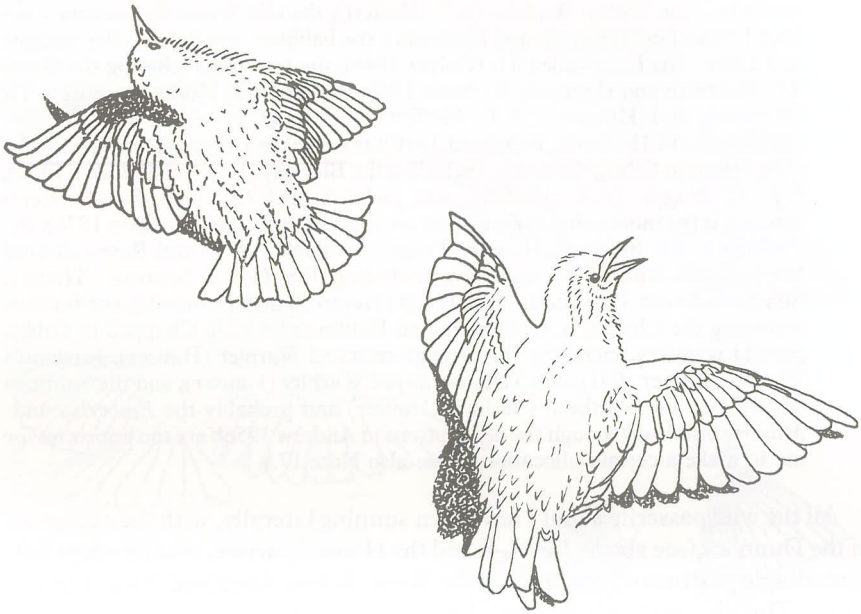
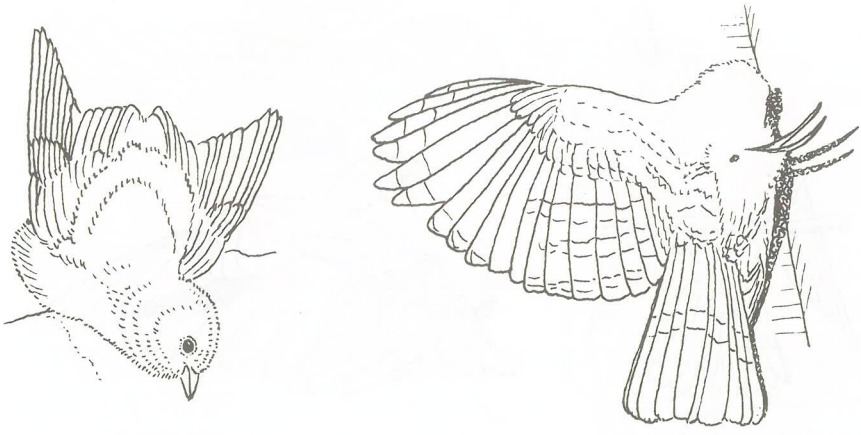


Fig. 60 *Two Starlings sunning together in 'spreadeagle' postures on lawn, lower bird in moult. This species in particular is prone to sun-bathe sociably, the behaviour often triggered by a 'pioneer' in the flock, or a sunning bird of another species, which may act as a focal spot for the rest which tend to cluster near it.*

I know the passerine spreadeagle posture best in the Blackbird, the description above being based mainly on the behaviour of this species. Like the Song Thrush and Robin, it may be seen to make its way from the shade to the sunning spot, immediately adopt the full-spreadeagle as it settles down, opening and extending the wings and fanning the tail all in one quick movement, and stay motionless. The bird may remain thus for the rest of the sunning spell, or change position (or even its spot) one or more times, or alternate between different forms of sunning behaviour – for example, leaning over, putting the wings away, and positioning (if necessary) into the lateral posture; at other times, it may go into the spreadeagle only after first sunning in another manner. The Starling too will settle immediately into the full-spreadeagle at times, pressed flat on the ground, but, more than the others, it may first half stand thus with wings and tail clear of the ground; it will also settle down tipped forward on the breast with only (say) the wing-tips against the ground and the tail fanned above it ('forward-spreadeagle'). House Sparrows were said by Summers-Smith (1963) to sun at times with the wings 'fully extended and laid flat on the tiles' and Hauser listed this species as one adopting her category of the 'compulsory exaggerated sun position', but I have



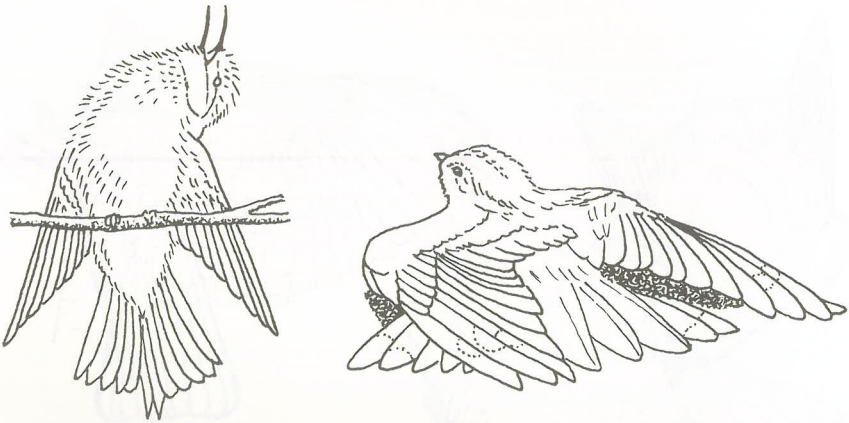
Figs 61–62 *'Spread-wing' sunning postures of Snow Finch ('forward semi-spreadeagle') on perch and, viewed from above, of Hoopoe ('half-spreadeagle') on ground against wall. The Hoopoe will also extend both wings, the site permitting; the position of the head and the open bill are typical for this species; a seemingly identical posture is said also to be adopted as a defensive concealing posture against aerial predators.*

never seen one yet in the full-spreadeagle; however, unlike Summers-Smith, I have observed sparrows sunning mostly on the ground where a 'semi-spreadeagle lateral' was the best posture recorded as the bird (a female) leaned away from the sun fully ruffled with wings partially spread, asymetrically (21 July 1982). What might be termed a 'forward semi-spreadeagle' with ruffled head held low was figured for the Snow Finch by Heinroth and Heinroth.

Among non-passerines, spreadeagle sunning postures have been recorded from the following groups, for example (see also Note 18):

> the woodpeckers, including the Northern Flicker and Red-bellied Woodpecker (Hauser); the hornbills, including the Crowned Hornbill and Casqued Hornbill (Kilham 1956); the Hoopoe (Poulsen 1974, Glutz and Bauer 1980); the bee-eaters (see below); the mousebirds (see below); the nightjars, including the Nightjar (Heinroth 1909, Turner 1914, Heinroth and Heinroth) and Common Nighthawk (Potter and Hauser 1974); the owls, including the Tawny Owl (Burton 1959); the gamebirds (Goodwin 1953, Nice 1962, Watson 1972); the pigeons (Goodwin 1967b); and some accipitrid and falconid birds-of-prey (see below).

The arborial woodpeckers and hornbills sun in spreadeagle postures off the ground, but exact details are lacking. The Hoopoe adopts a spreadeagle or half-spreadeagle sunning posture on the ground with the tail open, head and body feathers erected, and head thrown back with the bill open and pointing obliquely upwards. In the bee-eaters, a type of prone spreadeagle sunning has



Figs 63–64 *'Spreadeagle' sunning postures of Bee-eater (perched) and Nightjar (on ground).*

been observed in the wild from the Bee-eater, Blue-tailed Bee-eater, and Carmine Bee-eater (see Fry 1972) but only on cliff slopes facing the afternoon sun; it seems to be rather uncommon (C.H. Fry; see also Note 19). All species, however, when sunning at full intensity on a perch, either facing or turned away from the sun, frequently adopt an erect semi-spread posture with just the primaries fanned out sideways and the tail fanned. In the Bee-eater, for example, this posture, plus gaping and panting, is the last element in the intensity sequence described under Level-1 and Level-3 sunning (above); in captivity, it was only once seen on the ground, the bird lying flat, looking as if it were dead (Koenig 1951).

Prinzinger *et al.* (1981) figure a Red-rumped Mousebird clinging vertically to a perch, facing the sun with the wings loosely spread and tail slightly open, a posture recalling that adopted by many large non-passerines for sunning and wing-drying (see further, below). As well as sunning as described under Level-1, mousebirds of three southern African species studied by Rowan (1967) 'often "hang their wings out to dry" when wet, apparently in the sun (at least at times), much in the manner of cormorants'. The other groups mentioned above mostly adopt prone spreadeagle postures on the ground. The Palm Dove I watched sunning with the wing raised (see above) was first lying down in a semi-spreadeagle posture. Spreadeagle sunning, however, is uncommon amongst the pigeons and seems to have been recorded only from some *Streptopelia* doves (Goodwin) and the Mourning Dove (Hauser, B. King). The Nightjar performs both full- and semi-spreadeagle sunning with the tail fanned and feathers ruffled, often while gaping. The Common Nighthawk, too, has been observed in a 'full fluff' posture with 'tail widely fanned and wings fanned and drooped' (Potter and Hauser).

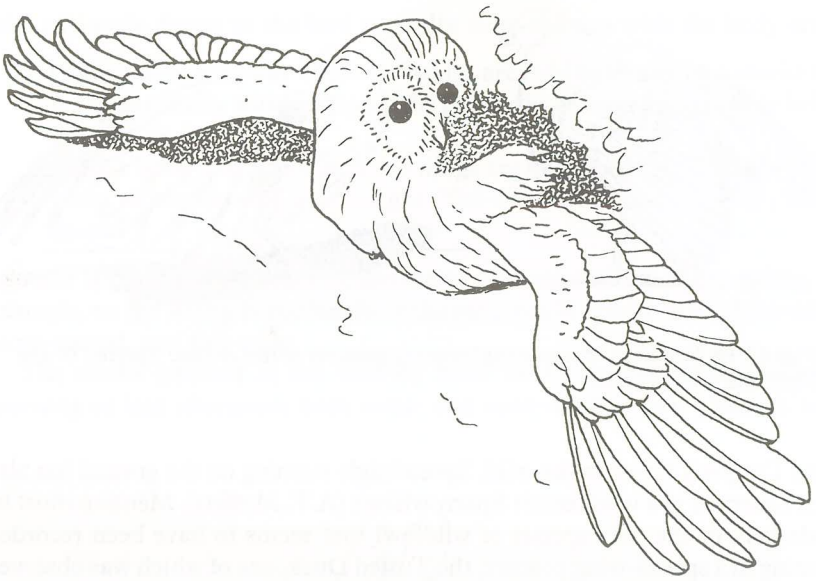


Fig. 65 *'Full-spreadeagle' sunning posture of Tawny Owl on ground.*

Gamebirds also lie flat with the wings outspread at times (see under Level-3). So will some of the owls and the diurnal raptors (though birds of both types will also assume other forms of spread-wing posture: see further, below). The Black Eagle lies down on a rock or the ground, back to the sun, both wings outstretched, and tail fanned (Gargett 1971). A captive Secretary-bird (Sagittariidae) was photographed in a similar pose on the ground with its back to the sun and the feathers of back and rump erected (see Haensel 1972; also Note 20). Some falcons will spread their wings fully while sunning in a prone position on the ground (Cade 1982); T.J. Cade informs me that he has seen the Peregrine, Gyrfalcon, Lanner, and Prairie Falcon sunning thus in captivity –

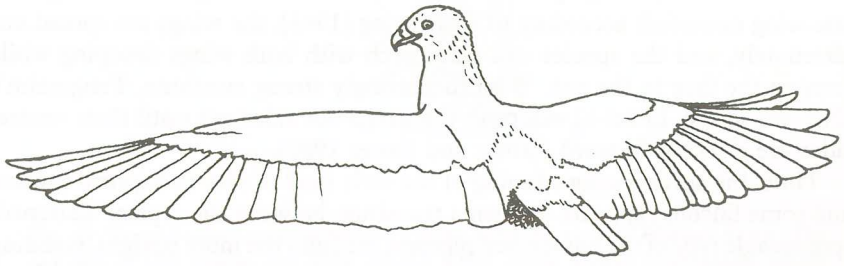
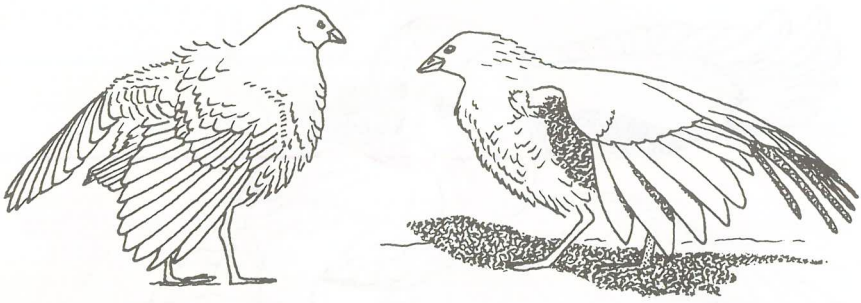


Fig. 66 *Secretary-bird in 'full-spreadeagle' on ground.*



Figs 67–68 *Standing 'spread-wing' sunning postures of two crakes: Spotted Crake (left) and Corn Crake.*

and a Cooper's Hawk in the wild. Spreadeagle sunning on the ground has also been observed in a wild female Sparrowhawk (A.T. Moffett). Mention must be made here of the only species of wildfowl that seems to have been recorded sunning in a spread-wing posture, the Tufted Duck, one of which was observed 'flopped on its breast with its wings half-spread' in the sun on a dam of a reservoir (Rogers 1950); see further in Chapter 7.

Spread-wing sunning takes other forms in many non-passerines. The rails in particular have a most peculiar standing posture (Heinroth and Heinroth) 'stretching their wings back, fanning them out and arching them over their backs' (Nice 1962), usually with the tail fanned. Such a posture seems to be the only one adopted by these birds when sunning and has been recorded, for example, from the King Rail, Virginia Rail, and Sora (Nice), the Water Rail, Corn Crake, and Moorhen (the Heinroths), and the Coot (Kornowski 1957). Judging from my own observations on the Red-and-white Crake and Baillon's Crake (Copenhagen Zoo, June 1967), a similar posture is used for drying, initially with a twitching-cum-shaking action while preening, etc.

As well as exposing the dorsal surface of the wings to the sun in the prone spreadeagle posture (see above), some owls at least will adopt a more upright posture and expose the undersurface of one or both wings frontally. The Heinroths had a photograph of a Short-eared Owl sunning thus on a log with one wing extended; according to Armstrong (1943), the wings are spread out alternately, and the species will also perch with both wings drooping while turning the face to the sun. With increasingly strong sunshine, Tengmalm's Owl (see above, Level-1) will push the wings out sideways until their ventral sides are directed forward (Glutz and Bauer 1980).

Thus, the spread-wing sunning of the owls (and of some accipitrid raptors and some falcons) appears to form a transition between the typical 'flattened' spreadeagle type of the passerines, pigeons, etc., and the more upright, standing sunning and drying postures of many large non-passerines (see especially Clark 1969, Curry-Lindahl 1970, Kahl 1971). Spread-wing postures of this latter type

take two main forms as the bird typically faces the sun with the body erect:

(i) the *'delta-wing'*, in which the wings are held half-open in a shield-like position usually with the tips of the primaries crossed in front of or below the tail; and
(ii) the *'open-wing'*, in which the wings are held out at right angles to the body, either more or less straight ('full-spread') or more angled ('loose-spread').

In some species, the sequence of increasing sunning intensity (depending, for example, on the strength and height of the sun) would appear to be: delta-wing, loose-spread, and full-wing.

The storks (studied in the wild by Kahl 1971) sun mostly in the early morning or late afternoon; both delta- and open-wing frontal postures have

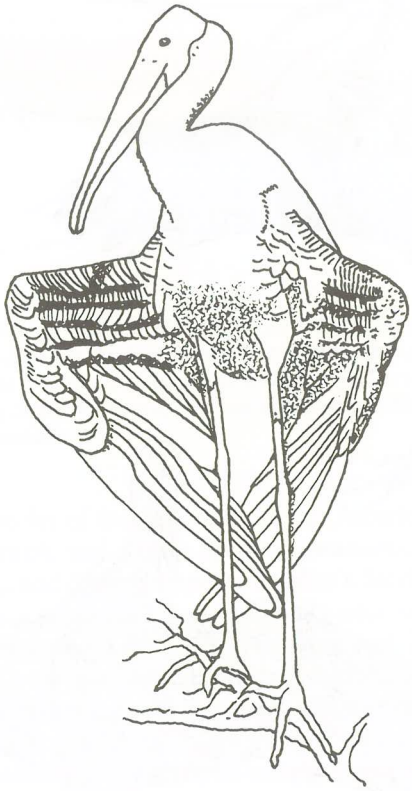
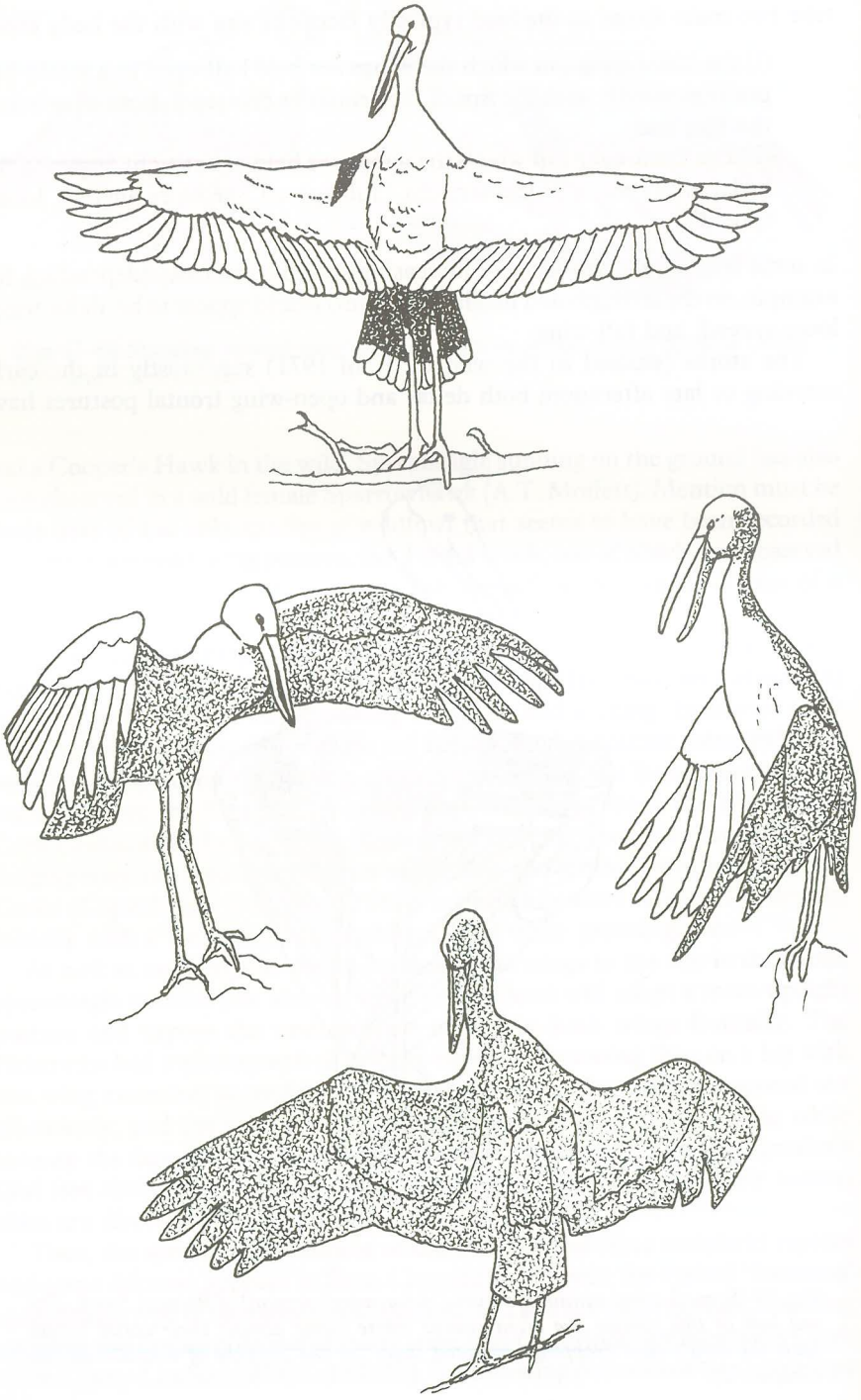
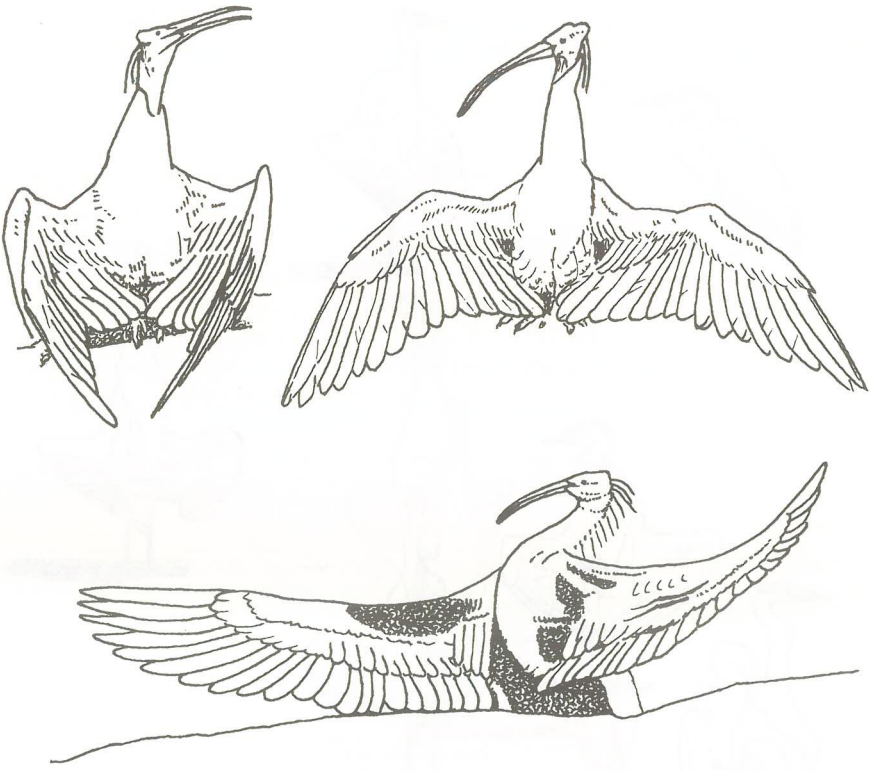


Fig. 69 *'Spread-wing' sunning posture ('delta-wing' version) of Painted Stork. The red legs of this species are often coated white along almost their entire length with the bird's own droppings excreted there for the purpose of urohidrosis (see Chapter 2).*

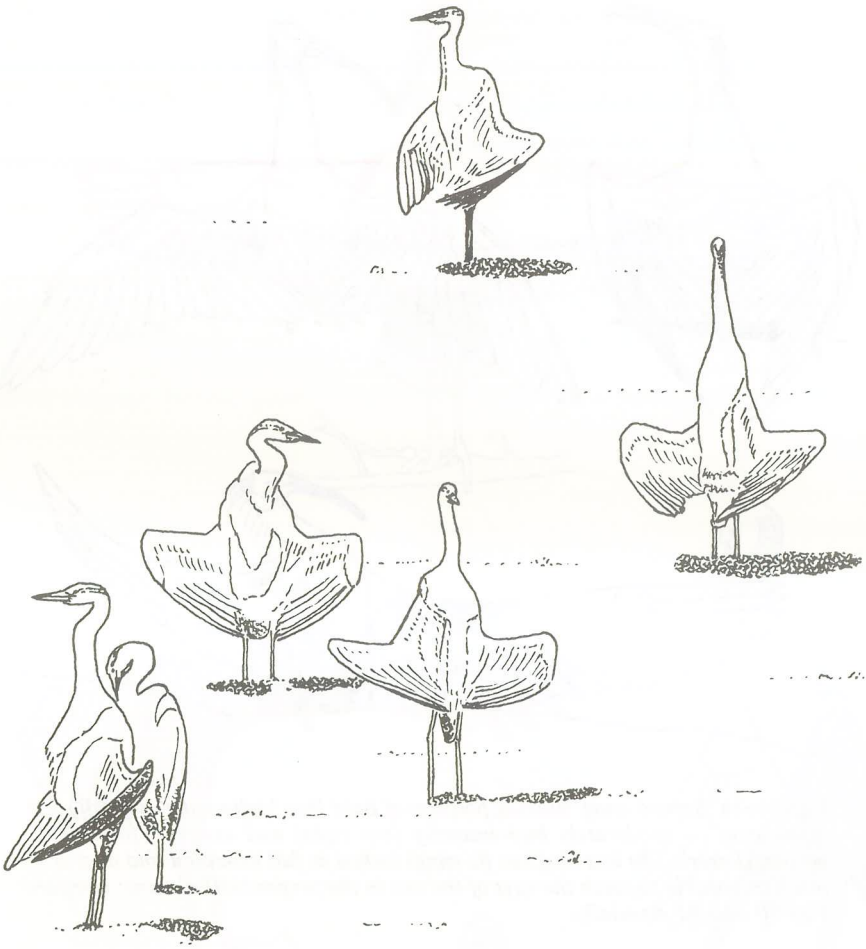




Figs 74–76 *'Spread-wing' sunning postures of Bald Ibis: 'delta-wing' (top left) and 'open-wing' — moderately high-intensity (top right) and extreme 'full-spread' version (lower). The last bird has its wings locked in full extension and angled as much as possible to catch the rays of the sun in the perpendicular plane: compare Figs 70 and 91 especially.*

been recorded in species of the genera *Mycteria* (American Wood Stork), *Ibis* (Yellow-billed, Painted, and Milky Storks), *Anastomus* (Asian and African Open-billed Storks), and *Sphenorhynchus* (Abdim's Stork); and the open-wing (full-spread version) in species of *Dissoura* (Woolly-necked Stork), *Xenorhynchus* (Black-necked Stork), and *Leptoptilos* (Greater and Lesser Adjutant and Marabou Storks). The White Stork, however, was seen only in a simpler wing-drooped posture (when drying) and no spread-winged postures at all seem to be known for the Black Stork and a number of other species. It must be emphasised that storks do not adopt open-wing postures of this type exclusively

Figs 70–73 (opposite) *'Spread-wing' sunning postures of Asian Open-billed Stork. Top bird in 'full-spread, open-wing' version, centre-right and lower birds facing the sun and centre-right with back to it.*



in the sun but use similar ones for wing-drying (facing into the wind whether the sun is out or not), for cooling (usually facing away from the sun with the feathers of the upper back erected, and accompanied by panting and urohidrosis), and for shielding the young (with the back to the sun).

The ibises, as well as sunning in the wing-drooped lateral posture (which could almost be classified as an 'oblique half-delta') and in the raised-wing posture (see under Level-3 and Level-4, above), also adopt spread-wing frontal postures at times. Both the full-spread and delta-wing forms, facing the sun, were observed in sunning Bald Ibises in captivity (Wackernagel 1964); the former posture has also been photographed in the wild by Hirsch (1979) and rather resembles that adopted by frigatebirds (see below). While a version of

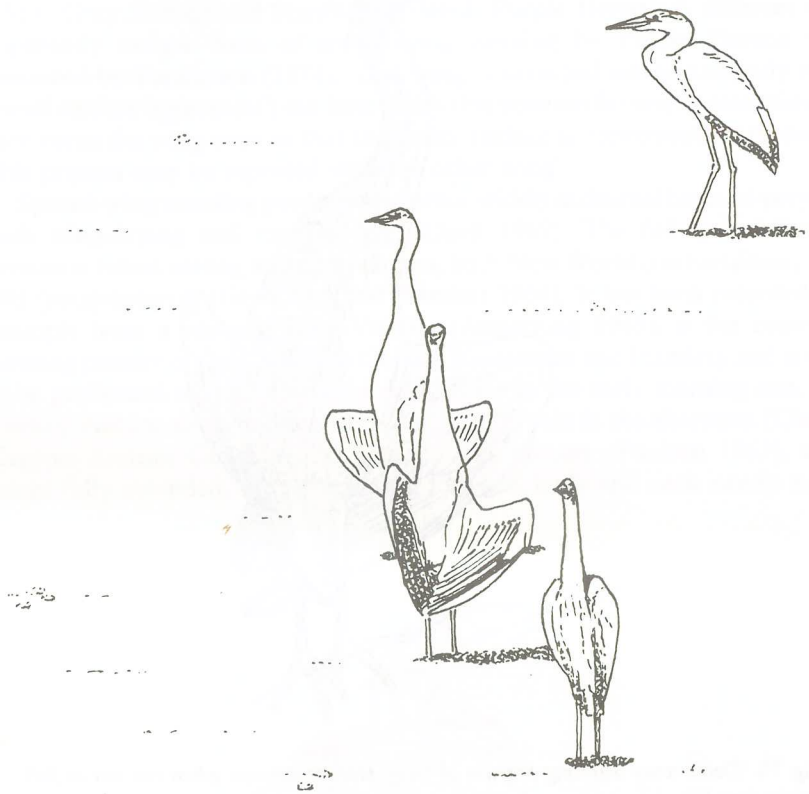


Fig. 77 (opposite and above) *Sunning group of Grey Herons at day standing-ground, Banc d'Arguin (off Mauritania), near middle of day. All seven of the sunning birds are in the 'delta-wing' posture, some in the up-tilted version when the sun is high, i.e., the angle of the undersurface of the wings tends to follow the perpendicular angle of incidence of the sun's rays.*

the open-wing posture was seen from a captive Hadada Ibis facing the sun (Wennrich 1982), and parent Sacred Ibises will shade the young with lowered wings and the back turned to the sun (Urban 1974), only the delta-wing sunning posture seems otherwise to have been recorded judging from a single observation by Hobbs (1958) on the Straw-necked Ibis.

Both delta-wing and open-wing (full-spread) postures occur in the herons, more exclusively it seems for sunning as the birds face the sun, though they can be drying the wings at the same time of course (see further, below). Only the delta-wing posture has been reported from the Great Blue Heron, Snowy Egret,

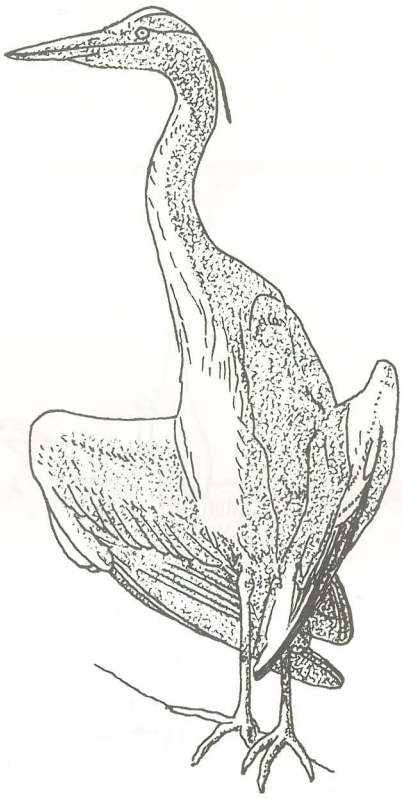


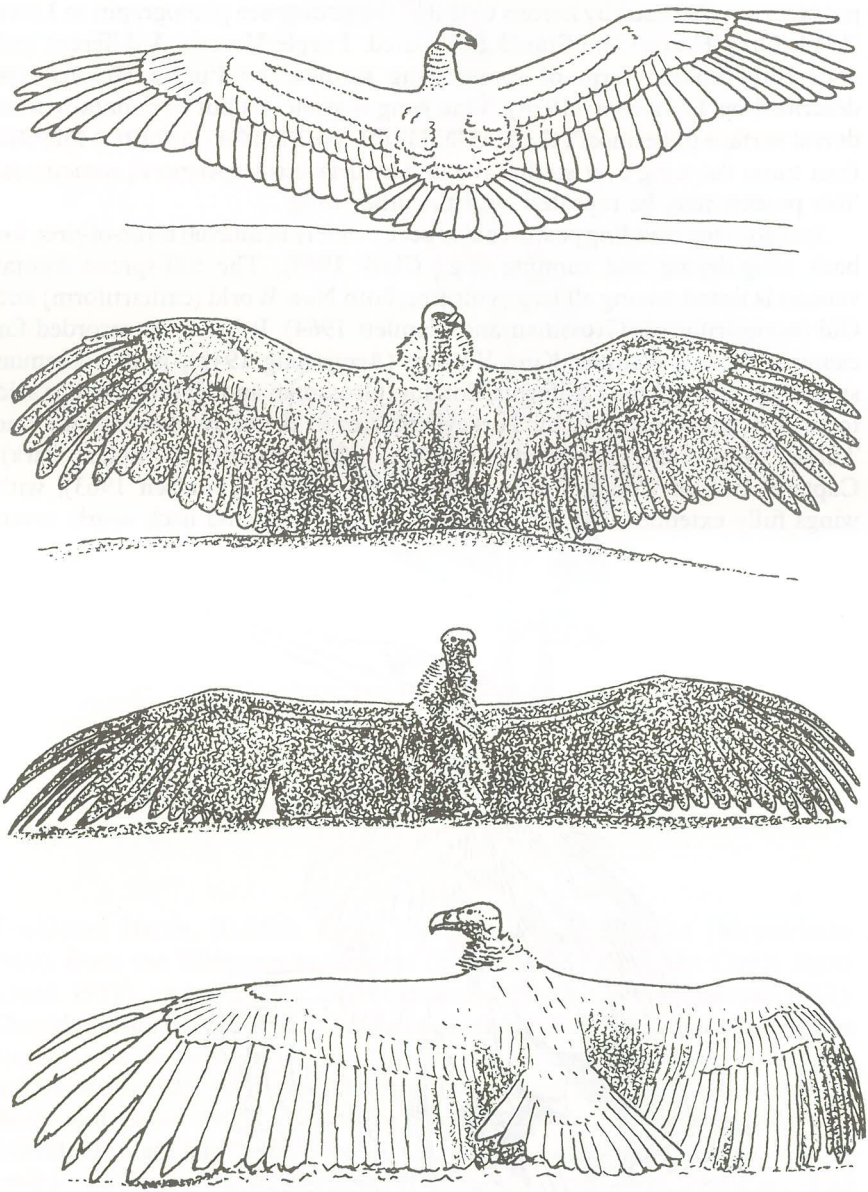
Fig. 78 *'Delta-wing' sunning posture of Grey Heron: version when sun not at full height (see Fig. 77).*

Tricolored Heron, Reddish Egret, and Green-backed Heron (Meyerriecks 1960), from the White-necked Heron (Hobbs 1958), from the Cattle Egret (Gush 1951), and from the Yellow-crowned Night Heron (Haensel 1972). Though the full-spread posture has been observed (Boyd 1950, Tully 1950), the delta-wing is the usual sunning posture also of the Grey Heron (e.g., Heinroth and Heinroth 1924–33, Rooke 1950 and others, Gush 1951, Milstein *et al.* 1970, Bauer and Glutz 1966); it was this version that was adopted by all three individuals that I have seen sunning (two together on the ground at the edge of a saline lagoon near Fayid, Egypt, on 7 October 1949, and one on the shore of an island in Cranemoor Lake, Englefield, Berkshire, on 4 August 1950). The delta-wing sunning posture has also been recorded in the Purple Heron by Gush (1951) on Java; like the Grey Herons and Cattle Egrets he also observed there, this species sunned mostly 'during the first four hours of daylight after late unseasonable night rains', but mainly on the ground, whereas the others did so

both on the ground and in the tops of small thorn trees. Delta-wing-like postures are also used by herons to shield the young; see photographs in Lowe (1954: Grey Heron) and Staněk (not dated: Purple Heron). A different and apparently unique form of spread-wing sunning by Purple Herons was described by Tomlinson (1974): 'One wing is stretched out horizontally with dorsal surface uppermost'; the bird 'holds this position for one or two minutes then turns the wing over so that the under surface is uppermost'; sometimes, 'this process may be repeated with the other wing'.

Spread-wing standing postures also occur widely in diurnal birds-of-prey for both wing-drying and sunning (e.g., Clark 1969). The full-spread frontal version is found among all large vultures, both New World (cathartiform) and Old (accipitriform) (Grossman and Hamlett 1964). It has been recorded for example from a sunning King Vulture (Armstrong 1943), is the common sunning posture of the California Condor (Grossman and Hamlet), and is said to be performed regularly by Turkey Vultures in the early morning sun, one Turkey Vulture also being seen thus during light rain in the afternoon (Clark). Captive Andean Condors also adopted this posture (Poulsen 1963), with wings fully extended, the tips curving forward, body and neck nearly erect,

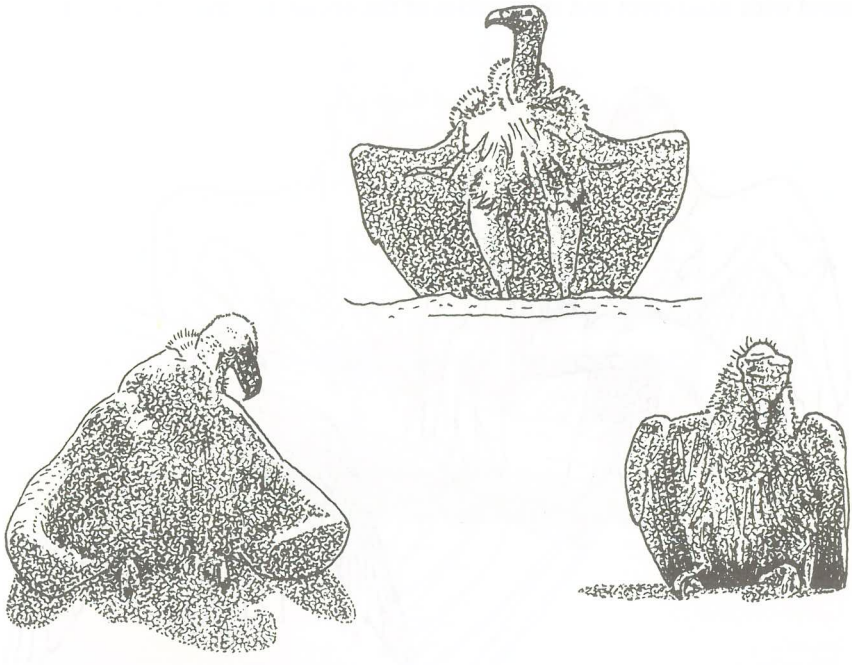
Fig. 79 *'Spread-wing' posture of Purple Heron on nest while sun-shielding young.*



Figs 80–83 *'Full-spread' standing sunning postures of one New World and two Old World vultures: Turkey Vulture (top), in moult; Himalayan Griffon; and Lappet-faced Vulture (bottom two) — squatting down (upper) and standing.*

and tail expanded, for sunning (in often-repeated spells of 2–10 minutes, 'both in cold and hot weather' when the sun was shining on the birds or at least when there was 'a sudden increase in brightness') and for drying after bathing (when the posturing was interspersed with wing-flapping).

The full-spread frontal posture is commonly used for sunning in vultures of the genus *Gyps*, which 'align their wings approximately at right angles to the direction of sunlight' (Houston 1980; see further in Chapter 3, above, particularly for the Indian White-backed Vulture); though not closely studied, the same sunning posture is particularly well-known in the Griffon Vulture. In captive Himalayan Griffons, the full-spread posture, with the wings opened wide, primaries splayed and tilted slightly forward, and neck ruff erected, was adopted in strong summer sun (for sunning) and also in dull winter weather (probably to air and dry the feathers) (Haensel 1972). Lappet-faced Vultures, studied by Sauer (1973) at two watering sites in the Namib Desert, adopted both full-spread and delta-wing postures on the ground for 'basking . . . thermoregulation . . . and also for drying the plumage' during their prolonged afternoon visits to drink, bathe, preen, and rest (the full-spread posture, at least, also being shown by the accompanying Cape Vultures). A Lappet-faced



Figs 84–86 *Sunning postures on ground of two vultures: Lappet-faced Vulture in 'delta-wing', standing (top, background) and squatting (bottom, right); and Black Vulture in 'delta-wing', squatting.*

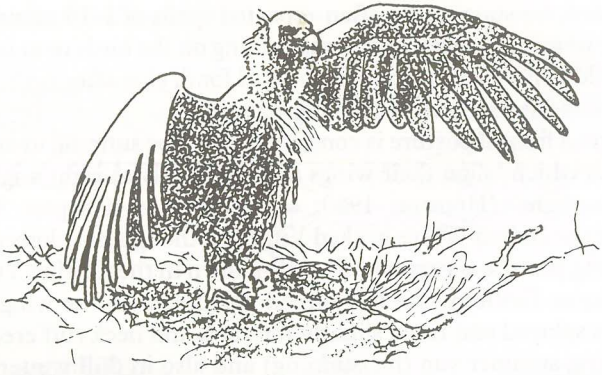
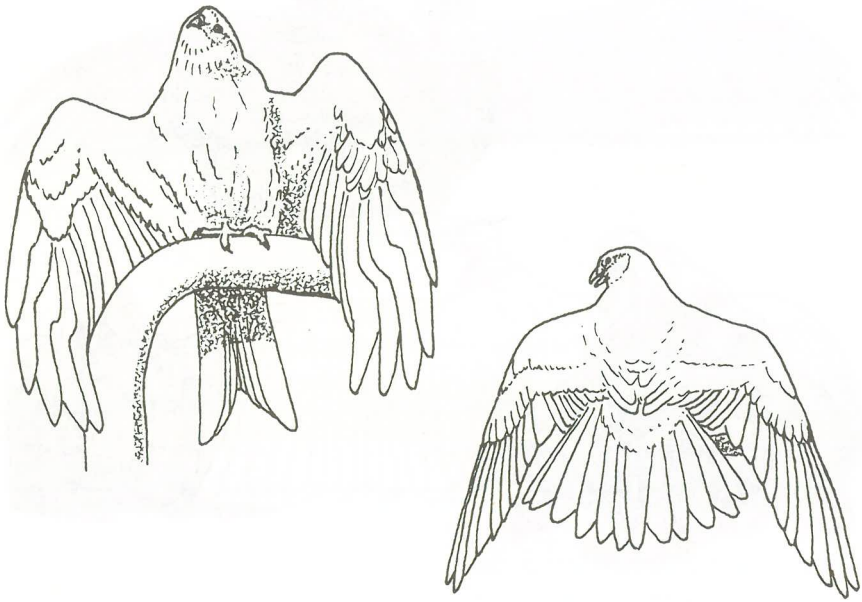


Fig. 87 *'Spread-wing' posture of Black Vulture on nest while sun-shielding young.*

Vulture on guard at the nest-site, however, sought shade on the ground to evade the heat of the noon-day sun instead of 'showing the common thermoregulatory activity exercised through panting, spread-wing postures and water-baths'. In the delta-wing posture, judging from Sauer's photographs, the bird may either stand with head erect and the hackles of the breast and mantle erected like a



Figs 88–89 *'Loose-spread' sunning postures of two diurnal birds-of-prey (a hawk and a falcon): Red Kite (upper) and Hobby.*

ruff, or squat down on the tarsi with toes bunched and head lowered. A similar version of the delta-wing sunning posture to the last was figured also in a captive Black Vulture: the bird would crouch on the ground with its back to the sun, so that the whole of the dorsal surface was exposed; its head was turned round to face the sun or drooped so that the crown and culmen rested on the ground between its toes (Haensel). This species also adopts standing full-spread postures, at least for shielding the young at the nest (see Meyburg 1976).

Standing spread-wing postures are probably widely adopted for sunning and wing-drying (as well as to shield the young) among other accipitrid birds-of-prey, and also among the falcons. Heinroth and Heinroth illustrated sunning postures of the loose-spread type for the Red Kite, Honey Buzzard, and Hobby (see also Note 21). This posture was the one observed in a sunning Bald Eagle by Bernard King: with back to the sun and tail spread, it perched thus for 30 minutes in the mid-day sun. A photograph of a sunning White-tailed Sea-eagle in Haensel (1972), however, shows a typical delta-wing posture. There are, it

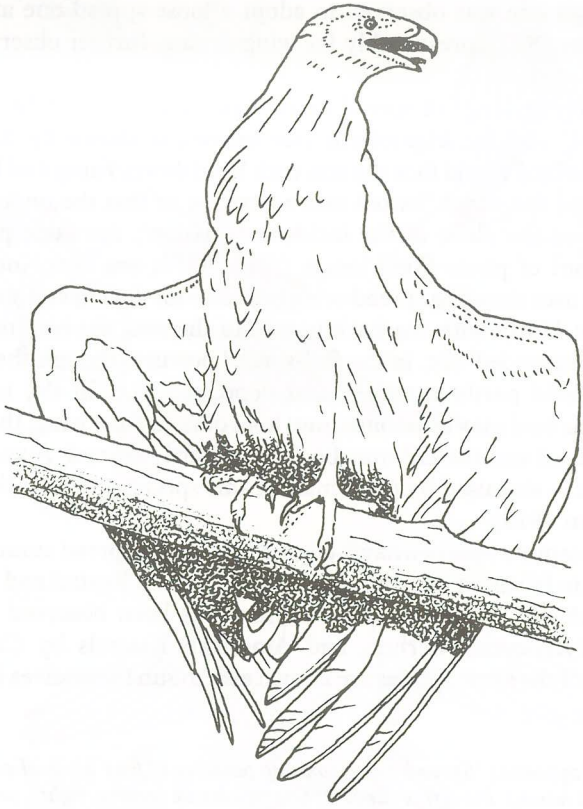


Fig. 90 *'Delta-wing' posture of White-tailed Sea-eagle.*

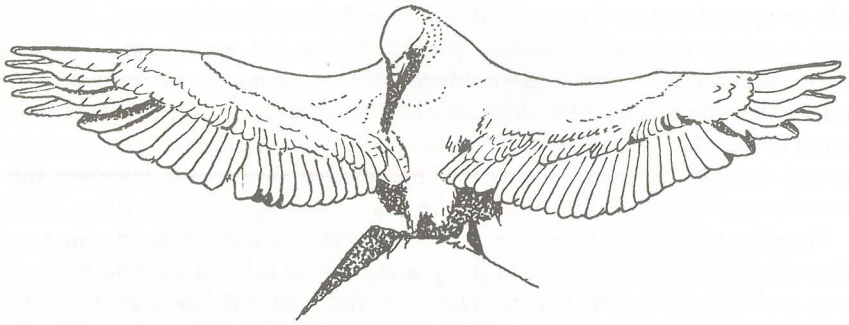


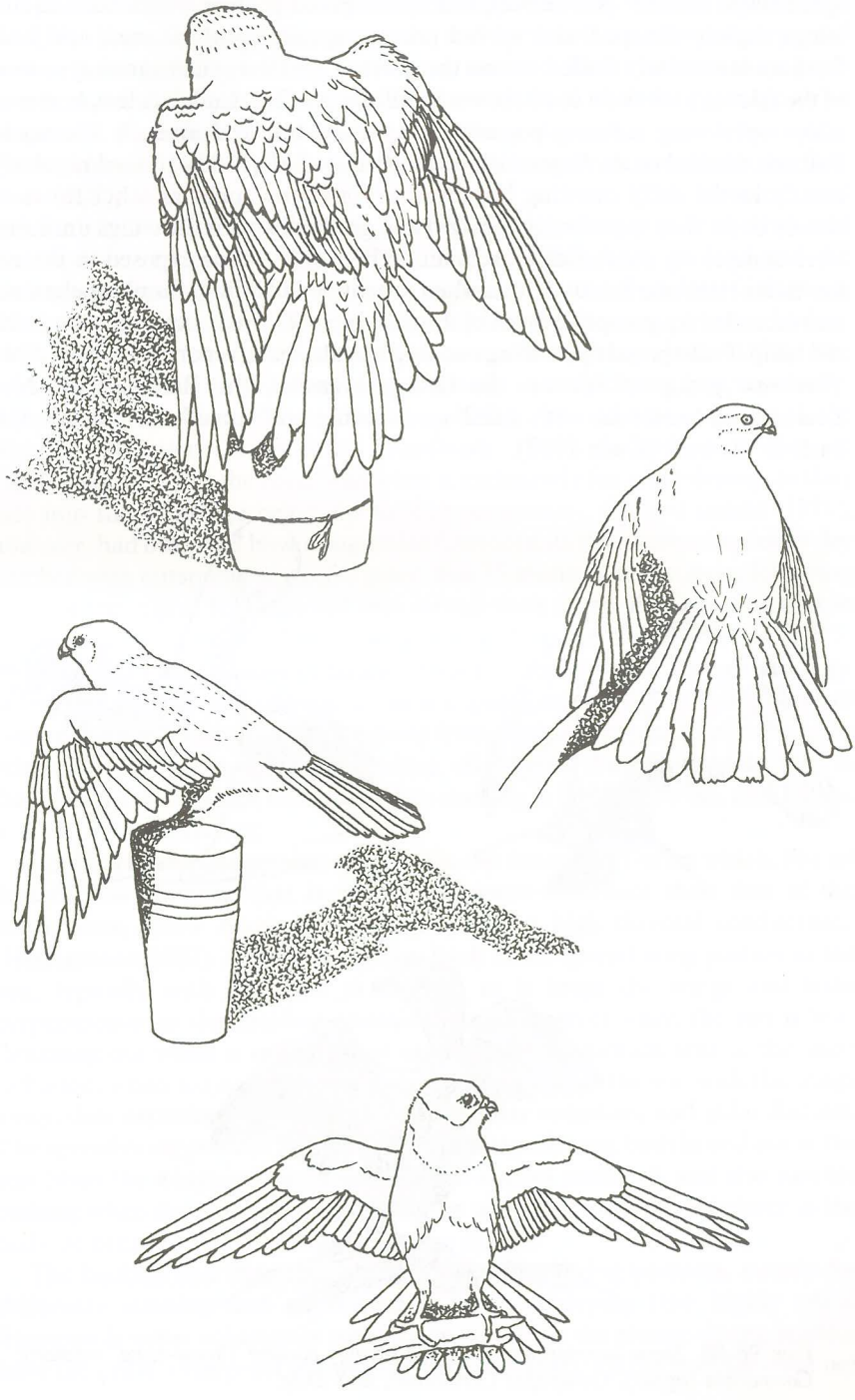
Fig. 91 *Extreme 'full-spread' sunning posture of Bateleur. The bird has its wings locked in full extension and angled as much as possible to catch the rays of the sun in the perpendicular plane.*

seems, no records of the Osprey (Pandionidae) using spread-wing postures for sunning; though one was observed to adopt a loose-spread one after fishing (Elowson-Haley 1982), presumably for wing-drying, further observations are needed.

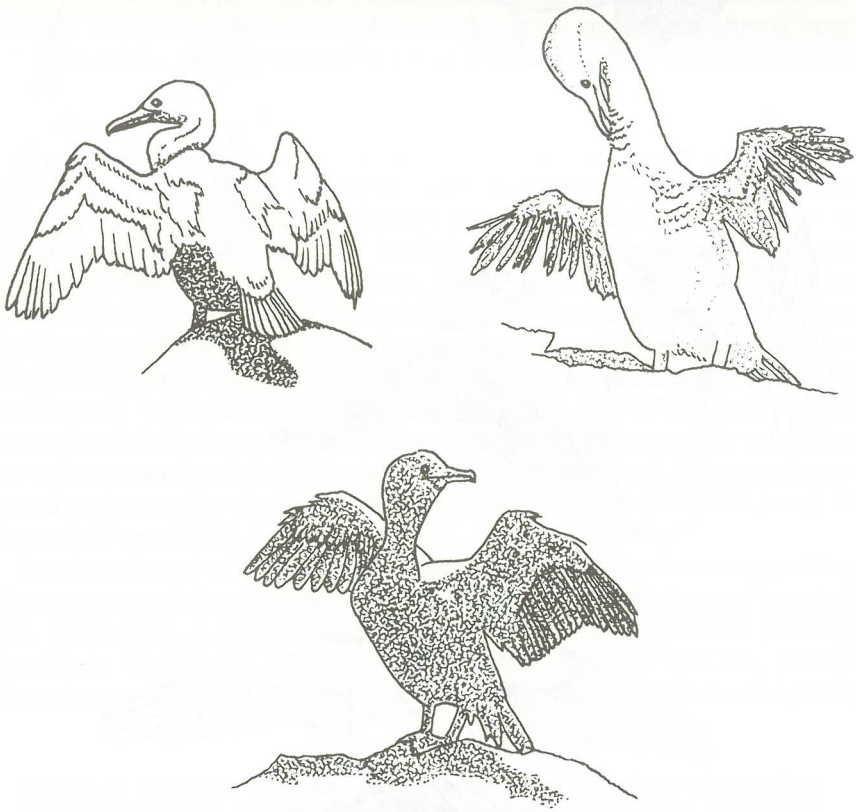
A particularly striking full-spread sunning posture, recalling that of the Bald Ibis (see above) and the frigatebirds (see below), is shown by the Bateleur Eagle: a captive bird would face the sun with head down, rump and leg feathers 'fluffed out', and the wings 'locked into a position so that the under surface is perpendicular to the plane of the incident radiation'; the same posture was adopted in front of photo-flood lamps (Cade 1973; see also Note 22). The Sparrowhawk uses standing spread-wing postures for drying and sunning after a bathe (Owen 1916): with the back turned to the sun, the bird may hold its wings 'widely expanded' (i.e. in the full-spread posture) though they are more usually only 'held partly extended and depressed' (i.e. in the loose-spread posture) and the bird may also sometimes hold out only one wing; the primaries are well separated and the tail may be fully or partly fanned. A variant loose-spread posture is also used by the female of this species to shade the young in the nest (Owen 1919).

A tethered captive Sparrowhawk adopted the loose-spread sunning posture when strong sun fell upon it, as did adjoining falcons – a Kestrel and a Peregrine (R.J. Prytherch). A similar standing posture has been observed in sunning Peregrines, Gyrfalcons, Merlins, and American Kestrels by Cade (1982). Though some of the same species are known also to sun themselves in the prone

Figs 92–95 (opposite) *'Spread-wing' sunning postures of four birds-of-prey (three falcons and a hawk): Peregrine (upper), Sparrowhawk (centre, right), and Kestrel as observed by R.J. Prytherch, all in 'loose-spread'; and Bat Falcon, in 'full-spread'.*



spreadeagle manner (see above), this loose-spread posture ('with back to sun, wings slightly drooped with spread primaries, tail slightly fanned, and body feathers moderately fluffed out on the dorsum') is the typical sunning posture of the falcons and likely to be shown by all species (T.J. Cade). A few, however, adopt open-wing sunning postures at times. Adult and juvenile Eleonora's Falcons, studied on an Aegean island by Ristow *et al.* (1980), sunned regularly, mostly in the early morning but also during sunny spells at other times on cloudy days; they would stand upright and gradually open the wings until they were completely outstretched, remaining motionless thus exposed to the sun for 'more than one minute', often then preening and oiling. Similar behaviour was recorded from captive birds of the same species when exposed to an infra-red lamp. Full-spread open-wing sunning has also been reported in three of the *'Nesierax'* group of falcons: the Orange-breasted, the Bat, and the New Zealand; all 'sunbathe with a full spread-wing and spread-tail posture with back to the sun' (Cade 1982).

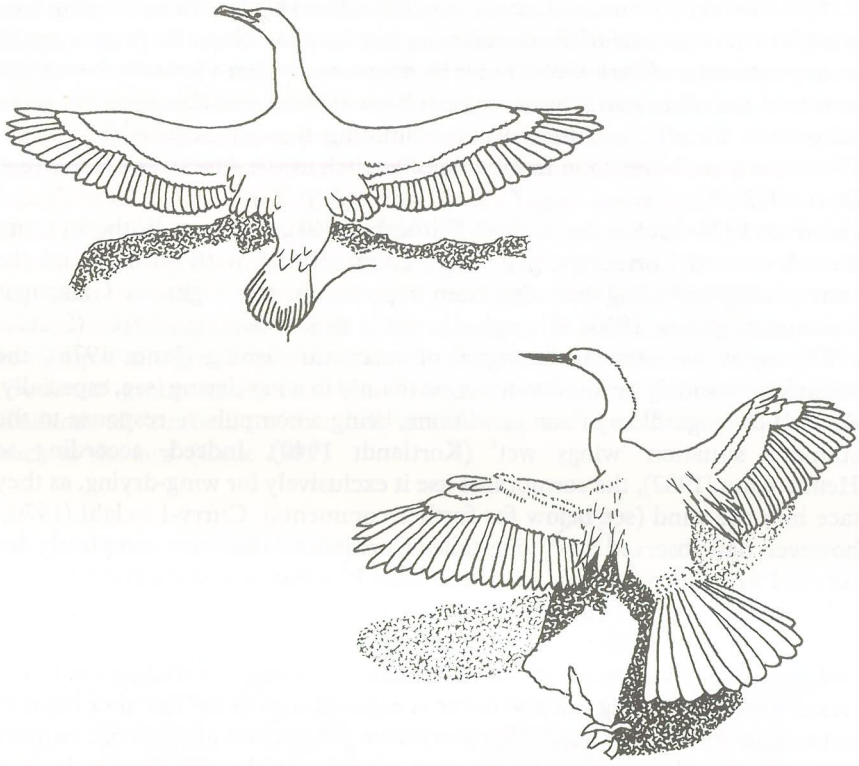


Figs 96–98 *Three cormorants in 'spread-wing' posture ('loose-wing' version): Cormorant (upper), Galapagos Cormorant, and Shag.*

Spread-wing postures also occur in pelecaniform birds. The open-wing type is highly characteristic of the cormorants and darters. It has also been reported from pelicans (see Clark 1969), but is by no means so firm a habit in these birds as it is in the other two groups – which have evolved wettable plumage as an adaptation for efficient underwater swimming through reduced buoyancy. Particularly well-known in familiar species such as the American Darter (e.g. Bent 1922), Cormorant (e.g. C.W. Townsend in Bent 1922, Heinroth and Heinroth 1924–33, Kortlandt 1940, Witherby 1940), Shag (e.g. Witherby), and Double-crested Cormorant (e.g. Bent, Palmer 1962), both on land and the water, wing-spreading has also been reported in the flightless Galapagos Cormorant (Snow 1966). Though dismissed as a balancing posture (Stabler 1957), or as an intraspecific signal of successful fishing (Jones 1978), the behaviour is widely believed to function mainly in wing-drying (see, especially, Rijke 1968) regardless of sun conditions, being a compulsive response to the stimulus situation 'wings wet' (Kortlandt 1940). Indeed, according to Hennemann (1982), the cormorants use it exclusively for wing-drying, as they face into the wind (see below for further comments). Curry-Lindahl (1970), however, had observed how Long-tailed Cormorants that were completely dry perched with outspread wings for more than 35 minutes near sunrise following a dry, warm night; he suggested that spread-wing postures might function in thermoregulation rather than in wing-drying. Further, Seigfried *et al.* (1975) had shown for four species of South African cormorants, including the Long-tailed, that wing-drying can also occur at exposed sites in the sun after bouts of swimming: the birds typically face away from the sun and perform one or more relatively short bouts of wing-spreading; afterwards, they continue to bask in the sun for a while, then, evidently when starting to feel heat stress, turn to face it while gular-fluttering.

Similar behaviour has been observed in the American Darter which, like all darters, has plumage that is even more water-absorbent than that of the cormorants, a low basal metabolic rate, and a high thermal conductance (Hennemann 1982). It too will position itself in the spread-wing posture in the sun, typically with the back to the sun as it keeps the wings and body perpendicular to the incident sunshine, standing erect when the sun is low, flattening out when it is high, thus exposing the maximum area to the solar radiation; when too hot, however, it typically faces into the sun with the wings away, thus exposing the minimum area to solar radiation, and gular-flutters. The spread-wing posture is also used for plumage drying, both in and out of the sun (then the wings are usually in the full-spread position), and also just for basking when the plumage is dry (then the wings are usually held closer to the body or occasionally just drooped at the sides).

The boobies and frigatebirds also adopt spread-wing postures, mainly for deliberate sunning and not typically for wing-drying (the highly aerial frigatebirds never voluntarily enter the water, while the plunge-diving boobies have the usual waterproof plumage of most seabirds). All the boobies – but not



Figs 99–100 *A cormorant and a darter in 'spread-wing' posture ('full-spread' version): Cormorant (left) and American Darter.*

the Gannet and its allies – sun in a delta-wing posture (see Dorward 1962, Nelson 1978); as I have studied the behaviour of the Brown Booby in some detail, a summary of the sunning and thermoregulatory behaviour of this species is given separately in Chapter 5. The typical 'inverted full-spread' sunning posture of the Ascension Frigatebird is particularly elaborate and is characteristic of all frigatebirds (see, e.g., Nelson 1980): it sits back on its tail facing the sun with the body and head erect and the wings extended fully along the ground and twisted 'inside-out' so that the undersurfaces are exposed perpendicularly to the incidence of the solar rays (the angle probably varying according to the position of the sun, as for example in the Bateleur Eagle which has a basically similar sunning posture: see above); the bill is usually open and the bird often gular-flutters. Such a posture was the one eventually adopted by a captive female Lesser Frigatebird I saw sunning in the Bristol Zoo on 3 May 1964; when first in the sun, however, it went into a delta-wing posture, keeping the elbows to its sides but the wrists held out, gradually going into the full-

Figs 101–102 *Two frigatebirds sunning: Great Frigatebird juvenile in 'inverted full-spread' posture facing sun, and Ascension Frigatebird in 'loose-wing' posture with back to sun.*

spread in stages via a series of posturally facilitated wing-flaps. A photograph of a sunning Ascension Frigatebird in Nelson (1975) shows a type of loose-wing posture with the back to the sun, but how common this less elaborate posture is remains to be established. It could, just conceivably, be the true sunning posture, for Nelson suggested that the habit of frigatebirds 'of turning the under-surfaces of their wings to the sky . . . tempts the suggestion that they are radiating heat' (i.e. heat-dumping). Such a unitary interpretation, however, seems certainly not to be true of the spread-wing sunning postures of birds generally; it would be more convincing for the frigatebirds if it could be demonstrated that the full-spread posture is adopted only when the birds are caught in the sun and that they otherwise seek the shade (see further in Chapter 5).

A COMMENT ON WING-DRYING, SUN-SHIELDING, ETC.

The whole question of sunning in cormorants and darters, and also in the ciconiiform birds and diurnal birds-of-prey, has been complicated by the problem of wing-drying, as well as being confused by those who maintain that spread-wing postures can only have the one main function (either wing-drying or sunning for thermoregulation). I will attempt to clarify the issue therefore. Firstly, there is the fact of wing-spreading by dry birds: when it is performed deliberately in the sun, then this should be counted as straightforward sunning (see, e.g., Bent 1922 for the Double-crested Cormorant). Secondly, there is

wing-spreading by wet birds to dry the plumage: when it is performed deliberately in the sun, then this too is a form of sunning: termed 'drying-in-the-sun' (above, under Level-1 sunning) but perhaps better shortened to 'sun-drying' (see further in Chapter 7, below); when not, then this is not sunning at all of course and is best termed 'wind-' or 'air-drying'. The same interpretation would also apply to the sunning and drying postures of the rails; also, presumably, to the wing-spreading of the mousebirds described above. (See also Note 23.)

If our understanding of sunning has been confused by the problem of wing-drying, it has been even more so by another category of sunning-like behaviour: those spread-wing postures which many large birds adopt at the nest when involuntarily exposed to strong sunshine that causes heat stress or when shading their young. Should such behaviour be counted as sunning? I think not, and prefer rather to classify the postures as 'sun-stress postures' (when the adults attempt to cool themselves) and as secondarily adapted 'sun-shielding postures' (when they use them to shelter the young).

CHAPTER FIVE

The Brown Booby

The following account is based on observations I made at Ascension Island situated in the tropical South Atlantic Ocean, eight degrees below the equator (see further in Note 1).

SUNNING

The typical sunning posture of the Brown Booby is a delta-wing one usually performed with the back to the sun so that the solar radiation falls on the dorsal surface. With head erect, the bird raises the wings at the carpal joints and stretches them backwards so that the elbows meet or overlap and the primaries extend over the rump and fanned tail, the latter acting as a brace to support the wings; the back feathers are well ruffled, especially those of the 'shoulder-ruff' (scapulars, etc.) and those round the feathered nipple of the oil-gland (which is thus exposed), the bill is open and often raised, and the bare gular skin and the

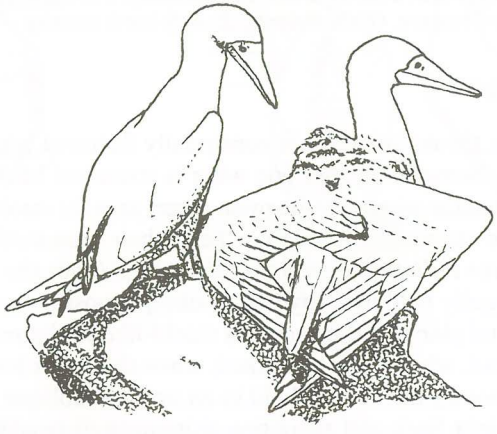
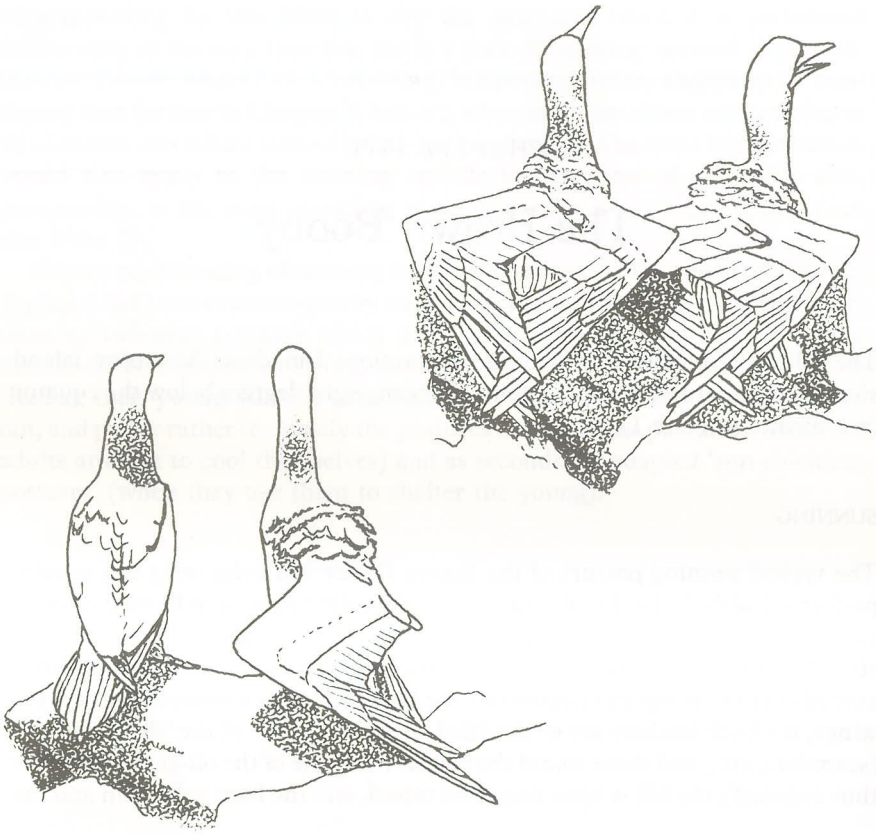


Fig. 103 *Pair of Brown Boobies in sun, right-hand bird in typical 'delta-wing' sunning posture with back to sun.*



Figs 104–105 *Pair of Brown Boobies in sun (two episodes). The upper birds are both sunning in the typical posture. Of the lower birds, only one is sunning — in the 'half-delta'.*

feathered area of the throat below it are continually fluttered with a throbbing or pulsating action. Sometimes, just one wing is stretched back (half-delta).

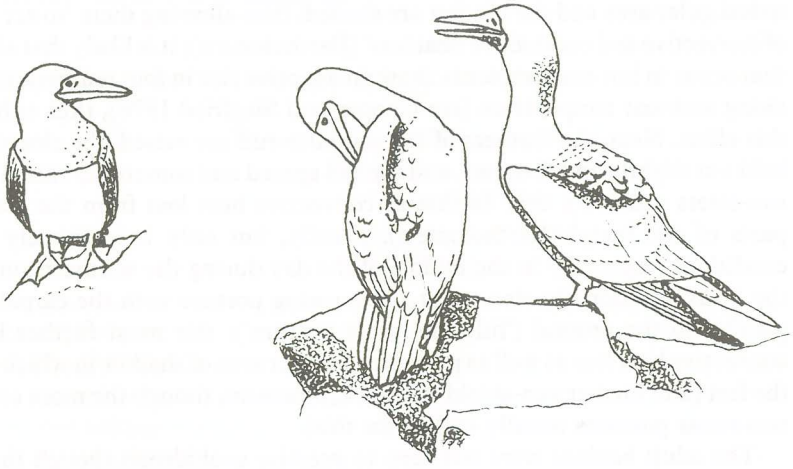
It is quite clear that the wings are the main target area for insolation. During a spell of deliberate sunning, the boobies keep their 'sun-surfaces' perpendicular to the incident radiation: when the sun is high (over the middle of the day), the body is usually held in a downward-oblique position with the wings lying in the horizontal plane on the back in a shield-like configuration with the tips crossed on the tail, which may be cocked; when the sun is lower in the sky (morning and afternoon), the body is held in an upward-oblique position with the wings sloping right back and their tips crossing well beyond the tail. At times, deliberate sunning follows a session of feather-care (bathing, oiling, preening, etc.); the birds will also preen during lulls in sunning (when the sun

appears fitfully from partial cloud) and after a sunning spell, giving special attention to the wings, and they sometimes head-scratch suddenly during a spell of sunning.

At times, the boobies will resort to special sunning spots on cliff ledges out of the wind, especially when their usual perching sites are in the shade. Sunning behaviour is performed deliberately throughout the year at Ascension but only when the sun is out, ceasing when it goes in. However, not all the birds present at the colony need be sunning at the same time, even in apparently ideal conditions of continuous strong sunshine. Outbreaks of sunning do occur at times, especially when the sun emerges after a continuous period of cloud or breaks out intermittently. On such days, the effect of the sun when it appears can be quite dramatic: where there is little or no wind, those birds that are in the sun immediately start either to sun themselves or to assume sun-stress postures only (see below); the same can happen on sunny days when the sunshine reaches previously shaded spots.

COOLING

As well as deliberately sunning, the boobies will also seek shade during the heat of the day, some birds having special 'shade-perches' which they can use at different times according to the position of the sun. When very hot, they cool themselves by flying out over the sea and carrying out a series of shallow



Figs 106–107 *Some postures of Brown Booby. The single bird (left) is in a normal relaxed perching posture, without any heat-stress. Of the pair in the sun, one is preening laterally (centre) and the other is in the cooling posture ('heat-posture' or 'sun-stress posture').*

Fig. 108 *Sun-stress posture of brooding Brown Booby while sun-shielding chick.*

plunge-dives under the water. Those forced to occupy fixed positions in strong sunshine (e.g. when defending a nest-site, incubating, or brooding small young), show an intensity sequence of responses when suffering from or attempting to reduce the effects of over-heating.

The first of these sun-stress cooling responses is sustained gular-fluttering which 'contributes to evaporative cooling' (see Bartholomew 1966 for the Masked Booby), performed with the head erect ('basic sun-stress posture'). While gular-fluttering, the bird typically turns its back to the sun so that the naked gular area and the big feet are shaded, thus allowing them 'to act as sites of convective and conductive heat loss' (Bartholomew); it is likely that all sulids that occur in hot environments show an adaptive rise in foot temperature with rising ambient temperature (see Cooper and Siegfried 1976), thus enhancing this effect. Next, the feathers of the shoulder-ruff are raised, the closed wings held out slightly and drooped, and the tail spread and sometimes raised ('main sun-stress posture'); this 'facilitates convective heat loss from the feathered parts of the body' (Bartholomew). Finally, but only in extremely taxing conditions (especially in the middle of the day during the southern summer), the birds occasionally also adopt a delta-wing posture with the carpal raised parallel to the ground ('full sun-stress posture'); this must further help in convective heat loss as well as providing a larger area of shadow in which to cool the feet (and further sun-shield the chick, if present, though the more common sun-stress postures usually suffice for this).

The adult boobies were not seen to practise urohidrosis though this may occur, perhaps only incidentally, in the young, which typically have dirty legs and feet before taking their first bathe when capable of flight. Instead of voiding well clear of the site as is usual at other times, both adult and young Cape Gannets suffering from heat stress in high ambient temperatures are known to

defecate deliberately on to or close behind their feet and to paddle in the excrement; they thus increase the rate of heat loss through evaporative cooling, both via the feet and the ground (Cooper and Seigfried).

COMMENT

All the major components of the posture that the Brown Booby adopts when sunning have a cooling function; however, to interpret deliberate sunning as merely an elaborate cooling response would be too simplistic. As the birds often seek the sun to perform thus, in spite of the problems of over-heating that follow, the behaviour must have some other function. The comments by Cullen and Ashmole (1963) on the sunning of the Black Noddy on Boatswainbird Islet, Ascension, are relevant here.

> 'The bird orientates itself so that the sun shines on the spread wing, and the head is inclined to the side so that the "cheek" receives the full force of the sun. The sunning posture is quickly given up as soon as the sun goes behind a cloud and the birds may preen instead – or leave the place if the sun remains in cloud for long. The noddies frequently resort to a sunny patch and adopt a sunning posture, when they could sit in the shade close by if they preferred, showing clearly that the behaviour is suited to warm, rather than to cool the birds.'

I take the word 'warm' here to mean 'obtain heat', i.e. for some other purpose than thermoregulation, for there can be no question of sun-basking (that is, sunning to gain heat) in either of these tropical species and the solution must lie elsewhere. (See further in Chapter 8.)

CHAPTER SIX

Sunning and Certain other Behaviour Compared

In my opinion, sunning has little if any equivalence with true bathing (i.e. in water) or with anting or dusting, though all in their different ways may help in feather maintenance. In the light of claims that there are causal and functional relationships between sunning and these other behaviour patterns (see Chapter 3), it is of interest to examine them in a little more detail so as to establish any differences and similarities. All have one feature in common, namely feather erection, and all are associated with preening and other feather-maintenance behaviour (head-scratching, etc.). Yet feather ruffling clearly serves more than one purpose, both within and outside thermoregulation, and it is not certain, though highly likely, that the preening and other activities that follow or intersperse bouts of anting and sunning are (as in the case of true bathing, and also that of dusting) part of a functional chain of feather-care behaviour or merely reaction to the displacement or soiling of the plumage.

BATHING

Bathing behaviour shows wide adaptive variety (see Simmons 1985, under 'Comfort Behaviour') but its main function, in addition to any cleansing of the feathers and skin and washing out of ectoparasites, is to wet the plumage so as to facilitate the oiling and preening which normally follow in functional sequence. There is no similarity at all between sunning and most forms of active bathing (i.e. what I have termed 'stand-out, stand-in, in-out, flight-, and plunge-bathing') but there is between some forms of sunning and one of the more passive forms of bathing, namely 'rain-bathing'. As we have seen (Chapter 4), this is especially true of the raised-wing posture in the case of the Columbidae, one of the few groups known to practise specialized bathing of this type (though some species, including the Diamond Dove, seldom if ever bathe at all in any way); the postures used in sunning and rain-bathing are identical or closely similar and aim to expose the flanks and probably the undersurface of the wing to the rain and solar radiation respectively, though obviously for quite different reasons. The same posture is used by pigeons for

sun-drying (see Goodwin 1967b) and probably also for wind- and air-drying, and perhaps for cooling, so the environmental pressures responsible for its evolution are clearly many and complex. There is little point, therefore, in attempting to establish a unitary explanation of either its causation or function, while the temptation to speculate as to which version of the posture was derived from which is best resisted. Incidentally, neither the Dunnock nor Reed Warbler have a raised-wing rain-bathing posture in their repertory of comfort behaviour in addition to the sunning one (see Chapter 4); neither do I believe that consideration of the one-wing 'flipping' display, performed by the Dunnock during antagonistic encounters, is in any way relevant to the derivation of its sunning posture (see Goodwin 1967a).

Some specialist rain-bathers adopt a sunning-like spreadeagle posture during precipitation: the feathers are ruffled, wings fully extended horizontally, and tail fanned. This is particularly characteristic of the parrots (Harrison 1961), the rain-bathing posture thus differing from the known (lateral and raised-wing) sunning ones of this group (see Chapter 4). Larks too will 'bathe in the rain, lying down in it with outspread wings' (Finn 1919); in this case, the rain-bathing posture does resemble the spreadeagle sunning one. American Robins (which are not specialist rain-bathers) have been seen in postures apparently resembling spreadeagle and lateral sunning ones while 'bathing' under lawn sprinklers (King 1981a), some of the birds sunning elsewhere afterwards (B. King).

ANTING

Typical anting is confined to the passerines and, in the wild, takes two main forms (Simmons 1957, 1966, 1985):

> (i) the bird applies single ants or wads of ants in the bill to the plumage, typically the ventral tips of the primaries, one wing at a time (active anting, direct anting, or ant-application behaviour);
> (ii) it postures among thronging ants so that they invade its plumage (so-called passive anting, indirect anting, or ant-exposure behaviour).

In both cases, formic-acid and other chemicals from the ants are introduced on to the feathers, principally those of the wings. There is no universal treatment of the skin, round the vent or elsewhere, as has been claimed (Whitaker 1957, Potter and Hauser 1974); nor do the great majority of species that show true anting behaviour use anything else but worker-caste ants or, in a few cases, other pungent invertebrates. Though, as with sun-exposure behaviour, the precise function of anting remains to be demonstrated, all the evidence suggests that it helps in the care of the feathers (the wings in particular), probably by supplementing the bird's own preen-oil with fluids from the ants (some of which are essential oils), removing stale preen-oil or excess lipids, and by

combatting ectoparasites (formic-acid and equivalent anal fluids of the ants being insecticidal). As reported in Chapter 3, most anting has been recorded (in the northern hemisphere at least) during the period when the post-breeding and post-juvenile moult is in progress; however, speculation that birds ant so as to soothe the skin during feather replacement (see Potter and Hauser 1974) seems ill-founded, the possibility that the correlation was between anting and the timing of nuptial swarming by the ants (see Simmons 1960), rather than between anting and the timing of the moult, not being considered. Likewise, speculation that anting is self-stimulatory, or even auto-erotic (see Whitaker 1957), appears to be even more misguided (Simmons 1966).

The typical posture adopted during ant-application is a lateral one in which one wing is positioned to give the bird access to the target area under the wing (see above) and the tail brought round to the same side. It thus resembles the typical lateral sunning posture of passerines but only superficially; for instance, the target area for sunning is different and the tail is positioned so that it is exposed to the sunshine, whereas in anting the tail is used to press against the wing-tip to facilitate the application of the fluid(s) from the worker-ants. (Both postures also resemble the one-wing stretch, a well-known comfort-movement which is often accompanied by the sideways fanning of the tail and the stretching of one leg; again the resemblance between this posture and the anting one appears superficial, though that between it and the sunning one may be due to their common origin – see Chapter 4.) The ant-exposure posture involves the extension of both wings and the spreading of the tail; especially when it is really being performed 'passively' (i.e. when the anting bird is lying down inactively in the ant swarm), it does quite closely resemble the typical spreadeagle sunning posture of passerines, though the results are wholly different: exposure to formic-acid on the one hand (sprayed out by the worker-ants as they attack the anting bird) and to solar radiation on the other. The resemblance diminishes, however, when the anting bird (as is more usually the case) performs dynamically in order to stimulate the ants to greater activity, often while applying ants at the same time; thus in the case of the *Turdus* thrushes, for example, the prone sunning posture is quite distinct from the more erect anting one (see Simmons 1982a).

It was an oversimplification on the part of Rothschild and Clay (1952), therefore, to state (referring to a photograph of a Blackbird in the typical spreadeagled sunning posture) that 'many birds when sunning themselves take up the passive anting position'. It has been this type of 'evidence' that has been responsible in part for the blurring of the boundaries between sunning and other forms of so-called 'bathing' behaviour, including ant-exposure (sometimes termed 'ant-bathing'). Burton (1959), for example, interpreted the rain-bathing behaviour of an African Grey Parrot as 'anting without ants' and found the rain-bathing posture of an *Amazona* parrot (species not indicated) 'indistinguishable from anting', though no parrot (or, indeed, any non-passerine) has been known to perform typical anting in any form (see also Harrison 1961).

Potter and Hauser placed great store on the fact that some birds may sun and dust at the same time and others sun during a spell of anting. Ignoring the complication that two of the latter cases involved woodpeckers, which almost certainly do not ant anyway, their conclusion that 'anting and sunning are not mutually exclusive forms of behaviour' was wholly misleading. I have seen anting Starlings break off to sun, but only when suddenly exposed to strong sunshine during a lull in anting, the two (quite distinctive) forms of behaviour being elicited serially in response to different stimulation; similarly, I have observed birds of a number of species sun suddenly when feeding or preening in comparable situations and bathing Blackbirds pause to sun where the water-dish was sited in the sun. Other forms of behaviour are also often interposed when a bird is engaged in sunning, anting, bathing, preening, and so forth, but always as a response to fresh stimuli; to seek casual and functional correlations in such cases (as, for example, when a Blackbird starts to display to its mate or to sing while sunning) would be ill-advised.

DUSTING

When dusting, the bird actively introduces particles of fine earth, sand, etc., into its plumage and later expels them. Though the movements differ between different taxonomic groups, most species toss the dust up into and on the plumage by scratching with the feet or flicking the wings and by ruffling the dust through their feathers and shaking it out, usually while squatting and shuffling around in a special dusting hollow. All the evidence, much of it recent, suggests that dusting functions in feather maintenance by removing excess preen-oil and feather lipids which are absorbed by the 'dust' and then removed with it (together with dry skin, feather debris, and the like); it may also help to re-align displaced feather barbs and help to combat ectoparasites (Healy and Thomas 1973, Borchelt and Duncan 1974, and others; see Simmons 1985 for recent summary). It has been suggested (Potter and Hauser 1974) that dusting soothes the skin during the moult by applying heat, in the form of warm sand (etc.) from dusting spots sited in the sun, to the feather tracts but such speculation seems ill-founded; neither does there appear to be any seasonal correlation (incidental or otherwise) between dusting and moulting (see Simmons 1985): indeed, domestic Japanese Quail have been proved to dust to a significantly lesser extent during the moult than at other times (Bliss and Heppner 1977).

Unlike sunning, dusting is essentially a dynamic form of behaviour as are most forms of bathing and anting. When lying over on its side, the dusting bird may adopt a posture resembling the lateral sunning one; the similarity is only superficial, however, and of no apparent significance. In its function, dusting appears to have more in common with bathing and anting than with sunning, though it cannot have exactly the same function even as bathing, which it

replaces in some groups that live in or originate from bare open habitats such as deserts and steppes (so many exceptions are now known to the rule that birds that dust do not bathe that it is clearly invalidated). The House Sparrow is the only species with which I am familiar that suns, dusts, and bathes (it is said also to ant but I have never seen it do so, even in experimental conditions, so confirmation is needed); there is clear similarity between its bathing and dusting movements (see Simmons 1954) but its sunning behaviour (described in Chapter 4) is quite different. It will, as we have seen, dust and sun after bathing as well as preen and oil. The Wren will also dust and preen after bathing (Nicolai 1962; Robert Gillmor) as will the Galapagos Dove (Nicolai). Like the sparrow, incidentally, the Wren, also a species that dusts, bathes, and suns (Simmons 1983), has not been recorded to ant.

COMMENT

The movements and postures involved in sunning, anting, and dusting mostly differ from one another, though there is some similarity in certain cases (as traced above); however, even if there were close resemblances in form, this would not prove functional co-identity, for which a common causal factor, namely heat, has been suggested. That heat is the main stimulus factor in the elicitation of sunning seems absolutely clear to me but I am convinced that attempts to link anting with the alleged thermal properties of ants is wholly misguided (see Simmons 1958, 1966) and based on a misunderstanding of the causal background of such behaviour, too much stress being placed on behaviour (reaction to fire and other 'ant-substitutes') resulting from ontogenetic abnormalities in birds reared in captivity. Neither am I aware of any convincing evidence that 'thermogenic' stimulation is involved in dusting (see above), even though some species will use sunny places in which to dust and will sun themselves at their dusting spots (see Chapters 3 and 4). As for bathing, there would seem to be little or no functional or causal equivalence between behaviour that involves water on the one hand and insolation on the other (but see the discussion on the function of sunning in Chapter 8).

Under normal conditions of ontogeny and performance in the wild, bathing, sunning, anting, and dusting each emerges, therefore, as a distinctive behaviour pattern in its own right.

CHAPTER SEVEN

Sun-basking

Much of the background information having been presented, we can proceed to examine the first of the two main types of sunning behaviour, namely sun-basking. That birds will at times use the sun deliberately to warm themselves or to prevent heat loss, especially when the air temperature is low, is now so well established that such thermoregulatory and energy-saving behaviour must be counted as one category of sunning (see Chapters 1 and 2). Mueller (1972), however (who used the term 'basking' for 'this perching in the sun without any extraordinary postures'), distinguished it from sunning proper and counted it as a form of 'heat-bathing' (a category in which he also included 'smoke-bathing'). I prefer to classify the general phenomenon as 'heat-basking', in which I would recognize:

(i) sun-basking itself, including sun-drying, and
(ii) other forms of heat-basking, including some aspects of so-called 'smoke-bathing' (see further, below).

GENERAL ASPECTS OF SUN-BASKING

I have seen much sun-basking among several species of garden passerines (particularly House Sparrows, Starlings, and Blackbirds), mainly during cool or cold clear weather in spring and autumn, when the ambient temperature is evidently at or just below their zone of thermoneutrality, and at various times of the day, but chiefly in the morning and late afternoon. Birds will also sun-bask in winter when the sun is strong, then mainly in the middle of the day while loafing. Such behaviour is particularly noticeable among flocking species, the members of the flock tending to loaf all together; I have noted it in the House Sparrow frequently and in other species (e.g. Fieldfare) casually. Sun-basking birds mostly perch above the ground out of the wind, e.g. in a sun-dappled creeper in the case of House Sparrows in my garden. They will also use sheltered spots on roofs and particularly warm spots on the ground at times. Much of the level-1 simple sunning behaviour described in Chapter 4 can be referred to sun-basking of this type, but some birds sunning in the wings-down (level-2) posture and some in level-3, level-4, or even level-5 postures seem at times also to be mainly heat-basking when they do so early or late in the main

sun-exposure season – or when drying themselves. These last examples, incidentally, invalidate Mueller's (1972) assertion that sun-basking involves no striking postures.

As already mentioned (in Chapter 3), many of the sunning records for hirundines may involve sun-basking; a further example is of a Swallow wintering in Cornwall which sunned itself on a beach in a sun-trap near the sea-wall (see King and Penhallurick 1977). Winter sun-basking by a Pied Flycatcher and a Collared Dove at a bird hospital in Cornwall has also been observed (B. King). The Hawfinch is very prone to sun-bask (see Mountfort 1957), doing so for long periods in the tree-tops or on the ground:

> 'It sits motionless, fluffed out like a ball, with its head sunk low between the shoulders and the flank feathers all but obscuring the wings'; sometimes, 'the long neck is extended, feathers on end, looking like a bottle-brush' and the tail 'tightly compressed . . . ridiculously short and narrow'.

The White-crowned Sparrows in the winter flocks mentioned under level-2 sunning in Chapter 4 were evidently sun-basking, this having 'adaptive value because it alleviates the energy costs of thermoregulation when the birds are in cold conditions below their zone of thermoneutrality' (Morton 1967); experiments on captives of the same species subjected to artificial insolation demonstrated that such birds had a lower oxygen consumption to controls at similar ambient temperatures (De Jong 1976).

The Turkey Vultures mentioned under level-1 sunning in Chapter 4 were also clearly sun-basking in the morning sun, such behaviour functioning 'to supplement metabolic energy in raising the body temperature from the nocturnal low-point' (Heath 1962). It is highly likely that the sunning behaviour of the mousebirds is largely concerned with sun-basking (see Cade 1973, Rowan 1967, Prinzinger *et al.* 1981); like the Greater Roadrunner (see below), these birds show adaptive hypothermia at times. The sunning behaviour of the African bee-eaters poses something of a problem, however. The simple perching-in-the-sun 'broken-neck' and ruffled-mantle postures of these birds, in which the skin is exposed, have all the features of sun-basking, especially when adopted early and late in the day; yet they are also often assumed in conditions of strong sunshine, when heat-absorption cannot be the purpose, and are then assumed to be anti-parasitic in function, the birds being exposed to high ectoparasite infestation in their nesting holes, especially towards the end of the breeding season (Fry 1972). On the other hand, bee-eaters observed in the prone spreadeagle posture – behaviour which has all the typical features of sun-exposure (see Chapter 8) – are thought probably to be sun-basking (C.H. Fry). Further study is obviously needed.

At least at times, sunning gamebirds are clearly sun-basking (see, e.g., Goodwin 1953); in winter, Ptarmigan 'usually bask where the sun is warm out of the wind, but sometimes in below-freezing winds' (Watson 1972). The Tufted Duck watched sunning by Rogers (1950) on a winter's day was one of

some 150 ducks of seven species (including a Gadwall, Pochards, and Goosanders) that had left the water to sun-bask at a spot that was a sun-trap and shielded from the cold wind, the Tufted Duck being the only bird to adopt 'extreme posturing', however (see Chapter 4).

Further examples of sun-basking for other species are given in Chapters 3 and 4 or may be deduced from the information there. Perhaps the most striking are the elaborate spread-wing (level-5) sunning postures of the storks which are definitely adopted for sun-basking at times, especially early in the day (see Kahl 1971).

SPECIAL CASES

A classic example of what I now call sun-basking has been reported in the Greater Roadrunner, a desert-living bird subject to low night temperatures that was studied in the field and captivity by Ohmart and Lasiewski (1971); its level-2 sunning posture was described in Chapter 4. Like the Turkey Vulture, this ground-cuckoo frequently suns during the early morning hours; it also suns intermittently during the day, but only if the weather is cool and clear, never if the ambient temperature is in or above its zone of thermoneutrality. Its 'sunning behavior, combined with an unusual pattern of cutaneous pigmentation' (see further, below) 'suggests that the absorption of sunlight is important in this species'; experiments demonstrated that it can use sunshine to reduce its energy expenditure, thus confirming the hypothesis of Hamilton and Heppner (1967a), 'the average energy saving' being 'equivalent to 41 percent of the standard metabolism predicted' for a bird of some 295 grams. Though the roadrunner suns throughout the year, the behaviour 'is probably most important during the winter when the productivity of the desert is low'.

Another good example is provided by certain grebes (Storer *et al.* 1975, Storer 1981, 1982). These are mainly small or medium-small species under 350 grams mean weight, from the size of the Least Grebe (131 g) to that of the Black-necked Grebe (334), though the Pied-billed Grebe (396), originally excluded, has now been added to the list (R.W. Storer). Sun-basking has also been recorded from certain larger species of South American grebes inhabiting high altitudes (the Junin Grebe and the Titicaca Grebe) or low latitudes (the Hooded Grebe of southern Patagonia). The typical sunning posture is described in Chapter 4; though its precise type (level-1 or aberrant level-2) was difficult to decide, the behaviour is clearly referable to sun-basking: 'an adaptation for utilizing solar energy' (Storer *et al.*). Sun-basking seems to have been first reliably reported for grebes by Bandorf (1970) in the Little Grebe (192 g); the sunning behaviour of this species has largely been overlooked in this country though evidently not rare (see Note 24). The Black-necked Grebe at least seems to restrict its sun-basking to that time of the day when the sun is high; at other times, presumably, the angle of the sunlight is too low to

penetrate between the raised back feathers, which are kept lowered early and late in the day so that heat is not lost to the air by radiation from the body between the feathers (Storer 1981).

The roadrunner when sun-basking 'exposes the black skin of the interscapular apterium and the black soft plumage of the dorsal spinal tract', all of which 'are covered by the scapular feathers and wings when the birds are not sunning' (Ohmart and Lasiewskii). Most of the species of grebes which sun also have heavily black pigmented skin on the back and black bases to the back feathers which are hidden much of the rest of the time (Storer *et al.*); as in the ground-cuckoo, such black areas absorb the solar energy directly when deliberately exposed in sunning. Though information from wild birds in relation to sunning is sparse, black pigmented feathers and other structures evolved for the purpose of using insolation probably occur widely in the bird kingdom; black coloration generally is known to facilitate this process greatly, hence reducing the metabolic expenditure required to maintain body heat, especially in low air temperatures (see, e.g., Heppner 1970, Walsberg *et al.* 1978, Lustick *et al.* 1980). In the cormorants, the predominantly black plumage, 'by being most receptive to solar radiation, assists . . . in supplementing metabolic heat for maintenance of normal body temperature' (Siegfried *et al.* 1975), this explanation being preferred by these authors to my own that dark plumages in such seabirds facilitate social inconspicuousness when feeding underwater (see Simmons 1972), though the two are not incompatible.

HEAT-BASKING

Heat-basking by other means than direct exposure to insolation is probably widespread in northern hemisphere birds in cold weather but is poorly documented except in the case of the use of the heat from the chimneys of man's houses and other artefacts. Usually (and often uncritically) termed 'smoke-bathing', this mainly involves rising hot air and radiated heat rather than the actual smoke itself; though the latter may often be there, of course, its presence seems as likely to act as a deterrent than an inducement to heat-basking. Besides true heat-basking, the phenomenon of 'smoke-bathing' would appear to involve at times (and probably only rarely in the wild) aberrant anting in the presence of pungent fumes which act as a 'substitute' (causally if not functionally) for formic-acid; it is easy, however, for inexperienced and uncritical observers to confuse anting with mere preening or active drying, which are much more likely to be the behaviour patterns involved. At other times, the birds seem to be attracted to the smoke in the hope of catching insects rising in the heat vortex, much as tropical birds attend bush-fires.

I do not propose to go into further details here, but the topic of 'smoke-bathing' has been discussed by a number of writers including Whitaker (1957), Burton (1959), and Mueller (1972); see also Brewer (1963).

CHAPTER EIGHT

Sun-exposure

If one type of sunning behaviour – sun-basking – helps birds to reduce the metabolic expenditure of raising the body temperature into the thermoneutral zone, or maintaining it there, such a function cannot apply when they deliberately position themselves in the sun ('sun-expose') in spite of the risk they run, and often face, of raising the body temperature near the upper critical limit and of suffering from heat stress. In such conditions, if a bird chooses to sun-expose itself rather than, for example, to seek shade, the adaptive significance of the behaviour must lie outside thermoregulation and energy conservation. This interpretation is strengthened when tropical species such as the Brown Booby are considered: they can be subjected to almost intolerable heat stress when engaged in the routine of the breeding cycle at the nest-site yet nevertheless deliberately increase such stress at times by engaging in sun-exposure. What has caused so much confusion in literature discussions of the possible basic function(s) of what I call sun-exposure behaviour, which is generally by far the more commonly *observed* form of sunning, is this apparent contradiction: that the bird, while sunning not for thermoregulation (i.e. heat-gain) but for some other purpose (see further, below), also suffers from and reacts against the effects of overheating, so it may have to perform thermoregulatory behaviour (i.e. heat-dumping in this case) and sun-exposure *at the same time.*

Thus, before discussing the function and motivation of sun-exposure, and considering certain other aspects of the behaviour, we first need to identify its components, especially the superimposed thermoregulatory ones. The latter have already been analysed in the case of the sunning posture of the Brown Booby (see Chapter 5).

COMPONENTS OF SUN-EXPOSURE BEHAVIOUR

At least sometimes, both sun-basking and sun-exposure may be involved simultaneously – e.g. when the sun is strong but the temperature otherwise low, as probably in the case of the House Martins observed by Prytherch (1981) – and, though weather and seasonal factors will obviously give clues, it may be difficult at times for the observer to judge which type of sunning is being

performed. Sun-basking, however, mostly involves level-1 and level-2 sunning behaviour (see Chapters 4 and 7). Such lower-level behaviour is also shown by sun-exposing birds, but mostly during lulls in higher-level sunning (e.g. during periods of fitful sun) or when sun-exposing at low intensity (e.g. during periods of weak sun, especially early and late in the season), though the sun-exposure postures of some groups (such as the skimmers) seem to be mainly simple ones. Then, while ciconiiform and certain other large birds seem to adopt their typical spread-wing (level-5) postures as much for sun-basking as they do for sun-exposure, it is clear that most birds engaged in the higher levels of sunning behaviour (i.e. level-3 upwards) are on the majority of occasions performing sun-exposure rather than sun-basking. Treatment in the rest of this chapter will, therefore, be confined to the higher-level (lateral, raised-wing, and spread-wing) sunning postures.

As we have seen, the main target areas for insolation in such postures are the wings (both upper and undersurfaces) and the tail (upper surface in most species but also the undersurface in some); thus, there appears to be no good reason to doubt that the extension of one or both wings, the raising of one wing, and the spreading of the tail can be regarded as the major postural components of higher-level sun-exposure behaviour. As well as adopting such postures, sun-exposing birds will often gape, pant, gular-flutter, and feather-ruffle; they often also expose the nipple of the oil-gland (in those species that possess one) and look up at the sun up in the sky ('sun-staring'). It seems unnecessary to argue the case for gaping, panting, and gular-fluttering being superimposed cooling components of sunning behaviour but what of feather-ruffling, oil-gland exposure, and sun-staring? Certainly the first two of these latter activities would also help to cool the sunning bird: the erection of the body feathers in the ways indicated in Chapter 2, and oil-gland exposure by convected heat loss. They could, however, also serve to expose the feather-bases, the skin beneath the feathers, the skin round the oil-gland, and the oil-gland nipple itself to solar radiation. I believe, therefore, that feather-ruffling and oil-gland exposure, as well as helping in heat-dumping in extreme conditions, are also important functional components of sun-exposure. The purpose of sun-staring is not clear but it could be the birds' way of monitoring the position of the sun as well as exposing any bare skin around the eye or, indeed, the eye itself to sunshine. There is also the strong possibility that sun-staring could be an anti-predator precaution, the sunning bird fleeing whenever any object (which could be a swooping bird-of-prey) interposed itself suddenly between the bird and the sun.

Besides functioning primarily in sun-exposure, the wing and tail postures themselves could well have a secondary thermoregulatory purpose also, namely to promote convective cooling at times. This is particularly likely of wing-raising, and could even be its primary function in pigeons (see Chapter 4). In the Dunnock, however, wing-raising now seems essentially a sun-exposure posture, often occurring early in the sunning spell before any other signs of heat

stress (gaping, etc.) are evident; moreover, as we have seen, the undersurface of the wing is always orientated so as to catch the sun's rays perpendicularly. Further study is needed, though, as wing-raising for the purpose of cooling in this species could have been adaptively incorporated into the sunning sequence at a low-threshold point through the evolutionary process of behaviour standardization, i.e. the bird is pre-programmed to lift the wing to cool itself before strictly needing to do so; the same could also be true of other cooling components of sunning (e.g. panting).

Thus, sun-exposure includes components that are wholly thermoregulatory in function and others which seem to serve the dual functions of sun-exposure and thermoregulation. It seems highly likely, therefore, that this form of sunning has been derived from behaviour that was once wholly thermoregulatory in nature (as we have seen, the sunning behaviour of the Brown Booby provides excellent evidence of this). Of course, if posturing for cooling gave rise to specialized sun-exposure behaviour, it is equally likely that posturing for warming (i.e. sun-basking) also did so in some cases.

SEASONAL AND RELATED ASPECTS

It is now quite clear that deliberate sun-exposure behaviour, involving the higher-level sunning postures, is a strictly seasonal phenomenon in temperate countries such as England. A preliminary analysis of my own observations on garden passerines indicates that such sunning typically occurs mainly in direct sunshine, most frequently, and at the highest intensities, at the hottest times of the day (when the sun is high in the sky), during the hottest months of the year (when the sun rises high above the horizon), and at specially favoured sites (see further, below). Depending on the weather, the sun-exposure season usually starts in mid-April and ends in early September, with peaks during the summer period May to August (see further in Note 25). Fuller information on seasonal and weather-related aspects of sunning is given by Stainton (1982; see Chapter 3).

It is also clear that certain weather conditions are highly conducive to sunning, often producing intense behaviour and affecting many birds at the same time. Poulsen (1974) found that sunning is especially likely to occur after a spell of cloudy weather and Teager (1967) characterized 'ideal sun-bathing weather' as that period on a hot summer's day when the sun shines with 'intense brightness and warmth' after the morning cloud has dispersed (see also Cade 1973). My own observations indicate too that the fitful appearance and disappearance of strong sunshine on cloudy days can be important, at times at least (see also Chapter 5, and below). The precise conditions remain to be fully established, however, and are likely to differ in different climatic zones; compare, for example, the findings of Stainton for southern England with those of Hauser (1973, also summarized in Chapter 3) for sub-tropical North

America. The possible influence of humidity also needs to be assessed.

As well as sunning deliberately during the sunning season, a bird may also be *induced* to sun-expose itself involuntarily in essentially the same way on finding itself exposed to strong sunshine suddenly in the course of other maintenance behaviour (such as feeding), especially when at or near a known sunning site; it may 'resist' such sunning (soon continuing as before or flying away) or engage in a full sunning session, for a while at least. As we have seen (Chapter 3), such enforced sunning was termed 'compulsory' sunning by Hauser (1957) and will be further discussed below (in Chapter 9). The bird may also alternate between sun-exposure (deliberate or induced) and active cooling behaviour; thus, for example, a sunning Blackbird will at times on very hot days seek the shade near by and may often be seen repeatedly popping back into cover between brief spells of sunning in the open. At times of fitful sun, with broken cloud partly or wholly covering the sun and reducing both its light and heat temporarily, the sunning bird may switch in and out of its sunning posture to a greater or lesser extent, or cease sunning entirely, until the sun shines strongly again. This, in my opinion, is a result, in part at least, of its monitoring the heat of the sun.

SUNNING SITES

The sunning sites of the Brown Booby were described in Chapter 5, and of some other species in Chapters 3 and 4. In the gardens of the houses in which I have lived and observed sunning behaviour, especially those in Leicester (see Note 1), certain general sunning areas and particular spots within them have been persistently used by garden passerines of more than one species when engaged in sun-exposure. Individuals of the same or different species may replace each other there at times within quite short time spans or sun-bathe quite near one another simultaneously (see also Teager 1967 and further in Note 26). They also follow the sun round, using alternative sites as necessary when sites come into and out of the shade; depending on the local topography, sunning sites tend to be on the western side of the garden in the morning and on the eastern side in the afternoon. The birds will also sun at times at other places where the sun is particularly strong, usually on lawns or paths, but even so may make for a favourite spot sooner or later (only the itinerant Starling will regularly sun almost anywhere where it happens to be, usually in parties on a lawn).

Sunning spots are mostly sited on the ground, where the temperature is at its highest, for example on bare earth in flower borders (etc.), on concrete or asphalt paths, and on the short grass of mown lawns (usually on or close to the edge). Typically, as also noted by Teager (1967), there are plants or other screens (fences, trees, walls, etc.) nearby. These provide shelter from any wind, which inhibits sunning, and also cover, into which, for example, the sunning

bird can retreat in the face of danger or, more usually, if it becomes overheated. A well-defined line of shade, from a building especially, is often used in the same way. As we have seen in Chapter 4, House Sparrows will also sun-expose off the ground on roofs, as will other species occasionally, the Blackbird and the Starling for example. In America, Hauser (1957) saw much 'voluntary' sunning, by birds of different species, often sociably, in a pear tree and in a fallen (but still living) pecan tree; another important site was a compost heap near the pecan tree, used when it was breezy at the latter site.

It is quite clear that sunning spots, especially those on the ground or similar hot surfaces, are chosen as sites of high temperature, provided they are safe. Temperatures on the heap in Mrs Hauser's garden rose to 60°C; on her feeding tray where 'involuntary' sunning was observed, they were as high as nearly 150°C at times! In his study, Weisbrod (1971) recorded ground temperatures ranging from 34 to 44 degrees at six sunning sites in the forest used by wild Blue Jays. As we have seen (Chapter 4), wild Diamond Doves will sun at times at ground temperatures of nearly 70°C. Most of the sunning spots used regularly in my own gardens have been sites of localized heat (sun-traps or 'hot-spots') at which the ambient temperature, from direct and reflected sunshine, is usually higher than the temperature elsewhere, even in the sun nearby at times, as proved by simple measurements made with a thermometer placed at the hot-spot and elsewhere. In particular, the difference between the shade (or air) temperature and the hot-spot temperature is often striking, by a factor of 100% or more at times. Failure to take into account the often marked difference between shade and hot-spot temperatures has been responsible for the dismissal of heat as the important factor in sun-exposure behaviour by some observers (see further in Chapter 3).

DURATION AND FREQUENCY OF SUN-EXPOSURE

Captive Blue Jays sunning on a perch did so in spells lasting from a few seconds to three and a half minutes; spells were longer on the ground, lasting up to 45 minutes and involving several changes in position, each position being held from several seconds to four minutes (Weisbrod 1971). Information on the frequency and duration of sunning by individual birds is, however, mostly lacking in the literature (though a number of examples were given recently by Prinzinger 1983). My own studies on garden passerines (particularly the Blackbird), to be published in detail later, indicate that, in optimum conditions, a bird can engage in sun-exposure repeatedly during the heat of the day, alternately sunning in the open and preening in the shade (see also Teager 1967), in spells of a few seconds to several minutes at a time, sometimes over several hours and on a number of successive days. At other times, however, in apparently similar conditions, little or no sunning at all may be seen. The factors involved are evidently complex, but the amount of sunning done (when

conditions are favourable) must depend, not only on the 'mood' of the bird (see further in Chapter 9), but on the competition that sunning faces from other essential activities in its daily time-budget, such as self-maintenance (feeding, drinking) and breeding duties. Thus, for example, a female Blackbird when incubating eggs will sun little if at all during her brief breaks away from the nest, feeding, while her 'unemployed' mate may be sunning frequently (see further in Note 27).

Safety is another factor affecting the frequency and location of sunning, the birds choosing areas where they feel secure and avoiding those where they are unduly disturbed or frightened. Gardens and parks, where the local birds are fed and provided with water, and are used to seeing people, are excellent places in which to observe sunning (see further in Notes 26 and 28).

SOME THOUGHTS ON FUNCTION

Following the survey of the literature, the descriptions of sunning behaviour, and the discussion of other topics including the other main adaptive type of sunning (sun-basking) in Chapters 3–7, I see no good reason to depart from the view I expressed in the Introduction to this work: namely, that sun-exposure is probably a subsidiary form of comfort behaviour functioning mainly in feather-care. The precise forms this function take remain a puzzle, however, at the present state of knowledge and in view of the virtual absence of systematic experimental evidence, though the benefits of sun-exposure must come, I am convinced, from the thermal properties of sunshine acting on the feathers and perhaps the skin. Such possible benefits (including the killing and discouragement of ectoparasites) have already been outlined earlier in the paper, especially in the review of the literature (Chapter 3), so there is no need to discuss them all again.

It should be stressed, however, that the effect of the sun's heat on the all-important wing and tail feathers may well be of the greatest significance, these being the areas that sun-exposing birds display most to the insolation; the maintenance of the good condition of the remiges in particular could well be a major aim of sun-exposure in birds generally, as in anting passerines. Further, both the preening directed to feathers near the neck and especially to the wings themselves – typically on the sun-side in the case of lateral sunning – plus the frequent head-scratching that accompanies or follows sun-exposure could well be components in a functional chain of feather-maintenance activities, though this remains to be demonstrated (it is possible that such behaviour is merely an incidental reaction to irritation caused by the displacement of feathers, the effect of the sun on the skin, or the sun-induced activity of ectoparasites). The full adaptive sequence could well be, however: bathing, oiling (in those species that have a functional oil-gland), preening, sunning, and further preening (with head-scratching). In those groups with powder-down replacing or

supplementing preen-oil, powdering could also enter the sequence. It should be noted, though of uncertain significance, that birds do not appear regularly to bathe *after* sunning (as often after anting, for example), not even when visiting the water to drink (as they often do); some, however (e.g. Eleonora's Falcon, Blue Tit) will oil after sunning (see Chapters 3 and 9).

Although sunning birds are sometimes in moult and the effects of sunning could perhaps be of some benefit to that state, any correlation between sunning and moulting may well be only seasonally coincidental, as in the case of anting and moulting. Speculation that sunning and anting are complementary activities that sooth the skin during feather replacement seems particularly ill-founded; if they complement each other at all, it is in the care of the wing feathers – the main target in both cases – each in its different way.

Lastly, the role of sun-exposure in the synthesis of Vitamin-D should not be finally discounted, especially in view of the work on doves (for other evidence, see Kennedy 1968 and Prinzinger 1983). Such a synthesis may not, in fact, involve irradiated preen-oil – indeed, it cannot in those few groups (including the parrots, nightjars, and bustards as well as the pigeons) which lack a fully functional oil-gland – but rather irradiated skin or irradiated feather lipids. The lipids are considered to be by-products of the keratinization process as the feathers form; they consist of cholesterol (mainly in the form of cholestanol) and other steroids together with fatty acids (see, e.g., Bolliger and Varga 1961).

CHAPTER NINE

The Motivation of Sunning Behaviour

The causal analysis of the motivational basis of behaviour, once a major task of ethological studies, is now out of fashion among zoologists in favour of the exploration of broader evolutionary themes. This neglect, understandable as it is, can, however, lead to errors of interpretation when only functional analysis is attempted. Certain features of any given behaviour may be better understood through consideration of the motivational basis of the behaviour pattern as a whole; thus, particular performances of sunning may occur in circumstances that give no true clue as to the function of sunning generally, indeed many may well fail to achieve that function at all. The following remarks are intended, therefore, as a brief guide to the likely motivational factors involved in sunning; they should serve as a useful background to the controversies indicated in Chapter 3.

Sunning has the features of what used to be called 'instinctive' behaviour; in this case, of that type (like bathing, anting, and dusting) in which an external 'medium' is employed to fulfil the biological function of the behaviour:

(i) it is 'species-characteristic': that is, the forms of the behaviour are stereotyped and found in all members of the species that perform them;
(ii) it is 'innate': that is, the forms of the behaviour do not have to be learned but are genetically 'pre-programmed' and appear more or less in their adult state at a certain stage in the ontogeny of the inexperienced bird, usually when it is still young (see Chapter 3);
(iii) it is motivated by internal as well as external factors, either of which can predominate at times;
(iv) it is 'self-rewarding': that is, the bird obtains satisfaction from just performing the behaviour (see also Note 29);
(v) it is not 'function-motivated': that is, performances of the behaviour are not primarily initiated by the need to achieve a certain function or ended by achieving it (see further, below);
(vi) it is 'self-exhausting': that is, performances of the behaviour reduce the internal motivation for it;

(vii) it is initially an unconditioned, automatic response to a simple 'basic-stimulus', some non-visual quality of the correct medium (Simmons 1966, 1982a), but
(viii) is later adapted more closely to the environment through learning; and
(ix) it often induces (facilitates or 'releases') the same behaviour in other individuals of the same species (and, in this case, of other species too).

There is good reason to suppose that these features are characteristic of both forms of sunning (sun-basking and sun-exposure), though their functions differ as must their internal motivation. Discussion here, however, is confined to sun-exposure.

The biologically correct object 'used' in sun-exposure behaviour is, of course, the sun. Each individual bird of a species that shows such behaviour has, however, to learn this: i.e., it is not born with an instinctive knowledge of the sun as an entity (just as a naïve bird does not recognize a worker-ant as the 'tool' for anting, water for bathing, or dry sand for dusting). As we have seen, there is controversy over the identification of the basic stimulus for sunning – light or heat? – to which the bird initially reacts instinctively. Most of the pertinent evidence, such as it is, points in my view to heat being the key basic-stimulus that first triggers performances of sun-exposure by the inexperienced bird (see reviews in Chapter 3) – not any source of heat, however, but a localized one coming from above. There is a clear indication, too, that a *sudden* warming of the bird's immediate environment is important. Thus, the bird learns to respond to the sight, and light, of the sun as well as to its heat.

> My hand-reared Blue Tit (see Note 1) first reacted to sunshine that came through the window strongly into its cage when it was about 17 days old, on 25 May: looking up at the sun, it raised its crown feathers with head turned sideways. Later that day, it behaved similarly in artificial light, orientating itself laterally to the bare 100W bulb several feet away in the centre of the room; evidently, though experiencing little if any heat from it on this occasion, the young bird had already learned from its experience of the sun earlier in the day to react to a 'suspended' light as a source of heat. Subsequently, however, it sunned to the light bulb only in certain circumstances. It did not do so again when experiencing just the light of the bulb at a distance; nor when it settled on the flex *above* the bulb, although then exposed both to the light and the heat emanating from it. But when I first held it close *under* the bulb (on 12 June), it responded immediately and, though clearly frightened at first, continued to do so that day, adopting a full-spreadeagle posture with all the contour feathers ruffled and bill open each time I held it there; after the two best spells of sunning, it obtained oil from the oil-gland, which had been fully exposed during the posturing, and applied it to the belly .It continued to sun thus for several days afterwards, and I noted that the intensity of the posture decreased as I lowered the bird away from the heat of the bulb. Later, however, it could 'resist' the stimulation and usually flew away as soon as I started to position it under the bulb.

It seems clear from the above observations, others on birds in the wild, and

from the literature (see Chapter 3), that sunning (like similar forms of instinctive behaviour) can at times be elicited more or less entirely by strong external stimulation from the environment ('involuntary', 'induced', 'purely instinctive' sunning) even in experienced individuals. Further, as we have seen above, the sight of other birds sunning is at times a strong inducement for others to perform through the process of social facilitation.

More normally, however, both external (environmental) and internal (cerebral and neuromuscular) factors are important in eliciting the behaviour ('voluntary', 'deliberate' sunning). At other times, even when the external stimulus is weak (e.g. in conditions of hazy or fitful sun), such sunning can occur more or less spontaneously when the internal motivation ('sunning mood') is at a high level. This 'sun-hunger' would appear to be determined primarily by a build-up of motivation for the performance of sunning *per se* in the central nervous system (if the bird has, for example, been unable to sun for some time). At times, however, there could perhaps also be strong secondary motivation originating from certain requirements of the body itself (e.g. the need for Vitamin-D) and by peripheral stimuli (e.g. the deformation of the flight-feathers, the presence of ectoparasites); peripheral stimuli could intensify at certain times, especially during the moult, when they need not necessarily be related to the achievement of any particular function. Finally, it may be noted that the continuation over several days of climatic conditions conducive to sunning may lead eventually to a marked decrease in the frequency and intensity of the behaviour through the process of habituation.

These determinants remain to be fully investigated and offer an interesting field of research, both observational and experimental. Care should be taken, however, to distinguish clearly between causal and functional aspects of the subject.

Summary

Sunning (or sun-bathing) – behaviour whereby the body is deliberately positioned in the rays of the sun – is widespread among birds. There appear to be two adaptive types:

(i) sun-basking (a form of heat-basking functioning to absorb heat, and therefore thermoregulatory and energy conserving in nature); and
(ii) sun-exposure, or sunning proper (of uncertain function but probably a form of feather-maintenance, as well as serving other purposes, for example, the synthesis of Vitamin-D).

In both types, solar radiation in the form of heat appears to be the key factor, causally and functionally. A classification of sunning is presented in Chapter 4, the following levels being recognized:

(1) simple sunning behaviour;
(2) the wings-down posture;
(3) lateral postures;
(4) raised-wing postures; and
(5) spread-wing postures.

These are described in detail, and forms of sunning-like behaviour (sun-stress postures, sun-shielding postures, wing-drying) are also considered. Sunning behaviour is briefly compared, in Chapter 6, with true bathing (in water) and with other forms of so-called 'bathing', i.e. dusting and anting. More detailed discussions of sun-basking (general aspects, special cases) and sun-exposure (components, seasonal and related aspects, sites, duration and frequency, function) then follow, in Chapters 7 and 8 respectively.

My own extensive observations on sunning in birds, especially certain garden passerines (Blackbird, Dunnock, and other species) and the Brown Booby (treated separately in Chapter 5), form the basis of this review (especially the descriptions of sunning postures). As a background to understanding sunning behaviour and the study of it, problems of thermoregulation (Chapters 2 and 5) and motivation (Chapter 9) are discussed and a wide, if not exhaustive, survey of the literature up to 1982 attempted (Chapter 3), with special reference to Holarctic birds. Some additional references and observations for 1983 and 1984 are added, mainly in the Appendix. It has not been possible, at this stage of knowledge, to explain all the phenomena covered, and much further study is needed, for example, on the functional relation between moulting and sunning (if any).

APPENDIX

Notes

1

My observations on sunning have been made intermittently over 35 years, mainly in England but also in Egypt (1949–50) and on Ascension Island (1962–64, and during later visits). For much of this time, incidents of the behaviour were mainly noted during the course of other work and many went unrecorded. Since 1978, however, and especially during 1981–84 (when this paper was being written or revised), I have made a special effort to record as much sunning as possible. Of a grand total of some 1600 records (but not including those for Ascension) the majority were obtained in the years 1976–84, mainly in the gardens of our homes in Leicester: at Oadby (1976–1981: 332 records) and Evington (1981–84: 1309). Most of these records refer to what may be termed 'garden passerines', namely:

> Blackbird (734 records), Dunnock (352), House Sparrow (297), Starling (193), and Song Thrush (49); and also (with under five records each) Robin, Fieldfare, Mistle Thrush (see Simmons 1982b), Wren (see Simmons 1983), Reed Bunting, Bullfinch, Blue Tit, Jackdaw, Rook, and Magpie.

In addition, during 1960, I was able to study the first performances of sunning by a hand-reared Blue Tit (see Chapter 9) and observe sunning by captive babblers (Timaliidae) – a Pekin Robin and a Rufous-chinned Jay-thrush. Other species seen sunning in England and Egypt were:

> Grey Heron (3 records), Feral/Domestic Pigeon (two incidents involving some 35 birds), and Greenshank, Palm Dove, Collared Dove, and Turtle Dove (one record each).

When at Ascension, I was able to include sunning among the topics investigated during a daily study of the Brown Booby at two rocky stacks inshore where the birds lived throughout the year (see Chapter 5). Some records were also obtained on the sunning of the Brown Noddy at one of the stacks and on the sunning of the Ascension Frigatebird elsewhere. These seabirds are exposed to high air temperatures and strong solar and background radiation, such conditions differing markedly from those normally experienced by the birds watched sunning in England, where the weather is highly seasonal and variable. By a strange coincidence, after returning to England from Ascension, I saw a captive Lesser Frigatebird sunning in the Bristol Zoo.

If these records do not yet amount to a really definitive study, they do contain a considerable body of descriptive material such as seems to have been available to few if any previous reviewers of the topic. They await full analysis but I have made a preliminary log of them on which I have drawn where useful in this review. Particularly valuable, and perhaps unique, are the records for individually known birds. These include 13 Blackbirds, with the highest totals from males TT (125), NY (87), DT (83), and DO (34), from females MB (54), ME (49), and MT (20), and from juvenile female GR (30); and also a breeding trio of Dunnocks and their young, with a total (up to 29

October 1984) of 76 from the two males CB and GT.

2

Prolonged panting and gular-fluttering without further intake of water can have their own costs at times, however, including the risk of dehydration and alkalosis.

3

Renolds' (1977) review of the thermoregulatory problems of birds nesting in arid areas, and the adaptations that they have evolved to avoid dangerous overheating, came to hand after Chapter 2 of the present review was written. Among topics he discussed, with special reference to East African birds, were: (i) the seeking of shade by off-duty and non-nesting birds; (ii) the reduction of metabolic rate; (iii) plumage adaptations (reflecting of solar radiation by white plumage and insulation through feather adjustments); (iv) heat loss from bare skin; (v) evaporative cooling; (vi) temporary hyperthermia; (vii) belly-soaking and foot-wetting; and (viii) the sharing of incubation by the sexes (with regular change-overs).

It is convenient here, also, to mention the book by Hamilton (1973) which was also seen too late for its contents to be noted in the main text of this review. Aiming at a biological evaluation of the coloration of man, it covers many of the topics treated here including thermoregulation and plumage colour, with a brief discussion of 'sunbathing' as a means of using the sun as 'an energy resource'.

4

There have been a few additions to the sunning literature during 1983–84 after this review was completed. As well as my own note on the Wren, they include: a spread of colour photographs showing a Robin, Blackbird, Wren, Great Tit, and Yellow Bunting sunning (Moffett 1983a, see also Moffett 1983b); a note on House Sparrows sunning inside glass jars (Rose 1983), accompanied by a most unhelpful comment by me (written before my current views on sunning were fully formed); a book on the effects of weather on bird life (Elkins 1983), which includes sections on responses to low and to high temperatures and a brief comment on 'sunbathing'; a review of sun-bathing by Prinzinger (1983); and Fry's book on the bee-eaters (1984), which includes information on sunning additional to that cited elsewhere in the present review. (See also Notes 23 and 30.)

Information from these sources will be picked up where useful in later notes in this Appendix but the main findings of the important contribution by Prinzinger are briefly summarized here. He noted that sunning is widespread in the animal kingdom generally and especially well-developed in birds, all species of which, he argues, show the behaviour to some extent at least. Sunning can be elicited mainly by light in some species, corvids for example, often being an automatic response to sudden increases in light intensity; in others, however, it is a reaction to warmth alone, as observed in captive mousebirds (Coliidae), four species of which adopted sunning postures under an ultra-violet lamp. Sunning by birds, he concluded, originated as a means of obtaining warmth (as in cold-blooded animals, including the reptilian ancestors of birds) and later evolved additional functions including, among others, the photobiological synthesis of Vitamin-D and the promotion of general good health (by stimulating the metabolism,

the peripheral circulation of the blood, and the central nervous system), the feeling of warmth or of well-being that the sun's rays provide being the 'reward' that the individual gets for performing the behaviour.

5

When drying itself in short grass, soil, or grit, the Dunnock may also flick aside debris with the bill as it settles down, peck up any tiny items of food within reach, or even (occasionally) make backward scraping movements with the feet while leaning forward on its breast. I interpret this last behaviour, not as incipient dusting, but as tactually induced nest-shaping, especially as the scraping is sometimes accompanied by functionally related wing-lowering movements.

6

In his book on the bee-eaters, Fry (1984) described the 'broken-necked' sunning (or sun-basking) posture as one 'with the head turned acutely aside, sunward eye closed and neck feathers on the sunny side fluffed'. He found it to be less common than the posture adopted mainly with the back to the sun in which the mantle feathers are 'raised and splayed', exposing the dark bases of the feathers; both postures, however, are followed by 'vigorous preening, and scratching of neck and head by the foot'. In Prinzinger's (1983) review, there is a photograph of two Little Bee-eaters sunning together on a cold African morning with only 'the feathers of the back' (actually the mantle) 'slightly fluffed for heat-absorption'. A drawing in the same review shows a Wall Creeper (Tichodromadidae) sunning in a sitting position with head turned at a right angle to the body and inverted so as to expose the chin and throat to the sun; and another shows a Jackdaw 'sunbathing at low intensity', facing the sun in a perched upright position with head to one side and slightly turned, exposing the side of the neck (Rollin 1948 has a photograph of a similar posture, but with the Jackdaw in a perched crouching position).

7

A drawing in Prinzinger (1983) shows a Guira Cuckoo perched in the wings-down sunning posture. For an amusing description of sunning by tame birds of this species, see Gerald Durrell's book *The Drunken Forest* (1956).

8

Recent observations on Blackbirds and Starlings reveal that, while the expanded-lateral sunning posture can be adopted immediately during a sunning spell or develop from the ordinary full-lateral, it also occurs at times as what I now term a 'decayed' posture; that is, it results from a switch by the sunning bird from the spreadeagle posture (see under Level-5) to the lateral, as it leans over into the lateral but does not retract the outstretched sun-wing fully. Such composite, often transitional, sunning postures are not uncommon and pose difficulties of interpretation only when the full sequence of posturing is not followed (see further in Notes 15 and 16).

9

A female Green Woodpecker was seen sunning on the stump of an old willow tree at 13:10 hours, 3 July 1982 (D.E. Ladhams).

> After some bark-tapping, it started sunning by turning right-side on to the sun with the right wing slightly lifted and head inclined to the left, opening the bill occasionally. At 13:13, it presented its breast to the sun with head held back; it preened a little and opened the bill occasionally. It returned to the sideways pose at 13:15, preening. It ceased sunning at 13:17, moving slowly round the trunk twice with some pecking. It sunned again at 13:18, back to the sun, moving to a live willow about 5 minutes later where it went on sunning in the same way, also preening (mainly at mantle and neck), before departing at 13:28.

10

On 26 July 1983, a hot, sunny day, I was fortunate to observe for the first time some sunning by Domestic and Feral Pigeons, at Burghley House, Huntingdonshire.

> The birds live in a large courtyard near the visitors' entrance with access to outbuildings for breeding, etc.; this yard is dominated by a huge spreading chestnut-tree. At 11:00 hours BST, several pigeons were noted in strong sun on one of sloping roofs above the yard; none was sunning. At 13:50, when checked again, some twenty of them were in the deep shade under the tree. Suddenly alarmed, they all flew out on another sloping roof in the full sun; here, 10–12 (both all-white and wild-type forms) almost immediately started to sun, aligning themselves side-on to and leaning away from the sun. Though a few of them went only into the wings-down posture (with or without the tail spread), most adopted the expanded-lateral, with the tail fully fanned and depressed (in some cases twisted towards the sun) and the sun-wing half open and spread down over the flank (clear of the tail or over or under it). Only one pigeon progressed from the expanded-lateral into a wing-raised posture, and then only briefly. After about 5 minutes, the sun went in; a few birds remained in the wings-down posture for a while, but the others immediately abandoned their sunning postures and started preening.

The most interesting feature of this incident was that the sunning was clearly induced when birds from the coolness of the shade suddenly found themselves in the full strength of the sun on an already heated surface (see Chapter 9).

11

In Fry's new book (1984), lateral sunning by Carmine Bee-eaters while 'sitting on the ground with wings folded and body rolled to expose the flanks on one side to a low sun' was described as a rare form of sun-basking; a lateral posture, with the closed wing slightly lifted to expose the flank, was also figured for the Red-throated Bee-eater.

12

In Prinzinger's (1983) review, there is a drawing of a Great Bustard (after a photograph in Heinroth and Heinroth) allegedly sunning in a most distinctive posture that exposes the underwings and belly; this seems clearly an error, a photograph (no. 6) of the full-stretch posture (a comfort-movement) in the Heinroths' book having been confused with the one of lateral sunning (no. 9).

13

Prinzinger (1983) has a drawing of a Domestic Fowl in the full-lateral posture with typical wing-fan.

14

The usual briefness of the Dunnock's wing-raising is confirmed by A.T. Moffett who, he told me, found it most difficult to get a good photograph of the posture because his subjects had usually lowered the wing, or were lowering it, while his shutter was operating.

15

Caution is needed in interpreting such cases of possible wing-lifting because of the possible occurrence of decayed and other intermediate or indeterminate postures at times (see Note 8). In the present context, I have recently observed lateral-sunning Blackbirds and Starlings wave the partly extended sun-wing about but have interpreted this as incipient spreadeagling, a surmise born out on occasion by the subsequent adoption of the spreadeagle posture by one of the birds involved. I have also seen a Dunnock adopt what appeared, superficially, to be a 'half-spreadeagle' posture (see under Level-5 sunning) when it was really in a decayed posture after making an incipient wing-raising movement.

16

In the case of spreadeagle sunning, there is also, once again, the problem of 'decay', etc., to be considered when interpreting incomplete-looking or atypical postures (see Notes 8 and 15).

17

Prinzinger's (1983) review contains a drawing of a Wall Creeper in a half-spreadeagle posture while lying forward on its breast with the tail spread; another of a young Magpie with its folded wings drooped and tail depressed and fanned; and one of a Red-billed Oxpecker (Buphaginae), observed on the back of a Rhinoceros, lying in a semi-spreadeagle posture, also with the tail fanned and depressed.

18

Chris Measures informs me that, during April 1979 in The Gambia, he and Martin B. Withers saw a Giant Kingfisher sunning at mid-day on a sandbank, with its wings and tail fanned out in the full-spreadeagle posture; its feathers were ruffled, especially on the head (where the crest was fully raised), and the head was thrown back and canted. This is the only record of sunning in the Alcedinidae known to me; neither Rosemary Eastman (1969) nor David Boag (1982), in their books on our species (both titled *The Kingfisher*) mention sunning, which is surprising.

19

Fry (1984) described how the Red-throated Bee-eater will sometimes 'spreadeagle on a vertical cliff near its nest entrance, clinging by its claws, the head hanging down over the back, fluffed throat to the sun, looking totally bemused'. He also reported that Red-throated Bee-eaters ('and doubtless other species') will 'occasionally adopt a variety of improbable basking postures on cliff or ground'; among those figured are the one described above and the full-spreadeagle while lying on the ground. Spreadeagled sunning on the sloping ground of the nesting cliff was also described for the Carmine Bee-eater.

20

In Prinzinger's (1983) review, there is a drawing of a sunning Secretary-bird lying down in a half-spreadeagle posture with one leg (the one on the same side as the extended wing) exposed and stretched out to the rear.

21

Drawings in Prinzinger (1983) show a Wedge-tailed Eagle and an Indian White-backed Vulture sunning in standing loose-wing postures.

22

This set-up with photo-flood lamps has been used for annual demonstrations of sunning at Cornell University, with the same individual Bateleur Eagle, in 1982, 'still going strong at it after twenty years of exposure' (T.J. Cade).

23

For recent contributions to the topics of feather wettability and spread-wing postures, see Mahoney (1984) and Elowson (1984).

24

Two Little Grebes, watched sunning at Chew Valley Lake by D.E. Ladhams at 14:40 hours on 28 August 1972, floated in full sunshine with their rear-ends turned to the sun, the tail-tuft and upper tail-coverts erected, wings slightly lifted away from the flanks, and body held with the rear humped up much higher than the depressed breast.

25

My first and last dates for higher-level sunning (level-3 or above) for the four most frequently observed species are as follows: Blackbird, 13 March/22 September; Dunnock, 31 March/10 October; House Sparrow, 14 April/25 October; and Starling, 18 April/29 August.

26

A good example of the multiple use of individual sunning sites is given by Moffett (1983b). In all, no less than 18 species were seen at the same site, sometimes side by side: Wren, Dunnock, Robin, Redstart, Blackbird, Song Thrush, Willow Warbler, Blue Tit, Great Tit, Jay, Magpie, Tree Sparrow, Chaffinch, Yellow Bunting, Green Woodpecker, Great Spotted Woodpecker, Wood Pigeon, and Sparrowhawk. I cannot match that but have had Blackbird, Song Thrush, Starling, Dunnock, and House Sparrow sunning together. On 23 July 1984, I wrote to Mr Moffett as follows:

> 'This multiple use of the same "hot-spot" is a particularly intriguing feature of sunning and your example . . . a particularly good one. Only the other day, I saw a similar case from my study window. The spot was first occupied by an adult female Blackbird; a little later, what I took to be the same bird was back, but the glass revealed it to be a juvenile Blackbird; I noted this down, then checked the spot again: sure enough, a bird was sunning there in the same spreadeagle posture but the glass now showed it to be an adult Starling!'

Pondering since on this phenomenon, it occurs to me that – as birds set a premium on using safe sites for sunning (see below) and as suitable sunning sites are limited – one way of discovering such sites, for young birds in particular, would be to watch where other birds are sunning and take a turn there, replacing or supplanting the occupant if necessary or settling close nearby. This is not the only factor, of course, ordinary social facilitation also being involved at times for example, behaviour of this sort being highly 'contagious' anyway (see Chapter 9). The interesting thing, too, is that all this can be an inter-species affair at times. I would add here also, as it has not been stressed elsewhere, that birds for the most part are wary when sunning, especially young birds performing for the first time. True, some individuals can be approached closely when sunning, but this is probably the exception rather than the rule and the idea that birds lose all sense of caution when sunning (see, e.g., Simmons 1964) is a misleading one.

27

Our two tame male Dunnocks (see Notes 1 and 28) not infrequently sunned this year (1984) when still feeding their fledged young.

28

It is no coincidence, I am sure, that our present garden in particular – where the birds are fed individually, become very tame, and are free from disturbance and domestic predators (not to mention noisy children and over-keen gardeners) – has proved to be an excellent place to observe sunning (with over 500 records so far this year alone). Our Dunnocks provide a particularly good example: over the past three years we have so tamed them that they now readily come to be fed at close quarters, one even entering the house (in 1981, when we first came to live here, any Dunnock that even saw us at the window promptly left the garden and there were few sunning records for this species here that year); in the next three years, however, I logged no less than 331 cases of sunning, compared with only 13 in six years at Oadby. An illuminating natural experiment also occurred here in 1983: the male Blackbird DT had been sunning well up to 11 July (with 81 records since 14 May) when he was suddenly frightened at very close quarters by a cat; he was so terrified that he was still giving cat-alarm calls next day and was only seen sunning twice more in the garden that year.

29

Do birds sun themselves because it gives them 'pleasure'? In many birdwatchers' view, as recently expressed to me by one of my informants, birds sun mainly because they enjoy doing so. Prinzinger (1983) put this more scientifically, suggesting that the feeling of warmth or well-being is the 'reward' that the bird gets for sunning (see Note 4). There are a number of reasons for discounting this as a major factor in the evolution of sunning, not least the selection pressure of predation which, surely, would mitigate against such 'indulgent' behaviour? The reward of warmth may be relevant at times, especially in the case of sun-basking, but other evidence suggests that the reward of performance itself is the key one: 'mental' or 'psychological pleasure' one might also term it (those intimately conversant with animal behaviour will know what I mean). Indeed, sunning birds get so hot and discomforted at times, yet persist or come back for more, that there can be no question then of any reward involving physical pleasure! The question of function, however, is another matter altogether, as I hope has been made clear.

30

After the rest of these notes was completed, I was sent a copy of a popular article on sunning by Horsfall (1984) which dealt in particular with plumage adaptations for the utilization of solar heat – 'solar freeloading' as the author strikingly characterized it – though possible further functions of sunning were also considered briefly. A number of interesting and highly relevant points are made, too late, alas, to be considered further here.

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Index of Birds

Numbers in italics refer to illustrations.

THE BOOK

- The first comprehensive review of the sunning behaviour of birds written specially for ornithologists and birdwatchers
- Critically reviews the literature, with special emphasis on European and North American birds
- Gives a new terminology and detailed descriptions of sunning postures — with comparative comments on bathing, comfort behaviour generally, anting, and dusting
- Identifies and discusses the two main types of sunning behaviour ('sun-basking' and 'sun-exposure')
- Gives background information on temperature control (thermo-regulation) in birds
- Over 100 line-drawings in the text

THE AUTHOR

Dr K.E.L. Simmons is a biologist with wide interests in ornithology, particularly in bird ethology, behavioural ecology, and taxonomy. He is currently working on a biography of the naturalist Edmund Selous as well as continuing with his long-term study of parent Great Crested Grebes and their young. His observations on comfort behaviour and associated activities, especially anting and sunning, extend over some 35 years. Because of his knowledge and experience of these topics, he has been dubbed by Dr Bruce Campbell (in the Summer 1982 issue of *The Countryman*) as 'our leading authority on all aspects of the avian toilet'!

THE CLUB

The Bristol Ornithological Club was founded in 1966 and now has over 430 members. As well as organising meetings, field-trips, and inquiries, it publishes a monthly newsletter *(Bird News)* and, unusually for a local bird club, an annual journal *(Bristol Ornithology)* containing papers and shorter items of wide interest. This book on sunning is its first venture into a more ambitious field of publishing.

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