Sunbathing behaviour of birds

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Many species of birds have been observed in sunbathing postures and it is clear that the behaviour is not rare, but its significance remains obscure. This short review discusses sunbathing in general terms and, in the hope of providing a basis for future work, lists the species for which I have been able to find records.

The literature on sunbathing by birds is small: it consists of short notes on specific records, tentative suggestions concerning its possible significance, and brief general summaries (e.g. Simmons 1964). The only detailed paper is that by Hauser (1957), which described sunning by 33 species observed over nearly a year in the United States of America. The subject has been neglected and largely left to amateur description, and almost no experimental work has been undertaken.

It is likely that I have overlooked many descriptions of sunbathing, especially where these are hidden away in literature which, by title, may not appear relevant. Nevertheless, that should not invalidate the general statements made here.

BEHAVIOURAL ASPECTS

Hauser (1957) distinguished two types of sunning. These were voluntary, 'an attitude assumed by a bird apparently for reasons of health and well-being, accompanied by preening', and compulsory, 'the same attitude assumed when a bird is suddenly and apparently unexpectedly exposed to direct sunlight, under more or less extreme conditions of humidity and heat. This response . . . appears to be unpremeditated and irresistable.'

The typical attitude is spread-eagled with tail and wings spread, contour feathers ruffled, mandibles parted and the eye facing the sun wide open (e.g. Dilger 1956). Ruffling of the feathers (complete erection) was distinguished from fluffing (partial erection) by Morris (1956). Fluffing improves insulation by increasing the volume of air trapped
Sunbathing behaviour of birds

in the plumage; ruffling, on the other hand, greatly decreases it. Morris considered that such ruffling was a thermoregulatory response and, associated as it is with gaping, this certainly is the likeliest explanation. It also has the effect, however, with the spreading of remiges and rectrices, of exposing the maximum possible surface area of feathers to the sun. Similar responses are shown by birds shielding their young from the sun: Brown and Davies (1949) described a sudden raising of one wing when a Reed Warbler *Acrocephalus scirpaceus* appeared to be suffering from heat exposure whilst shielding its young, and they suggested that this facilitated heat loss by exposing the subclavian vein to the air. It may therefore be significant that the underwing is exposed by some species during sunbathing—for example, pigeons (Goodwin 1967b), hirundines (Barlow, Klaas and Lenz 1963), Treecreeper (Buxton 1950) and Dunnock (Teager 1967).*

Hauser (1957), Barlow, Klaas and Lenz (1963) and Teager (1967) pointed out that sunning is frequently a social act, and that single birds attract others of the same and other species to do likewise. Aggressive displays and attempted copulation may occur at the same time, as has been noted among Cliff Swallows (Barlow, Klaas and Lenz 1963). This attracting of other birds can result in synchronised sunning, which may be advantageous in reducing the probably great risk of predation when a bird is in this vulnerable position. Hobbs (1958) recorded social sunning by White-necked Herons and Straw-necked Ibises in Australia, and it is interesting that Taylor (1957) described a similar incident with Grey Herons and Yellow-billed Storks in Africa, though he was unaware of its significance. Hauser (1957) noted that some birds favoured particular sites where repeated sunning might occur over a period of months.

Sunbathing has been classified under 'maintenance behaviour' and 'care of the body surface', and Nicolai (1962) has shown that the postures adopted by pigeons for rain-bathing and sunbathing are very similar, suggesting a common derivation. Rothschild and Clay (1952) thought it likely that anting had been derived in the course of evolution from sunbathing. The postures adopted in sunning vary somewhat between different families, and to a slight extent between related species, but far more detailed observation is necessary before this aspect can be usefully reviewed. The sunning bird is invariably orientated in such a way that the sun strikes the largest possible area of plumage. Lanyon (1958) showed that birds sometimes adopted a sunning posture when subjected to heat alone, and it is generally held to be a simple temperature response (Morris 1956, Simmons 1964). A very good case can be made for this being the explanation for Hauser's 'compulsory sunning', i.e. a heat dissipation mechanism, but the existence of 'voluntary

*Scientific names of species not given in the text will be found in the appendix on pages 256-258.
Simmons (1964) considered that sunbathing had both innate and learned components, and Nice (1962) and Dilger (1956) both established that the posture was adopted in early life. Many reptiles, especially lizards, sunbathe regularly, and in their case it is connected with temperature regulation, heat being absorbed (Prosser and Brown 1965). Hauser (1957) showed that birds often sunbathe after periods of rain and days without sun. Brown and Amadon (1968) noted that the New World vultures sun themselves especially in the morning, before leaving the roost, and in the evening. Since these authors also stated that the body temperature of the Turkey Vulture drops at night, sunning in this group is likely to be connected with heat absorption. This may apply as well to the nightjars, which are heterothermic.

THE FUNCTIONS OF SUNBATHING
The widespread occurrence of voluntary sunning among birds indicates that it is probably a basic and phylogenetically old response, common to most or all. As noted above, the risk of predation in this vulnerable posture is likely to be great. If this is so, the likelihood that the behaviour has survival value is increased. It is of course possible that sunning has different functions in different species or several functions in the same species. Its possible significance has been briefly discussed by Harrison (1946), Gibb (1947), Wynne-Edwards (1947), Simmons (1964) and Goodwin (1967a). The suggestions which have been put forward are reviewed below.

1. That it is a pleasurable stimulus connected with heat absorption
A bird undergoing voluntary sunning has, in anthropomorphic terms, the appearance of ‘ecstasy’, and it is a very reasonable supposition that it seeks out warmth and receives satisfaction from basking in the sun. This view has led some workers to dismiss sunning as a simple temperature response and of no further significance. There is no reason, however, why sunning should not have additional adaptive significance, at least at the ‘voluntary’ level: indeed, this is likely if the behaviour is old. Most birds are of course strict homoiotherms, and therefore sunning as a mechanism of raising body temperature must have far less importance than in reptiles. If other functions of sunning exist, then it is quite possible that selection has increased the level of ‘pleasure’, with the effect that the behaviour is indulged in frequently. But this is speculation.

2. That sunlight increases the mobility of ectoparasites, making easier their removal by subsequent preening
The only evidence to support this view is the fact that sunning is usually interspersed with, or followed by, preening. No analyses have
been made of the contents of the crops of birds which have been sunbathing, and to determine whether sunlight does have this effect would also necessitate a study of the effectiveness of normal preening. The responses of ectoparasites to sunlight and temperature are unknown; the results of the few studies made on the temperature responses of Mallophaga are ambiguous (Stenram 1956).

(3) That birds may sunbathe to dry wet plumage
This is certainly true in some circumstances, but is not of course applicable to all cases. Among the mousebirds (Coliidae), communal sunbathing is most frequent after rain or dew which has caused their soft hair-like plumage to be drenched with moisture (Rowan 1967). Bannerman (1956) recorded that when some Griffon Vultures had been wetted by a heavy shower and the sun then came out, they sat with outspread wings, drying their feathers: he also noted that this species uses the same posture for normal voluntary sunning. New World vultures likewise sit in the sun with outspread wings to dry their plumage—as has been observed in the California Condor and the American Black Vulture (Brown and Amadon 1968)—and this is an interesting case of parallelism. It is, of course, well known that similar behaviour in the cormorants (Phalacrocoracidae) and darters (Anhingidae) is almost certainly connected with plumage-drying (Rijke 1968).

(4) That sunbathing results in vitamin D production
It has repeatedly been suggested that sunning results in production of vitamin D from a precursor in the preen gland secretion which has been spread over the surface of the feathers during preening. Indeed, this has even been stated as fact by, for example, Moore (1953), Rothman (1954), Stoves (1957), Simmons (1964) and Prosser and Brown (1965). The evidence is ambiguous, however, and it was briefly reviewed by Kennedy (1968). Hauser (1957) stated: ‘When a bird is in the sunbathing position with its back to the sun, the feathers at the rump are raised so high that they fully expose the naked preen gland.’ A photograph of a sunning Blackbird by C. W. Teager (plate xiv in Rothschild and Clay 1952) illustrates this well: the upper tail-coverts and the feathers of the rump are raised, so that the nipple of the preen gland and most of its outline are clearly visible and exposed to the sun’s rays.

Hart et al. (1924) showed that, on a ration low in vitamin D, chicks receiving no sunlight were listless and inactive, rough of feather and awkward in gait, and that they died within six weeks, while others given sunlight were alert and active, with almost normal feathering. It is clear that sunlight has an alleviating effect on rickets in hens and turkeys (Reed, Struck and Steck 1939), but whether sunbathing in the wild has the function of producing vitamin D in the way outlined above is debatable. Kelso (1952, 1953), however, did demonstrate that
the Salkowski test for cholesterols gave a strong reaction with feathers previously exposed to sunlight. He also believed that feather-eating by captive Screech Owls *Otus asio* enabled them to procure vitamin D (Kelso 1946). Feather ingestion is well known for grebes (e.g. Nice 1962) and is a pathological condition among some domestic birds—for example, Muscovy Ducks *Cairina moschata* (von Faber 1964)—but in the case of grebes it has been suggested that feathers protect the gut from perforation by fish bones. Some groups—e.g. bustards (Otididae), some parrots (Psittacidae) and some pigeons (Columbidae)—are without preen glands, and these glands are atrophic in others. Do these birds indulge in sunning? The Blue-headed Quail Dove has been recorded sunbathing (Nicolai 1962), although it belongs to the genus *Starnoenas* in which the preen gland is absent (Garrod 1874).

Rickets has apparently never been observed in wild birds, although other avitaminoses have been, such as lack of vitamin A (Notini 1941), so it is difficult to guess at their vitamin D requirements and the sources available to them. It is likely that most of the vitamin comes from the diet, and there are likely to be differences in the amounts needed both by different species and at different times by the same individual. Irradiation of hens’ eggs increases hatchability (Reed, Struck and Steck 1939) and this may be because vitamin D is produced. What can be the vitamin D requirement of the developing embryos of hole-nesting species? Is more of the vitamin present in their eggs than in those of open nesters? It is possible that dietary vitamin D might be supplemented in some species with vitamin D formed during sunning, either from the provitamin circulating in the superficial blood of exposed areas of skin such as the legs or beak, or from the provitamin alleged to be present in preen gland secretions.

It is known that the calcium requirements of birds are increased during moulting (e.g. Meister 1951, Simkiss 1967), and Hauser (1957) stated from her experience of several hundred sunning incidents: ‘Young birds are seen sunbathing more frequently than adults except during the late summer molting season when many adult birds in all stages of molt may be seen preening and sunning.’ Similarly, records of sunning received by Gibb (1947) suggested that juveniles were more prone than adults to sunning, and he noted that the dates showed a tendency to concentrate round times of moult. Extensive field observations are needed to determine if this suggested tendency is a real one: it could simply be that, in general, the timing of moulting, by selection, coincides with sunny spells, since these are usually times when most food is available, and that sunning is indulged in as a natural consequence without adaptive significance to moulting.

(5) *That sunbathing plays a role in moulting*

Harrison (1946) suggested that sunning at the time of moulting might
have an effect unconnected with vitamin D production. He stated: 'It seems most significant that a crepuscular and nocturnal species such as the Tawny Owl should deliberately seek out perches directly exposed to the full influence of solar rays at the season of moult.' He was convinced that sunning had an important role in moulting: 'It seems reasonable to assume that this may operate not only through its local effects in stimulating the feather papillae to develop, but also through the central nervous and endocrine systems.'

(6) That it increases the flow of the preen gland secretion

As stated above, the preen gland may be exposed during sunning, and sunning is invariably followed by preening. The role of the preen gland secretion is as yet uncertain (Clark and Kennedy 1968), but it presumably functions in plumage care. Preen glands are homologous with mammalian sebaceous glands, and so it is of interest that sebaceous gland function is markedly dependent on atmospheric temperature (Rothman 1954). It is therefore possible that sunning does increase preen gland secretion, and that the behaviour is thus connected with feather care.

DISCUSSION

The most probable explanation for compulsory sunning is clearly heat dissipation. It is also likely that, in some circumstances, voluntary sunning is done to accumulate warmth. The suggested explanations of plumage care and vitamin D production are as yet speculative and need further evidence. The appendix on pages 256-258 may be more illuminating from the point of families not included, since it is evident that sunning is widespread. It seems clear from this list, however, that herons, birds of prey, rails, doves, larks, swallows, thrushes, finches and buntings are groups which are particularly prone to sunning. The further accumulation of single records of voluntary sunning is of least importance, and attention should now be given to the postures adopted, any associated behaviour and the frequency of occurrence throughout the year, as well as to the functional interpretation. A study of postures adopted may be of use in understanding the derivation of sunning and its connection with other 'comfort movements', as well as (with care) in shedding light on the relationships of different groups.

The sort of evidence which would shed light on, for example, the vitamin D hypothesis would be the incidence of sunning relative to the amount of sun in a temperate species (or population) relative to a tropical one. It would also be of interest to determine the amount of time which individuals of different species spend sunning during the day (which would best be done by colour-ringing) and to compare this with the amount of time spent on such essential activities as feeding.
It is possible that the amount of time spent on the various 'comfort movements' may be greater when more 'free' time is available. If this were the case, it would tend to suggest that such behaviour is of little importance in the lives of birds from the point of view of survival. It seems very likely that all movements concerned with care of the body surface are performed after other needs are satisfied, i.e. they are of secondary importance in the daily schedule and fitted into it as such. Above a certain minimal level, such behaviour may be entirely superfluous.

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SUMMARY
The sunbathing behaviour of birds is described and the very scattered literature reviewed. Various suggested functions are discussed under six appropriate headings on pages 251-254. At this stage it can only be said that the significance of the behaviour is as yet obscure, but it is certainly widespread among birds in many parts of the world. The appendix on pages 256-258 lists over 170 species of 48 families and subfamilies which have been recorded sunbathing. Groups which seem particularly well represented include the herons, birds of prey, rails, doves, larks, swallows, thrushes, finches and buntings.

REFERENCES
In view of the large number of references cited, this abbreviated list omits titles of papers.

Brown, P. E., and Davies, M. G. (1949): Reed-Warblers (East Molesey).
Hart, E. M., Steenbock, H.,
Appendix. Species recorded sunbathing

Where a date follows the authority, the relevant publication is listed in the references. Where no authority but a locality is given, the observation is by I. J. Ferguson-Lees. Where an authority but no date is given, the observation was in litt. to British Birds. It should be noted that this is necessarily a composite list, including both compulsory and voluntary sunning (see page 249).
Sunning behaviour of birds

PODICIPIDAE
Great Crested Grebe Podiceps cristatus (young) (Rankin 1947)

PROCELLARIIDAE
Fuller Puffinus glacialis (Mason 1950)

SULIDAE
Blue-faced Booby Sula dactylatra (Nelson 1967)
Red-footed Booby Sula sula (Nelson 1968)
Brown Booby Sula leucogaster (Darway 1962)
Australian Gannet Sula serrator (Warham 1958)

ARDEIDAE
Green Heron Butorides virescens (Hauser 1957)
Grey Heron Ardea cinerea (Boyd 1930, Brook 1930, Tully 1950, Low 1914, Taylor 1957)
Purple Heron Ardea purpurea (Gush 1951)
Great Blue Heron Ardea herodias (see Tully 1950)
White-necked Heron Notophaga pacifica (Hobs 1958)
Cattle Egret Bubulcus ibis (Gush 1951)
Bittern Botaurus stellaris (J. C. Rolls)

CICONIDAE
Yellow-billed Stork Ibis ibis (Taylor 1957)

THREKСIONITHIDAE
Straw-necked Ibis Threskiornis spinicollis (Hobs 1958)

ANATIDAE
Tufted Duck Aythya fuligula (Rogers 1950)
Mute Swan Cygnus olor (Hilary 1969)

CATHARIDAE
Turkey Vulture Cathartes aura (Brown and Amadon 1968)
Black Vulture Coragyps atratus (Brown and Amadon 1968)
California Condor Gymnogyps californianus (Koford 1951, Brown and Amadon 1968)

ACCIPTERIDAE
Griffon Vulture Gyps fulvus (Spain)
Bateleur Terathopius ecaudatus (Nigeria)
Black Kite Milvus migrans (Gibb 1947, Brown and Amadon 1968)
Double-toothed Kite Harpagus bidensatans (Brown and Amadon 1968)
Hen Harrier Circus cyaneus (Brown and Amadon 1968)

FALCONIDAE
Peregrine Falco peregrinus (Britain)
Eleonora’s Falcon Falco eleonorae (Vaughan 1961)
Spot-winged Falconet Spathopterus cirrochrous (Brown and Amadon 1968)

TETRANIDAE
Red Grouse Lagopus lagopus scoticus (Watson and Jenkins 1964)

PHASIANIDAE
Red-legged Partridge Akiaiarius rafa (Goodwin 1951)
Phesant Phasianus colchicus (Britain)
Domestic Fowl Gallus domesticus (Nice 1962)

BALLIDAE
Virginia Rail Rallus limicola (Nice 1962)
King Rail Rallus elegans (Nice 1962)
Water Rail Rallus aquaticus (Heinroth and Heinroth 1924)
Cayenne Wood Rail Aramides senex (Nice 1962)
Sora Rail Peregia carolina (Nice 1962)
Little Crake Porzana parva (Koenig 1941, Bauer 1960)
Corncrake Crex crex (Heinroth and Heinroth 1924)
Moorhen Gallinula chloropus (Heinroth and Heinroth 1924)
Coot Fulica atra (Kornowski 1937)

CHARADRIIDAE
Killdeer Charadrius vociferus (Davis 1943)

SCOLOPACIDAE
Snipe Gallinago gallinago (Mason 1950)

LARIDAE
Royal Tern Sterna maxima (Hauser 1957)
Snow Tern Sterna fasciata (Watson 1908)
Brown Noddy Anous stolidus (Watson 1908)
Black Noddy Anous stenorrhynchos (Darway 1962, Cullen and Ashmore 1963)

COLIIDAE
Stock Dove Columba oenas (Britain)
Rock Dove Columba livia (Nicolai 1962)
Woodpigeon Columba palumbus (Gibb 1947)
Turtle Dove Streptopelia turtur (Bentham 1957, Britain)
Laughing Dove Streptopelia roseogrisea (Nicolai 1962)
Collared Dove Streptopelia decaocto (Nicolai 1962, Britain)
African Collared Dove Streptopelia roseogrisea (Nicolai 1962)
African Mourning Dove Streptopelia decipiens (Nicolai 1962)
American Mourning Dove Zonitula monacha (Hauser 1957, Nicolai 1962)
Galapagos Ground Dove Neopelia galapagonensis (Nicolai 1962)
Ground Dove Columbifigans passeerina (Hauser 1957)
Inca Dove Streptopelia cineraria (Johnston 1960)
Blue-headed Quail Dove Streptopelia cyanopterola (Nicolai 1962)
Grey-faced Quail Dove Geotrygon caniseta (Nicolai 1962)
Ruddy Quail Dove Geotrygon montana (Nicolai 1962)
Gold-billed Ground Dove Columbina talpacoti (Nicolai 1962)
Plain-breasted Ground Dove Columbina minuta (Nicolai 1962)
Bare-faced Ground Dove Metopidius vicinis (Nicolai 1962)
Luzon Bleeding-Heart Gallicolumba lophaemica (Nicolai 1962)
Common Broodshewing Phaps chalopus (Nicolai 1962)
Brush Broodshewing Phaps elegans (Nicolai 1962)
Crested Pigeon Ocyphaps lophotes (Nicolai 1962, Goodwin 1967)
Zebra Dove Geopelia striata (Nicolai 1962)
Diamond Dove Geopelea concarta (Nicolai 1962)

CUCCULIDAE
Yellow-billed Cuckoo Coccyzus americanus (Cracraft 1964)
Guira Cuckoo Guira guira (Durrall 1916)

TYTONIDAE
Barn Owl Tyto alba (Gibb 1947, Bentham 1962)

STREIGIDAE
Little Owl Athene noctua (Gibb 1947)
Tawny Owl Strix aluco (Harrison 1946, Burton 1959)

CAPRIMULGIDAE
Nightjar Caprimulgus europaeus (Gibb 1947)

COLIDAE
Mousebirds Collurio spp. (Rowan 1967)

MEROPIDAE
Bee-eater Merops apiaster (Jordan)
Blue-cheeked Bee-eater Merops superciliosus (Nigeria, Jordan)
Least Bee-eater Merops pusillus (Nigeria)

UPUPIDAE
Hoopoe Upupa epops (Nigeria)

PICIDAE
Yellow-shafer Flicker Colaptes auratus (Hauser 1957)
Red-bellied Woodpecker Centurus carolinus (Hauser 1957)
Golden-fronted Woodpecker Centurus aurifrons (Hauser 1957)
Sunbathing behaviour of birds

**STENIIDAE**

Olive-backed Warbler *Hippolais pallida* (Nigeria)
Willow Warbler *Phylloscopus trochilus* (Harrison 1946)
Chiffchaff *Phylloscopus collybita* (B. King)
Bonelli’s Warbler *Phylloscopus bonelli* (B. King)
Blue Wren *Malurus cyaneus* (Goodwin 1967a)
Goldcrest *Regulus regulus* (Gibb 1947)

**MUSCICAPIDAE**

Pied Flycatcher *Ficedula hypoleuca* (Heinroth and Heinroth 1944)

**FURNIDIDAE**

Dunnock *Prunella modularis* (Beven 1946, Teager 1967; Britain)

**LAMIIDAE**

Masked Shrike *Lanius collaris* (Jordan)
Red-backed Shrike *Lanius collurio* (Gibb 1947)

**STURNIDAE**

Starling *Sturnus vulgaris* (Gibb 1947, Hauser 1957, Teager 1967)

**VIREONIDAE**

Red-eyed Vireo *Vireo olivaceus* (Barlow Klaas and Lenz 1963, B. King)