CHAPTER 1

Animal builders and the importance of bird nests

1.1 Introduction

Among the hundreds of bird nests carefully preserved in The Natural History Museum, London, is an unremarkable looking cup nest of grass and rootlets collected in New Zealand during the last century. It is the nest of the mournfully named *piopio or New Zealand thrush (*Turnagra capensis*). The interesting thing about the nest is that the builder is extinct, a victim of introduced mammals and its own over-confiding nature. The bird itself was last observed in 1947 (Fuller 1987). Possibly no other nest of this species remains in the world. It is an enduring expression of behaviour that can no longer be seen. To touch it is to be as close to its maker as to touch a brush stroke of a Van Gogh sunflower.

The structures animals build persist through time and in their construction the world is changed for the builders and for others. They may simply be regarded as objects of curiosity or wonder but, as products of evolution, they must embody principles of the organisation of the behaviour that created them, of functional design and of the evolutionary process itself; the scientific study of them should reveal some of these principles. This is the purpose of this book and the subjects to be examined are the nests and other objects constructed by that most consistently impressive group of animal builders, the birds.

So, in an important sense this is not a book about birds but about nests and related construction behaviour. Other groups of animals build nests or other structures, some much more remarkable than those built by birds. All these organisms share features in common with birds. They are equipped for building and have behaviour which ensures that the anatomy, even if unspecialised, is effectively employed on the chosen building materials. Consequently, the building activity of birds can be viewed as a model system, the study

---

* An asterisk is attached to any species referred to in this book whenever some aspect of its nest is referred to and that nest has been included in the museum nest survey, e.g. *piopio (*Turnagra capensis*).

of which allows generalisations to be made about all animal builders and all built structures. This chapter identifies important features of animal builders as a whole. In this way the relative importance of birds as builders can be judged and their ability to contribute to an understanding of building biology assessed.

1.2 Builders extend their control

The New Guinea ladder-web spider (Araneidae) builds a prey capture device which is like a conventional orb web except that the bottom sector of the web has been enormously extended downwards (Fig. 1.1). The length of the web is more than 130 times the body length of the spider, a huge extension of the capture range of the animal beyond the tips of its limbs. This extension of the animal also persists in time, although not for very long; built in the evening, it is dismantled before dawn. It is a design probably specialised for the capture of moths which, having hit the ladder, struggle to free themselves from its sticky threads by shedding their lose scales. In doing so they roll down the web and would fall off the bottom of a conventional orb web but in this case lose all their scales and are trapped as their supply of scales runs out (Robinson & Robinson 1972). Animals build artefacts to extend their control over the environment.

The highest mounds of some Australian termites of the genus *Amitermes* approach 7 m, with a similar girth near the base. This is large enough to contain a few million termites. When this is compared with the planned Millennium Tower, Tokyo, which will be about 800 m high yet accommodate only about 50 000 office workers, the scale of the termite building can be appreciated. The life of termites is, in fact, inseparable from the structures they build. A large proportion of colony members never venture out of the mound, which with maintenance may last decades, far longer than the individuals that built it. In some species the environment created inside the mound is regulated within narrow limits by its architecture. The mounds of so-called 'magnetic termites' (*Amitermes meridionalis* and *A. laurensis*) are laterally flattened near North–South axis, and taper to a narrow ridge at the top. This ensures that in the dry winter months the nest is warmed in the early morning by the sun striking its eastern face and its temperature is maintained into the late afternoon by the sun on its western face; at midday, however, the mound exposes little of its surface to the strong rays of the sun overhead. In this way the nest temperature remains quite constant during most of the day (Fig. 1.2, Grigg 1973).

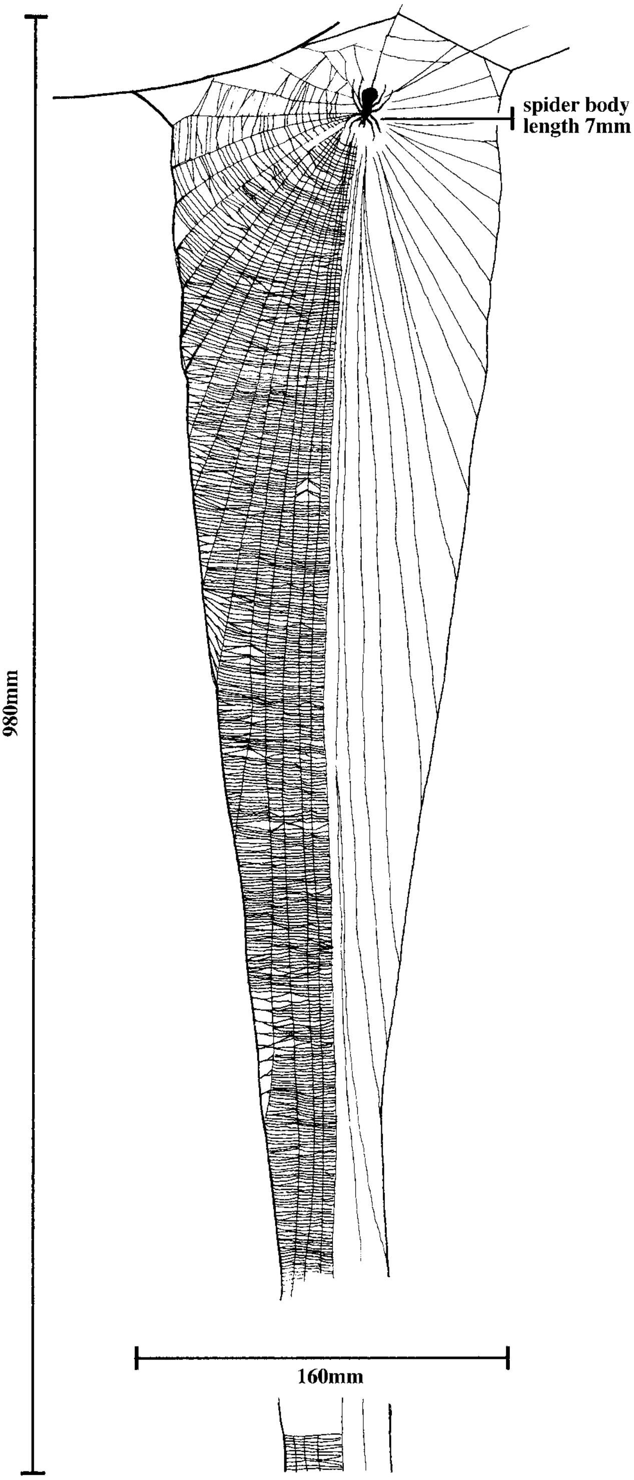

Figure 1.1
Builders extend their control: the elongated capture surface of the New Guinea ladder-web spider (Araneidae) is about 130 times the body length of the spider itself. (Adapted from Robinson & Robinson 1972.)

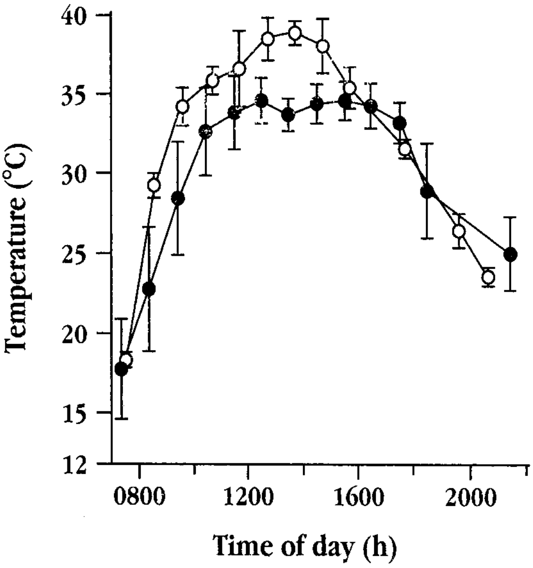

Figure 1.2
Temperature control through architecture: in its normal north–south orientation, the nest of the termite *Amitermes meridionalis* maintains a relatively constant temperature below 35 °C during daylight (solid circles). When the nest is rotated through 90°, nest temperature peaks at near 40°C (open circles). (Adapted from Grigg 1973.)

Heavy rains fall in the summer months, flooding the ground, but, with a height of 2–3 m, a mound of *A. meridionalis* keeps its one million or so inhabitants in safety well above the water level. As the water recedes the grass grows rapidly and the termites emerge to gather it into a multitude of storage chambers. This provides them with hay on which they can survive in the arid external world of the winter dry season. Temperature, humidity, food availability, these are all controlled by the agency of the mound itself. The termites' world loses its unpredictability, allowing them to transfer some functions formerly carried out by the bodies of their cockroach-like ancestors to the mound itself. Without the threat of desiccation or predation, their cuticles have become thin and soft. In their enclosed, darkened world, vision, body pigment and rapid escape responses have been almost lost. Birds' nests are by contrast designed to provide a controlled environment almost always simply to protect young. The few species in which adults sleep in nests outside the breeding season, even making dormitory nests (Skutch 1961), are the exception. The nests extend the control of parents in two respects: they help maintain the eggs near the typical avian body temperature of about 40 °C (Calder & King 1974), often considerably above the environmental temperature; and they reduce predation risk. A change in the structure of bird nests might therefore substantially alter the survival of eggs and chicks. This in turn might exert an indirect influence on the biology of the adults, for example the lifetime pattern of reproduction. This interaction between nest and the organisms whose world it controls is one which runs through this book.

1.3 The extended phenotype concept

The question of whether the artefact is in some respect part of the organism that created it was explored by Dawkins (1982) in *The Extended Phenotype*. He argues that, in the same way that there are demonstrably genes for body form or eye colour, there must be genes whose phenotypic expression is apparent in the architecture of a nest or web. This concept does not seem to me to pose any particular problems, although we know all too little about phenotypic variation in animal-built structures or its genetic basis. However, if we suppose that the number of radii in the orb web of the garden spider, *Araneus diadematus*, has a genetic basis, then it follows that, if web variants with more radii were more successful than those with fewer, then spiders with the genotype for many radii would increase in the population at the expense of those with the phenotype for fewer radii.

The relationship between genotype and extended phenotype may be more complex than this, and the evolutionary consequences difficult to predict. A nest builder may not affect its own survival but that of its offspring, which will die if the nest falls out of the tree. Nevertheless, better nest building will be selected for in the same way as any other kind of parental behaviour since the fitness of the builder is directly affected by the nest quality. Suppose, however, the nest is built by both parents – it is then an expression of aspects of the genotype of both; or that it is built by unknown thousands of individuals over many generations, as is a termite mound. With several individuals responsible for the architecture, what then is the effect of selection pressures acting upon the varied, mosaic nest phenotypes? Do they, for example, have consequences for mate choice or rates of evolution? None of this is known yet it is clear that, even in such complex systems of phenotypic expression, the architecture can be sophisticated and distinctive. The closed (Fig. 1.3) and open air conditioning systems of *Macrotermes* mounds (Luscher 1961, Darlington 1984) apparently attest to this.

The garden spider builds an orb web and rests at its hub awaiting the impact of flying prey. The related orb web spinner (*Zygiella x-notata*) hides in vegetation at the side of the web, holding one of the radii which connects directly to the web hub without contact with intersecting capture threads; this is a species-specific

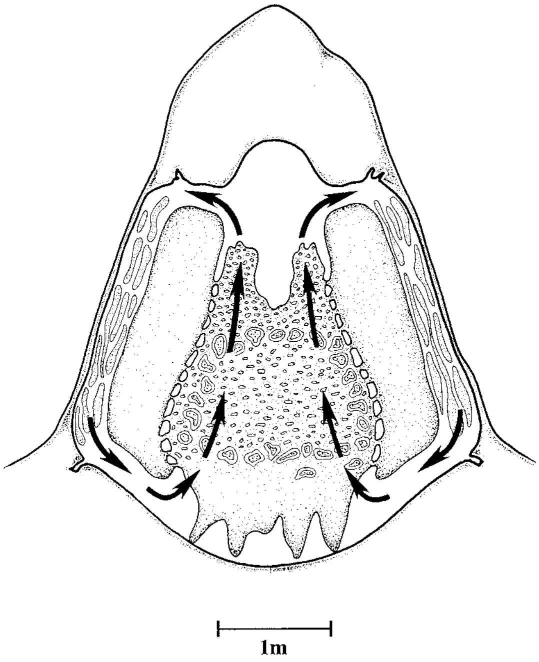

Figure 1.3
Collective extended phenotype: in the closed ventilation system found in some nests of the termite genus *Macrotermes*, the heat generated by the colony causes air to rise in the nest core, driving it round an air conditioning system that regulates temperature and gas exchange. The mound is built and extended by very large numbers of termites over many years. (Adapted from Luscher 1961.)

difference. The architecture of an extended phenotype may be as diagnostic of the species as the anatomy of its maker. Niche specialisation is, in fact, frequently expressed through species-distinctive architecture and may even be the feature which most readily identifies species in the wild. Species recognised through differences in their nest architecture have been labelled *ethospecies* because they are recognised through their behaviour. Examples have been described among wasps of the genus *Eustenogaster* (Stenogastinae, Vespidae) (Sakagami & Yoshikawa 1968, Hansell 1984, Fig. 1.4) and termites of the genus *Apicotermes* (Schmidt 1955). Bird nests also may be readily identifiable to species; the hanging nest of the *red-headed weaver (*Anaplectes rubriceps*, Ploceinae), made of fine twigs held together by twists of dried bark (see Fig. 9.2), is unique in construction.

Species-typical phenotypes may also be expressed with some degree of variation. Whether natural selection acting on this can produce evolutionary change depends upon whether the variation has a genetic basis. Here our ignorance is strongly evident. There are few systematic studies on the extent of variation in artefacts built by any one species, fewer still on its cause or relative fitness of the variants. The silk worm (*Hyalophora cecropia),* when it pupates, constructs a cocoon which may be either *compact* or

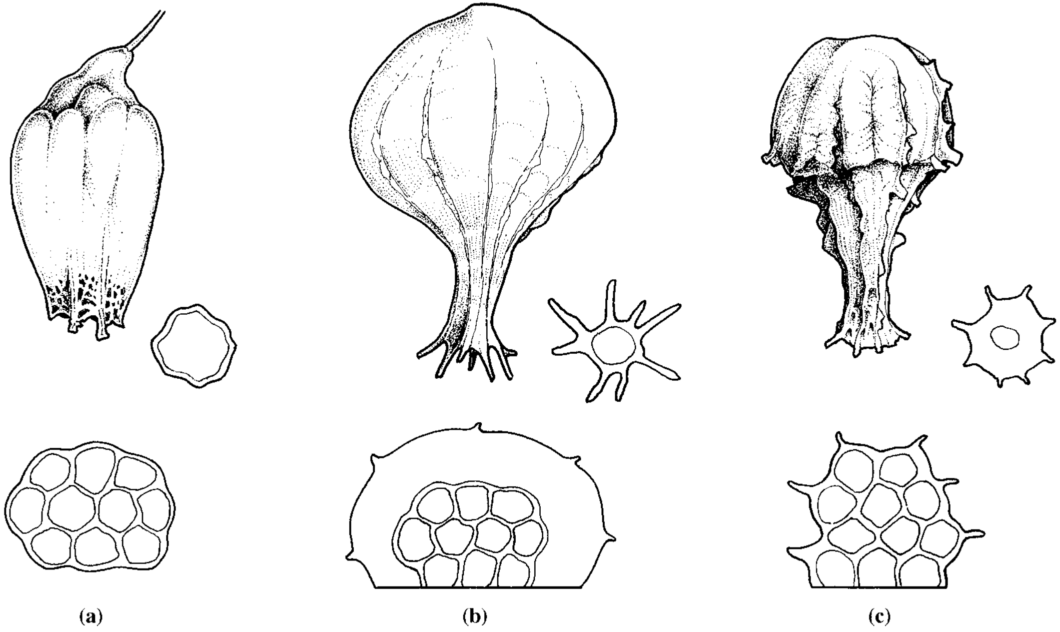

Figure 1.4
Ethospecies: the nests of three species of hover wasp (Stenogastrinae), each shown as side view, nest entrance shape and transverse section at the level of the brood comb. The nests are very distinctive, although it is difficult to distinguish the species on the basis of the wasps themselves. (Redrawn from Hansell 1984.)

baggy, but this polymorphism may not reflect genetic differences but be conditional upon the configuration of twigs where the caterpillar chooses to build (Waldbauer, Scarbrough & Sternburgh 1982). The stenogastine wasp *Parischnogaster mellyi* constructs a nest which may be a row of cells placed more or less end to end along a fine plant stem; cells may, however, be placed on the sides of previous cells to form a compact comb design or placed to generate an intermediate design. Again, the design appears to be conditional on environmental circumstances. The elongate design is preferred, more comb-like designs being adopted when the nest suspension is too short, suggesting that it might survive better, for example, through concealment from visually hunting predators (Hansell 1981). Within-species variation in nest design could alternatively be the result of differences in experience. Where construction behaviour is complex, individuals may improve with experience. Birds are potentially a very interesting group in this respect. They build rather elaborate structures and their capacity to learn is strongly evident in other aspects of their behaviour. In species in which this could be demonstrated, the prediction would be that experienced birds build better (more protective) nests.

1.4 Building behaviour changes habitats

By their behaviours, builders change the world and by their activity over succeeding generations, they may create distinctive new habitats, which represent a long history of occupation by the builders. In Cape Province, South Africa, the landscape is covered over large areas with more or less circular mounds 30 m across and 2 m high. These are apparently the consequence of the combined burrowing activities of termites (*Microhodotermes viator*) and mole rats (Bathyergidae) (Lovegrove 1991). This so-called *mima prairie* landscape is also found in the USA, created in this case by pocket gophers (*Thomomys*) (Fig. 1.5), and in Argentina, due to rodents of the genus *Ctenomys* (Cox 1984, Cox & Roig 1986). In South Africa the termite *Odontotermes* is thought to be responsible for creating a landscape of regular corrugations with parallel gullies about 50 m apart separated by ridges about 2 m in height which may be 1 km in length (Sattaur 1991). The period of time over which these landscapes have been shaped by burrowers is unknown, but the evenness of the mounds in *mima prairie* suggests that individual burrow systems may have been in more or less continuous occupation for decades and quite possibly a great deal longer (Hansell 1993a). An active mound of the termite *Macrotermes goliath* was found to

Figure 1.5
Builders change habitats: mima prairie in North America; a regular landscape, shaped over long periods of time by the burrowing activity of pocket gophers, *Thomomys*. (Photograph by V. Scheffer.)

contain archaeological remains dateable at 700 years old (Watson 1967).

The nests of birds, by contrast, are generally seasonal and short lived; the nest of a bird such as a *chaffinch (*Fringilla coelebs*) has a working life from first egg in to last chick out of no more than 35 days (Harrison 1975), although nests of large raptors may last for many years. The nests of megapodes are, in avian terms, exceptional. They may be used and added to year after year. In northern Australia there are sites where several hundred of these nest mounds occur together, some over 10 m high. As local megapodes weigh only about 1 kg, these mounds were originally identified as Aborigine middens (Bailey 1977) but now seem likely to be the nest mounds of the scrub fowl (*Megapodius* (*freycinet*) *reinwardt*) (Stone 1989). In New Caledonia mounds of 50 m diameter and 4–5 m high may be either archaeological sites or mounds of the extinct megapode *Sylviornis neocaledoniae* (Mourer-Chauviré & Poplin 1985).

1.5 Exploitation of the resources by others

The concentration of resources in a nest in the form of the occupants, their food supplies, the favourable microhabitat, even the nest material itself, creates a new range of niches to be exploited by a variety of specialists. The rich resources enclosed in social insect nests have led to the convergent evolution of a number of mammalian predators with long tongues and reduced dentition, including the aardvark (*Orycteropus*) in Africa and giant anteater (*Myrmecophaga*) in South America. Birds such as the honey buzzard (*Pernis apivorus*) and the red-throated caracara (*Daptrius americanus*) are specialist predators of the nests of wasps and bees (Thiollay 1991), as are some social insects themselves such as the tropical hornet (*Vespa tropica*) in Asia and the army ant (*Eciton hamatum*) in the New World tropics. A large number of arthropod species also exploit social insect colonies from within the nest itself in ways ranging from feeding on nest debris to obligate parasitism. Considering only ants, the arthropod symbionts found in their nests extend across six classes and ten insect orders which include 35 families of beetles alone (Hölldobler & Wilson 1990). Most obviously, however, the nest structure itself represents a resource which is of value to the conspecifics of the builder. The preferred method of nest foundation by the stenogastrine wasp *Eustenogaster calyptodoma* is by the acquisition of the nest made by another female (Hansell 1986). As rather ephemeral structures, bird nests provide fewer opportunities for exploitation, and the biodiversity of nest commensals is low. Nevertheless, chicks are a rich and vulnerable source of food, attracting predators or supporting a large population of nest parasites. This can have severe effects on chick survival or development, and has resulted in some construction behaviour and design features of nests to combat these problems (see Chapters 5 and 6).

1.6 Nests reinforce social life

Darwin, in *On the Origin of Species* (1859), admitted that he at first felt that the presence of sterile castes in the nests of social insects might be *'fatal'* to his theory of evolution by natural selection. He overcame the problem by suggesting that selection in social insects takes place at the level of the colony, allowing sterile morphs to be expressed in each generation. When, in 1964, Hamilton expounded his concept of *inclusive fitness* it could for the first time be clearly argued that individuals might benefit by sacrificing personal fitness