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137. HIRUNDINIDAE

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DEFINITION AND GENERAL DESCRIPTION

The Hirundinidae (swallows and martins) is one of 11 families of the passerine superfamily Sylvioidea (Sibley and Ahlquist, 1990). The family (of some 15 genera and 75 species) is widespread and distinctive with all species being small birds adapted for aerial insectivory: their bills are short and flat with a wide gape and they have long pointed wings and streamlined bodies. Two genera, *Hirundo* and *Cheramoeca*, occur in Australia.

Several features separate hirundines from other birds (Turner and Rose, 1989): a syrinx which is distinctive in having more or less complete bronchial rings (half rings are found in other Oscine families and anomalously in the river martins, *Pseudochelidon*); short tarsi sharply ridged at the rear (unlike other passerines) and sometimes feathered; a slender body with a short neck; long pointed wings with 10 primaries, the tenth being much reduced (absent in *Pseudochelidon*); a short compressed bill with a wide gape; a broad palate and a broad tongue tapering to a short, bifid tip; loral feathers which are directed forwards; dorsal pteryla forked on the lower back (except in *Pseudochelidon*); feet weak and with the front toes more or less united at the base; toes rarely feathered, claws strong in cliff-dwelling and burrowing species; tail medium to very long with 12 feathers, forked in about half the species with the outermost feathers sometimes elongated to form streamers.

HISTORY OF DISCOVERY

Hirundines are familiar birds throughout the world, often nesting in close association with people. *Hirundo rustica*, which migrates to Australia, was known to the ancient Greeks and Romans and formally named by Linnaeus in 1758. It is surprising that no other Australian species was described until 1817 (*H. nigricans*), with the remaining three (*H. neoxena*, *H. ariel* and *Cheramoeca leucosterna*) not being described until the early 1840s. (The Welcome Swallow *H. neoxena* was confused with *H.* (*tahitica*) *javanica* up until this time).

MORPHOLOGY AND PHYSIOLOGY

Hirundines have basal metabolic rates about half that predicted for similar sized passerines and the lowest recorded for birds of equivalent body mass (Prinzinger and Siedle 1988a).

External Characteristics

Diagnostic external features have been described above. Hirundines are small birds of 10-24 cm in length and 10-60 gm in weight (Turner and Rose, 1989). Australian species are 11.5-17 cm in length, with wing lengths of 85-110 mm and weighing 12-17 gm. Bill length is 8-12 mm and is greater than the breadth except in *Cheramoeca*. The tail is square to deeply forked. Plumage is compact and typically glossy above with paler, often streaked, underparts. The sexes are alike or nearly so in most species.

Moult is post-nuptial and usually slow and protracted because of the need for the bird to fly efficiently at all times in order to feed, but the sequence of moult follows the typical passerine pattern. Migratory species suspend moult during migration. Not studied in Australian species. The longest primary in Australian species is 9; rarely 8 is as long as 9. *H. rustica* has about 1500 feathers (Ginn and Melville 1983).

Locomotion

The legs and feet are relatively weak, and they rarely walk or run. In contrast, flight is strong and agile; the Barn Swallow has been recorded flying at speeds of up to about 75 km/hr. Deeply forked tails in many species provide them with an increased ability to brake and turn, allowing them greater efficiency in catching flying insects. Species with deeply forked tails can fly more slowly and catch more mobile types of insects than can square-tailed species (Turner and Rose, 1989).

Hirundines expend 50-70% of the energy required by other birds of comparable size, even during flight. The relatively high aspect ratio, low wing loading and generally streamlined features presumably all contribute to this efficiency; these factors also favour gliding flight, which conserves energy. Swallows are the smallest birds to employ gliding flight (Hails 1979).

Vision

Because hirundines must be good judges of speed and distance, they possess bifoveal retinas, unlike many passerines, and have eyes relatively frontal in their orientation, allowing a degree of binocularity. Swallows also have a ribbon-like area connecting the temporal and central foveas; this is thought to be a specialized condition (Sillman 1973).

Feeding and Digestive System

All species are aerial feeders; rictal bristles are present, wide mouths open wide and loral feathers point forward. In Europe, species feeding on large prey have stouter bills (Turner and Rose 1989). When feeding young, species feeding on smaller insects (eg *Delichon*) may glue "meals" together into a ball with saliva. Salivary glands are small, and no crop glands are present (Marshall and Folley 1956). The intestinal walls are firm, thickened and muscular, but coils are extremely simple (Lowe 1938).

Hirundines select prey items mainly by size rather than species and hence take a very wide range of taxa. Prey preference is a function not only of size but involves interaction between prey size, ease of capture and local density (Hespenheide 1975).

Reproduction

Hirundine eggs consist of 20.9% calcium, 0.60% sulphur and 38% protein by total dry weight (Turner 1982). In *H. neoxena* and *H. ariel* the shell, yolk, water and lipid content is typical for Australian passerines (Lill and Fell 1990). Eggs of Australian species are white, usually slightly lustrous, unmarked to boldly marked with spots and small blotches, particularly toward and over the larger end. Eggs are oval in shape, for *H. neoxena* about 18 x 14 mm (slightly smaller in Tasmania and south-western Australia than in south-eastern Australia) and 1.8 g in weight (Park 1981b, Serventy and Whittell 1967, Tarburton 1993, Vestjens 1977) and for *H. ariel* 17.0

x 12.2 mm and 1.3 g (Tarburton 1991). Laying in hirundines is determinate (Davis 1955). Onset of laying is determined by the abundance, quality and stability of the food supply (Turner 1982). In *H. neoxena* and *H. ariel* eggs are laid early in the morning at daily intervals; incubation can commence before completion of the clutch in *H. ariel* but this apparently does not occur in *H. neoxena*.

H. rustica warms eggs to a mean maximum of 35.7^{o}C; eggs may drop in temperature to about 26^{o}C during inattentive periods. Longer periods are spent incubating during low ambient temperatures in both *H. rustica* and *R. riparia* (Turner 1982).

Clutch size is typically 2-3 in tropical species and 4-5 in temperate species; rarely up to eight eggs are laid (Turner and Rose 1989). Among Australian species, only *H. ariel* and *H. neoxena* have been studied in any detail (Marchant and Fullagar 1983, A. H. Burbidge unpubl., Park 1981b, Brown and Brown 1991, Tarburton 1991, 1993, Schrader 1976)). Australian species lay 2-6 eggs, usually August to December but sometimes July to February and occasionally as late as April. Breeding synchrony within colonies is high. Mean clutch size for *H. ariel* is 3.5; multiple clutches may be laid. In *H. neoxena*, mean clutch size is 4.0 in eastern Australia and 3.2 in south-western Australia. First clutches average slightly less than second clutches and very late clutches are slightly smaller than clutches in the middle of the season. In *H. neoxena*, second and replacement clutches are slightly larger and slightly more successful than first or subsequent clutches.

Incubation is by the female alone in *H. neoxena* but participation by the male is known for some social species and may occur in *H. ariel*. Incubation in *H. ariel* is about 14 days with a hatching success of about 93% and in *H. neoxena* about 16 days with 70-80% success.

Time and duration of breeding, the occurrence of multiple clutches and degree of nestling mortality vary from year to year, apparently depending ultimately on weather conditions, particularly rainfall, through its effect on food supply and availability.

Embryology and Development

H. ariel nestlings hatch with very little feather down. The pattern of the feather tracts and nestling development is described by Tarburton (1991). Nestlings hatch at about 1.5 g and fledging occurs at about 22.5 days. About 90% of hatchlings fledge. Overall breeding success is about 80% with 2.3 young fledged per breeding attempt.

H. neoxena young are born blind and almost naked and soon acquire pale-coloured down (Marchant and Fullagar 1983). Pin feathers appear about the sixth day and are well developed by the tenth; the young are well-feathered at about 15-16 days and most down has disappeared by 20 days. Young increase in weight from 1.0-1.8 g at hatching at a rate of about 1.6 g per day (Park 1981b, Tarburton 1993). Incubation bouts are about 8 min and female foraging bouts almost 4 min; at one nest with 3-4 day old chicks, the chicks were fed 430 times in one day (Tarburton 1993). Both parents feed the young, which fledge at about 20 days. Inclement weather was the major cause of failure.

In *H. neoxena* in south-western Australia, clutches of four are most successful (although clutches of three are more common). More than 90% of hatchlings fledge and overall breeding success is about 75% with 2.4 young fledged per nest (Brown and Brown 1991). Breeding success may be slightly higher in isolated nests than in nests with neighbours; the difference may be due to agonistic interactions. In eastern Australia, overall breeding success is 53-62% (Marchant and Fullagar 1983, Park 1981b, Tarburton 1993); about 74% of hatchlings fledge, with 2.0 young reared per nest.

European *Delichon urbica* chicks (Prinzinger and Siedle 1988a,b) reach adult weight by about the 10th day, attain peak weight (about 27% above adults) by 17-29 days (through laying down of fats), declining through fledging at about 30 days to reach adult weight at about 40 days. These chicks reach relatively stable body temperature at about 12 days, when plumage insulating ability is well developed. Normal nestlings at 11 days old are able to undergo torpor, whereas younger nestlings react like poikilotherms. Normally the young enter torpor only after a long phase of starvation (with a severe loss of body mass). During torpor, *Delichon* can reduce body temperature from 41^{o}C to a minimum of about 18-20^{o}C and metabolic rate may be lowered by at least 80-90%. Metabolism in young *Delichon* older than ten days is 50-100% higher than in adult birds under similar environmental conditions, presumably because of ontogenetic energy expenditure for anabolism.

Compared with other passerines, young hirundines fledge with a comparatively greater proportion of primary feather growth completed (94% in *D. urbica* compared with 75-80%; O'Connor 1977). Tarsus and bill growth is completed early; gape is increased to a maximum about the middle of the nestling period, followed by a slight but significant decline. (Presumably, there is differential growth to increase the gape area presented to the parent (thus allowing the nestling to ingest larger food items) until the need to develop the more adult bill shape (required for independent foraging) becomes predominant as fledging approaches). Development of body feathers is preceded by the acquisition of a thick layer of down providing effective insulation ahead of feather growth. Flight feathers begin development earlier than the insulating plumage feathers, in contrast to the typical passerine pattern, suggesting an emphasis on the achievement of flight capacity. Tail growth is also more advanced than in other passerines, allowing the aerodynamic stability necessary for the precise flight required for aerial insectivory. Other aspects of growth are similar to those for other passerines. Legs, wings and pectorals of nestlings grow relatively slowly, while the head and body case are relatively fast growing components. (The increase in bill length and gape width during the first half of the nestling period probably also serve to increase parental feeding efficiency). The gizzard, alimentary tract and liver are disproportionately large in the early nestling period and decrease relative to other components later.

Growth of the integument (skin plus all feathers) increases with age more rapidly and reaches higher levels than in other passerines. As in other passerines, water content of body components decreases between hatching and fledging. There is a steady increase in lean dry weight during the first two thirds of the nestling period, after which it levels off (unlike in other passerines), due to water content declining sharply after day 19. Most water loss is from the integument and the digestive organs. At fledging, *D. urbica* chicks possess 2-3 times as much fat (per gram lean dry weight) as other passerines. Swallows depend on a food supply readily affected by poor weather and their high fat levels are presumably needed as a buffer against intermittent food shortage; they would also be advantageous to fledgelings should a period of trial and error learning be necessary to become proficient at taking aerial prey (O'Connor 1977). The young spend 15-30 days in the nest and lose weight in the latter stages, fledging at 73-85% of peak weight, itself greater than adult weight, mainly brought about by desiccation of the integument.

NATURAL HISTORY

Life History

Hirundines are typically monogamous with both sexes sharing in nest building and feeding the young and, in some species, incubation and brooding (Turner and Rose 1989). Males are often promiscuous, however, and females sometimes lay in another bird's nest, as has been demonstrated for *H. ariel* (Manwell and Baker 1975). The pair bond varies from "mutual tolerance" to strong mutual attachment, depending on the species. Species nesting in Australia do so solitarily or in loose groups, except for *H. ariel* which is strongly colonial, with adjacent nests usually touching. Various benefits of coloniality have been suggested, but *H. ariel* colonies may act as a focus for predators (Tarburton 1991). A colony of *Cheramoeca* in a quarry contained about 80 birds and a loose colony of *H. neoxena* under a jetty contained up to 25 nests (Blakers *et al*. 1984).

Hirundines are commonly gregarious when feeding, breeding, migrating: gatherings in excess of a million birds have been reported away from breeding areas. In Australia, *H. neoxena* has been reported in 1000s and *H. nigricans* in 10s of 1000s. *Cheramoeca* roosts communally, with up to 27 birds having been found in a single burrow at one time (Waterman and Llewellyn 1968). Solitary breeders may share feeding areas.

Overseas, *H. rustica* has been recorded living for up to 16.0 years (Turner and Rose 1989); the Australian *H. neoxena* to about 10 years. Data are lacking for Australian species but it is believed that breeding can occur in the first year.

Ecology

Swallows and martins typically occur in open habitats. Mud nesters are often associated with water, at least during breeding. *H. neoxena* and possibly *H. ariel* have benefited considerably from the provision by Europeans of water points and artificial nesting sites.

Many northern temperate zone hirundines undertake regular migrations to and from wintering and breeding areas, while tropical species tend to be sedentary or exhibit only local movements. Amongst the Australian species, *Cheramoeca* exhibits no large scale seasonal movements while some populations of *H. neoxena*, *H. ariel* and *H. nigricans* are partial migrants and *H. rustica* is a regular non-breeding migrant to northern Australia from northern Asia (Blakers *et al*., 1984). Migrants show little fat build-up prior to departure, presumably because diurnal movements allow for periodic feeding. *H. neoxena* and *H. ariel* may be sedentary in southwestern Australia (Blakers *et al*. 1984, Brown and Brown 1991).

Known predators of *H. neoxena* and *H. ariel* include *Falco cenchroides*, *F. peregrinus*, *Cracticus torquatus*, *Gymnorhina tibicen*, pythons (*Morelia* sp.), the introduced black rat (*Rattus rattus*) and domestic cats (*Felis catus*) (Carter in Mathews 1920, Barker and Vestjens 1989, Park 1981b, Ambrose and Congreve 1985). *Passer domesticus* has been reported removing eggs of *H. neoxena* (Park 1981b) and humans sometimes destroy nests around buildings.

H. ariel is subject to competition for its nest from House Sparrows, pardalotes and Zebra Finches and to nest predation by kingfishers and nests disused by martins are sometimes used by a number of other small birds and bats (Hyett 1980) but the degree of competition is unknown; Budgerigars have been known to use holes previously used by *H. nigricans* (Schrader 1975).

Food consists almost entirely of insects caught in flight, with winged Diptera, Hymenoptera, Hemiptera, and Coleoptera featuring prominently in the diet, but Trichoptera and wind-drifted spiders (Araneae) are also taken (Barker and Vestjens 1990, Park 1981b). A few extra-Australian species supplement their diet with seeds and berries in times of low insect abundance (Turner and Rose, 1989), and some species will take grit and occasionally food from the ground. Specialists on small prey items tend to feed higher, less vigorously and further from the nest. Amongst European species at least, those with stouter bills take larger insect prey. Colonial breeders often form feeding flocks, but even solitary breeders will feed communally outside the breeding season. *H. neoxena* has been recorded foraging 10 km and more off-shore (Amiet 1964, Latham 1981).

Ectoparasites of swallows include ticks and mites (Acarina), chewing lice (Phthiraptera Mallophagans), bugs (Hemiptera: Cimicidae), fleas (Siphonaptera) and flies (Diptera: Hippoboscidae, Calliphoridae) (Campbell and Lack 1985, Kaczmarek 1988, McLure 1967, Vestjens 1977, Allen and Nice 1952).

Infection levels of the parasitic haematophagous tropical fowl mite (*Ornithonyssus bursa*, Macronyssidae, Gamasida) have a direct effect on fitness of adult *H. rustica* (Moller 1990). McLure (1968) in 315 blood smears of hirundines of 6 species found 2.2% positive, all *H. rustica*, for internal parasites (haematozoa, microfilaria or trypanosomes).

Behaviour

Nests are of three types (Mayr and Bond 1943):
1) natural holes eg in trees or caves (thought to be primitive, generally solitary species),
2) excavated burrows eg *Cheramoeca*,
3) mud nests, ranging from a simple cup (*H. neoxena*) to an enclosed chamber with entrance passage (*H. ariel*) (thought to be specialized species, usually more or less colonial).

Swallows in groups 1) and 2) lay white eggs, but while some species in group 3) lay white eggs, others lay spotted eggs (Turner and Rose 1989). *Cheramoeca* has white eggs while *ariel*, *nigricans* and especially *neoxena* have spotted eggs (Beruldsen 1980).

In *H. neoxena* nest building (by both sexes) takes 6-29 days, with most nests being rebuilt on existing ones from previous years; *H. ariel* takes about 30 days but it is not known whether both sexes build. Nest construction varies from none in *nigricans* which simply nests in a tree hollow (sometimes narrowed at the entrance with a little mud), sometimes in a building or a bridge (Blakers *et al*. 1984) while *ariel* makes a bottle-shaped nest of mud and clay lined with feathers and fine grasses - one bird stays inside constructing while five or six others bring mud in their bills (Gould 1865). *H. ariel* nests under culverts and bridges, in or on other man-made structures, on cliffs or large rocks, creek banks, and under overhanging branches (Tarburton 1991). *Cheramoeca* constructs a nest of dried leaves of grasses and twigs at the end of a metre long burrow in the side of a bank (Gould 1865, Hindwood 1941). Compared with other Australian species, *Cheramoeca* has relatively long claws and tarsus, and tarsus relatively stout, presumably as adaptations for burrowing. *H. neoxena* constructs the familiar mud nest bound with grass or straw, lined with fine grass and feathers, on a more or less vertical surface on a cliff, in a burnt out tree or, more commonly, in or under man-made structures, especially buildings, bridges and jetties (Marchant and Fullagar 1983). Occasionally, in the absence of mud or vertical surfaces, nests may be made of seaweed on a horizontal surface (Ambrose and Congreve 1985).

Partners generally stay paired from year to year (Park 1981a). Males advertise by singing from the nest site. Pairing and courtship displays are brief and courtship feeding is rare in the Hirundinidae (Turner and Rose 1989). Courting male *H. neoxena* descend on stiffly downheld quivering wings (Pizzey 1980). Copulation has been observed in *H. neoxena* near the nest, in *H. ariel* in a nest and in *H. nigricans* on the wing (Park 1981b, Hastwell 1985, Tarburton 1991, 1993). Male *H. neoxena* guard their mate during incubation and both sexes guard the young (Tarburton 1993).

Adults of *H. neoxena* remove faecal sacs from the young for about the first week, but thereafter the sacs pile up under the nest (Park 1981b).

Some swallows (apparently including *Cheramoeca* (Congreve 1972)) are capable of going into torpor in times of low food availability (and hence low body weight). The ability to go into true torpor is rare in birds, particularly in passerines.

Newly fledged *H. neoxena* return to roost in or near the nest for up to several weeks after fledging. In *H. ariel* the territory comprises the nest interior, exit hole and approach route alone. *H. neoxena* defends the nest site and several metres of nearby airspace (Brown and Brown 1991, Park 1981b).

H. neoxena occasionally engage in dusting behaviour and, more commonly, sunning themselves by exposing their sides to the sun, with the wing on the sun side spread and elevated (Park 1981b, Klapste and Klapste 1985). *H. nigricans*, *H. ariel* and *H. rustica* have been reported bathing (Slater 1961).

Voice

Song in Australian species is an attractive or animated twittering, uttered in flight or from a perch or nest. Alarm calls and contact calls are brief twittering, "churring" or high pitched sounds.

Economic Significance

The positive economic significance of hirundines (not quantified) lies in their harvesting of small flying insects (including aphids, flies, midges and mosquitoes) for food. In a few species, some negative effects may occur as a result of nesting and roosting in buildings and defecating therein.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Hirundines are almost cosmopolitan (they are absent from the high Arctic and Antarctica). They may have originated in Africa, where 50% of species breed (and 39% breed only there). On the other hand, almost all species nesting in natural cavities occur in the Americas and almost all African species nest in burrows or construct mud nests, thought to be a derived condition.

Affinities with other Groups

The Hirundinidae is a well defined group (in terms of osteology, morphology, and DNA sequences) but there has been little consensus concerning their relationships. Their closest relatives appear to be the Northern Hemisphere Regulidae (kinglets) and Aegithalidae (long-tailed tits and bush-tits) of the Sylvioidea (Sibley and Ahlquist 1990).

Affinities within the Family

There are two subfamilies: Pseudochelidoninae (2 species) and Hirundininae (about 73 species, including all Australian species). The leg myology of the Pseudochelidoninae is intermediate between that of Hirundininae and that of other passerines; variation in swallows is negligible below the level of sub-family (Gaunt 1969).

All except one Australian species are perhaps best placed in Hirundo, the largest, most specialized and recent genus in the family. *Cheramoeca* is a monotypic genus of uncertain affinity, probably relictual, and usually considered to be unspecialized relative to other Australian species on the basis of nest construction.

Intergeneric hybridization (*Hirundo* x *Delichon*) is sufficiently frequent to emphasize the taxonomic uniformity of the family. Not surprisingly, there is little agreement concerning generic limits.

Fossil record

Hirundine material has been identified from Quaternary-aged deposits in Australia, but identification past that of family is unreliable (Baird 1985). The earliest Australian record is from the Quaternary, about 30 000 - 40 000 years BP (Rich and Baird 1986). Brodkorb (1978) lists only one pre-Quaternary (Upper Pliocene) hirundine fossil but a fair amount of Quaternary material is known.

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Illus: tarsus and foot of *Hirundo* and *Cheramoeca*.
ariel at nest