

Order FALCONIFORMES

Small to very large diurnal birds of prey. The terms 'diurnal birds of prey' and 'raptor' are used broadly to cover the convergent group of predatory and sometimes scavenging birds, much as 'seabirds' is used for the convergent assemblage of many sorts of marine birds, but not all are diurnal. About 280 species in 70 genera. Three families: Accipitridae, Sagittariidae and Falconidae. Monotypic Sagittariidae (Secretarybird *Sagittarius serpentarius*) extralimital in sub-Saharan Africa (Ethiopian region); other two cosmopolitan, except Antarctica, and represented in HANZAB region by 25 breeding species and one confirmed accidental (24 breeding and one accidental in Aust.; two breeding species and one non-breeding visitor in NZ). Traditionally (e.g. Amadon & Bull 1988; Peters) all diurnal birds of prey have been placed in a single order of four families (three above plus American Vultures Cathartidae). However, general uncertainty about the relationships of the higher taxa and recent studies of DNA-hybridization (Sibley *et al.* 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990) have led to the removal of the Cathartidae either into a separate order (Cathartiformes) or into a sub-family of the storks Ciconiidae, to which they are most closely related. Other arrangements of the higher taxa have been to put the Accipitridae into one order, with or without the genus *Pandion*, and the Falconidae into another or to put *Pandion* into its own monotypic family (BWP). Here we treat the Accipitridae, including *Pandion*, and the Falconidae as the two families of one Order. The Order may be of Gondwanan origin (Kemp & Crowe 1990).

As a whole, diurnal birds of prey have rather drab plumage in shades of brown, rufous, grey, white and black; patterns on underwings are sometimes important for identifying birds in flight. Field identification often depends more on general characters or jizz (structure, proportions, attitudes of wings in flight, and actions in flight) than on characteristics of plumage. These general characters are hard to describe succinctly and space does not allow us to discuss them exhaustively. Experience in the field with careful instruction from knowledgeable observers is really the only way to acquire skill in identification. However, Porter *et al.* (1986), though dealing specifically with European raptors, give useful information on fundamental differences between the various groups into which Accipitridae and Falconidae are divided.

Silhouettes and attitudes in flight being so important for identification, we have modified the section on Field Identification by adding a section on flight, in which these matters are described. It is as well to define standard terms for the sorts of flight that these birds use. Emarginations of inner and outer webs of primaries, leaves gaps between the feathers and gives a slotted or fingered appearance to wings; obvious and prominent in many Accipitridae, less so in Falconidae. **Gliding**: coasting forward on stiff wings without or between wing-beats; wings flexed according to angle of descent. **Soaring**: maintenance of height above ground or rising and circling up on stiff, fully spread wings and tail. **Hovering**: active flapping into wind to maintain position in relation to the ground. **Poising** (wind-hanging or kiting): facing into wind to maintain position but without flapping. **Stooping**: steep or shallow dive with wings folded close to the body; sometimes at great speed. The term **dihedral** (having two plane faces) describes the V-shaped attitude of the wings when raised above the plane of the body; qualified by **strong**, **medium** and **slight** to denote the degree to which the wings are raised to form a smaller or larger angle between their planes ($>15^\circ$, $5-15^\circ$, $0-5^\circ$ respectively); **modified dihedral** is when the innerwings are raised above the plane of the body but outerwing flat for the most part.

Members of the Order readily recognized by hooked, sharply pointed beaks with waxy membrane or cere at base through which nostrils open, strong powerful feet and sharp curved claws, otherwise found only in owls (Strigiformes), which resemble this order only by convergence. Palate imperfectly desmognathous with palatine processes of maxillae separated for much of their length and so grading into schizognathous type as found in some forms. Basipterygoid processes, absent in all except *Sagittarius*. Generally 14 cervical vertebrae but 15 in Falconidae and *Pandion*, 17 in some vultures (*Gyps*). Often no paired foramina or notches on sternum or else only one of pair. Holorhinal, nares impervious. Two carotids. Caeca, reduced except in *Pandion*. Crop, nearly always well developed; gizzard, poorly developed; fur, feathers, scales, insect chitin and many bones remain in crop and are later regurgitated as a compact pellet. Highly acid stomach for digesting all but chitinous or keratinous parts of prey. Syrinx, tracheo-bronchial. Ambians muscle present. Muscle formula, typically A (BXY in *Sagittarius*). No biceps slip; expensor secundariorum only in *Falco* and a few others. Ten functional primaries, eleventh vestigial or lacking; 11-25 secondaries; diastataxic. Tail with 12-14 rectrices. Feathers with aftershaft, except *Pandion*. Underdown present in varying amount; patches of powder-down in *Elanus*, *Circus*, *Gypaetus* and some others. Oil-gland, well developed, feathered except in *Microhierax*. Eyes, large with high density of cones in retina, giving high resolution; wide field of binocular vision. Hearing, acute. Sense of smell, poor; do not detect prey or carrion by smell, even in Old World vultures (cf. New World vultures [Cathartidae]).

Male nearly always smaller than, or same size as, female; thus different from most other birds; dimorphism greatest in bird-catching *Accipiter* and *Falco*. This reversed sexual dimorphism in size discussed by Reynolds (1972), Amadon (1975), Mendelsohn (1986a,b), Olsen & Olsen (1987), Pleasants & Pleasants (1988, 1989), Montgomerie & Lundberg (1989), J. Olsen (1989, 1990), P. Olsen (1991), Ydenberg & Forbes (1991) and Brown & Amadon¹ and others. Habits normally diurnal but sometimes crepuscular; a few nocturnal (e.g. Letter-winged Kite *Elanus scriptus*). Comfort behaviour includes bathing in water and dust; most adopt a characteristic posture for drying and sunning.

Raptors occur in all land faunas and a variety of climatic zones and habitats. Communities of raptors richest in Tropics and Subtropics and poorest in high latitudes. Patterns of movements vary: resident, migratory or dispersive; juveniles dispersive. In A'asia, small and medium-sized species breeding at high latitudes or altitudes or feeding on seasonally fluctuating prey tend to undertake seasonal movements, which are often towards coast, north (some to New Guinea) or to lower latitudes (Baker-Gabb & Fitzherbert 1989).

In A'asia, local threats to populations include illegal shooting, trapping and poisoning for supposed or real damage to livestock or poultry, or simply because they kill other birds. Egg-collecting, while illegal, is also a threat to some species. Some species have been or are used in falconry, an illegal activity in Aust. Secondary poisoning from pesticides is still a problem. Deforestation and other habitat degradation are the major threats. In consequence, some species are probably declining. Three endemic species are threatened: Square-tailed Kite *Lophoictinia isura*, Red Goshawk *Erythrotriorchis radiatus* and Grey Falcon *Falco hypoleucos* (Brouwer & Garnett 1990).

Further information on behaviour and biology of raptors in Newton (1979), Newton *et al.* (1990) and BWP.

(1) Because this reference and two others are so often used throughout the species accounts for the birds of prey, they are given in the texts without date and not listed in the references; they are Brown & Amadon (1968), Cupper & Cupper (1981) and Hollands (1984). For full details of these references, see the Introduction under Simplified References.

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Family FALCONIDAE falcons

Small to medium-sized diurnal birds of prey; about 60 species in ten genera. Four subdivisions or sub-families recognized: (1) about nine species of caracaras (Polyborinae), extralimital in the Americas; (2) monotypic *Herpetotherinae*, extralimital in Neotropics; (3) forest falcons (Micrasturinae), five species extralimital, also in Neotropics; (4) falconets, pygmy falcons and typical falcons (Falconinae), 44 species in four genera, widespread in all continents except Antarctica. Seven of c. 37 species of *Falco* (Falconinae) breeding in HANZAB region, of which one endemic in NZ. These divisions would be treated as full families if whole assemblage treated as separate Order from other Falconiformes. Here we need to consider only Falconinae, and of that sub-family only the genus *Falco*, which has been analysed by Cade (1982), and tentatively revised by Olsen *et al.* (1989) on the basis of study of feather-proteins. Further discussion in Amadon & Bull (1988), Sibley *et al.* (1988), Kemp & Crowe (1990) and Sibley & Monroe (1990).

Falco has been divided informally (Olsen *et al.* 1989) into adaptive groups: (i) typical kestrels; (ii) desert falcons and gyrfalcons; (iii) merlins; (iv) peregrines; (v) aberrant kestrels; (vi) typical hobbies and similar species. In HANZAB region, *longipennis* (Australian Hobby), *subniger* (Black Falcon), *hypoleucos* (Grey Falcon), *berigora* (Brown Falcon), and *novaeseelandiae* (New Zealand Falcon) thought to belong to the hobbies. Merlins and desert falcons not represented. Strongly resemble other families of Falconiformes, having sharp talons and hooked bills; very acute sight; powerful flight; furcula free of sternum; similar moult of secondaries; and some common feather-lice. Differ in some important details of skull; in having bony tubercle in nostrils surrounded by almost completely ossified nasal bones; in details of sternum; in moult of primaries; in chemical and other characters of egg-shell; in chemical composition of feathers; in extra bones at base of pygostyle for insertion of powerful muscles; and in having projections, or tomial teeth, on upper cutting edges of upper mandible on either side correspond with notches on lower mandible. Usually, droppings let fall, not squirted out as in Accipitridae (Kemp & Crowe 1990; Newton *et al.* 1990). Some (e.g. Starck & Barnikol 1954; Starck 1959; Sibley *et al.* 1988) have considered that the Family is related to owls Strigiformes but now generally considered close to Accipitridae (Sibley *et al.* 1988; Sibley & Monroe 1990).

Falcons have strong rigid bodies, thoracic vertebrae being ankylosed, not free as in other Falconiformes; necks, short; wings, long and pointed in contrast to short and rounded in *Accipiter*. Ten functional primaries, p1 minute; 11 secondaries; diastataxic. Wing-beats strong; hunting action characterized by diving or stooping at prey but species such as kestrels hover and drop on prey, and hobbies and merlins tail-chase. Tails, narrow, of medium length; 12 rectrices. Bills, short, strongly hooked with single tomial teeth; in some, if prey not killed by strike, killed by bite to neck. Short fleshy tongue. Cere found in all groups. Nostrils, typically rounded, opening in cere. Syrinx, large with tympaniform membrane. Lores, feathered; many species have dark malar stripe. Orbital skin bare. No marked brow-ridge. Tarsi, fairly long in most; usually reticulate (except Brown Falcon); toes, powerful with long claws; strike down prey with open feet. Stand erect or diagonally when perched or settled; can walk and even run surprisingly fast. Oil-gland, feathered. Feathers with aftershaft. Thin-walled, large, distensible ventriculus of stomach. Caeca minute. Eyes, usually brown; large with acute vision.

Plumages vary considerably; generally rather drab in greys, black and rufous; some species have colour morphs. Often various shades of grey above and rufous below; black moustachial stripe characteristic of many species; kestrels typically rufous above. Sexes alike except in size. Iris dark as are bills and claws. Cere, eye-ring and legs usually brightly coloured. Complete annual moult. Moult of primaries inwards and outwards from p4; similarly, of secondaries from s5 (centrifugal). Young semi-altricial, nidicolous; hatched with eyes closed and ears open; down, white; first down soon overgrown by dense second down. Juveniles often darker and streaked, with dull bare parts; usually acquire adult plumage after moult at end of first year.

Distributed almost world-wide and adapted to nearly every zone of latitude and climate in a great many habitats; some individuals range far in aerial search and pursuit of prey. Species vary greatly from fully migratory to resident or even sedentary, but in Aust. and NZ apparently mostly non-migratory, or dispersive or nomadic, perhaps moving to some extent according to climatic condition, though some species apparently undertake regular migrations (e.g. Australian Kestrel to PNG). Migrations, diurnal, typically with flapping flight, when rarely gregarious and rarely soaring. Generally suffer from persecution and other human pressures such as degradation of habitat, persistent pesticides, collection of eggs and young for falconry and direct slaughter but Aust. species may be less affected than those in Europe and Middle East.

Highly predatory; seldom eat carrion. Large falcons specialized to take large birds such as pigeons, ducks and grouse, typically attacking by stooping at great speed and striking down prey with feet, usually at no great height and even taking prey that is much larger than themselves on the ground; thus much exploited by falconers. Hobbies specialize on chasing smaller birds and insects, often high above ground or at level of canopy in Aust.; Brown Falcon takes insects and ground-dwelling and aerial prey (and even carrion). Merlins hunt at lower levels and persist in chasing small birds like larks and pipits till they catch them or become tired out. Kestrels (and Brown Falcon) typically adapted to take insects, small rodents and reptiles on the ground by hovering and dropping on them. Most species hunt solitarily but many species may

congregate at swarms of insects and fires. Aerial hunters may eat prey on wing; larger species usually take prey to perch or plucking station where typically kill victim with bill if not already dead, pluck or skin it and then break it up. Indigestible matter regurgitated as pellets. Food may be cached.

Generally, displays consist of aerobatics and ritualized attack and defence with stereotyped postures on perches or nest (cf. Accipitridae) (see BWP; Cade 1982). Usually solitary outside breeding season, frequenting home-range or exclusive feeding territory. Roost at night alone or loosely as a pair; some insectivorous species (kestrels particularly) may form loose communal roosts near swarms of locusts or termites. For the most part also breed solitarily but some, e.g. kestrels, form loose colonies. Pair-bond normally monogamous, probably usually long-term; bigamy by males occasionally reported but no regular polyandry or polygyny. Nesting territories advertised by aerial displays and calling. Flight-play often spectacular with high-circling, talon-grappling and cartwheeling; high-speed chasing with complicated manoeuvres occurs. Nest-sites shown by males to females by ledge-displays accompanied by calling and even scraping out depressions to form potential nests, and by ritualized inspection of holes. Courtship feeding starts well before laying; male provides food for female, often using spectacular aerial food-passing. Males generally continue to bring food to female and young until young well feathered; typically, females become active in defending eyrie and in hunting when young no longer need brooding. Copulation occurs well before it is necessary, to fertilize the eggs and far more often than is necessary so is part of courtship; accompanied by special calls and displays. Frequent copulation probably a behaviour to avoid cuckoldry. Contact behaviour includes billing and allopreening but more usually avoid close contact. Nest-relief without ceremony, male simply replacing female if she leaves nest for feeding, loafing or preening. Voice unspecialized and usually consists of monosyllabic *keks* or *kiks* in series, chattering, chittering, trilling or cackling; shrill, piercing, loud, harsh; may differ in pitch between sexes. Loaf with head drawn in to shoulders, typically standing on one foot with other drawn up into feathers; may doze or sleep with bill under scapulars in middle back. Clean feet with bill after feeding and wipe bill on perch. Some bathe in shallow water, perhaps daily; sometimes dry themselves with wings partly spread; drink even when cold. Dusting widespread in Family. Sunbathing with fully spread wings occurs in hobbies; shield young from sun or rain by mantling over them. Comfort behaviour may be performed in flight as in Accipitridae. For fuller information on behaviour see Cade (1960, 1982), Glutz *et al.* (1971), Village (1990), BWP.

Timing of breeding season varies, perhaps with latitude. Nest-sites on ledges and in holes on cliffs, even on buildings, in holes and hollows in trees, in old stick-nests of other species and sometimes on ground. In spite of claims to contrary, no true building by any species, though hollows may be scraped out with feet and small pieces of material added or removed, e.g. sprays of leaves, bits of bark. Eggs, broad or rounded ovals; mat; white or whitish ground-colour, intensely or entirely blotched with reds and browns. No vacuoles in outer layer of egg-shell; inside of egg-shell, ochre. Usual clutch-size: 2–3 in hobbies; 3–6 in kestrels and other small falcons; 3–5 in large species. Annual variations at times of plagues of rodents less marked than in some accipitrids. Laying interval usually 2 days in all species but 3 days has been recorded for all species, including kestrels. Typically females show period of lethargy before laying. Single-brooded but losses of eggs replaced in 11–16 days (Newton 1977). Incubation mostly or entirely by female. Period: 25–31 days in kestrels; 28–35 days in merlins and hobbies; 32–35 in large falcons. Usually starts with second egg. Egg-shells often eaten by females (P.D. Olsen) (cf. Accipitridae). Parental duties divided much as in predatory Accipitridae; male may feed young bill to bill but often only in absence of female; can rear young alone if mate lost soon after hatching. Nestling period: 25–32 days in most small and medium-sized species; 35–49 days in large. No siblicide in nest. Depend on parents after fledging for 1–3 weeks in kestrel-like species; 2–3 weeks in hobbies; 4–6 weeks in larger falcons. Age of first breeding usually 2 years or older; earlier in small species.

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Falco novaeseelandiae New Zealand Falcon

COLOUR PLATE FACING PAGE 304

Falco novae-Seelandiae Gmelin, 1788, *Syst. Nat. ed* 13, 1, p. 268; based on 'New-Zealand Falcon' of Latham, 1781, *Gen. Synop. Birds*, 1, p. 57, pl. 38 — Queen Charlotte Sound, New Zealand.

OTHER ENGLISH NAMES New Zealand, Bush or Quail Hawk and in error Sparrowhawk.

MONOTYPIC

FIELD IDENTIFICATION Length 40–50 cm; wingspan male c. 60 cm, female c. 80 cm; weight: male 240–350 g, female 410–640 g. Medium-sized falcon, about one-third larger and more robust than Australian Kestrel *Falco cenchroides*; about one-third smaller than Swamp Harrier *Circus approximans*. Slender-bodied with narrow well-protruding head and neck in flight, and rather long tail, gently rounded at tip; wings, shorter, much broader and more rounded at tips than other falcons. Flight silhouette resembles more an accipiter than any falcon in HANZAB region. When perched, wing-tips reach half-way to tail-tip, again recalling an accipiter. Three forms: Bush, Eastern and Southern, which differ in size, plumage, habitat and range. Birds from NI and nw. SI (Bush form) smaller than birds from open areas over most of SI (Eastern form); birds from extreme sw. SI, Stewart and Auckland

Is intermediate in size. Sexes differ; female larger than male. No seasonal variation. Juvenile separable.

Flight Wings held flat when **soaring** and **gliding** (Fig. 1). Flight silhouette, especially when soaring, more like *Accipiter* than *Falco*. When **soaring**, wings held straight out from body, carpals pressed slightly forward and primaries directed slightly back (giving gently angled leading-edge); trailing-edge curved forward; primaries well spread, giving well-rounded, slightly fingered wing-tip; narrow head and neck protrudes well in front of



Fig. 1 Soaring and gliding

wings, and long tail held partly spread, appearing rounded at tip. When **gliding**, carpals pressed well forward and closed primaries directed back, tapering to rather blunt wing-tip for a falcon; folded tail appears long, gently rounded at tip. Flight typical of genus, with bursts of rapid powerful wing-beats between glides. Soar and sometimes hang on wind; make fast slanting dives at prey.

Description All forms: **Adult male** Cap and ear-coverts, uniform bluish-black with thin buff supercilium; prominent black moustachial stripe set off by whitish chin and throat and buff patch on lower cheeks. Upperparts, bluish black, with varying narrow dull-rufous, grey or white bars on saddle and wing-coverts, and narrow rufous barring on rump and upper tail-coverts. Remiges and secondaries, black, with faint narrow grey bars; bold white barring on inner webs of primaries; normally concealed from above but partly visible when primaries well spread, showing as rows of white spots on outer primaries. Tail, black, narrowly tipped buff when fresh and with 7–10 narrow broken white bands, usually evenly spaced. Underbody varies: palest birds, mostly white or creamy, with rufous-brown wash across foreneck and breast, fine dark streaking on throat, bold black streaking on foreneck, breast and upper belly, and bold black barring on flanks; lower belly finely streaked rufous-brown; thighs, vent and under tail-coverts, rich rufous-brown, finely streaked and more broadly barred with black. Darkest birds similar, except foreneck to upper belly, washed rufous-brown. Undertail, black with 7–10 narrow white bands. Underwing: lesser and median coverts, dull rufous-brown, densely spotted white; remiges and greater coverts, black with bold narrow white barring; tips of outer primaries unbarred, forming solid black wing-tip; white barring can be strongly translucent when backlit. Bill, black, blue-grey at base. Cere, orbital ring, legs and feet, deep lemon-yellow, richer during breeding season. Iris, dark brown. **Adult female** Similar to male but duller, less blue on head; some lack pale barring on upperparts, and underparts often darker (more heavily marked). Cere, orbital ring, legs and feet, pale yellow. **Juvenile** Sexes similar; plumage varies considerably, especially below. Similar to adult but upperparts appear uniform and underparts darker, browner and less heavily streaked and with no barring on flanks. Head-pattern as adult; upperparts uniform black with bluish bloom initially, fading to dark brown; some, especially males, have pale barring similar to adult and rufous spots on nape. From none to ten pale bars on upper side of tail, fainter than on adult and usually not on distal third. Underparts vary; on palest, chin and throat, white with fine dark streaking on throat; foreneck, breast and upper belly, creamy or white, densely streaked blackish brown (streaks more diffuse than on adult); flanks solid dark brown to blackish brown, sparsely spotted with white or dull rufous-brown; lower belly, creamy or white, finely streaked dark brown; thighs, vent and under tail-coverts, dull rufous-brown, finely streaked dark brown. Darkest birds similar, but foreneck, breast and upper belly, uniform dark reddish-brown with scattered rufous-brown, creamy or white spots. Underside of tail, black, with faint pale barring as above. Underwing as adult but with paler buff leading-edge. Bill and iris, as adult. Cere, orbital ring, legs and feet, dull blue-grey, becoming olive-green then yellow with greenish tinge by middle of first winter.

Similar species Unlikely to be confused with other raptors in NZ. **Swamp Harrier** about one-third larger and paler, with much longer, more rounded wings, longer legs and lazier slower flight on wings held in shallow V; has conspicuous pale patch on upper tail-coverts. **Australian Kestrel** (irregular visitor to NZ) is smaller, with much narrower, more pointed wings, persistent hovering flight; much paler (whitish) below and chestnut above,

with contrasting black outerwing, conspicuous black subterminal tail-band visible from above and below.

Usually solitary falcon of forested areas and rough open high country; often seen in pairs before breeding. Combines hunting methods of typical falcon with those of accipiter. When hunting, fly rapidly low over ground, weave between trees, pursue prey into cover; also hawk for insects. Most common call, rapid piercing chatter, sometimes with squeaky quality; also whining, chattering, squealing and chipping calls.

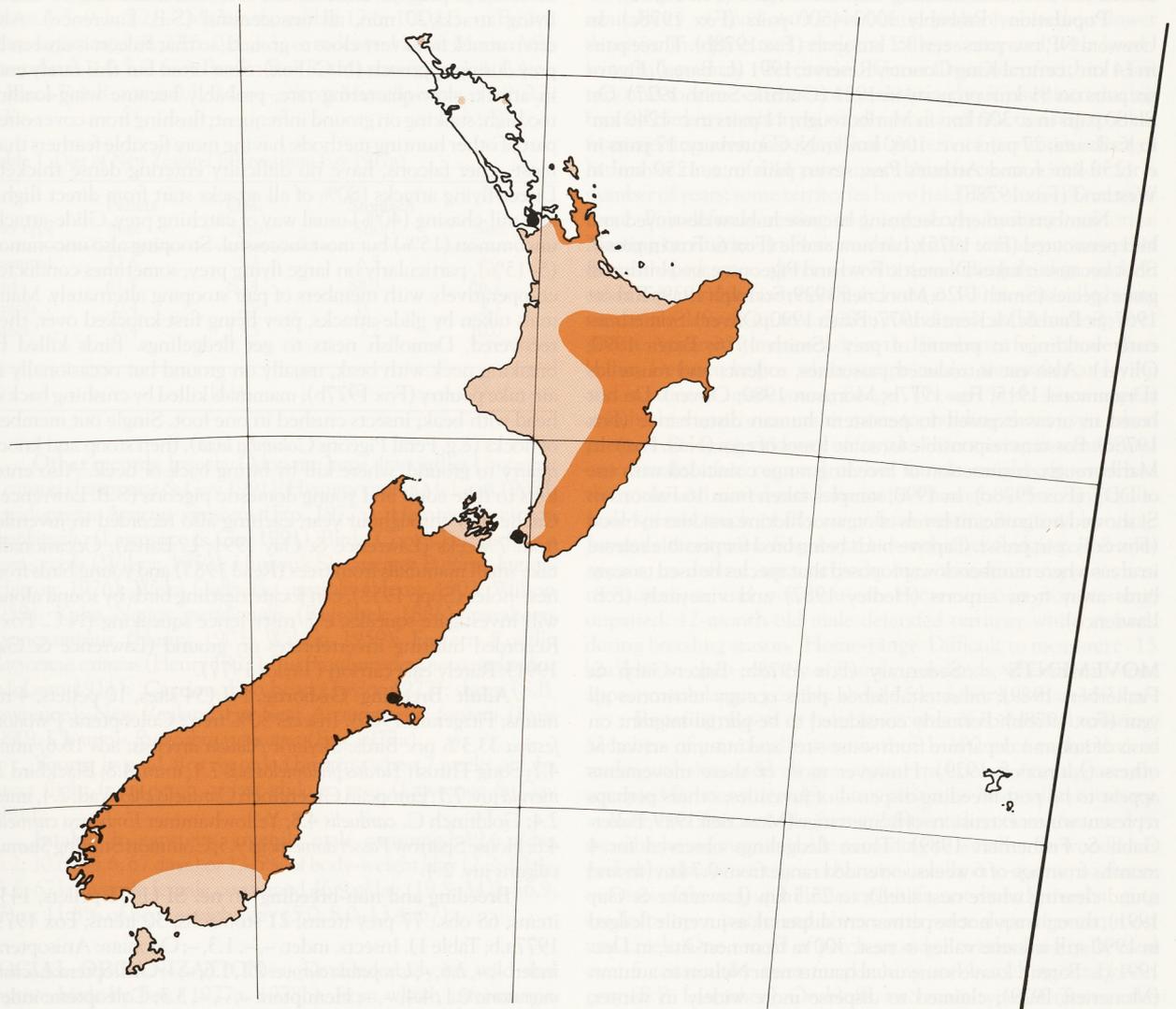
HABITAT Over open country and wooded lands of NZ and subantarctic islands. Particularly inland in main mountain ranges and some isolated ranges; recorded to 2100 m asl (Soper & Jardine 1957; Child 1975). Typically in mosaic of open country, where most hunting occurs, and forest, used for perching, roosting and nesting; particularly pastoral land, subalpine tussock grassland (*Poa*, *Festuca*, *Danthonia*) or herbfield with beech forest, podocarp-hardwood or tawa *Beilschmiedia tawa* forest, or tall shrubland; also in large forested areas, but at lower density. Hunt in more open parts of range, where prey accessible; occasionally in forest, particularly at edges or where emergent trees or clearings break canopy (Fitzgerald 1965; Harrow 1965; Challies 1966; Powell 1972; Child 1975; Gill 1976; Fox 1978b; Hedley & Hedley 1982a; Lawrence & Gay 1991). Sometimes hunt over wetlands, and, where hunting range includes ocean shores, take seabirds and carrion (Taylor 1977); often hunt in river valleys (Fox 1977a; S.B. Lawrence). Transient, probably mainly immatures, in settled and urban areas, cultivated land and snow-covered ground. Falcons visiting small offshore islands probably derived from breeding population on mainland (Fox 1978c).

Breed in hills and ranges, to at least 1500 m asl (Fox 1978c). Nest where small birds abundant, usually in sites offering unobstructed view, easy access, protection from weather and freedom from disturbance, though one record of successful nesting in 2 consecutive years c. 150 m from road and 200 m from house (L. Barea); in trees in forested part of home-range, on ledges of cliffs, or ground on steep broken hillsides. Nests near but not directly over water; sea-cliffs not used (Powell 1972; Fox 1977a). Search for prey on wing or from perch. Perches include rocks, trees, shrubs, telegraph poles, fence posts; sometimes within tree-canopy. Hunting flight high or low; contour-hunt at low level over ground or canopy, at times below tree-tops; soar, usually at heights of 50–200 m, sometimes up to 1000 m. Agile on ground, stalking prey among grass and shrubs.

Clearing may have reduced breeding range, but density higher in partly cleared areas, even where original forest makes up only 5% of area, than in continuous forest. Partial clearing, low-intensity logging and road-making provide open country and edges favoured for hunting. Selective logging of mature podocarps and tawa may have reduced potential nesting sites (L. Barea). Intense pastoral use of land not detrimental when affecting hunting habitat, but may have adverse effect when occurs in breeding habitat (S.B. Lawrence). Few birds in cultivated and settled areas. Not known if birds occupied lowlands before European settlement, but certainly now unsuitable because settlement intense. Monocultures of exotic pines not used, especially mature stands with even canopy (Fox 1977a, 1978b,c). Rarely nest on artificial structures; nest under stack of fence posts unsuccessful (Young 1959).

DISTRIBUTION AND POPULATION Endemic to NZ. Mainly in ranges from e. Taranaki to East Coast on NI; widespread SI.

NI Rare or absent N of 37°S; occasional records Great



Barrier I. (Bell 1976). Isolated populations Moumoukai district, Coromandel Ras, and from Te Aroha to Rotorua and King Country (Fox 1978c; Hedley & Hedley 1982b; NZ Atlas). Mainly from Raukumara Ra., SW through Volcanic Plateau and n. Hawke's Bay to w. Manawatu, Wanganui and Taranaki districts. Also in s. Hawke's Bay and Torarua, Rimutaka, Aorangi Ras and Hapuakohe Ra. (Gill 1976; Fox 1978c; Moynihan 1979; NZ Atlas; L. Barea). **SI** Widespread in n. central, w. and s. regions; from Wakamarama Ras and Tasman NP, S to Lyell Ra. and Nelson Ls NP; Marlborough Sounds, S through Kaikoura district, and SW through central and w. regions, E to e. foothills of Southern Alps, and S to Fiordland; also n. and central Otago. Largely absent from E (S of Conway R., although occurs in Kakanui Ras) and S (E of Te Waewae Bay). Recorded Stewart I. and associated islets (Blackburn 1968; Fox 1978c; NZ Atlas).

Chatham Is Egg recorded by Buller before 1888 (Turbott 1967). Probably extinct by 1892; no further records other than subfossil bones (Forbes 1893; Scarlett 1955; Dawson 1957).

Auckland Is First recorded 1839; several records since; 5–6 pairs found in 1972–73 mainly on Adams I. (Fox 1978c); ten nests found in 1990 (NZDOC; R. Wheeldon).

Campbell I. No authenticated records (Westerskov 1960) though listed as straggler (Oliver).

Macquarie I. Single doubtful record by Buller (Turbott 1967).

Breeding Throughout most of range. Confirmed breeding records: **NI** Round Firth of Thames, Coromandel Ra., King Country (Hedley & Hedley 1982b; Fox 1978c), from East Coast to Volcanic Plateau and Hawke's Bay, Tararua Ra (Fox 1978c) and Rimutaka Ra. (Moynihan 1979; Fox 1978c). In Otago, breeding recorded Taeri Ridge, Nenthorn, and extensively in Taeri Gorge System (N.C. Fox). **SI** Throughout range except Marlborough Sounds, Alexandria–Ranfurly district, Hokonui Hills and Longwood Ra., where breeding has not been confirmed (Fox 1978c). Since 1988, 2–3 pairs nested Banks Pen. after 40-year absence; field-study 1990–91 found most sites in Marlborough occupied, but not all breeding (N.C. Fox).

Range has contracted; now rarely seen N of Auckland (Oliver); not recorded Hen and Chickens Is since 1924: Hen I., 1924; Chickens Is, 1880; E. Chicken I., 1914 (Merton & Atkinson 1968); now mainly recorded in more remote districts (Turbott 1967). Breeding in marginal areas of Marlborough reduced or

ceased since 1940s coinciding with use of DDT (Fox 1978c).

Population Probably 3000–4500 pairs (Fox 1978c). In Urewera NP, two pairs seen 3.2 km apart (Fox 1978b). Three pairs in 14 km², central King Country Reserve, 1991 (L. Barea). Five or six pairs on 81-km² property in 1921 (Guthrie-Smith 1927). On SI: 80 pairs in c. 300 km² in Marlborough; 11 pairs in c. 1240 km² in Kaikoura; 27 pairs in c. 1060 km² in N. Canterbury; 17 pairs in c. 1250 km² round Arthur's Pass; seven pairs in c. 1250 km² in Westland (Fox 1978b).

Numbers formerly declining because habitat destroyed and bird persecuted (Fox 1975), but now stable (Fox & Fox in press). Shot because it takes Domestic Fowl and Pigeons, caged birds and game species (Smith 1926; Moncrieff 1929; Stidolph 1939; Turbott 1967; St Paul & McKenzie 1977; Barea 1990; Oliver). Sometimes enter buildings in pursuit of prey (Smith 1926; Barea 1990; Oliver). Also eat introduced passerines, rodents and mustelids (Drummond 1915; Fox 1977b; Morrison 1980; Oliver). Do not breed in areas exposed to persistent human disturbance (Fox 1978c). Possums responsible for some losses of eggs (N.C. Fox). In Marlborough, contraction of breeding range coincided with use of DDT (Fox 1978c). In 1990, samples taken from 16 Falcons in SI showed insignificant levels of organochlorine residues in blood (Fox & Fox in press). Captive birds being bred for possible release in areas where numbers low; proposed that species be used to scare birds away from airports (Hedley 1987) and vineyards (S.B. Lawrence).

MOVEMENTS Sedentary (Fox 1978b; Baker-Gabb & Fitzherbert 1989); most established pairs occupy territories all year (Fox 1978b). Formerly considered to be partial migrant on basis of autumn departure from some sites and autumn arrival at others (Moncrieff 1929). However most of these movements appear to be post-breeding dispersal of juveniles; others perhaps represent winter extensions of home-range (Moncrieff 1929; Baker-Gabb & Fitzherbert 1989). Three fledgelings observed for 4 months from age of 6 weeks, extended range from 0.7 km (in and round clearing where nest sited), to 25.5 km (Lawrence & Gay 1991), though may not be permanent dispersal, as juvenile fledged in 1990 still in same valley as nest, 300 m from nest-site, in Dec. 1991 (L. Barea). Leave some usual haunts near Nelson in autumn (Moncrieff 1929); claimed to disperse more widely in winter, when food scarcer (NZRD); noted as occasional non-breeding visitor to Great Barrier I. (Fox 1978c). Some birds may move north in autumn, following sources of food; others may move to lowlands (Cade 1982). Juveniles regularly recorded from agricultural districts and towns in autumn–winter (Moncrieff 1929; Fox 1978c; CSN). Pairs or single adults occasionally recorded from towns and lowland districts in winter (P. Croxford; CSN). Philopatric; recoveries of ten banded birds show mean distance travelled of 4.4 km (maximum 10 km); continuous occupation of some nesting territories for 30 years indicated; some roosting sites used for decades or centuries (Fox 1978b).

FOOD Mostly small birds but can take ducks and herons; third of food, by weight, from mammals (rabbits, hares and stoats); take insects and lizards but rarely carrion. **Behaviour** Seven methods of searching (Fox 1977a): still-hunting, contour-hunting, soaring, slow-quarterming, stalking, listening, flushing from cover; four methods of attack noted: direct flying attack, tail-chasing, glide-attacks and stooping. Of these, still-hunting or searching from perch most often used, though contour-hunting most effective. Further studies discovered indirect attack also very successful: Falcon spots distant prey and flies in another direction, gains height, moves over quarry at height (≥100 m) and corkscrew

dives on to prey. Juvenile female recorded launching 13 direct-flying attacks/20 min, all unsuccessful (S.B. Lawrence). Also often attack from very close to ground, so that Falcon is unseen by prey during approach (N.C. Fox). Soar often but this rarely ends in attack; slow-quarterming rare, probably because wing-loading too high; stalking on ground infrequent; flushing from cover often part of other hunting methods; having more flexible feathers than most other falcons, have no difficulty entering dense thickets. Direct-flying attacks (80% of all attacks start from direct flight) and tail-chasing (40%) usual way of catching prey. Glide-attacks uncommon (15%) but most successful. Stooping also uncommon (5–15%), particularly on large flying prey; sometimes conducted co-operatively with members of pair stooping alternately. Mammals taken by glide-attacks, prey being first knocked over, then recovered. Demolish nests to get fledgelings. Birds killed by breaking neck with beak, usually on ground but occasionally in air; take poultry (Fox 1977b); mammals killed by crushing back of head with beak; insects crushed in one foot. Single out members of flocks (e.g. Feral Pigeons *Columba livia*), then stoop and knock quarry to ground, where kill by biting back of neck. Also enter lofts to take adult and young domestic pigeons (S.B. Lawrence). Cache prey throughout year; caching also recorded in juveniles from 7 weeks (Lawrence & Gay 1991; L. Barea). Occasionally take small mammals from trees (Read 1985) and young birds from nest-holes (Sopp 1958); can locate nesting birds by sound alone; will investigate squeaks, e.g. rusty fence squeaking (N.C. Fox). Recorded hunting invertebrates on ground (Lawrence & Gay 1991). Rarely eats carrion (Taylor 1977).

Adult Breeding Gisborne, NI (34 sites, 10 pellets, 4 remains; Fitzgerald 1965). Insects 50% freq.: Coleoptera: *Pyronota festiva* 33.3% no. Birds: Skylark *Alauda arvensis*: ads 16.6, imm. 4.7; Song Thrush *Turdus philomelos* ads 7.1, imm. 4.8; Blackbird *T. merula* juv. 7.1; European Greenfinch *Carduelis chloris* ad. 2.4, imm. 2.4; Goldfinch *C. carduelis* 4.8; Yellowhammer *Emberiza citrinella* 4.8; House Sparrow *Passer domesticus* 9.5; Common Starling *Sturnus vulgaris* juv. 2.4.

Breeding and non-breeding In ne. SI (1371 pellets, 1434 items; 68 obs., 77 prey items; 21 stomachs, 30 items; Fox 1975, 1977a,b; Table 1). Insects: indet. –, –, 1.3, –, Odonata: Anisoptera: indet. –, –, 2.6, –, *Uropetala curovei* 0.1, 1.6, –, –, Orthoptera: *Locusta migratoria* 0.1, 4.4, –, –, Hemiptera –, –, –, 3.3; Coleoptera: indet. 0.2, 7.6, 1.3, 3.3; *Pyronota* –, –, 1.3, –, Tenebrionidae –, –, 1.3, –, Reptiles: lizards: gecko *Naultinus elegans* tail –% est. wt. in pellets, –% no. in pellets, –% no. in obs., 5.3% no. stomach contents; skink *Leiopisma* 0.4, 2.9, –, –, Birds: indet. –, –, 10.4, 26.7; White-headed Petrel *Pterodroma lessoni* –, –, 3.3; White-faced Heron *Ardea novaehollandiae* –, –, 2.6, –, Cattle Egret *A. ibis* –, –, 1.3, –, Domestic Duck –, –, 1.3, 3.3; Pacific Black Duck *Anas superciliosa* –, –, 1.3, –, Domestic Fowl *Gallus gallus* –, –, 6.7, 3.9; Californian Quail *Lophortyx californica* 4.2, 2.2 –, –, Masked Lapwing *Vanellus miles* –, –, 1.3, –, Kelp Gull *Larus dominicanus* 1.1, 0.1, –, –, New Zealand Pigeon *Hemiphaga novaeseelandiae* –, –, 3.9, –, Feral Pigeon 1.0, 0.2, 9.1, –, Sacred Kingfisher *Halcyon sancta* 0.1, 0.1, –, –, Skylark 0.2, 0.3, 2.6, –, Skylark or Richard's Pipit *Anthus novaeseelandiae* 4.2, 8.1, 1.3, 3.3; Grey Warbler *Gerygone igata* 0.1, 1.3, 1.3, –, Song Thrush 5.2, 3.6, 1.3, –, Blackbird 8.3, 4.4, 3.9 (incl. 2.6 juv.), –, Bellbird *Anthornis melanura* 0.1, 0.3, –, –, Silveryeye *Zosterops lateralis* 2.2, 0.5, –, 3.3; Greenfinch 3.9, 7.1, –, 3.3; European Goldfinch 0.3, 1.3, –, –, Redpoll *Carduelis flammula* 0.1, 0.6, –, 6.6; Chaffinch *Fringilla coelebs* 1.5, 4.0 (incl. 1.3 juv.), 3.9, –, Yellowhammer 3.9, 7.8, 10.3 (incl. 3.9 juv.), 10.0; Yellowhammer or Greenfinch 6.3, 12.1, –, –, Richard's Pipit 0.1, 0.2, 1.3, –, Dunnock *Prunella modularis* 0.7, 1.9, –, 3.3; House Sparrow –, –, 2.6, 3.3; Common Starling 4.2, 2.9, 1.3 (juv.), 6.6; Grey Fantail

Rhipidura fuliginosa 0.1, 0.5, —, —; Australian Magpie *Gymnorhina tibicen* 1.3, 0.3, 5.2, —. Mammals: rabbit 12.6, 1.3, 1.3, —; Brown Hare *Lepus capensis* 22.5, 0.8, 1.3, —; rodents: House Mouse *Mus musculus* 0.1, 0.5, 2.6, —; Brown Rat *Rattus norvegicus* 1.4, 0.4, —, —; Black Rat *R. rattus* 0.1, 0.1, —, —; Stoat *Mustella erminea* 0.9, 0.2, 1.3, —.

Table 1 Diet of New Zealand Falcon (from Fox 1977a)

Prey type	Pellets	Obs.	Stomach	
	%wt	%no.	%no.	%no.
Mammal	37.6	3.2	6.5	0
Bird	61.5	80.4	88.3	86.7
Lizards	0.4	2.9	0	3.3
Insect	0.4	13.5	5.2	10.0
n		1434	77	30

Other records Insects: Odonata: large dragonflies *Uropetala c. carovei* (Lawrence & Gay 1991); Hymenoptera (McLean 1907); Lepidoptera: *Aenetus virescens* (Fox 1977a); Hemiptera: cicada *Amphipsalta* (Lawrence & Gay 1991). Birds: Cook's Petrels *Pterodroma cooki* (Wilson 1959); Hutton's Shearwater *Puffinus huttoni* (Harrow 1976); Weka *Gallinallus australis* (Henry 1903; Wilson 1959); Kaka *Nestor meridionalis* (Reischek 1885); parakeets *Cyanoramphus* (Henry 1903; Wilson 1959); Eastern Rosella *Platycercus eximius* (Henry 1903); Tui *Prothemadera novaeseelandiae* (McLean 1911). **Carrion** Fish head (Taylor 1977); sheep (S.B. Lawrence); New Zealand Fur Seal *Arctocephalus forsterii* (Russ 1990); Chamois *Rupicapra rupicapra* (Fox 1977a).

Young In wild, first recorded hunting when 7 weeks old, by direct flight from perch or fast glide to prey (Lawrence & Gay 1991).

Intake In captivity, juvenile male consumed 39.6 g/day (6.2; 30.6–45.6; 67 days) or 13.5% of body-weight/day (2.2; 10.4–15.6; 67); juvenile female consumed 46.9 g/day (19.8; 34.0–56.9; 67) or 11.8% of body-weight/day (5.0; 8.0–13.4; 67).

SOCIAL ORGANIZATION Detailed study on wild and captive birds by Fox (1977a, 1978b), from which information taken unless stated. Often seen singly or in pairs. Throughout year, adults appear to remain within home-range, possibly continuing to defend territory; pair may hunt co-operatively at any season. Occasional small groups of 6–12 seen during autumn, probably transient associations of dispersing juveniles.

Bonds Probably monogamous; pairs of adults often seen in winter, which suggests some pairs remain bonded throughout year. At least 20 months old before starting breeding activities, though twice females tried unsuccessfully to breed during first moult; sometimes scrape made but eggs not laid because one partner immature. **Parental care** Both sexes prospect for nest-site, incubate, and tend young. Male does 20–35% of incubation (n=4 pairs). Only female feeds young. If female killed, male can raise nestlings (Soper & Jardine 1957; Fox 1977a). **Co-operative breeding** Two instances of third Falcon at nest; in one, supernumerary, probably juvenile, assisted in defence of nest when adult female on eggs.

Breeding dispersion Single pairs, in territories. In scrub and grasslands, most pairs 2–5 km apart, averaging 3.8 km (n=94 pairs) and 4.0 km (n=21 pairs) in different areas; in woodland, seemed much farther apart (14 km), though probably not all pairs found. Two pairs, 3.2 km apart in partly logged forest; 5–6 pairs in 80-km² holding (Guthrie-Smith 1927), pairs therefore being c.

4.3 km apart. Spacing markedly non-random, and may depend on availability of food within habitats; probably breed at lower densities in alpine and subalpine valleys compared with lower-lying hill-country. **Territories** Generally resident within territory and to some extent territorial throughout year; introducing trained birds to territory in winter produced reactions up to 1 km from nesting area. Geographical pattern of territories changes little over time; of 144 pairs, most have been on location for a number of years; some territories have held Falcons for 30 years or more. Pair defends nesting and, apparently, hunting territories. **Nesting territories** In Fox's model, nesting territory consisted of dome-shaped space above nest-site (excluding dead ground on other side of ridge from nest), and area c. 100 m vertically below nest; male defends up to c. 500 m round nest, and female up to c. 400 m. Apparently more sensitive to disturbance from above than below. Defence begins when scrape made, intensifies at laying and continues until young fledge. Though both sexes appear attached to territories, males more so, holding them even when partners die; some evidence of females intermixing in winter, and one female, after removal of her female neighbour, switched territories and mated with lone male. Throughout breeding cycle, male spends much of day away from nesting territory, hunting. **Juvenile territories** For about 1 month after fledging, juveniles appear to defend area actively but, as autumn approaches, territorialism and vocalizations decrease; one non-nesting, unpaired, 12-month-old male defended territory while at hack during breeding season. **Home-range** Difficult to measure; c. 15 km²/pair in open country of mainly grasslands, whereas in forest, appear much larger, possibly about 75 km², but less than 189 km².

Roosting Roost as pair; no records of communal roosting. Members of pair usually roost within 1–100 m of each other at traditional sites used all year; some traditional sites apparently occupied for many decades, if not centuries. Normally pairs have at least two sites, usually facing different directions; assumed to use whichever more suitable according to weather. In woodlands probably always use trees; otherwise usually one-quarter to three-quarters of the way up hillsides on bluffs, not directly overhanging creeks or open water, and always with scree slope between roost and creek. One record of perch on ridge overlooking gully used over 5 consecutive years for perching and launching attacks on prey (S.B. Lawrence). On bluffs, two main types of roosts: cake and splash. **CAKE-ROOSTS:** are pot-holes in bluffs where cakes of white droppings accumulate, sometimes into mounds exceeding 100 kg; birds using these usually have small hard balls of uric acid on tips of rectrices; one cake-roost at alternative site was used by nesting Paradise Shelducks *Tadorna variegata*; when Falcon's nest failed at first site, evicted Shelducks and reared young 10 m from roost-site (N.C. Fox); build-up of droppings can eventually block roosting hole, or cause collapse of cliff face, leading to desertion of site; some desertion attributed to disturbance by Brush-tailed Possums *Trichosurus vulpecula*. **SPLASH-ROOSTS:** are simply rock perches under sheltering overhangs where mutes splash rock-face, making site visible for some distance; droppings constantly weathered, so age of sites unknown; can be temporary or permanent. During breeding season, unless permanent roosts near (30 m) nest, generally pair uses temporary splash-roosts, usually within c. 20 m of nest; more randomly oriented than permanent roosts possibly because smaller choice of sites near nest. Once fledged, young use temporary or permanent roosts of parents until independent; if use permanent, site within 500 m of nest often <100 m. Permanent roosts usually higher above foot of bluffs, varying from 2 to 19 m (n=27) with mean of 8 m (n=15), than those of temporary roosts with mean 3.5 m (0.3–8.0; 17). **Arrival and departure at roosts** In wet weather, roost for long periods in

daylight; in fine weather, do not roost until well into dusk, sometimes hunting until it is quite dark.

SOCIAL BEHAVIOUR Detailed study on wild and captive birds by Fox (1977a, 1978d) from which information taken unless otherwise stated. Calls, postures and displays used during breeding essentially similar in nearly all species of falcon. Following activities recognized: **MANTLING**: wings and tail spread, forming protective cloak over food; usually head low, feathers of body and head raised; seen in dependent young and captive birds with food, though all birds will freeze or mantle over prey if potential robber sighted. **PLAYING** Seen in captive birds regardless of age or sex, specially in spring and summer; solitary play usually consists of mock-attacks, clutching at clumps or roots, toying with sticks or rocks, or catching and releasing prey several times; when two Falcons play together, whether mated or not; play reflects courtship, rearing of young and prey-catching activities, e.g. talon-grappling. Birds turning their heads upside down while perching, probably at play. Juveniles in wild observed pulling moss, twigs and pieces of bark from trees, carrying for a short distance and discarding them; one tried twice to break off branchlet by hanging upside down and flapping; one spent 15 min dismembering a lump of lichen, watched by a sibling; sometimes, when an object was dropped, the juvenile that dropped it and a sibling would pursue and try to catch it (Lawrence & Gay 1991). **LONG-DISTANCE VIEWING**: when viewing distant object in sky, usually look at it directly with eyes slightly closed; occasionally squint or cock head slightly. **FLIGHT-INTENTION MOVEMENTS**: spread wings horizontally and fan tail (Fig. 2); intently watch object that stimulates movement and then launch into flight or relax; often very brief,

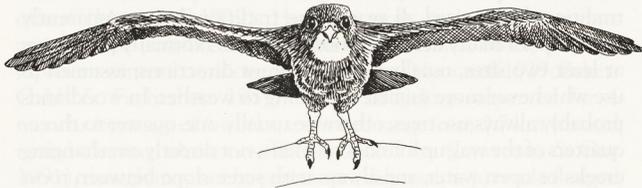


Fig. 2 Flight-intention movement

sometimes just lean forward and flick wings slightly. **LAYING POSTURE**: about time of laying, females appear very lethargic: scapulars, rump, under tail-coverts and small feathers and rictal bristles round cere and chin, fluffed; one or both wings drooped, body set well back on tail, eyes often not fully open and foot, if raised, not tucked up properly. **Comfort behaviour** **ONE-WING STRETCH**: (Unilateral Stretch of Snyder 1974): stretch wing, leg and tail on one side; may repeat on other side; sometimes associated with yawning or violent exercising of wing. **TWO-WING STRETCH**: lean forward, fanning tail and stretching both wings upwards and forwards as far as possible; often associated with excretion. **ONE-LEG STRETCH**: lower one leg until proximal end of tarsus almost touches perch and lower part of leg projects forwards; then stretch leg clear of body and return to tucked-up position; often associated with yawning. **ROUSE (Body-shake)**: slowly raise all body-feathers then shake violently. **SCRATCHING**: bend slightly and scratch directly using digit II or III; feathers of head often raised, and eye half-closed. **BILL-WIPING**: rub one side of bill, then other, against rock, branch or grass in up-and-down motion; afterwards often paddle with feet, doubtless to clean toes. **PREENING**: occupies a significant part of day, specially for growing or moulting birds. **SUNBATHING** (Fig. 3): fan tail, wings slightly drooped and spread, back to sun (S.B. Lawrence). Often in captive birds for 0.5–30 min when first placed in sun in morning: wings and tail spread,

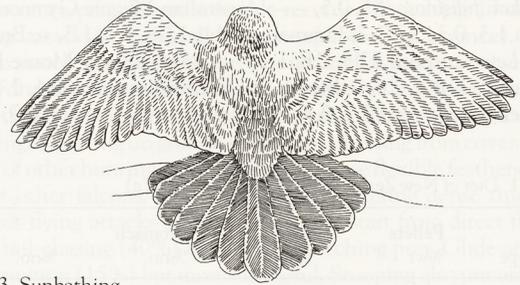


Fig. 3 Sunbathing

usually with back toward sun.

Aerial activity During breeding, either sex, especially male, circles over territory, intermittently giving Chattering call. Probable **MOCK CHASES**: spectacular noisy flight, initiated mainly by male, where pair chase each other performing aerobatics, accompanied by Chattering and Whine (Powell 1972). After Passing and Leading (see Courtship), male flew slowly, weaving round trees, gliding for spells with wings in V, and pursuing female often used Flutter-glide or Cuckoo-flight (form of aerial food begging; see Relations within family group). **FLITTER FLIGHT**: performed by males, not females or juveniles, and function unknown; while flying high (50+ m) and steadily with intermittent glides, suddenly change wing-beat into fast deep-pumping beat, causing rapid acceleration and rocking from side to side through angle of c. 30°; ends abruptly after travelling c. 30 m; seen in autumn and breeding season. Perhaps similar to flight recorded by Edgar (1963) in Oct.: single bird glided with angled wings and then, high in air, performed fairly slow flight, which alternated with sharp side-slips, shallow swoops and quick lifts. See also Agonistic and Sexual behaviour below.

Agonistic behaviour Individual distance in wild, in absence of territorial attachment, probably around 2–5 m; members of pair sit beside each other, and usually roost within 1–100 m. Defend nesting territory, occasionally hunting range and perch, roosting site and disused nest-sites. **TERRITORIAL ADVERTISING**: probably flights over territory accompanied by Chattering, though aerial or perched displays do not appear to deter intruders (Fox 1978e). **Threat** Apparent threat posture: **FRONTING** (Fig. 4; Crowding-off): with very erect, almost backward-leaning stance, individual approaches, and stares straight at, another Falcon, which may leave perch if intimidated, though one female started



Fig. 4 Fronting



Fig. 5 Angel Posture

to play in response. **ANGEL POSTURE** (Fig. 5; Weir & Picozzi 1975): bird directs eyes at opponent with feathers of body raised, wings partly opened, tail fanned, and weight on tail, leaving feet free to lash out; sometimes even goes over on back to defend itself; may squeal intermittently; a threat or defence posture seen during

close physical confrontations between conspecifics and sometimes interspecifics, e.g. with Swamp Harriers, or with potential prey, such as Australian Magpies *Gymnorhina tibicen*, that defend themselves strongly. Juveniles recorded being mobbed by Chaffinches *Fringilla coelebs*, attacked by Australian Magpies, and swooped at closely, but without contact, by Tuis. Juveniles dodged attacks by Magpies and remained perched, whining (Lawrence & Gay 1991). **Attacks** When defending nest, attacks involve stooping and calls; in experiments, trained males released into other bird's territories were routed by residents. Swamp Harriers do not usually nest near Falcon's nest; nesting adult Falcons, and even newly fledged juveniles and non-nesting subadults, chase those approaching within 0.5 km of centre of territories; talon-grappling with Harriers and falling downwards (Fox 1978a). Juveniles have driven off Great Cormorants *Phalacrocorax carbo* from nesting clearing; two siblings flew hard at Cormorant, swooping and diving at it for several hundred metres (Lawrence & Gay 1991). Intruders seldom attacked when perched (Fox 1978e). Also see Parental anti-predator strategies below.

Sexual behaviour In captivity, chittering call only given by pair during breeding season. **Courtship** Many displays similar to those described for Peregrine Falcons. During courtship, the following aerial displays noted. **PASSING and LEADING:** male comes in with food and swoops past female who then follows him. **MOCK CHASES** (see Aerial activity) often precede copulation (Powell 1972). **MOCK-ATTACKING (=Dive Display)** (Walpole-Bond 1938; Nelson 1973): male stoops at female. **CLIFF-RACING:** aerobatics performed using rising air currents on nest-cliff; male flying 20–30 horizontal figure-of-eight patterns swooping 1–2 m above female's head; aspects of territorial defence and advertising displays. Figure-of-eight display-flight also recorded over bush habitat (L. Barea). Also semi-static displays: prominent perching; play, possibly including talon-grappling when perched or on ground (not known between conspecifics in air), though also used in defence of nest (Fox 1978a); food-transfers; nest-prospecting and scraping; mutual preening and billing. Often in early courtship, and throughout incubation and brooding periods, adult female Whines plaintively and softly when male away hunting (L. Barea). Wild and aviary birds generally behave similarly. **Courtship feeding** Almost from beginning of courtship, female solicits food from male in a similar manner to young (see Relations within family group); male **BOWS** (Fig. 6) and **BOBS** (Fig. 7) rapidly when he gives food to mate. Food-transfers take place bill to bill on ground, or

perspersed with Bowing and Bobbing. During laying, female relies totally on food from mate. Once young hatch, to maintain food supply to female, male has caches for storing food, and transfer takes place near nest. One adult female Whined for food for her 17-day-old nestlings. **Greeting** Incubating male flies off as female approaches, occasionally Chittering as he does so. **Mutual preening** and billing observed. **Copulation** Probable sequence of events: male with food performs Passing and Leading, chase ending near future nest-site with male presenting food to female; he waits while she eats and copulation follows; during these events, female often Whines. Copulation usually performed on stable perch, wide branch or rock; generally favour one or two particular dead trees, or ground below them, or in absence of trees, rocky bluff. Before copulation male, with feathers sleeked down and 5–10 m from feeding or waiting female, assumes horizontal posture and flits nervously between branches, and makes fast jerky short runs; several times Bows head right down and Bobs, jerks head up again, often giving Chup or Chittering call. Female, spontaneously or after eating food, indicates willingness to copulate by squatting, lowering head almost down to her feet and giving soft Whining call. Male mounts female and balances by flapping wings, while female raises tail vertically (Fig. 8; Powell 1972). Complete copulation averages 10 s (7–15; 6) with 89 min (35–105; 4) between copulations during middle of day in one pair;

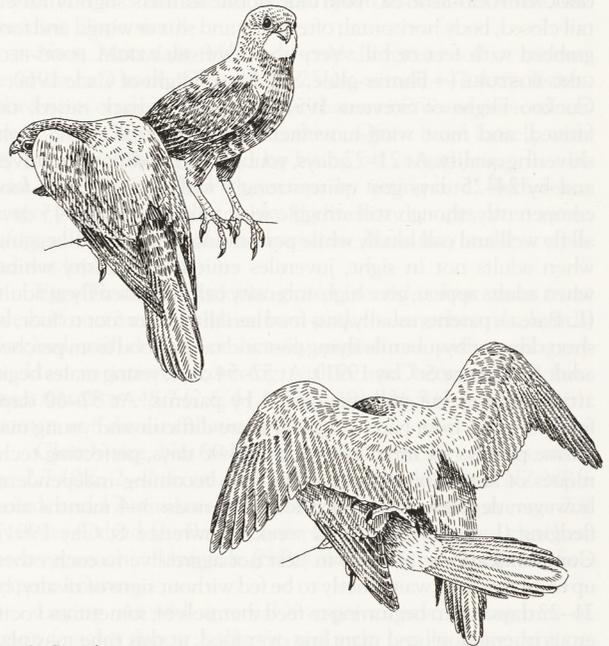


Fig. 8 Copulation

possibly pair were still at early stages of courtship. Male often Chitters after copulation; female may Whine, and one female maintained semi-copulatory position for up to 12 min afterwards, occasionally performing thrusting abdominal movements. Some courtship displays may continue into later stages of breeding cycle; copulation sometimes occurs after start of incubation (L. Barea); female with young begging for food, see Relations within family group.

Relations within family group In two pairs, males examined potential nest-sites during courtship by poking under rocks or logs, occasionally scraping substrate; tried to entice female to site by leaving prey there; behaviour continued until nest-site finally chosen by female. Scraping performed by both sexes but

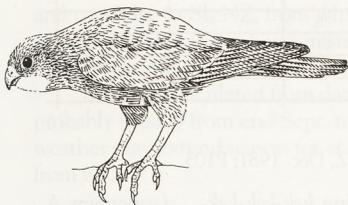


Fig. 6 Bow



Fig. 7 Bob

foot to foot in air (copulation on perch often follows). In captive pair, at first, male was aggressive to female's approaches; at other times he performed COWLING and would not release food immediately, but walked about on stiff upright legs with food in bill and wings drooped, turning away from female; Cowling often inter-

probably more so by female, though captive males often scrape, even during incubation. During incubation female sits tightly. After hatching, male hunts more but does some brooding; when male tries to take over brooding, female sometimes refuses to leave; male retreats and tries again later. During breeding, female gives whining call to prompt male to hunt. In captivity, where male unable to leave, female emphasized call by flying at male, driving round pen (N.C. Fox). When 14 days old, young brooded only during periods of stress, such as cold weather. One female seen to preen one of her 16-day-old young. Male passes food to female who feeds young. All food-soliciting postures associated with Whine, which develops when 4 days old. At first, nestlings direct begging at parent's bill; by 7 days, Whine call well developed and young gape with upright body-posture and tarsi flat on ground; by c. 10 days, begging also directed at parent's feet. From this time on food-begging postures stay same; two begging postures, on ground and aerially, seen only in dependent young or nesting females. From 6–8 weeks, whine for periods of up to 10 min. Whining especially heard from unfed juveniles when sibling just fed by adult; from 9–13 weeks juveniles spend less time perching quietly, more time flying and chasing one another; intensity of whining increased when adult appeared; while whining, fluff out plumage, droop wings and hold head at 45° angle; at 14 weeks, heard male, during 30 min period of whining, give a double or treble Whine every 15 s (Lawrence & Gay 1991).

GROUND FOOD-BEGGING POSTURE: dorsal feathers slightly raised, tail closed, body horizontal; often beat and shiver wings, and food grabbed with feet or bill. Very characteristic **AERIAL FOOD-BEGGING POSTURE** (= Flutter-glide, Sandpiper Flight of Cade 1960; = Cuckoo Flight of Stevens 1957): feathers of back raised, tail fanned, and most wing-movement occurs at tips giving slight shivering quality. At 21–22 days, young begin feeding themselves, and by 24–25 days grip quite strongly with feet and pull food competently, though still struggle with tough items. At 45 days, all fly well and call loudly while performing Aerial Food-begging; when adults not in sight, juveniles emit low-intensity whine; when adults appear, give high-intensity call and often fly at adults (L. Barea); parents usually pass food aerially, either foot to foot, by short drop, or by juvenile flying past and taking food from perched adult (Lawrence & Gay 1991). At 52–54 days, young males begin attacking prey but still mainly fed by parents. At 57–60 days, food-transfers from parents appear more difficult and young may pursue parents for up to 100 m. By 70–90 days, perfecting techniques of searching and attacking and becoming independent; however, dependent for much longer periods: 3–4 months after fledging (L. Barea); up to 22 weeks (Lawrence & Gay 1991).

Communications Siblings in nest not aggressive to each other; up to 14 days old, wait quietly to be fed without signs of rivalry; by 21–22 days, when beginning to feed themselves, sometimes vociferous interactions and mantling over food; at this time may play together; at 28–29 days, play together roughly. Two fledging males, aged 35 days, performed together: mutual preening, talon-grappling, and mandibulating feet. At 6–7 weeks, observed siblings (two females, one male) chasing one another in flight, driving one another off perches, occasionally screaming; at 7 weeks siblings became more aggressive when one received food from adult, trying to steal food from fed bird; unfed juvenile once knocked adult female off perch after she had passed food to another sibling; 7–8 weeks made longer, faster, more aggressive flights, constantly changing roles of 'prey and pursuer'; sometimes caught talons in flight and tumbled end over end before disengaging; sometimes made physical contact during direct stoops; occasionally pursuer stalled, extended talons, and came up from below pursued sibling; by 15 weeks, play between siblings seemed to

have stopped; adult male recorded diving at 17-week-old juvenile male (Lawrence & Gay 1991). Just before hatching to c. 12 days old, nestlings often respond to disturbance and stress, specially cold, by *peeping*, but can thermoregulate at c. 11 days; at 3 days, also huddle when cold, and sprawl and pant if too hot; by 14 days, seek shade to avoid stressful weather but seldom go more than 2 m from scrape. **Anti-predator response of young** Mainly concerned with human disturbance: by 7 days, freeze; by 11 days, give Chatter; at 14 days may freeze, scuttle into surrounding vegetation or Chatter and rush out 1 m or more to attack intruder's feet; at 28–29 days, run off and hide. **Parental anti-predator strategies** Chattering given in alarm. From laying to when young fledge, pair respond to human intrusion by calling and repeatedly stooping, sometimes striking; male arriving with food may cache it or pass it to female before starting to stoop, care of prey apparently taking precedence over nest-defence. When only one or two young, parents usually defend them; three or four, as they grow, are often left alone while parents hunt, and when c. 35 days old, parents spend no more than 2 min with them. Nest defended against: Swamp Harriers, Kelp Gulls, Great Cormorant, White-faced Herons, people, dogs, cats, Chamois, horses and helicopters; one pair successfully evicted nesting pair of Paradise Shelduck. When 21–22 days old, young may stray from scrape but usually return nightly for food; spend much time preening and can perform One-wing and Two-wing Stretch. At 24–25 days, a few broods move from nest, using as base a similar site nearby. At 28–29 days, frequently exercise wings, and still sleep lying down. At 32 days, males sleep at night on one foot, some tucking their heads into their scapulars; females appear 4 days behind in development. By 28–29 days, many broods have deserted nest-sites; once left, young seldom return to the scrape. When 45 days old, roost at permanent or temporary sites, with adults or separately.

VOICE Reasonably well known; study by Fox (1977a), on which account based. Noisy during breeding season, particularly in defence of nest, which makes species conspicuous (St Paul & McKenzie 1977; Fox 1978b; Moynihan 1979). Only Chatter likely to be heard at any time of year. Also utter chitters and whines and, less often, chups and squeals. All calls made by both sexes but Chatter and Whine of female deeper; Chatter of male faster than that of female (L. Barea). Individual differences and regional variations not known.



A L. McPherson; Mt Cook NP, NZ, Dec. 1981; P103

Adult CHATTER: chattering *kek-kek-kek...* (sonagram A, male); usually 3–12 syllables, c. 7 syllables/s. Uttered by both sexes, at any time of year. Given when excited and when alarmed or angered; also to advertise presence on territory. Often uttered by male circling over territory, heard over long distances (St Paul & McKenzie 1977). Large females have deep quacking *kek*, small males much squeakier call. **WHINE:** one or more drawn-out calls sounding like *whee-up* or *wa-ik*, with emphasis on first syllable. Given softly by females early in courtship while male away hunting, though may continue through to incubation period.

Female gives soft whining call, *whew-whew-whew-whew...* when in submissive posture before copulation. Continues during copulation. Not given at any other time (N.C. Fox). When more highly excited, e.g. when food visible, Whine louder, more strident, insistent and demanding and given more often. Ground and Aerial Food-begging postures (see Social Behaviour) almost always associated with high-excitement whining. Used in courtship flight before copulation (Powell 1972). Used during breeding to stimulate male to leave nest to hunt (N.C. Fox). Derivative low-excitement calls, particularly in captivity; described as *chirrup*, *quack* and so on. **CHITTER**: chattering *i-i-i...*; about 11 syllables/s. Most often uttered in flight; when on ground normally associated with pre-copulatory posture of male and with food passes. Given once or twice immediately after copulation (six of seven observations of same male), when swooped by mate (ten of ten observations of same male; two of two of same female). Given by one captive pair only during breeding season (e.g. by male flying off just after female had landed abruptly beside him) but throughout winter by captive yearling male when given food. Invariably associated with physical confrontations, usually sexual, between two birds. Thought to be social rather than territorial, reflecting excitement and requiring stimulus of close physical, non-hostile confrontation with another bird. **CHUP**: usually monosyllabic *chup*, occasionally with preliminary short *ee*. Not loud. Heard occasionally and only during breeding season. Similar to first syllable of Chitter and used in similar situations, e.g. in captivity by male when surprised by female, when confronted by her in playing on ground (although Chitter more common if two birds playing together). Often uttered by imprinted captive male, particularly at play. **SQUEAL**: short (c. 5 s), shrill and undulating squeal. Probably rarely heard in wild. Given by captive birds in serious interactions with other predator, e.g. when disputing over food with Swamp Harrier or when handled. Combinations of calls possible, particularly Chatter, Whine and Chitter.

Young PEEP: utter audible *peep* before hatching, interspersed with bouts of tapping at egg-shell. Captive-bred chick *peeped* 3 times/s if stressed or disturbed, particularly if cold. Seldom used once capable of thermoregulation (c. 11 days). Carries remarkably far for such a quiet call. **WHINE**: first heard at 4 days (captive-bred chick), well-developed by 7 days old. Penetrating, occasionally audible over 1 km from nest. Similar to Whine of adults. Male 4 weeks old, during 30-min period of Whining gave double or treble *whew-up* every 15 s (Lawrence & Gay 1991). **CHATTER**: in captive birds appeared to deepen slightly when bare parts became yellow, at about 9 months.

BREEDING Not fully known. Studies by Fox (1977a) in field and captivity in SI, NZ, from which information derived. Breed solitarily in simple pairs in forested areas and in grasslands with remnant wooded areas in hilly and mountainous country.

Season Calculated from dates of hatching: in n. SI: laying, probably usually from end Sept. to mid-Nov. Prolonged cold wet weather may extend season for at least 1 month. No information from NI.



Site Four types used. (1) Ledges of cliffs, usually upper third; ledges 1–6 m long and 0.6 to 2.5 m deep, average c. 1 x 0.6; sheltered by pronounced overhang and screened by vegetation, sometimes with narrow entrance c. 30 cm wide. (2) On ground on steep broken hillsides, easily accessible, at foot of rocky over-

hang and usually screened by vegetation. (3) On ground under log without much screening vegetation; once under dense Kowhai bush, having effect of Type (2) sites. (4) In epiphytes on trees, dead or dying; probably a common site in areas of continuous bush. Also recorded in emergent Rimu *Dacrydium cupressinum*, NI (Hedley & Hedley 1982a; L. Barea), emergent Tawa (L. Barea), hollow tree-trunks (A. Blackburn) and once under stack of fence posts by road (Young 1959). Altitude of sites (n=118), from 100 to 1500 m asl, average 672; all within 50–100 m of creek suitable for bathing. Sites (n=42) tended to be fewer facing N and NW (into hot midday sun or violent hot nw. winds) and SW (direction of persistent cold wet winds). Pairs (n=11) tended to select same type of site from year to year, with one exception; did not switch from cliff-sites to ground-sites or vice versa. One pair recorded nesting in hole on cliff-face, then following year 100 m away under small bush on rock stack c. 50 m high (S.B. Lawrence). Sites generally on lower two-thirds of hill-slopes. Used traditionally for many years. Males may be more firmly attached to territory or site than females; selection of site may be affected by conditions of wind and air currents at particular locations, which probably influence perching, flight and approach behaviour of birds and may even affect breeding success. Male first examines site during courtship period and may try to attract female by bringing and leaving food there; female makes final choice. Pairs and perhaps sites mostly 2–5 km apart, average 3.8 and 4.0 km in two similar e. study areas; 14 km apart in w. forest area (see Breeding Dispersion).

Nest, Materials Merely a scrape in grassy soil or humus, never on bare rock, typically 20–25 cm across, 4–7 deep. Established nests on deep soil are deeper than more recent ones, which may have rocks protruding into them. Often lined loosely with dry grass; probably gathered by biting off or gathering, live or dead, and being pushed into scrape by sitting bird. Both sexes scrape, probably mainly female. Preliminary scrapes often made before selection of final site. Immature birds may make scrapes and not lay.

Eggs Rounded oval; not glossy; ground-colour varies from pale buff or cream through salmon-pink to deep chestnut, lightly blotched with brown or heavily pigmented with mahogany speckles; variations occurring within and between clutches. **MEASUREMENTS**: 48.7 (2.6; 41.4–54.3; 69) x 36.7 (1.4; 33.6–39.6). **WEIGHT**: at 8 days incubation, 45.4 g.

Clutch-size Not well determined. From 25 nestings, average 2.7 (0.6; 2–4) from one captive, four wild, three NZ NRS records and 17 museum collections; from four nests, average 2.8 juveniles fledged (L. Barea); one pair in captivity, two clutches, three eggs each, all infertile (S.B. Lawrence); no clutches of five or more known.

Laying At 48-h interval in captive birds. During time of laying females appear lethargic and sick, totally dependent on males for food. Replacement laying known, possibly 2–3 times; once at interval of 14–16 days after loss; once in captivity 20 days after first clutch removed (S.B. Lawrence).

Incubation By both sexes; captive male incubated with eggs touching, female with eggs apart. Starts with laying of first egg but incomplete until last egg laid. Male's share 20–35% from laying of first egg but female dominated so that she sometimes refused to leave when male approached or male left as soon as she appeared. Change-overs brief, averaging 1.4 min (0.5–2.0; 10) in wild, 1.0 (n=4) in captivity. When settling on eggs, movements of foot, with toes bunched and flaccid, very careful to avoid damage to eggs. **INCUBATION PERIOD**: not known but probably 29–35 days; 31 days recorded in captivity and 29 days in wild (NZ NRS), but both perhaps in unnatural or exceptional circumstances.

Young Semi-altricial, nidicolous. Hatching lasted c. 2 days for one egg; almost synchronized or up to 2 days apart. At hatching, covered with white protopile, sparse in places to reveal pink skin; iris, black or dark brown, with eyes closed except when being fed; bill and claws, translucent pale pinky-cream. At 7 days, able to crawl short distances, Whining call developed, gape vigorously. Thick grey woolly teleoptile obscures white protopile, except on crown at 11 days. At 14 days, down covers crown and rest of body, rectrices and primaries appear. At 18 days, feathers of body appear, especially on scapulars and round face, and egg-tooth usually lost; size of adults, able to run short distances. At 21–22 days, begin to feed themselves, may stray some distance from scrape but usually return for meals and at night. At 24–25 days, bill, dark horn; cere, legs and feet, pale sky-blue or olive-green. At 28–29 days, mostly feathered except on crown, nape and rump; very active, often leave scrape, and will run off and hide when inspected. Still have some down on crown and rump at 32 days.

Growth At 1 day: weight, c. 31 g; length of body, c. 70 mm; tarsi, c. 20 mm. At 7 days: weight, c. 41; length, c. 110; tarsi, c. 26. At 14 days: weight, 220 (male), 380 (female); tarsi, c. 50. At 18 days: weight, 310 (male), 500 (female); rectrices, c. 20 mm. No further increase in size after 21–22 days, growth concentrated on feather development. Length of rectrices at 21–22, 28–29 and 35 days: 30–40, 60–70 and 95 respectively. **Parental care, Role of sexes** Female usually broods continuously for first 10–14 days; male generally visits very briefly after hatching, broods occasionally till young 10 days old; thereafter brooded, or sheltered only in hot, cold or wet weather but after 16 days young tend to seek their own shelter. Nestlings not mutually aggressive. Fed solely by female. Male provides food and has plucking posts usually 50–200 m from nest and out of sight. Females start to hunt when chicks can thermoregulate, from c. 11 days old. Surplus food often cached and brought to nest after unsuccessful hunts. Young eject faeces over edge of nest.

Fledging to maturity At 32 days, males can fly, owl-like; some females try to fly at 35 days; all young flying well by 45 days, can soar; seldom return to scrape. Fed by parents, usually by aerial passes. Young chase parents, screaming loudly; roost with adults or separately. By 52–54 days, males start to hunt and kill but still mainly fed by parents. Between 70 and 90 days, young perfect hunting techniques and are becoming independent of parents. Probably all young sexually mature by age 20 months but some try to breed as yearlings and when in heavy moult.

Success No accurate details. During three years, nine of 32 pairs probably produced no young, but observations vitiated by tendency of birds to make preliminary scrapes, by immatures making scrapes and not laying and by irregular observations. Average number of young reared for all nests 1.9 (0–4; 32) and for successful nests 2.6 (n=23). Variations according to nest-site: Type 1, 3.0 (2–4; 7); Type 2, 1.6 (0–4; 22); Type 3, 1.7 (0–3; 3). Most losses probably during hatching and first few days thereafter. Success tended to be best in nests protected from bad weather, i.e. those facing N, NW, SW. High levels of DDT can cause thinning of egg-shells and repeated breakage.

PLUMAGES Prepared by D.J. James. Much variation; three poorly differentiated forms: Bush, Eastern and Southern. Following are composite plumage descriptions; differences between the three forms are discussed under Geographical Variation. Age at first breeding unknown although juveniles have tried to nest (Fox 1977a).

Adult male Acquired by 16 months (Fox 1988) (not 11 months *contra* Fox 1977a). **Head and neck** Crown, nape, hindneck, ear-coverts and moustachial stripe, uniform black-

brown (119), with dark blue-grey tinge when fresh; moustachial stripe extends for one-quarter length of neck, bordering lower margin of narrow rectangular patch of brown (121C) feathers with dark-brown (121) shaft-streaks on side of neck. Narrow supercilium, of brown (121C) feathers with dark-brown (121) shaft-streaks, extends short distance behind eye. Lores, white with short black-brown (119) bristles. Chin, pale buff (124), grading to brown (121C) on throat; feathers have narrow dark-brown (121) shaft-streaks on chin, broadening towards throat; bases of feathers, white. **Upperparts** Black-brown (119) with dark blue-grey tinge when fresh; feathers, narrowly fringed rufous-brown (38), most narrowly on upper mantle, progressively broadening towards upper tail-coverts. When worn, feathers dark brown (119A) and fringes narrow or lost. Scapulars and lower mantle feathers have two narrow white bars on each web, broadly separated at shaft, giving appearance of four isolated spots, two on each web; more noticeable on scapulars; scapulars also have narrow white tips. Upper tail-coverts have two narrow light-brown (39) bars interrupted at shaft. **Underparts** Feathers of breast, white to pale buff (124) with broad dark-brown (121) central streaks that become narrower dark-brown (119A) shaft-streaks towards abdomen; sometimes narrowly fringed light brown (39). Feathers of vent, light brown (223C) with still narrower shaft-streaks. Feathers of abdomen, long and flimsy. Feathers of flanks, dark brown (121), with large white spots on edges and narrow white tips; spots, varyingly tinged brown (121C) at edge of feathers. Thighs, rufous-brown (38) with narrow black-brown (119) shaft-streaks, sometimes narrowly fringed light brown (39). Under tail-coverts, brown (37), with obscure dark-brown (121) markings beside shaft, narrow black-brown (119) shaft-streaks and moderately large light-brown (39) spots on edges. Axillaries, dark brown (121), with white spots on edges slightly smaller than on flanks. **Uppertail** Black-brown (119), with narrow buff (124) to light-brown (39) tip 1–2 mm wide; rectrices have 7–11 narrow (c. 3 mm wide) white bars (often tinged rufous near rachis) that are widely and evenly spaced (13–23 mm apart); these are interrupted and not aligned (offset from each other) at shaft on t2–t6 but do align on t1; bars on adjacent rectrices align when tail spread but not when folded. **Undertail** White bars are often less distinct and lacking in contrast. **Upperwing** Mostly black-brown (119). Primaries and secondaries have broad white bars on inner web (8–10 on p8), broadest at edge and petering out before shaft in sawtooth pattern; outer web has small indistinct white spots corresponding to bars on inner web; when wing spread, spots on edge of outer web and some bars on inner web show clearly on secondaries and on p7–p10; spots align with those on neighbouring feathers to give slightly barred appearance. Tips of remiges, edged whitish. Greater coverts, black-brown (119), with small white spots along outer web and obscure white bars on inner web. Rest of coverts lack spotting but are fringed rufous-brown (38); fringes become broader from marginal coverts towards median coverts. **Underwing** Remiges appear dark brown (119A) to brown (28), boldly barred white; trailing-edge of wing, uniform dark brown (119A), broadest at outer primaries, narrowing towards body. Greater coverts, dark brown (121) with moderately large white spots or bars on both webs and narrow black-brown (119) shaft-streaks. Lesser and median coverts similar but paler brown (37), with smaller spots that often coalesce along edges to produce streaked rather than spotted appearance. Marginal coverts, buff (124), to light brown (39), with dark-brown (119A) shaft-streaks and no spotting on edges. Subhumeral, as axillaries.

Adult female Similar to male but slightly darker. On average, differs in: upperparts and upperwing, slightly darker and browner, lacking blue-grey tinge; underparts, darker and slightly

more spotted; rectrices have fewer (6–10) bars; remiges average c. 0.3 more bars (9–11 on p8) (Fox 1977a). See also Measurements, Weights and Bare Parts.

Downy young Protophyle, white and thin; mesophyle, grey, thick and woolly at 11–12 days. Feathers appear from 14 days; males fledged by 52 days, females a week later (Fox 1977a, 1988).

Juvenile Fairly similar to adult but most appear uniform dorsally, and darker, less streaked ventrally; some are difficult to tell from adults on plumage alone. **Head and neck** Crown, nape, hindneck, ear-coverts and moustachial stripe, dark brown (121–119A). A few palest birds have a patch of feathers on each side of hindneck with large buff to rufous-brown bases visible and forming indistinct spots; these never so distinct as in some falcons (e.g. Australian Hobby). Moustachial stripe, slightly more distinct than in adult, appearing longer; borders an indistinct narrow rectangular patch of buff (124) feathers with dark-brown (121) shaft-streaks on side of neck. Supercilium, buff (124); broader than adult. Chin, lores and throat, white with narrow dark-brown (121) shaft-streaks, broadening towards base and sides of neck. Bases of feathers, white, mostly concealed. **Upperparts** Uniformly dark brown (121–119A), usually lacking fringes and barring of adult; a small proportion of birds (mostly or only male Eastern form) are barred dorsally like adults; all such birds have spots on hindneck and are pale ventrally, making them difficult to tell from adults except on bare parts (Fox 1977a). Some have slight off-white to pale-buff (pale 124) barring on mantle and scapulars, not as pronounced as in adults. Upper tail-coverts, usually uniform dark brown (119A), but often with indistinct light-brown (39) bars that are interrupted at shaft. **Underparts** Most birds lack the vertically streaked appearance of adults, appearing darker and spotted or barred; palest birds (mostly male Eastern form) are streaked on breast like adults. Feathers of breast, usually dark brown (119A) or brown (37), with narrow to broad dark-brown (121) shaft-streaks, pale-buff (124) spots at edges, and (sometimes) brown (33) tips. Feathers of flanks, usually darker brown (121), with larger, clearer buff (124) to yellow-brown (123B) tips and spots on edges. Abdomen, light brown (123A) with narrow brown (28) shaft-streaks; when fresh, feathers often narrowly fringed off-white. Thighs, brown (121C) to rufous-brown (c38) with varying brown (28) shaft-streaks. Under tail-coverts, like breast but with smaller spots on edges. Axillaries, dark brown (119A) with small white spots on edges. **Tail** Similar to adult; rectrices have 0–10 bars in a pattern similar to adult, but fainter and often obscure, especially on distal third; average 1.8 fewer bars than adult. **Upperwing** Similar to adult, but white bars on inner webs of remiges duller and smaller; average 0.5 fewer bars than adult of corresponding sex. Also lack white bars on inner webs of greater primary coverts (but these present on greater secondary coverts). Fringes, absent (or very thin and quickly lost) from all coverts. **Underwing** Greater coverts similar to adult, but lack shaft-streaks. Median and lesser coverts have fewer white spots on edges; they are brown (121C), with narrow brown (28) shaft-streaks and slightly paler brown (121C) fringes. White bars on inner web of remiges smaller than, but otherwise similar to, those of adult. Subhumeral, as axillaries.

BARE PARTS Based on Fox (1977a), freshly dead specimens at NMNZ, and photos (Moon 1979; NZRD; unpubl.).

Adult male Bill, grey-black (82), with grey (84) or light-grey (85) base. Cere and orbital ring, yellow (153). Iris, dark brown (223). Feet, yellow (56) or straw-yellow (57). Claws, grey-black (82). In breeding condition, colour of skin intensifies to bright yellow or orange-yellow but fade again by time eggs hatch (Fox 1977a). **Adult female** Similar to male except cere and

orbital ring, yellow-brown (123B); legs, yellow (55); feet, dark olive-green (49). Colours of skin do not intensify in breeding condition (Fox 1977a). **Downy young** Iris, dark brown. Bill, legs and feet, pink, becoming dull grey at c. 10 days (Fox 1977a). **Juvenile** Iris, similar to adult. Cere, orbital ring and feet vary greatly: from olive-green to pale blue, dull grey or brownish grey; change to yellow after 9 months; diet profoundly influences development of colours (Fox 1977a).

MOULTS Summarized from Fox (1977a); about 95 dated observations of live birds and skins (NMNZ, CM).

Adult post-breeding (Pre-basic). Complete; apparently can be interrupted at any stage of cycle. Primaries, centrifugal from p4; sequence, similar to but apparently less rigid than other falcons in HANZAB area; wings, often slightly asymmetrical; usually a maximum of 2–3 primaries growing at once. Secondaries, centrifugal from s5 or thereabouts; moult slightly later than corresponding primaries. Tail starts with t1 often followed by t2; rest of tail irregular, often rapid and asymmetrical; begins when remiges about one-third replaced. Timing varies somewhat; remiges and rectrices can be in moult most months but especially Nov.–May. Most nesting females observed were at some stage of moult but probably suspend when chicks are growing, so protracted. Nesting males observed were not moulting; moult may not begin until Jan. **Post-juvenile** (First pre-basic). Probably complete. Remiges and tail probably moult earlier than in adults (Sept.–Feb. at end of first year). Small proportion begin body-moult in late autumn or winter of first year. Two juvenile females trying to nest were moulting heavily in Dec. Sequence of main feathers, similar to adult post-breeding.

MEASUREMENTS Eastern form (Fox 1977a): (1) adults; (2) juveniles; includes combined live and freshly dead birds and skins from AMNH, BM, AWMM, Wanganui Mus., NMNZ, CM; skins from some museums measured for Fox by other workers; for wing-lengths from live and freshly dead birds, 1 mm was deducted to allow for shrinkage in skins; ages combined for tarsus; (3) skins at NMNZ, ages combined (measured by R.M. O'Brien).

	MALES	FEMALES	
WING	(1) 255 (6.70; 245–267; 14)	297 (7.00; 285–308; 16)	**
	(2) 260 (5.10; 250–268; 11)	296 (7.40; 280–308; 20)	**
8TH P	(3) 177, 177, 179	196, 198	
TAIL	(1) 175 (6.70; 165–189; 11)	207 (6.50; 195–222; 16)	**
	(2) 182 (5.30; 172–190; 8)	208 (5.90; 194–216; 13)	**
BILL C	(3) 22.7 (0.57; 22–23.4; 3)	24.1, 27.3	
BILL F	(3) 17.6, 18.3, 18.7	20.4, 22.5	
TARSUS	(1) 56.1 (1.50; 53.3–59.5; 18)	64.9 (3.80; 61.0–74.0; 23)	**
TOE	(3) 49.0, 53.0, 57.3	59.2, 65.1	

Southern form (Fox 1977a): (4) adults; (5) juveniles; as for (1) and (2) above. (6) Skins, ages combined; data as for (3) above.

	MALES	FEMALES	
WING	(4) 248 (8.40; 230–257; 7)	281 (4.40; 274–287; 10)	**
	(5) 248 (2.90; 243–251; 10)	280, 282, 284	
TAIL	(4) 167, 169	194 (5.20; 186–198; 4)	
	(5) 171 (2.90; 167–175; 7)	193	
BILL C	(6) 22.6, 28.2		
BILL F	(6) 21.4, 24.7		
TARSUS	(4) 56.6 (3.00; 55.1–58.2; 9)	61.2 (3.90; 54.0–65.7; 5)	*

Bush form (Fox 1977a): (7) adults; (8) juveniles; as for (1) and (2) above. (9) Skins, ages combined; data as for (3) above.

	MALES	FEMALES	
WING	(7) 236 (5.5; 226–244; 15)	273 (5.1; 268–281; 7)	**
	(8) 241 (5.2; 230–261; 22)	274 (4.5; 266–285; 16)	**
STH P	(9) 167 (2.98; 163–171; 6)		
TAIL	(7) 165 (7.0; 148–172; 12)	186 (3.4; 182–194; 8)	**
	(8) 166 (4.2; 159–174; 16)	189 (4.0; 181–195; 14)	**
BILL C	(9) 21.5 (0.79; 20.5–23; 6)	24.4, 26.4	
BILL F	(9) 17.4 (0.55; 16.8–18.4; 6)	20.7, 20.9	
TARSUS	(7) 54.9 (2.30; 51.5–62.5; 24)	60.7 (2.50; 55.1–66.0; 22)	*
TOE	(9) 49.5 (1.54; 46.7–50.7; 6)	56.0, 70.6	

Wing-length in each form is significantly different from the other two (Fox 1977a).

WEIGHTS (1) Eastern; (2) Southern; and (3) Bush forms. Data from live birds, corrected for estimated weight of contents of crop (Fox 1977a).

	MALES	FEMALES	
(1)	330 (12.0; 307–342; 6)	531 (37.0; 461–594; 16)	*
(2)	434–500		
(3)	264 (11.0; 252–280; 5)	474 (30.0; 420–507; 8)	*

The weight of four captives each varied by 50–70 g (13–19%) between measurements. Nestlings weighed c. 31 g when 1 day old, 32 (3 days), 41 (7 days), 100 (11 days), 220 (male) and 380 (female) (14 days) and reached adult weight by 18 days (Fox 1977a).

STRUCTURE Wing, fairly broad for falcon; tip, somewhat rounded. Eleven primaries; p8 longest, p10 41–53 mm shorter in adults (31–38 in juveniles), p9 4–21, p7 5–13, p6 23–30, p5 38–45, p4 51–58, p3 64–75, p2 77–91, p1 84–105, p11 minute. Outer web emarginated on p9–p8. Inner web emarginated on p10–p9, slightly so on p8. Thirteen to 14 secondaries including 3–4 tertials; longest tertial falls between p2 and p3 on folded wing. Tail, long (68–70% of wing-length); square at tip; 12 rectrices; t1 usually longest, t6 14–21 mm shorter; sometimes t2 longest (by 2–3 mm), if buff tip on t1 abraded. Cere, rounded. Bill, laterally compressed with sharp dorsal ridge; tomial tooth, small. Tarsus, slender, feathered on basal quarter; scales, rather large, reticulate; for details of pattern of scutellation, see Fox (1977a). Outer toe without claw almost equal to middle, inner c. 84% of middle, hind c. 66%.

GEOGRAPHICAL VARIATION Often treated as two species by early workers but now recognized as single highly varied species (Fox 1977a, 1988; NZCL; Peters). No subspecies currently recognized, but Fox (1977a, 1988) distinguished three forms: Bush, Eastern and Southern that differ in size, plumage, ecology, habitat and range, but intergrade considerably.

Bush form mostly inhabits native bush on NI and nw. SI as far S as Greymouth; Eastern form occupies more open country on SI along dry e. coast and from coast to coast across the centre; Southern form is coastal bird of Fiordland, Stewart I. and Auckland I. (Fox 1977a). Eastern form largest, averaging c. 21 mm longer in wing than Bush Falcon sex for sex. Southern form, intermediate but nearer Bush. Cline in size correlates better with habitat

than latitude. Eastern palest form; on average has more white bars on rectrices; pale bars on inner web of remiges may coalesce into pale panel along edge of feathers; in adults no consistent difference in body-plumage between forms was detected among strong individual variation (Fox 1977a); some juvenile male Eastern forms (5/27 skins) had pale dorsal barring and streaked underparts like adult and spots on hindneck (see Plumages), but this not recorded in other forms; one female and one male Eastern had some faint dorsal barring less pronounced than on adult (Fox 1977a). Bush and Southern forms are similar to each other though Southern are somewhat intermediate. Affinities of Southern form are poorly understood; three populations included herein unlikely to have much genetic exchange. Only one skin from Stewart I. was examined by Fox and although it had a wing-length intermediate between Eastern and Southern it was placed with the latter on ecological grounds. Fox (1977a) considered Fiordland and Auckland Is populations morphologically similar, but Auckland Is birds generally appear to show more rufous in adult plumage than do other forms (N. Hyde).

Brown & Amadon considered New Zealand Falcon an aberrant Hobby, allied with Brown Falcon. Based on morphological features, Fox (1977a) tentatively placed it with three S. American falcons, Orange-breasted *F. deiroleucus*, Bat *F. rufigularis*, and Aplamado *F. femoralis*; Cade (1982) followed Fox (1977a). Recent electrophoretic studies of feather-proteins suggest closest ties are with Brown Falcon (Olsen *et al.* 1989).

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Volume 2, Plate 25

New Zealand Falcon *Falco novaeseelandiae* (page 279)

1 Adult, bush form; 2 Juvenile, bush form; 3 Adult, eastern form; 4 Juvenile, eastern form; 5 Adult, eastern form; 6 Juvenile, eastern form; 7 Adult, eastern form; 8 Juvenile, eastern form; 9 Adult, bush form; 10 Juvenile, bush form