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THE MORPHOLOGY OF THE BROWN GOSHAWK *Accipiter fasciatus*

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Sexual, age, seasonal, population and subspecific differences in the morphology of the Brown Goshawk *Accipiter fasciatus* are described on the basis of data derived from birds captured near Macclesfield, Victoria, and from museum specimens. The physical characteristics of this species are also considered in the context of the genus *Accipiter*.

INTRODUCTION

The genus *Accipiter* comprises approximately 45 small to medium sized raptor species with short, rounded wings and long tails. Most of the smaller species (commonly termed 'sparrowhawks') have long, slender legs and toes, with an especially long middle toe. Larger species (commonly termed 'goshawks') generally have relatively shorter, thicker legs and toes. Females are larger and heavier than males in all species (Brown and Amadon 1968).

Despite numerous taxonomic studies (Hartert 1910, Stresemann 1923, Mayr 1957, Wattel 1973, 1981, Stresemann and Amadon 1979), Brown and Amadon's (1968) contention that the genus *Accipiter* is puzzling and insufficiently known remains valid. For example, several similar species exist sympatrically in some areas (such as Sulawesi, Indonesia), while some species (such as the Grey Goshawk *A. novaehollandiae*) exhibit considerable geographical variation. In Australia, the Brown Goshawk has obvious morphological similarity to both the Grey Goshawk and the Collared Sparrowhawk *A. cirrhocephalus*, however its intra- and interspecific taxonomy are controversial (Condon and Amadon 1954, Wattel 1973, 1981, Ford 1986). Here, morphological data for *A. f. fasciatus* are presented and discussed in relation to those for conspecific subspecies and congeneric species.

METHODS

Fieldwork was undertaken from early March to late August in 1980 and 1981, from late February to late July in 1982 and from late January to late April in 1983, in a 64 square kilometre area centring on Macclesfield (37°54'S., 145°30'E.), 50 km east of Melbourne, Victoria. Two major creeks and their tributaries flow through the area, approximately 65 per cent of which has been cleared and sown to pasture. The vegetation of the district has been described by Gullan *et al.* (1979).

Brown Goshawks were captured in 600 x 600 x 900 mm traps similar to the 'falling lid' traps of Kenward and Marcström (1983), baited with live white Feral Pigeons *Columba livia*. Eight to 12 traps were set at any one time, each placed in one of 49 positions used. Up to 14 linear measurements were taken for captured birds, using the procedures of Baldwin *et al.* (1931) and Gurr (1947). Wing areas were measured, regardless of moult condition, by tracing opened wing outlines onto paper, then measuring the silhouette areas with a leaf area index machine. Mass was recorded (±5 g), an estimated crop contents mass being deducted where appropriate. Wing loadings were calculated following Brown and Amadon (1968). Dimorphism indices (DI) were calculated following Storer (1966):

$$DI = \frac{\text{mean } ♀♀ - \text{mean } ♂♂}{½\,(\text{mean } ♀♀ + \text{mean } ♂♂)} \times \frac{100}{1}$$

As suggested by Earhart and Johnson (1970), square and cube roots of means were used to calculate dimorphism indices for non-linear measurements. The degree of dimorphism was categorized as 'weak', 'moderate' or 'strong' following Snyder and Wiley (1976). In order to determine the magnitude of dimorphism relative to size (wing length) in *Accipiter* a 'relative dimorphism index' (RDI) was calculated:

$$RDI = \frac{DI \times (\text{mean } ♂♂ \text{ wing length} + \text{mean } ♀♀ \text{ wing length})}{100}$$

Using Wattel's (1973) wing length data, dimorphism and relative dimorphism indices were calculated for 41 *Accipiter* species.

Specimens in the National Museum of Victoria collection were examined and measured prior to the commencement of trapping. Females (sexed by dissection) generally weighed more than 430 g, had tail lengths equal to or greater than 220 mm, and wing lengths equal to or greater than 275 mm. Subsequently, captured Brown Goshawks failing to meet at least two of these criteria were sexed as male. Birds were aged as 'first year', 'second year' or 'third year and older'. The ageing criteria of Condon and Amadon (1954) were used at the outset, although these were modified as the study progressed (see Results).

Specimens from the National Museum of Victoria, South Australian Museum, Museum of Western Australia and H. L. White Collection were also measured (12 linear parameters) to investigate possible differences between Victorian and south-western populations of the nominate subspecies, and between the nominate subspecies and *A. f. didimus*, the other widely accepted (far northern) Australian subspecies. The '97 per cent from 97 per cent' form of Amadon's (1949) '75 per cent rule for subspecies' was used to check the validity of *didimus*, and to test the possibility that south-western and Victorian populations of the nominate subspecies should be split at the subspecific level.

The plumage and bare parts of captured Brown Goshawks were examined to determine age class characteristics. Colours were standardized using Smithe's (1975) charts. Moult condition was recorded following Hamerstrom and Hamerstrom (1971). Since most trapping occurred during autumn and winter, supplementary moult data were obtained by observing birds in flight and at the nest, and through collection of moulted feathers. All captured individuals were fitted with stainless steel bands.*

The following nomenclatural conventions have been adopted: species names are given as binomials (e.g. *A. fasciatus*), subspecies names either as trinomials (e.g. *A. f. fasciatus*) or as the subspecific epithet (e.g. *fasciatus*).

RESULTS

Measurements

Sexual differences

Female Brown Goshawks were significantly larger ($p<0.001$) than males for all measurements taken on captured birds, with little range overlap for most parameters (Tables 1 and 2). The species was found to be strongly dimorphic for 16 of 17 parameters measured (Tables 1 and 2).

Age differences

Calculated means for third year and older Brown Goshawks were larger than those for first year birds for ten (males) and 13 (females) of the

*Bands were supplied by the Australian Bird-banding Scheme, CSIRO, Division of Wildlife and Rangelands Research, Canberra.

14 linear parameters measured, however the differences were not significant. Third year and older birds were 7.6 per cent (males) and 9.8 per cent (females) heavier than first year birds, combining the data for all seasons. The differences were significant for males ($t = 3.89$, $p < 0.001$) and females ($t = 5.60$, $p < 0.001$). Although there were no significant age differences in wing area, wing loadings were greater for third year and older birds: significantly so for females ($t = 4.17$, $p < 0.001$). In contrast, third year and older birds had shorter tails than first year birds: significantly so for males ($t = 2.94$, $p < 0.001$).

Seasonal differences

Brown Goshawks of both sexes increased in mass from summer to winter (Table 2). This trend, apparent for both first year birds and third year and older birds, was stronger for males than females. Wing areas and wing loadings of both sexes also increased from summer to winter (Table 2).

Differences between populations and subspecies

Brown Goshawks from south-western Australia were larger than Victorian birds for seven (males) and six (females) of 12 linear measurements on museum skins (Table 3). Although several differences were significant ($p < 0.05$), none were close to satisfying Amadon's (1949) rule for subspecies. However, the average dimorphism index was higher for the south-western population (16.9) than for the Victorian population (15.8).

TABLE 1

Linear measurements (mm) and dimorphism indices (DI) for Brown Goshawks captured near Macclesfield, Victoria.

Parameter	Sex	Mean	SD	Range	n	DI
Exposed culmen length	M	24.4	1.0	22.0-26.0	49	13.4
	F	27.9	1.2	24.5-30.7	63	
Exposed culmen length less cere length	M	17.2	0.8	15.1-20.1	49	15.1
	F	20.0	1.0	18.3-22.4	63	
Culmen depth	M	16.2	0.9	14.4-18.6	49	13.8
	F	18.6	1.0	16.0-21.2	63	
Hind toe length	M	20.7	1.8	17.1-24.4	50	18.4
	F	24.9	2.2	20.4-31.3	65	
Inner toe length	M	22.2	1.6	19.8-27.1	50	16.1
	F	26.1	1.7	22.2-30.2	64	
Middle toe length	M	39.6	2.5	34.1-44.5	50	13.2
	F	45.2	3.8	37.4-53.1	65	
Outer toe length	M	27.5	1.9	22.7-31.0	50	15.7
	F	32.0	3.1	26.1-43.1	65	
Hind claw length	M	19.8	1.0	18.3-24.4	50	19.6
	F	24.1	1.0	22.3-26.8	64	
Inner claw length	M	19.1	0.8	17.3-20.8	50	19.0
	F	23.1	1.0	20.6-25.8	64	
Middle claw length	M	15.2	0.8	13.0-16.9	50	19.0
	F	18.4	0.9	16.5-20.9	65	
Outer claw length	M	13.2	0.8	11.4-14.6	50	14.8
	F	16.1	0.9	14.5-19.1	65	
Tarsus length	M	74.5	2.3	69.1-79.2	81	10.4
	F	82.7	2.3	75.5-89.7	121	
Tail length	M	204	9.3	165-225	81	15.4
	F	238	8.8	220-260	122	
Wing length	M	263	8.1	235-280	81	13.8
	F	302	7.6	275-320	122	

Females referred to *didimus* using Condon and Amadon's (1954) plumage criteria were significantly smaller ($p < 0.05$ or $p < 0.001$) than Victorian and south-western *fasciatus* for all parameters (Table 3). Tarsus and inner claw length differences satisfied Amadon's (1949) rule for subspecies.

Differences between species in Accipiter

Of the 41 *Accipiter* species for which Wattel (1973) provided wing length data, only five exceed *A. f. fasciatus* in mean wing length for both sexes (Table 4). On the basis of wing length the Brown Goshawk is of average reversed size dimorphism in the context of a highly dimorphic genus. For its relatively large size, however, it is highly dimorphic, with a relative dimorphism index exceeded by only four of 40 other species for which Wattel (1973) gave wing lengths (Table 4).

Plumage and bare parts

By examining captured Brown Goshawks of known age, distinguishing plumage and bare parts characteristics were determined for three age classes (Table 5). Five individuals of each sex previously captured as first year birds were recaptured in their second autumn or winter. A further 18 birds were initially captured in second year plumage. However, none of these were recaptured in the ensuing year, preventing the establishment of a duration for this plumage.

Observation at nests indicated that there was considerable variation in the timing of moult commencement for breeding female Brown Goshawks. While some lost the first primary (numbered from the carpal flexure outwards) at about the time of laying (usually October), others appeared not to begin moult until about the time their eggs hatched (approximately 30 days after laying) or later. Primaries were replaced progres-

TABLE 2

Seasonal variation in mass, wing area and wing loading for Brown Goshawks captured near Macclesfield, Victoria.

Parameter	Season	Sex	Mean	SD	Range	n	Dimorphism Index
Mass (g)	Summer	M	335	44.6	260-385	7	
		F	549	47.8	500-610	7	
	Autumn	M	345	27.0	290-425	55	
		F	558	51.0	440-700	98	
	Winter	M	365	23.1	335-415	20	
		F	583	47.6	505-655	16	
	All seasons	M	349	29.3	260-425	82	15.8
		F	561	50.8	440-700	121	
Wing area (sq cm)	Summer	M	823	45.0	776-883	4	
		F	1 167	30.5	1 129-1 210	6	
	Autumn	M	877	75.2	778-1 089	21	
		F	1 190	89.7	984-1 399	12	
	Winter	M	909	62.1	815-1 034	16	
		F	1 192	84.6	1 058-1 379	12	
	All seasons	M	884	71.3	776-1 089	41	14.8
		F	1 188	81.6	984-1 399	43	
Wing loading (g/sq cm)	Summer	M	0.39	0.08	0.29-0.47	4	
		F	0.46	0.04	0.41-0.53	6	
	Autumn	M	0.40	0.03	0.33-0.45	21	
		F	0.48	0.05	0.40-0.60	25	
	Winter	M	0.41	0.04	0.33-0.46	16	
		F	0.49	0.04	0.42-0.54	12	
	All seasons	M	0.40	0.04	0.29-0.47	41	18.2
		F	0.48	0.05	0.40-0.60	43	

sively outwards, old feathers being shed when the new neighbouring feather was approximately half-grown. Secondary wing and tail feathers started to drop three to four weeks after the start of primary moult, secondaries being lost from various positions almost simultaneously. During November to January females often had two or three gaps with partly grown feathers among the secondaries. The central tail feathers were the first to be replaced, but data were insufficient to identify any further pattern in tail replacement. Three breeding males commenced moult during the first three weeks after their mates eggs hatched. Their feather replacement followed the same general pattern as that of the breeding females.

Most third year and older females (11 of 12 captured between 29 March and 29 April) had replaced all primary and secondary feathers by late March, however three of four males of this age class had not completed primary or secondary moult when captured in April. Third year and older birds of both sexes finished tail feather replacement later than primary replacement. The duration of moult for breeding females was 150 to 180 days, and breeding males appeared to complete moult in 130 to 170 days. Data were insufficient to ascertain the timing or duration of moult for first year birds acquiring second year plumage.

DISCUSSION

Measurements

Sexual differences

The pronounced reversed sexual dimorphism found for Brown Goshawks captured near Macclesfield is consistent with Baker-Gabb's

TABLE 3

Linear measurements (mm) from museum specimens of Victorian and south-western *A. f. fasciatus* and *A. f. didimus*.

Parameter: Length	Sex	Victorian *fasciatus*				south-western *fasciatus*				*didimus*			
		Mean	SD	Range	n	Mean	SD	Range	n	Mean	SD	Range	n
Exposed culmen	M	24.3	0.9	23.1-25.8	23	23.3	0.9	21.9-25.5	13	22.4			1
	F	27.1	1.0	25.0-29.3	19	27.2	1.7	23.5-30.0	16	25.6	0.3	25.3-26.0	5
Tail	M	200.0	7.2	186-211	22	199.3	7.8	187-214	12	167			1
	F	231.2	7.4	217-242	18	229.5	9.7	213-246	16	209.6	9.0	198-219	5
Wing	M	260.0	5.8	242-269	23	254.7	6.4	242-265	12	240			1
	F	294.5	7.8	275-307	19	296.1	7.4	282-309	16	274.6	5.6	268-280	5
Tarsus	M	73.9	2.3	70.0-79.2	23	74.8	1.3	73.2-77.4	13	71.0			1
	F	82.3	2.4	76.5-87.0	19	84.0	1.4	82.3-87.0	16	73.8	2.4	70.8-76.4	5
Inner toe	M	21.1	0.7	19.5-22.0	22	21.3	0.7	20.0-22.8	13	20.2			1
	F	25.5	1.1	23.2-27.0	19	25.3	1.3	22.5-27.3	16	22.0	1.5	20.0-23.7	5
Middle toe	M	37.4	1.1	33.9-39.0	22	38.4	1.5	36.5-40.4	13	34.1			1
	F	44.0	1.8	40.5-47.1	18	44.0	2.0	39.2-47.3	16	39.0	1.8	37.5-42.0	5
Outer toe	M	27.0	0.9	24.8-28.3	22	26.9	0.9	25.3-28.8	13	25.0			1
	F	32.1	1.2	29.9-34.7	19	32.0	1.4	29.5-35.0	15	28.1	1.2	26.5-29.7	5
Hind toe	M	19.6	0.9	16.9-21.2	22	19.7	0.7	18.7-21.0	13	18.7			1
	F	24.0	1.1	22.4-26.8	18	24.0	1.2	22.4-26.6	16	20.4	0.8	20.0-21.5	5
Inner claw	M	18.9	0.8	17.8-20.6	23	19.0	0.7	17.6-19.9	12	17.2			1
	F	22.4	1.0	20.1-24.2	19	23.1	0.9	21.1-25.1	16	20.2	0.5	19.4-20.7	5
Middle claw	M	15.2	0.9	14.0-17.3	23	15.3	0.4	14.6-16.0	12	13.8			1
	F	17.5	0.8	16.0-18.7	18	18.4	0.9	17.2-20.4	16	16.2	0.7	15.6-17.0	5
Outer claw	M	13.1	0.6	12.2-14.6	23	13.2	0.3	12.7-13.9	11	11.3			1
	F	15.4	0.7	14.6-17.0	19	16.0	0.7	15.0-17.0	16	13.9	0.9	12.5-14.7	5
Hind claw	M	19.6	0.9	17.8-21.5	23	19.5	0.7	18.3-20.4	12	17.0			1
	F	24.2	1.1	21.0-25.0	16	24.2	1.1	22.7-26.5	16	20.9	0.9	19.8-21.7	5

TABLE 4

Wing length*, dimorphism index (DI) and relative dimorphism index (RDI)** in *Accipiter* species.

Accipiter species	Wing length (mm) Mean ♂	n	Mean ♀	n	DI	RDI
A. poliogaster Grey-bellied Goshawk	251.0	2	273.7	4	8.7	45.6
A. trivirgatus Crested Goshawk	198.5	2	220.2	4	10.4	43.5
A. griseiceps Celebes Crested Goshawk	177.1	8	201.9	9	13.1	49.6
A. tachiro African Goshawk	210.4	7	241.4	13	13.7	61.8
A. castanilius Chestnut-bellied Sparrowhawk	154.0	4	180.7	4	16.0	53.5
A. badius Shikra	176.4	5	198.7	4	11.9	44.6
A. brevipes Levant Sparrowhawk	221.6	7	234.9	9	5.8	26.4
A. butleri Nicobar Shikra	168.5	2	181	1	7.2	25.1
A. soloensis Grey Frog Hawk	186.8	13	195.5	11	4.6	17.5
A. francesii France's Sparrowhawk	158.2	9	175.7	7	10.5	35.0
A. trinotatus Spot-tailed Goshawk	151.3	10	164.9	25	8.6	27.1
A. *fasciatus* Brown Goshawk	**262.1**	**14**	**302.3**	**21**	**14.3**	**80.7**
A. novaehollandiae Grey Goshawk	259.6	10	308.4	9	17.2	97.6
A. melanochlamys Black-mantled Goshawk	219.4	5	253.2	5	14.3	67.5
A. albogularis Pied Goshawk	209	1	245.3	6	16.0	72.6
A. rufitorques Fiji Goshawk	201.7	11	236.7	7	16.0	35.1
A. haplochrous New Caledonia Sparrowhawk	204.0	7	236.5	11	14.8	65.1
A. henicogrammus Gray's Goshawk	224.2	5	245.4	12	9.0	42.2
A. luteoschistaceus Blue and Grey Sparrowhawk	191.3	3	211.5	2	10.0	40.2
A. poliocephalus Grey-headed Goshawk	194.8	10	218	1	11.2	46.2
A. superciliosus Tiny Sparrowhawk	139.2	4	161.2	4	14.6	43.8
A. collaris American Collared Sparrowhawk	148.5	2	172.8	5	15.1	48.5
A. erythropus Red-thighed Sparrowhawk	148.4	7	170.0	6	13.6	43.3
A. minullus Little Sparrowhawk	141.7	27	160.8	24	12.6	38.1
A. gularis Japanese Lesser Sparrowhawk	165.9	32	189.1	21	13.1	46.5
A. virgatus Besra	147.4	15	173.3	10	16.2	51.9
A. cirrhocephalus Collared Sparrowhawk	208.4	17	241.0	17	14.5	65.1
A. erythrauchen Moluccan Sparrowhawk	166.5	2	201.2	4	18.9	69.4
A. rhodogaster Vinous-breasted Sparrowhawk	165.0	9	203.3	12	20.8	76.6
A. ovampensis Ovampo Sparrowhawk	224.4	22	250.9	13	11.2	53.2
A. madagascariensis Madagascar Sparrowhawk	178.0	3	225.0	13	23.3	93.8
A. nisus Sparrowhawk	200.6	101	237.8	67	17.0	74.5
A. rufiventris Red-breasted Sparrowhawk	201.2	24	232.6	15	14.5	62.9
A. striatus Sharp-shinned Hawk	173.5	12	207.1	15	17.7	67.3
A. bicolor Bicoloured Sparrowhawk	206.7	3	240.0	4	14.9	66.5
A. cooperii Cooper's Hawk	233.2	9	262.4	9	11.8	58.4
A. melanoleucus Black Sparrowhawk	293.3	10	340.7	3	15.0	95.1
A. henstii Henst's Goshawk	280.7	7	322.5	2	13.9	83.8
A. gentilis Goshawk	323.0	5	362.7	3	11.6	79.5
A. meyerianus Meyer's Goshawk	300.0	2	332	1	10.1	63.8
A. buergersi Bürger's Goshawk	296.3	3	323.0	2	8.6	53.2

*Mean wing lengths were obtained from Wattel (1973) and are for nominate subspecies excepting:

A. striatus – The mean used is for *A. s. velox*.
A minullus – The mean used is derived from a sample including specimens of both *A. m. minullus* and *A. m. tropicalis*.

**Dimorphism and relative dimorphism indices (defined in Methods) were calculated from wing length means.

(1984) data for museum specimens. The dimorphism indices calculated by that author for exposed culmen length (16.7) and wing length (13.8) are similar to those calculated here, though the mass dimorphism index he reported was comparatively high (20.1 versus 15.8). The dimorphism indices reported here for middle, inner and hind claw length (19.0, 19.0 and 19.6 respectively) suggest the possibility of greater niche separation between the sexes (in diet, for example) than might be predicted from the wing length index (13.8).

As reported previously (Condon and Amadon 1954, Disney 1963), Brown Goshawks can be readily sexed in the hand on the basis of size. Despite overlap in the range in measurements for most parameters (including overlap in wing and tail length not previously reported), an individual in south-eastern Australia weighing more than 450 g and with tail and wing lengths exceeding 225 and 280 mm respectively is almost certainly female. One with mass less than 400 g and with tail and wing lengths less than 200 and 275 mm, respectively, is probably male.

TABLE 5

Plumage and bare parts characteristics* for three *A. f. fasciatus* age classes.

	first year birds	second year birds	third year and older birds
Head and nape plumage	Streaked white: most feathers are white with a dark brown 'teardrop' at the tip. Some individuals are rufous (Colour 39 or 139) across the lower nape. Rufous edging to crown feathers gives the head a pronounced rufous appearance in some individuals.	Crown feathering is brown with some white streaking. Rufous nuchal collar (from Colour 240 to Colour 38) present for six of ten birds captured in their second winter.	Crown feathering is uniformly grey despite underlying white feather bases. Rufous nuchal collar is always present: often brighter and relatively wider in males.
Ventral body plumage	Brown streaking (Colour 2 to Colour 20) on throat and chest. Grey interspaces appear as dark as Colour 86 where they overlie brown areas.	Broad transverse barring with pronounced dark brown (Colour 20, 21 or 129) edging to rufous bars. Throat usually coarsely dappled brown.	Transverse barring is finer than in second year birds and paler due to reduced brown bar edging. Rufous in barring is paler than in second year birds. Throat dappling fine and grey (Colour 85).
Dorsal body plumage	Brown (Colour 20 or 21) with rufous (Colour 38 or 39) edging. Rufous edging often lost from the upper feathers by mid-winter.	Similar to that of first year birds, but feathers lack rufous edging.	Generally grey (Colour 83) but can be much lighter (rarely to Colour 85). Females generally (but not always) 'browner' than males.
Tail and tibiae barring	Variable in conspicuousness, but generally distinct. Tibiae barring brown (Colour 38 or 39) edged darker.	Tail barring indistinct, often barely visible on central feathers. Tibiae barring is fine and tawny, usually edged brown.	Tail barring as for second year birds. Tibiae barring very fine and tawny. Brown edging to tibiae bars is reduced or absent.
Eyes	Iris dark after hatching but light brown (Colour 119B to 219B) by fledging. Iris changes to cream or pale yellow after fledging, with some brown flecks. Some birds have bright yellow irides by May, often paler near the circumference, but others still have pale irides in August and possibly later.	Irides are generally bright yellow (Colour 55). A few birds of both sexes have pale yellow irides.	Irides bright yellow (Colour 55) most birds. A few males have darker (Colour 18) irides, while other individuals of both sexes have pale yellow irides.
Tarsi and feet	Tarsi are pale yellow (Colour 54). The feet are more intensely pigmented.	Tarsi and feet more intensely pigmented than in first year birds, sometimes close to orange (Colour 18).	Tarsi and feet are as for second year birds.

*Colour numbers refer to those in Smithe (1975).

Age differences

That third year and older Brown Goshawks were found here to be larger for most parameters than first year birds supports similar findings for other accipiters (Mueller and Berger 1968, Marcström and Kenward 1981, Newton *et al.* 1983). Similarly, the finding that older Brown Goshawks generally have shorter tails than first year birds parallels data for the Goshawk *A. gentilis* and Sparrowhawk *A. nisus* (Mueller and Berger 1968, Amadon 1980). The last author hypothesized that long tails would help inexperienced birds master flight and reduce their injuries in collision with prey and vegetation during foraging. Long tails probably also produce more buoyant flight by increasing the surface expanse presented to the air.

Seasonal differences

The summer to winter increase in mass reported here for Brown Goshawks is known for many mammals and birds including several accipiters (Mueller and Berger 1968, Newton 1973, Mueller *et al.* 1981a, b). Thus, Brown Goshawks have least mass in summer when their flight surface area is reduced by moult. If mass peaked in summer, loadings would be greatly elevated during that period, possibly necessitating changes in foraging and other behaviour. Instead, wing loading was calculated to increase from summer to winter, as previously noted for Cooper's Hawk *A. cooperii* (Mueller *et al.* 1981b).

Differences between populations and subspecies

On the basis of limited data, Debus (1984) suggested that Brown Goshawks in south-western Australia might be larger than those from the south-east, where the sympatric Grey Goshawk females might have imposed an upper limit on the size to which the former species could evolve. The data presented here add qualified support to this view, particularly for females, which might be expected to expand their niche more than males in the absence of a similar large competitor. If Brown Goshawk movements are largely internalized in the south-west (Aumann 1986), the population might have undergone the niche broadening characteristic of isolated contexts (Keast 1976). The greater reversed dimorphism found in the south-west would be a long term product of this isolation, competitive release, and niche expansion (Cody 1974, Opdam 1975, Clouet 1978). Australian *Accipiter* assemblages lend themselves well to the investigation of intra and interspecific niche utilization and reversed size dimorphism in raptors, and additional morphometric and ecological data for populations throughout the continent would be valuable.

The nominate *A. f. fasciatus* is the largest subspecies of the Brown Goshawk (Wattel 1973), a size superiority expected on the basis of variation in accordance with Bergman's Rule (larger-bodied forms being found at higher latitudes). That *didimus* is sufficiently smaller than *fasciatus* to merit subspecific status without recourse to plumage differences is interesting in view of Ford's (1986) suggestion that the two might warrant separation at specific level. There is strong evidence, however, for a winter invasion of the range of *didimus* by *fasciatus* (Condon and Amadon 1954, Wattel 1973, Aumann 1986), and a few museum specimens have intermediate characteristics. Furthermore, Wattel (1973) argued persuasively for an Australian origin for *didimus*, rather than the New Guinean origin proposed by Condon and Amadon (1954). If the Brown Goshawk has been a successful island colonist (Mayr 1944, Wattel 1973), producing subspecies as different as *hellmayri* (on Timor and similar to *didimus*) and *vigilax* (on New Caledonia and similar to *fasciatus*), the elevation of *didimus* to specific status would present a series of taxonomic problems.

Differences between species in Accipiter

The nominate subspecies of the Brown Goshawk is one of the largest of the accipiters; however, it has an unusual combination of characteristics for a large form. Its long tarsi are more typical of small bird-catching species than of larger species, but it lacks the relatively long middle toe characteristic of the small bird-catchers. Furthermore, the Brown Goshawk's tarsi and toes are heavy, particularly in females, and the bill is fairly strong. Although similar tarsus, foot and bill structure occurs in the African Goshawk *A. tachiro*, Black-mantled Goshawk *A. melanochlamys* and the New Caledonia Sparrowhawk *A. haplochrous*, these are all much smaller than *A. f. fasciatus* (Wattel 1973). Wattel (1973) also noted Brown Goshawks to have relatively long tails and long, pointed wings in the context of *Accipiter*. He considered these characteristics to be associated in the genus with use of open

habitat and with migration. There is evidence that the Brown Goshawk is a partial migrant over much of its Australian range (Aumann 1986), and it certainly uses more open habitat than its Australian congeners. The species appears to have benefited from partial forest clearance, possibly at the expense of its congeners (Blakers *et al.* 1984). Further, the Brown Goshawk seems to have been better adapted morphologically, through its size, long tarsi, and bill, toe and claw strength, to capitalize on large introduced avian and mammalian prey animals. At Macclesfield the species eats many Rabbits *Oryctolagus cuniculus* and Common Starlings *Sturnus vulgaris* as part of a very broad prey spectrum (Aumann 1986). This dietary breadth can probably be attributed to the species' relatively large size, to its high degree of sexual dimorphism, and to a predatory versatility derived from its unusual combination of physical characteristics.

Plumage and bare parts

Plumage changes with age in most (probably all) accipiters. Generally, a first year plumage characterized by vertical streaking on the throat and breast is replaced by an 'adult' plumage with horizontal ventral barring prior to the second winter (Brown and Amadon 1968). An intermediate plumage is known for some species. There is wide agreement between the Brown Goshawk ageing criteria of Condon and Amadon (1954) and those described here, however important differences are as follows: 1. second year Brown Goshawks often have full nuchal collars; 2. upper surface feathers of second year birds are brown, similarly coloured to those of first year birds; 3. conspicuousness of tail barring is not useful for distinguishing second year from older Brown Goshawks; 4. though tarsal scute fusion is generally more complete in older individuals, this characteristic is not reliable for separating second year from older birds.

There is considerable variation among individual Brown Goshawks in each age class. Although the ventral barring of second year plumage is browner than in older birds, even this character is variable. A progressive reduction in the brown edging to ventral barring may occur over several years, raising the possibility that 'second year' plumage as described here lasts for more than one year (at least for some individuals). Although environmental factors are manipulated in studies with captive birds, monitoring captive Brown Goshawks through several moults would provide useful evidence in this regard.

The duration and pattern of Brown Goshawk moult described here is consistent with that reported for captives (Morris 1976). In most respects this pattern is typical for *Accipiter* (Stresemann and Stresemann 1960, Voitkevitch 1966), though tail moult finishes before primary moult in the Sparrowhawk (Newton and Marquiss 1982). As reported here for Brown Goshawks, breeding Sparrowhawk males commence moult at about the time their young hatch, three to four weeks later than females. During incubation, male accipiters provide food for themselves and their mates (Brown and Amadon 1968), and delayed moult commencement may be a response to the need for effective foraging capacity during this period. Although food needs increase after hatching, loss of flight capacity may be offset by increased prey availability (Newton 1979).

The apparent variability in the timing of moult commencement for breeding female Brown Goshawks requires investigation in temperate and tropical areas. In several temperate accipiters females commence rapid moult at about the time of laying (Newton and Marquiss 1982); thus, much of the period of diminished flight capacity coincides with the only period of the year when foraging is not required. Olsen *et al.* (1982) noted a captive Brown Goshawk to drop her first primary five days before laying. Moult during incubation is not known for females of tropical accipiters, although Schmitt *et al.* (1982) reported W. R. Tarboton to have seen a female Shikra *A. badius* in primary moult while feeding nestlings.

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