BREEDING BEHAVIOUR AND ECOLOGY OF THE AUSTRALASIAN HARRIER (Circus approximans) IN THE MANAWATU-RANGITIKEI SAND COUNTRY, NEW ZEALAND

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ABSTRACT

During 1976-78, 212 Australasian Harriers *(Circus approximans)* were trapped and individually marked, and a total of 220 retraps and 319 resightings were made. During two breeding seasons the population density averaged one bird per 50 ha.

Seven territories averaged 31 ha each, and the home ranges of four pairs averaged 900 ha each. Some of the behaviour and displays described have not been previously recorded for the Australasian Harrier, including territory-boundary display flights, border patrolling, eviction of intruders, nest inspection, courtship feeding, copulation, and post-fledging behaviour and dispersal. Also described are display soaring, display diving, feeding at plucking stations, aerial food passes and the post-hatching parental division of labour. Nineteen pairs fledged an average of 1.0 young per nest site and 1.8 young per successful nest. Birds observed breeding at Pukepuke Lagoon for a second consecutive season were more successful than new arrivals. Two cases of polygyny were observed.

INTRODUCTION AND METHODS

The Australasian Harrier *(Circus approximans)* is one of only two diurnal raptors resident in New Zealand. It is slightly heavier than its close relative the European Marsh Harrier *(C. aeruginosus)*, which is the largest of the European harriers (Brown & Amadon 1968). Throughout its range in Australasia and Oceania the Australasian Harrier is a bird of the open country, where it slowly quarters reeds, rushes, fields of tall grass, and crops. It is common and widespread in New Zealand, but its breeding biology has received little study except for the work of Stead (1932) and Soper (1958), who described some of the displays that occur during the breeding season. Soper also recorded data on clutch size and incubation period.

I studied Australasian Harriers during 1976-1978 as part of a wider investigation of the influence of predators at Pukepuke Lagoon Game Management Reserve (175°15'E, 40°10'S). Pukepuke Lagoon is situated 3 km from the coast near the centre of the Manawatu-Rangitikei sand country, an area of approximately 4200 km^2 on the south-west coast of the North Island. Detailed descriptions of the region

can be found in the New Zealand Ecological Society Proceedings (1957), Cowie & Smith (1958) and Cowie *et al.* (1967).

The 1200 ha study area was dominated by rows of vegetated sand dunes, which ranged between 5 and 20 m above sea level. Between these low dunes were extensive sand plains and peaty swamps. Marram *(Ammophila arenaria)* and spinifex *(Spinifex hirsutus)* were the dominant plants on the foredunes and marram and tree lupins *(Lupinus arboreus)* on the moderately well stabilised dunes immediately inland. Pines *(Pinus radiata)* had been planted on some dune ridges and covered about 12% of the study area. On the ungrazed sand plains and peaty swamps, red rush *(Leptocarpus simplex)*, raupo *(Typha orientalis)* and cabbage trees *(Cordyline australis)* were the dominant plants. Intensively grazed and well-drained pastures of introduced grasses covered about 50% of the study area.

Six cage traps adapted from a design by Hollom (1950) and three automatic bownets (Tordoff 1954) were used. They were baited with rabbits *(Oryctolagus cuniculus)* shot by the Manawatu Pest Destruction Council.

Birds were sexed by weighing with a spring balance accurate to 10 g and by examination and measurement of their tarsi, feet and culmen, females being significantly larger for all these measurements (Carroll 1970, Fox 1977). Adults and juveniles were distinguished by moult differences. The rectrices of juvenile harriers *(Circus)* also often contain stress marks (Hamerstrom 1967).

All adults and most juveniles were fitted with individually colour-coded patagial tags similar to those made by Fitzner (1975). All birds were also banded with individually numbered stainless steel bands provided by the New Zealand Wildlife Service.

Trapping locations and sightings of individually marked birds were plotted on maps of the study area so that their home range and territory sizes could be estimated. Within each resident bird's home range was a smaller favourite hunting area where 75% or more of trappings and resightings were made. Observations were usually made from a high vantage point through 7 x 50 binoculars.

Because Australasian Harriers readily desert their eggs and young if disturbed by man (Stead 1932, Soper 1958), I seldom visited nests until after the young had fledged. Hence, I have no data on clutch size, incubation period or hatching success.

Following Newton's (1976) guidelines, I have used the term " nest site " for the nest and its immediate surroundings, " territory " for the area that was defended around the nest site, and " home range " for the area that included the territory and hunting areas of the pair. Birds were considered to be permanent residents if they were seen or trapped regularly for 9 months.

RESULTS

Trapping, resightings, and population density

Of the 212 Harriers trapped, 76 were retrapped a total of 220 times and 56 were resighted a total of 319 times. Nineteen (9%) of the trapped birds were adult males, 81 (38%) juvenile males, 34 (16%) adult females and 78 (37%) juvenile females.

During the 1976-77 and 1977-78 breeding seasons, averages of 18 breeding birds and six juveniles were resident in the 1200 ha study area, giving a population density of one bird per 50 ha.

Territory size, formation, and maintenance

During both breeding seasons the number of breeding birds and

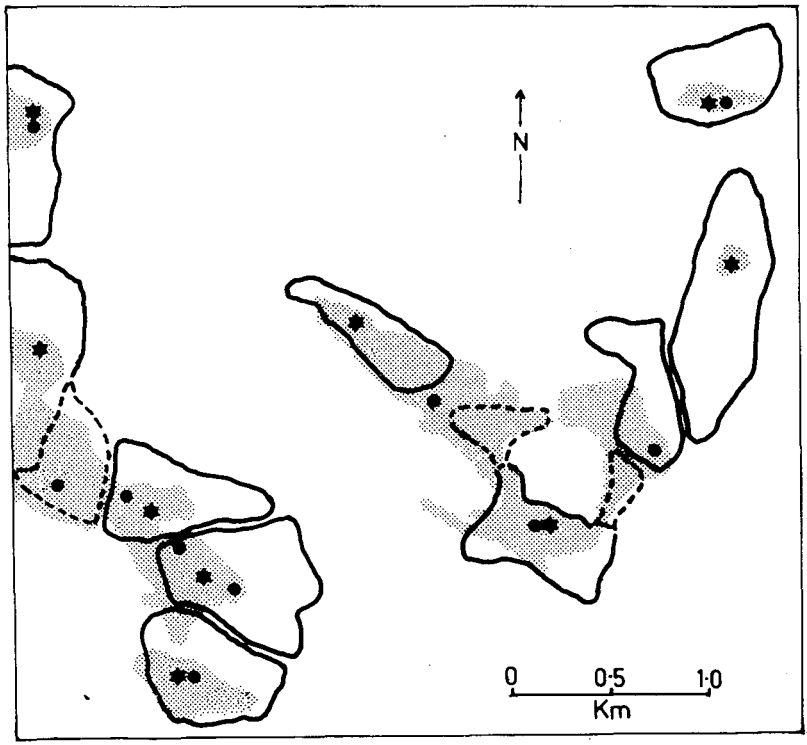

FIGURE 1 — Australasian Harrier territories and nest sites. Light stipple = swampland; unshaded area = open farmland, dune ridges and pine plantations; solid lines = territory boundaries 1976-77; dotted lines = parts of territories not defended after young hatched 1976-77; stars = nest sites 1976-77; dots = nest sites 1977-78.

the number of territories defended (10) in the study area remained constant (Fig. 1). Territory sizes were calculated during the 1976-77 breeding season only. Territory boundaries were clearly demonstrated during border disputes and evictions of intruders. Seven paired birds' territories averaged 31 ha (range 18-55 ha). Two of these decreased in size by about 20% after the young hatched during November, and average territory size was then 27 ha (range 18-42 ha). Neighbouring males then hunted but did not defend the areas that the former territory owners had relinquished. The territory was defended to a height of about 20 m at the boundary and 20-30 m over the nest site. Territory boundaries often corresponded to dune ridges or ecotones such as that between swamp and farmland. All parts of the territory were defended with equal vigour. Males and females defended the same territory, except in cases of polygyny, when each female defended about half the area defended by the male. Co-wives in contiguous territories defended them against each other as well as other intruders.

All adult males and females formed pairs and defended territories, whereas most first-year birds did not. However, two different first-year males established small territories of about 12 ha in August 1976 and 1977. One of the males was paired with a marked adult female for about 6 weeks, but both males' territories were abandoned 3 months after their establishment.

Neighbouring Harriers influenced the size and shape of one another's territories through boundary displays, border patrols and eviction of intruders. In late May the first evictions from incipient territories were seen, and in mid-July the first territorial displays were seen.

Rival males displayed by flying in the same direction on each side of the territory boundary about 10 m apart and at a height of about 15 m. They flew with their wings held at an exaggeratedly high angle and with their bright orange-yellow tarsi thrust straight down. Their flight was slow with very few wing-beats and their pale ventral surfaces and dark underwing bars were conspicuous. Territorial displays were usually silent, the sharp *chit-chit-chit* threat call being voiced only during interspecific territory defence. However, a *kirrk* call similar to the male's courtship call was occasionally heard when both birds landed on prominent trees or knolls in their respective territories. They would remain perched for about 5 minutes and then usually leave the area and begin hunting.

Territory boundaries were not clearly defined until September. Territory display flights were observed as often as six times a day but decreased in frequency as the breeding season progressed. They were replaced by border patrolling, which was characterised by males flying unaccompanied along the contours of their mutual territory boundary but without adopting the territory display flight. One of two neighbouring adult males was seen patrolling 12 times and the other six times during one afternoon in December. Although females

often evicted intruders from the territory, they were seen only twice to make territory display flights and twice to fly border patrols. These occurred after they had built nests in October.

Once nest building had started, the rate of observed evictions of intruders from territories increased markedly from two per 100 hours' observation (300 hours of observation) in August and September to 20 per 100 hours' observation (450 hours of observation) from October until the end of December. This change was due to an increased intolerance of intruders rather than increased provocation by them. Until the nest was built, adult males and females usually evicted only birds of their own sex, but after this time they were usually indiscriminate in their evictions. On four occasions, however, males were seen to start courtship diving when females intruded on their territories.

To evict intruders, the defending bird flew fast, low and directly at the intruder, attacking it or pursuing it closely in a fast chase until it either crossed the territory boundary or climbed to at least 20 m. Once the intruder was above this height, female territory owners usually returned to the centre of the territory, whereas males " escorted " the intruder to the boundary, flying below and often ahead of the intruder, which followed him. The male often thrust its tarsi down when it reached the boundary and flew along the boundary for a short way before returning to the centre of the territory or continuing hunting.

Adults usually had no difficulty evicting intruders, but repeated disturbance from other Harriers probably caused at least two pairs that began nest building in a communal roost area to abandon their breeding attempts. The communal roost was used throughout the year by non-breeding birds and occasionally by breeding adult males. The territory owners were unable to evict the birds that came to the roost in the evening, although the males spent about an hour each evening trying to do so.

Home range

In the 1976-77 breeding season, the home ranges of four pairs averaged 900 ha and overlapped those of their neighbours by about 75%. Within each 900 ha were a pair's favourite hunting areas, which totalled about 300 ha. Each bird in a pair sometimes hunted over areas that were regularly hunted by its mate and sometimes over other areas where its mate was rarely seen. Favourite hunting areas varied from one or two large areas of swampland to many small areas of tall vegetation interspersed with open farmland. The four pairs' favourite hunting areas overlapped those of their neighbours by about 25%, but birds from different pairs were seldom seen in the same area at the same time. First-year birds were not usually evicted from a pair's favourite hunting area unless they flew within about 100 m of a hunting adult.

First-year birds' daily home ranges during the breeding season were similar in size to the adults' favourite hunting areas, but the total area they ranged over was much larger. I was uncertain how far they ranged, but reported observations of marked birds and banding returns from outside the study area (Baker-Gabb 1978, Robertson 1978) indicated that usually they did not leave the sand country. This extends 20 km north, 20 km south and 15 km east of Pukepuke Lagoon.

Courtship displays

During June, with increasing frequency, pairs of adult Harriers were seen soaring together on a thermal. When they soared in display their wings were raised high and bent slightly back. The male, which was often the higher bird, occasionally stooped close to the female. The female then sometimes flew on a fast zig-zag course away from the male with him in close pursuit for about 20 seconds. More often, however, she flipped over and thrust her tarsi at the male, a manoeuvre reminiscent of the aerial food-pass seen later in the breeding season. Pairs soared and chased most often late on warm sunny mornings.

Soaring usually preceded display diving. In July, the first shallow undulating display-flights were performed by the male, accompanied by the male's short *kee-a* courtship call. When flying lower than 50 m above the ground, the displaying bird occasionally abruptly reversed its flight direction or " switched-back " (Hamerstrom 1969). If a female was displaying above her mate which was perched near the nest site, she regularly gave a loud *kee-o* call, which the male answered with a soft *kyuck*.

Shallow display flights rapidly progressed into the spectacular diving display, which was performed by both sexes but most often by the male. The full diving display or " sky-dance " (Hamerstrom 1969) consisted of a series of U-shaped dives at heights varying from 50 to 200 metres above the ground. The displaying bird flew with deep exaggerated wing beats as it dived steeply for about 25 m, and then sailed out of the dive on upraised wings and executed a full- or half-barrel roll at the zenith. The courtship call was given during display diving. If the female had been soaring with the male before he made his diving display, she either descended slowly with her wings held high and landed in tall vegetation or she left the area and began hunting. If the female landed, the male continued diving and began twisting like a falling leaf before eventually alighting near her.

No first-year Harriers were seen courting. However, some first-year birds must have been involved in courtship display because one first-year female fledged young from Pukepuke Lagoon. Males were not observed courting and breeding successfully until they obtained paler adult plumage in their second or third year.

Courtship feeding

Courtship feeding usually took place out of sight in tall raupo or red rushes. However, two males were seen to feed their mates regularly at "cock nests," the unlined platforms built by the male from early September onwards. These males flew to the cock nest with prey, raised their wings high, and gave the courtship call. The female, which was usually perched on a cabbage tree nearby, then flew to the cock nest and took the prey. As the female landed, the male left and perched nearby. Males that were not seen at cock nests fed their mates in a similar way on an area of dry ground in their territories. Courtship feeding took place probably once a day for about 6 weeks, beginning in mid-September.

Nests

While looking for a nest site during September, the pair flew low over their territory. When one bird landed, the other continued to soar at a low height. The roles were then reversed. When on the ground, the male frequently gave a short quickly repeated *see-o* call.

Females began nest building in late September and early October. The main nest was built within 50 m of the male's cock nest. Nest building was unobtrusive, the female flying low to areas about 50 m from the nest site to gather material. Nest material was carried in the beak or claws. Nests took about 4 weeks to complete.

Of the 19 nests built in the study area during the two breeding seasons, 11 were in dune-hollow swamps that had been fenced to keep out domestic stock and eight were in raupo swamp. The average distance between each nest site and its nearest neighbour was 910 m (range 300-1600 m).

Ten nests were examined only after the young had fledged. They averaged 80 x 50 cm with the base of the cup 40 cm above ground level or water level. The oval nests commonly consisted of a sturdy base of lupin, thistle, toetoe, and flax stems with cabbage tree leaves, marram and grasses forming a lining. All seven nests examined in dune-hollow swamps were built on red rushes with a toetoe growing beside and to the west of the nest. The three nests examined in raupo swamp were built on sedges *(Carex)*. All ten nests were surrounded by tall vegetation on three sides with an opening to the east. Thus, they were protected from the potentially strong rain-bearing westerly winds that prevail in the study area.

Copulation

I observed copulation on only three occasions, during October. Twice the female was initially soaring high over the male, which was hunting in the territory below. When the male caught a green and golden bell frog *(Litoria aurea)* in a farm drain, the female began a diving-display descent and landed 2 m from the male. He flew 20 m away with the prey and continued feeding. The female's high-pitched

soliciting *seee-uh* call was heard as she once again flew to the male. This time he left the frog and flew 3 m away. The male stood side-on to the female with his wings raised. The female was in a crouched posture facing the male and the soliciting call was again given as she pecked at the frog. The male then flew and alighted on her back. Copulation was completed in about 10 seconds with the male flapping to maintain balance. He then flew 30 m away and began preening. The female completed her meal and then bathed in the farm drain. The third copulation was essentially the same, except that the male flew into the territory and presented the female with a small prey item before copulation occurred.

Incubation and the aerial food-pass

Male Harriers were not seen to land at the nest once the females had begun incubating eggs in early November. From this time onwards food was passed from male to female only by the aerial food-pass. Small prey about the size of a house mouse *(Mus musculus)* was transferred on average three times a day. Although aerial food-passes varied, they commonly consisted of the male calling the female from the nest with a quiet *chuck-chuck-chuck* and then flying slightly above and ahead of her. The male then dropped the prey about 2 m to her. The female flipped over to catch the prey in one or both of her feet. On three occasions I saw passes made from claw to claw. The food item was not missed by the female in a total of about 150 aerial food-passes. After the pass the female flew to eat the prey at a plucking station, a regularly used area of dry ground some 30 m from the nest.

Division of labour and post-hatching behaviour

During the 12 weeks between the time nest-site inspection was observed and the time the young were 2 weeks old, all females seldom left their territories, where they were fed by the males. When not incubating, they were often seen perched on prominent cabbage trees for periods of up to an hour, soaring over their territories, or making short flights to collect nest material. The males were away hunting for most of this time.

A change in the female's behaviour in early December indicated that hatching had occurred. She no longer took prey to the plucking station after an aerial pass but returned with it to the nest. When the nestlings were about 1 week old the female began to spend long periods perched within 30 m of the nest, although whenever it rained she returned to the nest to cover the young. The male's behaviour also changed. He no longer perched in the territory after passing prey to the female but usually left the area and continued hunting. If the male had not recommenced hunting by the time the female had fed the young, she often dived at him and chased him from the territory.

Males landed and deposited food items at four of the five successful nests during the 1976-77 breeding season, but only after the nestlings were at least 2 weeks old. They did not stay long enough to feed the nestlings.

Nesting success and fidelity to breeding area

During the 1976-77 breeding season, nine young were fledged from five of the nine nests, giving an average fledging success of 1.8 young per successful nest, or 1.0 young per nest site. In the 1977-78 season, 11 young were fledged from six of the ten nest sites, giving the same (1.8) average fledging success for successful pairs and 1.1 young fledged per nest site. In both seasons four pairs fledged no young.

Ten of 15 individually marked adults resident at Pukepuke Lagoon during 1976-77 re-established territories during 1977-78, eight of which became resident on their former territories and six of which paired with their mate of the previous breeding season. Breeding success was highest among those adults known to be breeding in the study area for a second consecutive season. Of the ten adults that returned, six had successfully fledged young the previous breeding season but eight were successful in the second observed breeding season. Only four (44%) of the nine new birds in the study area fledged young during 1977-78. The Fisher exact-probability test indicates that returned breeders were not significantly more successful ($p > 0.05$) than birds breeding for the first time, but sample sizes are small.

Polygyny

I observed one case of polygyny in each of the two breeding seasons. Three of the four females and both of the males were individually marked. The observed breeding histories of these six birds are summarised in Table 1.

During 1976-77, male A defended two territories which were not adjacent and where the distance between nest sites was 1300 m. Often, one of two or more wives may be favoured by a male harrier (Balfour

TABLE 1 — Breeding history of polygynous Australasian Harriers at Pukepuke Lagoon

1976-1977	Young fledged
Male A x Female W (polygyny)	0
Male A x Female X (polygyny)	0
Male B x Female Y (monogyny)	2
1977-1978	
Male A x Female X (monogyny)	1
Male B x Female Y (polygyny)	0
Male B x Female Z (polygyny)	2

& Cadbury 1979), but in this case neither of the two females (X and Y) appeared to receive more food from their mate than the other, nor did one begin nest building earlier. No young were fledged from either of the nest sites. The following year, female X again paired with male A, but in a monogynous relationship this time, and fledged one young.

During 1977-78, a second polygynous male (B) defended one territory and the two nest sites were 350 m apart. In this case the females both defended a territory within the male's territory. The first wife (Z) began nest building about 1 month before the other (Y) arrived in the area, and she received more food from the male. The first wife fledged two young, and the less-favoured second wife fledged none. Male B had been paired with the less-favoured second wife (Y) in a monogynous relationship during the previous breeding season, when they had fledged two young.

The average success of the two polygynous matings was 0.5 young fledged per female, or 1.0 young fledged per male. These success rates are lower than the 1.2 young fledged per adult ($n = 15$) in monogynous matings, but sample sizes are too low for statistical comparisons.

Fledging

The mean fledging dates recorded for the two breeding seasons were 13 and 18 January (range 1-27 January). For the first week after the fledglings left the nest, they remained within their parents' territory and perched together on prominent bushes. Males were more precocious than their larger sisters and accomplished most activities such as leaving the nest site and making their first flight outside the territory about a day earlier. One week after fledging, the young flew strongly after their parents and gave the soliciting call. The adults usually dropped the prey, and the fledglings all dived to catch it before it hit the ground. The first fledgling to see the adult returning to the territory usually secured the food item.

After the young had fledged, two adult males were seen less often over their territories but continued to hunt in their home ranges. In these cases, the females continued feeding the fledglings alone. At the nine other successful nests, both parents fed the fledglings at about the same rate. After fledging took place, adult females were seen up to 2.5 km from the nest site on five occasions, whereas before this time they were not seen more than 1 km from the nest site.

Four weeks after fledging, individually marked fledglings were seen up to 2 km from the territory, but they returned to roost near the nest site in the evenings. During this period they were seen to make their first successful captures of large insect prey, and from then on they were not seen to be fed by their parents, although this may have occurred.

There was a general dispersal of the young away from the study area about 7 weeks after they had fledged, that is, in February and early March. Most of the adults that had successfully fledged young left the study area in March. Their departure was preceded by that of the unsuccessful adult females, which left in December and early January. The adult males that had fledged no young left at the same time as the successful adults in March. Presumably the unsuccessful adult females were not as familiar with the pair's home range as the males, and when they no longer received food from the male, they left in search of areas where food was more readily available.

I do not think any birds were fed by their parents after they had left the study area because the adults left about a week after their young and because the many juveniles that passed through the study area in the ensuing weeks were not seen flying near unmarked adults or soliciting prey from them.

DISCUSSION

Population density and spacing mechanisms

The number of territories was identical in 1976-77 and 1977-78. This stability was probably due to the wide range of live prey and carrion items in the Australasian Harriers' diet (Carroll 1968, Redhead 1969, Douglas 1970, Baker-Gabb 1978). Raptor populations that feed on a wide spectrum of prey items are much more stable than those that are food specialists (Newton 1976). For example, Hen Harrier *(Circus cyaneus)* breeding populations may fluctuate greatly when feeding primarily on small mammals, whose numbers are subject to large fluctuations (Hagen 1969, Galushin 1974, Hamerstrom 1979). When feeding mainly on small birds, rabbits and hares, the density of breeding Hen Harriers is much more stable (Picozzi 1978).

Newton (1979) pooled data from more than 50 studies on 22 raptor species, which demonstrated a linear relationship between female body weight and breeding density for populations in which individual pairs foraged in more-or-less exclusive home ranges. The population density I recorded of one Australasian Harrier per 50 ha and one breeding pair per 120 ha was approximately twice as high as that predicted by Newton's (1979) data. However, home ranges of individual pairs of Australasian Harriers overlapped extensively. If breeding density is considered only in relation to the area in which each pair of Australasian Harriers had exclusive hunting access (about 225 ha), a value within the upper limits of Newton's (1979) data is obtained. The high Australasian Harrier breeding density was probably the result of a favourable distribution of prey and of hunting habitat, and a complete lack of competing raptor species at Pukepuke Lagoon.

Besides the availability of food, both the availability of nesting habitat and territorial behaviour influence the density of breeding raptors (Moore 1957, Southern & Lowe 1968, Newton 1976). The

breeding density of Australasian Harriers at Pukepuke Lagoon seemed to be limited by nesting habitat because nests were built only in raupo and red-rush swampland and all the suitable nesting habitat was defended.

Home range

The home range size observed for Australasian Harriers was slightly larger than that recorded for Marsh Harriers in Europe by Schipper (1977). This concurs with observations by Schoener (1968) and Newton (1979), who demonstrated that territory and home range size increase with increase in raptor size.

Breeding behaviour

Some of the behaviour and displays I observed have not been previously described for the Australasian Harrier. These include territory-boundary display flights, border patrolling, eviction of intruders, nest inspection, courtship feeding, copulation, post-fledging behaviour and dispersal. Other workers have noted similar Australasian Harrier behaviour for display soaring (Stead 1932), display diving (Sharland 1932, Stead 1932), feeding at plucking stations (Fletcher 1909, Soper 1958) and the post-hatching parental division of labour (Soper 1958). Soper stated that the female seldom brooded the nestlings once the oldest was 4 days old and the youngest about 24 hours old. From fledging dates, I calculated that the females I observed ceased brooding when the nestlings were 7-10 days old. I did not observe groups of Australasian Harriers display diving during courtship, as noted by Sharland (1932) and Fox (1978).

Descriptions of some behaviour similar to that which I observed have been recorded for other harriers: display diving and aerial food passes by *Circus aeruginosus, C. cyaneus,* and *C. pygargus* (Breckenridge 1935, Robinson 1950, Benson 1958, Hamerstrom 1969, Sondell 1970, Johannesson 1975, Brown 1976, Watson 1977); escorting of territory intruders by *C. aeruginosus* and *C. cyaneus* (Sondell 1970, Watson & Dickson 1972); and feeding at cock nests by *C. aeruginosus* (Witherby *et al.* 1943, Johannesson 1975).

Nesting success

Clutch sizes recorded for the Australasian Harrier vary from two to seven eggs with a mean of 4.4 (Table 2). New Zealand

TABLE 2 — Australasian Harrier clutch size

Reference	Mean	Range	Number of nests
OSNZ nest record scheme	4.6	2-7	25
RAOU nest record scheme	3.7	3-5	11

populations lay significantly more eggs than southern Australian birds ($t = 2.72$, $p < 0.01$). This is probably due to geographical influences because an increase in clutch size with latitude has been well documented by ornithologists (Moreau 1944, Cody 1966).

From two of 15 nests studied, Soper (1958) concluded that the incubation period was 31-34 days. The mean fledging success I recorded (1.8 young) was similar to the mean of 2.1 young fledged from 13 successful nests in New Zealand (OSNZ nest record scheme) and the same (2.1 young) fledging success from 14 successful nests in southern Australia (RAOU nest record scheme). Comparisons cannot be readily made between my data (1.1 young fledged from 19 nests) and the means of 1.3 and 1.6 young fledged from 20 and 19 nests in the OSNZ and RAOU nest record schemes respectively (Table 3). This is because I included both non-breeding territorial pairs and pairs that laid eggs but failed to fledge young as unsuccessful breeders (Postupalsky 1974), whereas birds were included in the nest record schemes only if they laid eggs.

TABLE 3 — Australasian Harrier fledging success

Reference	Young fledged per nest			
	0	1	2	3
Pukepuke Lagoon	8	4	5	2
OSNZ nest record scheme	7	2	8	3
RAOU nest record scheme	5	2	8	4

Polygyny

Monogyny is the dominant avian mating system, occurring in more than 90% of the bird species studied (Lack 1968). Although the Australasian Harrier has been previously recorded as monogynous (Sharland 1932, Stead 1932, Soper 1958), I found that it is sometimes polygynous. Polygyny has been recorded in at least 11 other species of diurnal raptor and is most common in the genus *Circus* (Schipper 1977, Newton 1978).

The Australasian Harrier hunts mainly swamplands and open grasslands. This behaviour links it with other polygynous raptor species because Newton (1976) stated that polygyny occurred mainly among diurnal raptors found in open country and was most prevalent in areas or years that were unusually rich in food. Orians (1969) suggested that birds inhabiting marshes were also more likely to be polygynous.

Male Australasian Harriers defended all the available nesting habitat at Pukepuke Lagoon. This was a resource with a patchy distribution (Fig. 1) that seemed to limit the density of breeding birds. As in the Australasian Harrier, links between polygyny and patchy resource distribution have been found in other polygynous birds

(Verner & Willson 1966, Zimmerman 1966, Orians 1969, Martin 1974, Stewart *et al.* 1977). This form of polygyny, whereby some males monopolise an important and spatially clumped or unevenly distributed resource, has been termed " resource defense polygyny " by Emlen & Oring (1977).

By monopolising the available nesting habitat, male Australasian Harriers may have increased their likelihood of being polygynous and thereby fledging more young. Although my sample was too small to provide evidence about the fledging successes of polygynous and monogynous males, Balfour & Cadbury (1979) stated that 87 polygynous male Hen Harriers fledged significantly more young per male than 55 monogynous birds. Similarly, other data on polygynous species (Emlen & Oring 1977) agree with Orian's (1969) prediction that polygyny should be advantageous for males and that there should not be a negative correlation between the number of females mated to a given male and the average reproductive success per female. Where this is not the case (Downhower & Armitage 1971, Elliott 1975), differential survival of independent young of monogynous and polygynous pairs may exist, but this is often more difficult to substantiate.

In the one case in my study area where there were two Australasian Harrier nest sites in one male's territory, the first wife was dominant and favoured by the male. The favoured female had a similar fledging success to monogynous females. Similarly, Balfour & Cadbury (1979) found that polygynous Hen Harrier groups which contained up to six females had a favoured first wife. In such groups the first wife had the same fledging success as monogynous females. The Hen Harrier nests socially (Balfour 1962), whereas the Australasian Harrier does not, and the wives of the polygynous male I observed interacted aggressively along their territory boundary. However, once the first wife was incubating eggs she could do little to exclude the second wife.

To gain a mate and a suitable nesting site, a female Australasian Harrier may sometimes improve her chances of reproductive success if she becomes a second wife and mates with an already mated older male. This may result in lower than average breeding success for the second wife, but at Pukepuke Lagoon the only alternative was to pair with first-year males, which held small territories only briefly. If a female is to be a second wife she should, in theory, select an older male because older males were four times more successful hunters than juveniles (Baker-Gabb 1978) and should therefore provide more food. Both of the polygynous males I observed were older birds, distinguishable from young males by their paler ventral surfaces (Oliver 1955, Baker-Gabb 1978).

No differences were apparent between polygynous and monogynous males in the quality of their territories and hunting areas. Perhaps second wives selected a mate on the basis of courtship feeding, which took place daily for at least 6 weeks before the first wife laid

eggs. Courtship feeding would test a male's ability to supply food for himself and his mate or mates and would presumably have a selective advantage for greater egg production. It would also act as a predictor of a male's ability to feed the nestlings adequately. Nisbet (1973, 1977) found that courtship feeding indicated the potential of a male Common Tern *(Sterna hirundo)* as a provider. Males made a substantial contribution to the nutritional requirements of the laying females. The amount of food the males provided was one of the factors limiting the number and size of the eggs and also fledging success.

It has been possible to classify the type of polygyny exhibited by Australasian Harriers and some of its characteristics in this study. However, more data are required on its breeding biology before we can understand what balance of environmental and behavioural selection pressures causes the Australasian Harrier to become polygynous.

Conclusion

The breeding behaviour and ecology of the Australasian Harrier have been shown to be similar to those of other harriers that have been extensively studied in the northern hemisphere. A lack of competing open-country raptors in New Zealand, therefore, appears to have had little effect on these aspects of its biology. All harriers except the Spotted Harrier *(C. assimilis)* nest on the ground and all hunt over open grasslands and marshes (Brown & Amadon 1968). This behaviour has probably influenced the similarly spectacular aerial courtship and territorial displays that are accompanied by vocalisations and are performed by all harriers that have so far been closely studied (Witherby *et al.* 1943, Brown 1976, Watson 1977). These displays are a most effective means of communication in habitats that usually have few conspicuous perches to display from. For the same reason, food transfers from male to female are most effectively accomplished in the air. The hunting and nesting habitat may also have an influence on harrier mating systems, for Orians (1969) predicted that birds that inhabit marshes are more likely to be polygynous. If the availability of nesting habitat is often an important limited resource for other harrier species, as it was found to be for the Australasian Harrier in this study ("resource defense polygyny" of Emlen & Oring 1977), this may further explain why polygyny is so common within the genus *Circus.*

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SHORT NOTE

MIGRATORY MOVEMENT OF SILVEREYES AT FAREWELL SPIT

While working in the 8-10 km part of Farewell Spit on 15 May 1980, we realised that the faint background sounds of Silvereyes *(Zosterops lateralis)* were coming not from the dune vegetation but from high overhead. During this and the next two days, whenever we were away from the sound of wind or surf on the Central Flats of the spit or on the farm at the base, we recorded a daytime passage of small flocks of Silvereyes.

From about 1100 on the 15th, when we first noticed that the calling was from overhead, calls were continuous until nearly 1200. Judging by sound, most flocks comprised 20-30 birds. They were seldom visible to the naked eye, and few were seen even with binoculars. Two flocks of c.30, two of c.60, and one large one of c.100 were seen, all tightly bunched, flying eastwards along the spit about 150-200 m above the ground. Only one flock of c.30 was seen in the dune lupins, the birds calling excitedly and taking off eastwards along the spit.

On the 16th, four small flocks were heard flying high over the base of the spit between 0600 and 0700. At 7 km on the spit, at least 18 flocks passed high overhead between 0815 and 1200, but we spent about an hour of this time within sound of the Ocean Beach surf, and we were travelling and not listening between 0700 and 0815. Flocks passed at intervals ranging 1-20 minutes apart, and four flocks sounded large. The audible passage diminished toward midday, and only occasional small flocks were heard thereafter. The only Silvereyes