Australian Field Ornithology 2025, **42**, 116–124
http://dx.doi.org/10.20938/afo42116124

Breeding biology and behaviour of the Eastern Barn Owl *Tyto javanica delicatula* in north-western Victoria

John G. McLaughlin[1] and S.J.S. Debus[2]

[1]1Deceased
[2]Zoology, University of New England, Armidale NSW 2351, Australia
Email: sdebus@une.edu.au

Abstract. The breeding biology and behaviour of the Eastern Barn Owl *Tyto javanica delicatula* were studied by JGM in north-western Victoria during 1987–1990, in agricultural and woodland areas (*n* = 14 nests). Overall, clutch size was 3–6 eggs (usually 4 or 5, mean 4.7), and fledgling productivity was 2–5 fledglings per attempt (mean 3.6). Incubation lasted 33 ± 1.5 days, the nestling period *c.* 46–57 days (mean *c.* 53 days), and the post-fledging dependence period 3–5 weeks. Consecutive successful clutches within the same year (autumn and again in spring) were recorded during periods of highest prey density. At lower prey densities Barn Owls laid significantly smaller clutches and were seasonal (spring) breeders. Levels of nestling mortality were significantly higher during low prey abundance than during high prey abundance. Breeding behaviours, including courtship and copulation, are described. Evidence was obtained to indicate a lengthy courtship period, territorial defence, and the maintenance of pair bonds during the nonbreeding period.

Introduction

The breeding biology and behaviour of the Eastern Barn Owl *Tyto javanica delicatula* in Australia, to the extent then known, was summarised by Higgins (1999), based substantially on an unpublished thesis by McLaughlin (1994). Since then, there has been a brief account of territory and nest occupancy, breeding chronology, clutch and brood sizes and the fledgling period for one pair (Courtney & Debus 2006); brief observations on nest sites, vocalisations and fledgling behaviour (Hollands 2008); and description of a perched display posture that preceded allopreening (Fisher & Fisher 2014). Subsequently, some other aspects of breeding biology or behaviour, including brood sizes, were described in reports of Barn Owls breeding in purpose-built nest boxes, or in artificial or natural hollows (Meaney *et al.* 2021; Mawson *et al.* 2024). Here we present the detail supporting the summary statements of Higgins (1999) that cited McLaughlin (1994). Aspects of the breeding biology of Indian/Asian populations have also been studied (Lenton 1984; Nagarajan *et al.* 2002; Mahmood-ul-Hassan *et al.* 2007; Pande & Dahanukar 2012), in the monsoonal tropics north of the equator, where site productivity and the prey base may confer substantial differences from the Australian population.

The Eastern Barn Owl (hereafter Barn Owl) in Australia is generally considered to exhibit a boom-and-bust life-history strategy adapted to periods of prey superabundance, by responding at any time of year with successive large clutches and large broods (e.g. Fleay 1968; Schodde & Mason 1980; Hollands 2008). However, in temperate Australia plagues of potential prey such as rodents may be infrequent, interspersed by 9–22 leaner years (e.g. Saunders & Giles 1977; Singleton & Redhead 1989), and the question becomes what Barn Owls do in normal (i.e. non-plague) years. Hence, Barn Owls in Australia are likely to pursue a breeding strategy that has received little attention.

Described here are aspects of the breeding biology and behaviour of Barn Owls during a period of moderate abundance of the primary rodent prey (House Mouse *Mus musculus*). A rapid decline in prey abundance (McLaughlin 1994; McLaughlin & Debus in press) also provided an opportunity to examine the effect of a variable food resource on Barn Owl breeding biology and behaviour. Mouse density declined by ~80% from a high in 1987–1988 to a low in 1988–1989.

Taxonomic note

The Australian Barn Owl is currently classified by BirdLife Australia as subspecies *delicatula* of the global *Tyto alba*. After some taxonomic confusion in the recent literature, several definitive genetic studies have split the complex into three regional species: *T. alba* of Europe, the Middle East and Africa; *T. furcata* of the Americas; and *T. javanica* of Asia to Australasia (including subspecies *stertens* of India/South-East Asia and *delicatula* of Australia), each species having a distinct ecological niche (Jønsson *et al.* 2013; Aliabadian *et al.* 2016; Uva *et al.* 2018). Thus, aspects of the biology of European, African or North American populations need not necessarily apply to those in Australia.

Study area and methods

Study area

Barn Owls were studied by JGM from July 1987 to December 1990 in the semi-arid Mallee wheat-belt of north-western Victoria, at two main sites: one was intensively managed agricultural land (1030 ha) at the Mallee Research Station at Walpeup (35°08′S, 142°02′E), ~30 km west of Ouyen; and the other was state forest (~1000 ha) ~7 km west of Red Cliffs, immediately north-east of Thurla (34°20′S, 142°08′E). Regionally, >50% of the original vegetation of the area has been cleared for agriculture, with <20% of the original vegetation remaining in intensively farmed areas. Land use was dryland cropping of winter cereals, mainly

Wheat *Triticum aestivum* with some Barley *Hordeum vulgare*. Mean annual rainfall is 250–400 mm and winter-dominant. Summer temperatures frequently exceed 34°C, often 40°C, and winter minima are often below 2°C.

The Walpeup site consisted of 805 ha of cleared land (intensive dryland cropping for wheat and barley ~300 ha, pasture or fallow 500 ha, grazed by 500 sheep) and ~20 ha of retained shelter belts and woodland patches. Native vegetation at Walpeup consisted of medium to tall (5–12 m) mallee eucalypts, most notably Oil Mallee *Eucalyptus oleosa* and White Mallee *E. gracilis* on sandy soils, and Belah *Casuarina pauper* and Slender Cypress-pine *Callitris preissii*, often with Cattlebush *Alectryon oleifolius*, on loamier soils; both had an understorey of chenopods and exotic grasses. Vegetation at the Thurla site consisted of a closed woodland of Grey Mallee *E. socialis*, Dumosa Mallee *E. dumosa* and Slender-leaved Mallee *E. leptophylla* with an understorey of Porcupine Grass *Triodia irritans* on sand-dune crests; and tall open mallee woodland of large (>12 m tall) Oil Mallee and some White Mallee and Grey Mallee with a midstorey of scattered small stands of Cattlebush, Sugarwood *Myoporum platycarpum,* Desert Cassia *Senna artemisioides*, Slender-leaved Hopbush *Dodonaea angustissima* and various *Acacia* spp. (e.g. Umbrella Wattle *A. oswaldii*) and a ground layer of chenopods and others (e.g. Ruby Saltbush *Enchylaena tomentosa*, Rosy Bluebush *Maireana erioclada* and Shrubby Twin-leaf *Zygophyllum aurantiacum*) on the heavier soils in swales.

Field methods

Nest sites were located by following calling Barn Owls at night or searching potential areas (i.e. those with hollow trees) during the day and inspecting tree hollows. Pre-recorded Barn Owl calls were sometimes broadcast in an attempt to elicit a response. Artificial structures (e.g. sheds, water tanks, old car bodies, agricultural machinery) were also searched, and Barn Owl records were sought from local residents and naturalist groups. A systematic survey at Walpeup aimed at locating all potential nest and roost sites (i.e. tree hollows) was conducted in September–November 1987. From December 1987 onwards, all known and potential sites were inspected at least once every 6 weeks, except March–May 1989 and September–December 1990 when sites were checked once, and concentrating on areas with a greater density of suitable hollows. The site at Thurla was searched less regularly, concentrating on areas with high potential. Most nests at this site were located, although some might have been missed after February–March 1990 when access to the area was hampered by high rainfall. Each nest (or roost) was visited at least once every 6–8 weeks. Active nests were visited and their contents inspected usually at intervals of 2–3 weeks, sometimes longer, without causing unnecessary disturbance. In JGM's absence, some breeding data were collected by local naturalists. Additional breeding data were sought from the Royal Australasian Ornithologists Union's Nest Record Scheme, and the Atlas of Australian Birds database (Blakers *et al.* 1984).

Observations at nests were made from ground-level hides (two-person tents), situated 4–6 m from the base of the nest tree, with an unobstructed view of the hollow. Binoculars (7 × 50, i.e. high light-gathering power) were used. Lighting was provided by one or two broad-beam electric torches, modified to enable the power source to be controlled from inside the hide. Torches were covered with red filters (e.g. Southern 1955) and mounted on tripods 3–4 m from the nest tree. Hides were entered at dusk, before first Barn Owl activity. Observation periods varied in length, and overall were strongly biased toward the first half of the night. Night-vision equipment was not available, so fieldwork was conducted during periods of maximum moonlight (a source of potential bias).

Observations at nest sites were also conducted from distances of 50–100 m, with binoculars and usually without a hide, on nights with good moonlight, and at some sites where the presence of a hide near the nest might have been disruptive (e.g. during incubation). A hand-held 50-watt spotlight covered with a red filter and powered by a 12-volt battery was occasionally used. Care was taken to minimise any disturbance caused by artificial lighting.

Details of breeding behaviour were obtained from 12 sites (11 breeding pairs), representing a total observation period of 94.6 hours. Effort was divided as follows: courtship and pre-laying period 14.3 hours (three sites); laying and incubation period 10.6 hours (four sites); nestling and fledging period 55.9 hours (six sites); post-fledging dependence period 13.8 hours (seven sites). Additional information on nestling and fledgling behaviour (two sites) was obtained in JGM's absence by J. Kiley (pers. comm.). As birds were not individually marked or sexed, specific reference to the sexes is made only where that (or similar) behaviour has been observed elsewhere, and sex roles have been defined.

Caution was used when attributing behaviours to male or female. Plumage differences between the sexes are slight (e.g. degree of spotting on underparts: Schodde & Mason 1980; Higgins 1999), and require adequate views under good light. Bunn *et al.* (1982) and other authors (e.g. Hollands 2008) have noted slight sexual differences in the delivery of the usual screech call, but the variation observed precluded confident separation of the sexes. Differences in call occasionally enabled the identification of individuals at nest sites, and some calls were sex-specific (e.g. persistent adult female 'snoring').

Despite their adult-like plumage, fledgling Barn Owls show obvious traces of mesoptile down for at least the first week after leaving the nest, and are more heavily spotted on the ventral surfaces (mainly breast and underwing-coverts: Schodde & Mason 1980; Higgins 1999). Behaviour, including vocalisations, is a more reliable guide to identifying fledglings (described by McLaughlin 1994 and herein).

At one nest, where the nestlings were accessible, weights and morphometric measurements were obtained for five nestlings, and later two Barn Owls were banded before they fledged (bands supplied by the Australian Bird and Bat Banding Scheme).

Assumptions

Barn Owls begin incubation before completing a clutch of eggs and hatching is asynchronous (Higgins 1999; Hollands 2008). For Australian Barn Owls, various authors

(e.g. Higgins 1999; Hollands 2008) cite a laying interval of 2 days, not determined in this study, so an approximation of 2.5 days (consistent with Barn Owl studies elsewhere, e.g. Bunn *et al.* 1982; Lenton 1984; Wilson *et al.* 1986) was used when calculating incubation periods. When calculating the age of nestlings and fledglings, it was assumed that the interval between successive hatchings matched the interval between laying. Clutches were considered complete if the number of eggs present had not increased over 4 days or longer.

Definitions

Parental active prey-delivery time was taken as from the first to last delivery within a given nest watch. Fledging is usually defined as the first flight. Undetermined in this study, fledging was therefore defined as the first occasion on which a young Barn Owl ceased to roost diurnally at the nest site (i.e. in the nest hollow). However, because young Barn Owls may roost diurnally at the nest site after their first flight (for up to 7 days: Bunn *et al.* 1982; Steyn 1982; Lenton 1984), true fledging age was likely slightly younger than estimated. Independence was assumed when a juvenile owl was no longer present at night in the vicinity of the nest, or was actively dispersed by adults. Territorial here is taken to mean resident, nesting owls defending a breeding territory against conspecifics.

Analysis

Comparisons of nest productivity before and after a decrease in the abundance of prey were conducted by JGM using non-parametric Mann-Whitney *U*-tests (Siegel 1956). In most cases, averages are given as medians. For χ^2 tests with one degree of freedom, the Yates's correction for continuity was incorporated (Fowler & Cohen 1987).

Where the age of a nestling or fledgling was known only approximately, a range of ages is given. For the calculation of maximum nestling (to fledging) period (below), the mid-point of these ranges was used.

Results

Most nests were found during the incubation or nestling periods (86%, $n = 12$). Consequently, the limited information on the timing of courtship and nest-site establishment behaviours was obtained after the mouse crash in July 1988.

Nests

Fourteen nests (sites where at least one egg was laid) were located, one of which was abandoned before the first egg was laid and was excluded from the analysis of breeding success. Two pairs of Barn Owls were believed responsible for two nests each, herein treated as independent events.

Nine nests (64%) were found in intensively managed agricultural land (including two at Walpeup) and five (36%) on primarily non-agricultural land (including four at Thurla). Thirteen nests (93%) were located in tree hollows, and one (successful) on baled hay in a hayshed. Ten nests were found by inspecting tree hollows during the day, two by following calling Barn Owls, and two were located from information provided by local residents. Details of parameters of nest sites are provided elsewhere (McLaughlin 1994; McLaughlin & Debus 2025) and have been summarised by Higgins (1999).

Breeding density and inter-nest distances

One breeding pair of Barn Owls at Walpeup (in two separate nest sites) gave a breeding density of one pair per 1030 ha (total area) or 220 ha (treed areas only), if this was the only pair present. The closest known concurrently active nests were ~1.5 km away, in September–November 1987 and March–May 1988. At Thurla, the nearest known concurrently active nests were 2.0 km away in July–August 1987 (one abandoned before laying) and 1.8 km away in September–November 1989, giving a breeding density of ~500 ha per pair. The distance between known active Barn Owl nests before the crash in mouse populations in June–July 1988 (see McLaughlin 1994; McLaughlin & Debus in press for mouse population data) was not substantially less than the corresponding distance after the crash. However, in the 2.5 years following the crash, fewer nests were found than during the 9 months from June 1987 to March 1988 (although search effort was less in 1990). Following the prey crash, Barn Owls did not breed at Walpeup for the remainder of the study, nor at or in the vicinity of any of the agricultural sites used before the crash.

Breeding chronology

At one nest, male incessant stationary screech calls were first noticed 8–10 weeks before eggs were laid. About 40 days later, and 2–4 weeks before laying, courtship flights and copulation were observed, although they might have occurred well before this period. At another nest, an increase in calling activity, including male incessant stationary screech calls, was recorded *c.* 12 weeks (*c.* 85 days) before the earliest possible laying date. Courtship flights, female 'snoring' and copulation were first observed 9 weeks (*c.* 60 days) before the first egg was laid.

Before the prey crash in July 1988, two pairs of Barn Owls had re-nested following successful nesting attempts, near their initial nest sites. In one case the pair nested in a different hollow of the same tree. Although JGM was often present in each of these areas after the first nesting attempts, and usually found Barn Owls in the area then, no overt courtship displays were recorded for their second attempts.

Overall, Barn Owls incubated eggs or had nestlings in all months of the year except January (June 1987–December 1990; $n = 14$ breeding events). Eggs were recorded in nests during 9 months of the year, and nestlings in all months except January and February. For two pairs that laid consecutive clutches before the crash in mouse populations, the period between fledging of the first brood and laying of the next clutch was similar, *c.* 12 weeks.

Most clutches (86%, *n* = 12) were initiated in June–October: February–March (23%, *n* = 2) and June–September (77%, *n* = 7) before the mouse population crash, although Owls found nesting in the first 6 months of the study (June–December 1987) might have nested earlier that year; and August–October (most, 80%, *n* = 4 in September–October) after the prey population crash. Clutches were laid during the latter half of each year of data collection except for 1988 (i.e. immediately following the crash in prey populations), after which Barn Owls were not found nesting at either study site until September 1989 (at Thurla), *c*. 15 months later.

Clutch size

The overall median clutch size for completed clutches was 5.0 (range 3–6, usually 4 or 5, *n* = 9; mean 4.7 ± standard deviation 1.0). Clutches were larger (4–6 eggs, usually 5 or 6, median 5.0) before the mouse crash than after (3–5, usually 4, median 4.0) (one-tailed Mann-Whitney *U* = 3.0, *P* <0.05).

Incubation period

Inspections of nest contents at two nests enabled the incubation period for two eggs to be estimated. The contents of both nests were examined before the last egg was laid, and were re-examined before the last egg hatched. Assuming a laying interval of 2.5 days, both nests gave an incubation period of 33 ± 1.5 days per egg.

Nestling period (age to fledging)

Sufficient data from three nests (*n* = 11 fledglings) enabled an estimate of the nestling period. The youngest age of diurnal roosting outside the hollow was 46 days, and the oldest age of roosting in the nest hollow was 52 days. The overall range of estimated maximum age to outside diurnal roosting was 46–63 days, and the range of midpoints was 46–57 days (mean 53 ± 4 days); the mean is probably longer than the true nestling period.

Period of dependence

For the oldest fledgling at one nest, the young owl finally left the nest area at 74–76 days after hatching (*c*. 20–22 days post-fledging). At another, only three of the four fledged owlets were present in the nest area when the oldest owlet was 72–77 days old (18–23 days post-fledging). Otherwise, all young at all sites monitored had vacated the area by a maximum of 90 days after hatching (*c*. 37 days post-fledging).

Breeding success

For nesting attempts in which clutch size was known (*n* = 10), young hatched in eight attempts (80%). For completed clutches (*n* = 9 for clutches, *n* = 42 for eggs), 38 eggs in eight clutches hatched (90%), giving a mean brood size at hatching of 4.2 ± 1.9). One nest was abandoned after two eggs were laid, probably because of the partial collapse of the floor of the nest hollow. All four eggs at another disappeared during incubation (cause unknown). Otherwise, for successful clutches (*n* = 8 for clutches, *n* = 38 for eggs), all eggs hatched (86% hatched of 44 eggs in total). There was no indication of egg infertility. Hatching success was 93% (26 chicks/28 eggs laid) before the prey crash and 75% (12 chicks/16 eggs) post-crash.

Overall, Barn Owl nesting attempts produced a median of 4.0 fledglings (completed clutches: 2–5 young, mean 3.6 ± 1.5; all clutches: 0–5 young, median 4.0). Nesting attempts before the mouse crash produced a greater median number of fledglings than those after the crash (all nests: 0–5 young, median 4.5 vs 0–4 young, median 3.0; successful nests: 3–5 young, median 5.0 vs 2–4, median 3.5), although this difference was not significant (one-tailed Mann-Whitney *U*-test: for successful nests *U* = 6.0, *P* <0.10; for all nests *U* = 10.5, *P* <0.10). From small sample sizes, fledgling productivity was highest for nests commenced in 1987 (3–5 young, median 5.0, *n* = 5) and early 1988 (4–5, median 4.5, *n* = 2); lowest for nests in 1989 (0–2, median 1.0, *n* = 2) when the Owls next bred after the mouse crash; and intermediate in 1990 (3–4, median 4.0, *n* = 3) when mouse numbers were probably increasing in 1990, although low compared with 1987–1988 (McLaughlin 1994; McLaughlin & Debus in press).

At nests where the brood size at hatching and the number of fledglings was known (*n* = 7), 88.9% (32 of 36) of nestlings survived to leave the nest. Two nests (28.6%) produced fewer fledglings than nestlings hatched. At one nest, the bones of a nestling Barn Owl were found in the nest hollow after all other owlets had fledged. There was no evidence to indicate the fate of three of the five nestlings at another. When first located, another nest contained four nestlings, although one was substantially smaller and weaker than its siblings, and 10 days later only three nestlings were present.

For completed clutches where the number of fledglings was also known (*n* = 4 each for pre- and post-crash nests), 36 eggs produced 28 fledglings (77.8% success). Levels of egg to fledgling mortality before the prey crash were significantly lower than after the crash: 19 young/20 eggs (95%) vs 9 young/16 eggs (56.3%) (χ^2_1 = 5.42, 2 × 2 contingency table, *P* <0.05). In 1989, eggs and some nestlings disappeared without any signs of predation, suggesting possible cannibalism of eggs and chicks during food shortage, whereas the increase in productivity in 1990 might have been a result of enhanced prey availability.

Aspects of breeding behaviour

The earliest indication of breeding activity was the male incessant stationary screech call. The male perched in a prominent position on or close to the potential nest tree, and screeched persistently (call duration *c.* 1 sec., one call every *c.* 2–5 sec.) for periods often exceeding 10 minutes. These calling bouts usually commenced *c.* 20–40 minutes after twilight. Females were already present where this behaviour was observed. Incessant stationary screeching was not observed after laying had commenced.

Courtship flights were observed on 12 occasions at two sites, <9 weeks before clutch initiation. These flights typically consisted of tail-chasing or close-pursuit flights, centring on the nest tree. Most flights were brief (<2 min.), within ~100 m of the nest tree, ~15–25 m above ground. On two occasions, they exceeded a height of ~50 m. In all cases, courtship flights were accompanied by frequent screeching (and similar vocalisations). Most flights concluded with one or both birds entering the nest hollow. More frequently (*n* = 19), the male alone undertook similar flights around the nest tree, usually when the female was in the nest hollow. At least two of these flights concluded with copulation, with the female perched near the nest hollow.

Within *c.* 8 weeks of laying, female behaviour became juvenile-like. Females at this time gave the repetitious food-soliciting snoring call, a brief but persistently repetitious raspy or wheezy call characteristic of dependent young. Females also became sluggish, were reluctant to fly during the night or flush from the hollow during the day (a feature also of recently fledged dependent young).

Where observed, copulation took place in the nest tree within 2–4 m of the nest hollow (nine observations at two sites). Copulation was twice preceded by male-only courtship flights. Both female snoring and male rapid high-pitched twittering increased in frequency immediately before copulation. Copulation lasted for *c.* 10–20 seconds, accompanied by rapid vocalisations. On one occasion, copulation occurred following the presentation of food by the male, with the female holding the prey in her bill during copulation, and once following a brief period of allopreening. Immediately following copulation, frequency of calling rapidly diminished, and the male usually flew to a branch within 10 m, occasionally after a short flight around the nest tree. At one nest, copulation occurred seven times in 191 minutes, including three occasions when copulation was assumed to have occurred (based on pattern of vocalisations) but was not seen.

Two to four weeks before laying, female nest attendance was high. Other than during the early evening (<20–40 min. after dark) when both birds were active away from the nest tree, the male delivered food to the female in the hollow. At one nest, the female spent 230 minutes of a 235-minute observation period (98%) either in the hollow or perched within 2 m of its entrance. During 198 minutes of observation at another nest, the female remained in the nest hollow the entire period; the male entered the hollow on seven occasions for a total of *c.* 6.5 minutes (delivering food on at least three occasions). The uneaten bodies of four House Mice were found during one of four prospective nest inspections at this stage of breeding. Two of four nest inspections revealed both adult Owls roosting together.

Laying and incubation

Laying was coincident with a marked decrease in calling activity. Both adults were still active and called in the early evening, though the intensity of calling during this active period appeared less than before clutch initiation. Subsequently, calls were very infrequent. In 14 nest inspections at eight sites during the incubation period, both adults were flushed from the hollow on only one occasion (7.1%).

Nestling period

Nestling age: hatching to c. 15 days

Adult vocal activity appeared to increase slightly at hatching. The female continued to roost in the nest hollow; however, during the entire nestling period there were no records of both adults roosting together. During 9.5 h of observation (over two nights) at one nest (oldest chick aged 12–14 days) the female was absent from the nest on seven occasions for a total of 63 minutes (11%). After the chicks hatched, the female no longer gave the soliciting snoring call. From the hide 4–6 m from the nest, nestlings at 4–6 days were heard giving a soft *gobble-gobble* call. The adult female often gave a squeaky *e-e-e-e-e* call either in or close to the nest hollow, probably a food-offering call. Delivery of food to the nest was infrequent (1.2 deliveries/h or 1.7/h of active delivery time) and only by the male, which spent *c.* 15–30 seconds in the nest hollow when delivering prey (*n* = 3 nests, 4 observation periods, total 15.4 h of observation; a mean of 4.5 chicks gave 0.28 delivery/chick/h, and 0.43/chick/h of active delivery time). During most of this period, the male was also responsible for feeding the female. At one nest, the male roosted >500 m from the nest, although closer suitable roosting sites were available.

Nestling age: c. 16–30 days

Feeding rates of nestlings increased (data combined with Days 30–45: see below), and nestlings were noticeably more vocal, frequently hissing and emitting a variety of twittering sounds. When the nest was examined during the day, nestlings emitted a sustained defensive hiss. The female ceased diurnal roosting in the nest hollow during this period, and the adults now visited the hollow only to deliver prey, indicating that chicks were now feeding themselves. When entering the hollow, adults always held the prey item in the bill, and entered the hollow head first. Each prey delivery lasted *c.* 10–15 seconds.

Nestling age: c. 31–45 days

Vocalisations by adults and chicks increased during this period. When adults returned with food, the calls of nestlings increased in rapidity and intensity over background calling when the adults were absent. The most common call given by nestlings was a well-developed food-soliciting snore. By *c.* 40 days, nestlings typically ascended the inside of the hollow, spending much of the observation period looking out. However, when given food by an adult, nestlings backed away and descended into the hollow. Wing-stretching and exercising of flight muscles commenced by nestlings standing in the entrance of the hollow, which often became crowded; at one nest, a nestling was knocked to the ground by the wing-flapping exercises of another but climbed adeptly back to the hollow, maintaining a hold with its bill, claws and possibly wings. For Days 15–45, the parental prey-delivery rate was 2.3 deliveries/h or 3.0/h of active delivery time (*n* = 2 nests, 3 observation periods, total 11.1 h of observation; a mean of 4.3 chicks gave 0.53 delivery/chick/h, and 0.68/chick/h of active delivery time).

Nestling age: c. 46 days to fledging

Approaching the end of the nestling period, young climbed or jumped and flapped out of the nest, and flew around the nest tree and adjacent trees and onto the ground within 6–8 m of the nest tree. The food-soliciting calls at this time were frequent and loud (at this time snoring may also act as a contact call), and food-delivery rates by adults appeared to reach their maximum (3.3 deliveries/h or 4.3/h of active delivery time; *n* = 3 nests, 5 observation periods, total 15.8 h of observation; a mean of 4.8 chicks gave 0.69 delivery/chick/h, and 0.91/chick/h of active delivery time). Young engaged in apparent play or learning behaviours, including dropping and then pouncing onto prey delivered by adults, preening, allopreening, and apparent bill-fencing (interlocking of bills). After apparent food satiation, as indicated by a marked decrease in the rate and intensity of snoring calls, the owlets dozed, typically standing on one foot with the other drawn into the feathers of the belly. At two sites, at least four owlets spent extensive periods (>30 min.) dozing on the ground. At one nest, an owlet spent *c.* 10 minutes dozing while perched on the observation hide.

Morphometrics of nestlings

At one nest in November 1989 (Thurla, 1 year after the prey crash), nestling body mass, culmen length and tarsus length increased linearly with nestling age, from a starting point of 2–4 days old over a brood age range of up to 12–14 days old (Figure 1). The calculated rate of mass increase was ~22 g per day over that interval, from a small sample of a single brood of five owlets in intact mallee woodland in a normal prey year.

Post-fledging

The nest tree remained the centre of all activity while any owlets remained in the nest hollow. Following fledging of the last owlet, activity was no longer centralised, and feeding of young occurred anywhere within ~200 m of the nest tree. However, the fledglings tended to remain closely associated, engaging in occasional bouts of allopreening and bill-fencing. Immediately post-fledging, young were typically inactive, and called mostly with the food-soliciting snore call. Increasing mobility and activity were associated with the development of a typical Barn Owl screech call, although raspy and imperfectly delivered. Both adults were vocal and active during this period. Parental prey-delivery rates appeared lower than during the immediate pre-fledging period. No observations of prey capture by recently fledged owls were made.

On three occasions at two sites, fledglings were found roosting during the day in exposed positions when suitable tree hollows were available nearby. Recently fledged owlets did not flush easily from diurnal roost sites, and were reluctant to fly from perches at night, despite being able to fly reasonably well. When approached within 2 m, one fledgling roosting in an exposed position adopted a defensive mantling posture (wings outstretched and bent down and forwards) and emitted a series of sustained defensive hisses and bill-clacking.

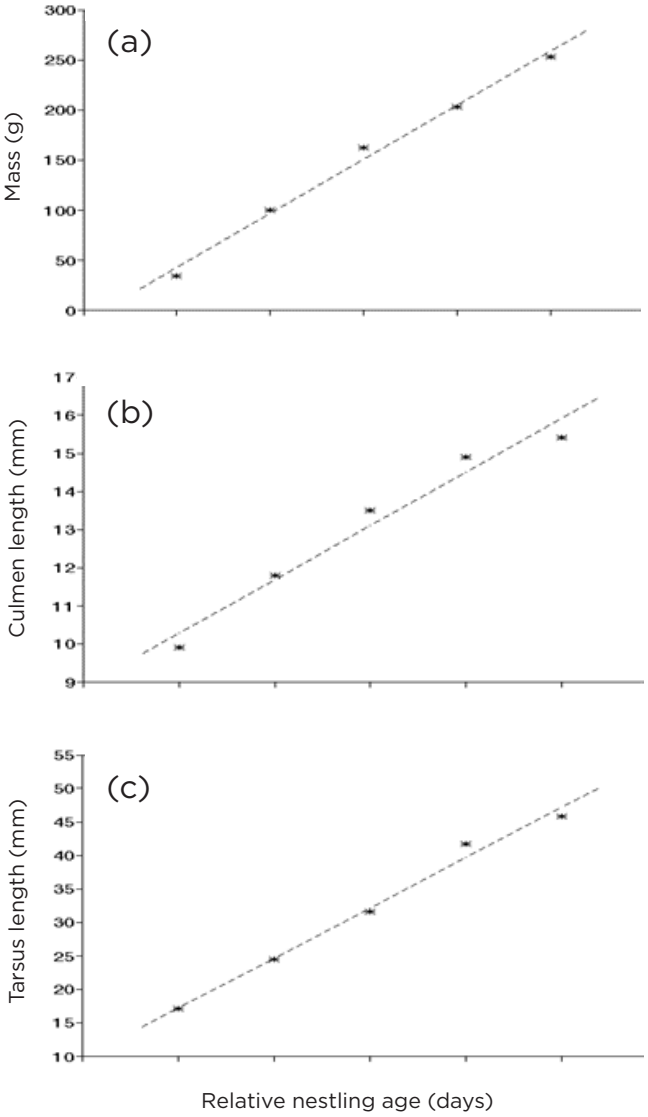

Figure 1. Relative age-related mass and linear measurements of five nestlings from one Barn Owl nest, 2 November 1989. Approximate age of youngest nestling 2–4 days; assumes a hatching interval of 2.5 days. (a) body mass vs age, (b) culmen length vs age, (c) tarsus length vs age.

One case of aggression by adults toward a juvenile that was no longer giving the snoring call was observed. This owl (aged 74–76 days), which was flying well but emitting an imperfect screech call, perched next to a stationary juvenile that was persistently snoring. An adult dived at the juvenile after delivering prey to the younger owl, and both adults subsequently chased the juvenile in flight for >80 m. Adult vocalisations during pursuit were loud and rapid, with an explosive quality. Similar calls were not noted during any other stage of breeding.

Territorial behaviour

The following observations indicated probable territorial behaviour. Initial evening activity was typically the period of greatest vocal activity for Barn Owls at most sites, during both breeding and nonbreeding periods. Based primarily on vocalisations, the Owls were frequently noted to fly from

and around their roost or nest sites. Calling during these flights was brief (0.5–1 sec.), and typically comprised a series of 5–15 calls delivered over 30–60 seconds (flights either lasted this length of time or continued beyond audible range). On three occasions at two sites during summer (just before total darkness), visual observations of these flights were made (nonbreeding birds, roosting areas known). In one case, an Owl flew ~350 m from its roost site, described a small arc, flew almost directly back over the roost and out of sight. Two observations made on successive nights at the same site were almost identical. In each case the Owl flew ~400 m from its roost area, changed direction (~30º), flew ~200 m, changed direction again (~45º), before being lost to view. In all cases, the birds flew at heights of ~10–30 m. A variation of male incessant stationary screech calls, delivered usually for <1 minute from various positions (>200 m) from the nest tree during the early evening, was commonly observed. This call behaviour occurred with varying intensity throughout most of the breeding period.

The response of Barn Owls to playback of Barn Owl calls was variable, and the factors accounting for this variation were not determined. However, on at least four occasions (at two sites) during the nonbreeding period, when Barn Owl screech calls were broadcast within 250 m of a pair of Barn Owls, both owls responded. This response was characterised by screeching, flying in directly over the source, and perching nearby.

During the early nestling period at one nest, J. Kiley (pers. comm.) twice observed a single Barn Owl ~50 m from the nest site being vigorously pursued away from the nest by the resident male. These chases involved loud and prolonged screeching. An encounter near the nest tree was also observed the following night. On this occasion two owls made physical contact (possibly by locking talons), and tumbled to the ground where they fought for *c.* 15 seconds, emitting high-pitched and rapid screams. During this fight at least one owl lost many body and some flight feathers.

Pair bonds

Because Barn Owls were not individually marked during this study, no unequivocal data concerning pair bonds during the nonbreeding period could be obtained. However, of 19 records obtained at night of Barn Owls in the vicinity of known breeding sites during a nonbreeding period (i.e. sites from where young had dispersed, and where no breeding or overt courtship behaviour was currently taking place), 15 (79%) were of two closely associated owls (suggesting a pair).

Discussion

Mating and egg-laying

Laying seasonality in Victoria in times of high prey abundance, including second broods in a year, was similar to that of subspecies *javanica* and *stertens* in the productive tropics, allowing for the inverse seasons in opposite hemispheres (cf. Lenton 1984; Mahmood-ul-Hassan *et al.* 2007). Mating behaviour and associated vocalisations were also similar to that described for *javanic*a by Lenton (1984).

Breeding parameters

Clutch size (mean, mode and range) in the Victorian Mallee was generally consistent with other Australian data (cf. Olsen & Marples 1993; Higgins 1999; Beruldsen 2003; Courtney & Debus 2006; Mawson *et al.* 2024), although the present study confirms that clutch size is larger in boom times (e.g. rodent plagues) than in leaner times (*contra* Schodde & Mason 1980). Well-fed captive Barn Owls also lay large clutches (5–7 eggs: Fleay 1968). Clutch size was also similar to, or slightly smaller than, that of overseas populations, notably subspecies *javanica* and *stertens* of the productive tropics (cf. Lenton 1984; del Hoyo *et al.* 1999; Mahmood-ul-Hassan *et al.* 2007; König & Weick 2008). Alleged clutches of 12 or more eggs, in Australia (Higgins 1999) and overseas (del Hoyo *et al.* 1999), may represent two females laying in the one nest, given the occasional occurrence of polygyny (e.g. Taylor 1994; König & Weick 2008; Roulin 2020).

The incubation period (*c*. 33 days) was consistent with other data for Australian Barn Owls (34 or 32–33 days in captivity: Fleay 1968; J. Norman pers. comm.), and similar to or at the higher end of values given for overseas populations (e.g. del Hoyo *et al.* 1999; König & Weick 2008; Roulin 2020), notably for *javanica* (32.6 days: Lenton 1984). Hatching success was similar to or somewhat higher than for tropical subspecies *javanica* and *stertens*, including for first versus second clutches of the year (cf. Lenton 1984; Mahmood-ul-Hassan *et al.* 2007).

Brood size was consistent with other Australian data, and in at least some cases similarly related to food abundance (cf. Fleay 1968; Purchase 1972; Hutton & Brickhill 1985; Courtney & Debus 2006; Hollands 2008; Fisher & Fisher 2014; Meaney *et al.* 2021; Mawson *et al.* 2024; 2–4 chicks in Royal Australasian Ornithologists Union Nest Record Scheme). Meaney *et al.* (2021) recorded fledged broods of up to six (mean four) from an optimal next-box design; and Figure 2 of Mawson *et al.* (2024) shows a brood of four including a large feathered nestling (with wisps of natal down) incorrectly labelled as an adult, as well as another brood of five chicks (their Figure 4). There are few comparative Australian data for measures of breeding success, which is probably region- and year-specific according to climate, weather and food supply. Meaney *et al.* (2024) recorded at least 32 young, possibly up to 35, fledged from 11 nesting events in nest boxes, or 2.9–3.2 young per attempt.

Growth curves for body mass, culmen and tarsus for subspecies *javanica* and *stertens* were also almost linear over the owlets' first 2 weeks (Lenton 1984; Nagarajan *et al.* 2002), as for the brood in Victoria. The inferred daily rate of mass increase for the single Victorian brood, based on an assumed hatching interval, exceeded that measured for broods of the large subspecies *javanica* (cf. Lenton 1984).

The approximate nestling period (*c*. 53 days to outside roosting), possibly an over-estimate of the true fledging age, is similar to values obtained in the wild (50–55 days: Hollands 2008) and in captivity for Australian Barn Owls (8 weeks: Fleay 1968; fledged in 40–45 days if food is

provided *ad libitum*, otherwise 50 days: J. Norman pers. comm.). It is also similar to values obtained for the larger subspecies *javanica* (59–65 days: Lenton 1984), and for other continental populations (*c.* 56 days: Bunn *et al.* 1982; *c.* 52–56 days: Wilson *et al.* 1986; 45–55 days: Steyn 1982; 55–65 days: Roulin 2020), and shorter than the 9–10 weeks given by Schodde & Mason (1980). Most radio-tracked nestlings that first roosted outside the nest box at ≥59 days (mean 75 days) returned to the nest to roost on subsequent day(s) to a mean of 79 days old (Almassi *et al*. 2021).

The minimum post-fledging dependence period (*c*. 3–5 weeks) was similar to previous inferences for Australia, allowing for age since fledging rather than since hatching (i.e. fledged *c*. 4 weeks: Fleay 1968; 3 weeks: Courtney & Debus 2006), and for *javanica* (*c*. 3 weeks, with returning to the nest to roost during that time: Lenton 1984). However, it is difficult to follow juveniles after they range away from the immediate nest site. Overseas values generally agree (independence at 28–46 days, 3–5 weeks or *c*. 1 month post-fledging: Bunn *et al.* 1982; Steyn 1982; del Hoyo *et al.* 1999; König & Weick 2008), supported by observation, radio-tracking and banding of juveniles dispersing from their natal area from as little as 2–3 weeks post-fledging, though usually 4–6 weeks, and settlement on future breeding areas at 2 months post-fledging (Taylor 1994). Radio-tracked juveniles left their natal home range (1.5-km radius from the nest) at a mean of 97 days of age (Almassi *et al.* 2021), i.e. a mean of 22 days post-fledging. These values are shorter than the 12 weeks stated by Schodde & Mason (1980).

Prey abundance and breeding

The findings of this study support the view that Barn Owls are multi-brooded (laying in autumn/winter as well as spring), and have larger clutches and broods and greater breeding success in boom times than in leaner times, when breeding is more seasonal (spring) and pairs may even forego breeding during food shortage, in Australia (e.g. Fleay 1968; Schodde & Mason 1980; Olsen & Marples 1993; Higgins 1999; Hollands 2008; Mawson *et al.* 2024) as well as overseas (e.g. Bunn *et al.* 1982; Lenton 1984; Taylor 1994; König & Weick 2008; Jackson & Cresswell 2017; Roulin 2020). However, the interval between successive breeding events (fledging to next egg-laying) was longer in the Victorian Mallee than in the tropics for *javanica* (a few days to a month: Lenton 1984). Overlapping breeding cycles (new clutch before the previous brood fledges), as can happen overseas when food is abundant (e.g. del Hoyo *et al.* 1999), are unconfirmed for Australia, although possibly occur during prey plagues (Higgins 1999). Cannibalism of eggs and/or chicks, as occurs in Australia and overseas during food shortage (Bunn *et al.* 1982; Higgins 1999), was suspected in the present study.

Behaviour

In this study, courtship behaviours and other activity preceding breeding were extended (*c.* 8–10 and 12 weeks before clutch initiation), and it appeared that pair bonds were maintained during the nonbreeding period (*contra* Schodde & Mason 1980). Meaney *et al.* (2021) observed fledging 3–5 months (mean 4.5) after courtship, suggesting a courtship/pre-laying phase lasting on average *c*. 7 weeks. Elsewhere, pre-breeding activity can take 2–3 weeks (subspecies *javanica* during continuous breeding: Lenton 1984) or 6–8 weeks (Bunn *et al.* 1982; Taylor 1994). Conversely, in this study overt courtship behaviour was not detected when pairs, with established pair bonds, laid second clutches within a year. The male perched display posture to a female as both emerged from different roost holes in the same tree, before they allopreened and after local fledging dates (Fisher & Fisher 2014), was not observed.

Allopreening by nestlings (this study) has also been recorded overseas (Ducouret *et al.* 2020). The intensity of food-begging calls by nestlings during absence of the adults serves to establish which nestling receives the next prey delivery, based on degree of hunger or satiation (Roulin *et al.* 2000).

Territorial behaviour occurs in Barn Owls overseas (e.g. Bunn *et al.* 1982; Cramp 1985; Roulin 2020), and was observed in this study at low breeding density and prey abundance, thus contrasting with the lack of territoriality in times of high breeding density and prey abundance (e.g. Schodde & Mason 1980; Hollands 2008). Similarly, this study obtained evidence of pair bonds persisting between breeding events, *contra* Schodde & Mason (1980) who suggested that Barn Owls in Australia are solitary birds that maintain pair bonds only for the duration of a single breeding event. SJSD also observed similar territorial behaviour to that described by JGM (above): in northern inland New South Wales in October 2024 (no mouse plague), when a pair of Barn Owls was breeding as indicated by incessant screech calls, in response to playback of screech calls one or two Barn Owls screeched, performed fly-overs and landed nearby, appearing agitated.

Conclusions

The findings of this study suggest how Australian Barn Owls behave during normal years and situations: they breed at low densities, with moderate reproductive output, and exhibit seasonal breeding and territorial behaviour. Such an interpretation is also supported by the observations of Courtney & Debus (2006).

Acknowledgements

This paper formed part of an MSc thesis at La Trobe University, supervised by the late Peter Rawlinson, the late Dr Richard Zann, and Dr David Baker-Gabb; the University, staff and fellow students (notably Dr Beverley Van Praagh, Bruce Quin, Martyn Summers and Evan Schmidt) are gratefully acknowledged for supporting and/or facilitating the project. The Wheat Research Committee for Victoria and the M.A. Ingram Trust provided financial assistance. The Department of Agriculture and Rural Affairs enabled access to the Mallee Research Station, and the officers and staff of Mildura Region of the Department of Conservation and Natural Resources facilitated the study. Thanks go to John Kiley, Gary Leamon, Chris Johns, David Whelan, Bruce Quin, Alex Peart, Tania and Zac Rajic, Terry Mazzer and Les McLaughlin for field assistance. Thanks also go to Jon Starks for access to the Royal Australasian Ornithologists Union Nest Record Scheme and Australian Bird Atlas data; Julie Norman (Healesville Sanctuary) for data on

captive Barn Owls; the Bureau of Meteorology for providing climate data; Richard Loyn and the late Ken Rogers for statistical advice; and Louise Currie for help with banding Barn Owls. The co-operation of the many landholders, especially Florence Beaton of Sunshine Farm, Carwarp, is gratefully acknowledged. This study was carried out under DCNR Research Permit numbers 88-134/140, 89-151 and 90-025. Chris Pavey, Alexandre Roulin and Matthew Johnson provided helpful comments on a draft of this paper.

References

Aliabadian, M., Alaei-Kakhki, N., Mirshamsi, O., Nijman, V. & Roulin, A. (2016). Phylogeny, biogeography, and diversification of barn owls (Aves: Strigiformes). *Biological Journal of the Linnean Society* **119**, 904–918.

Almassi, B., Massa, C., Jenni, L. & Roulin, A. (2021). Exogenous corticosterone and melanin-based coloration explain variation in juvenile dispersal behaviour in the Barn Owl (*Tyto alba*). *PLoS ONE* **16** (9), e0256038.

Beruldsen, G. (2003). *Australian Birds: Their Nests and Eggs*. Author, Brisbane.

Blakers, M., Davies, S.J.J.F. & Reilly, P.N. (1984). *The Atlas of Australian Birds.* Melbourne University Press, Melbourne.

Bunn, D.S., Warburton, A.B. & Wilson, R.D.S. (1982). *The Barn Owl.* Poyser, Calton, UK.

Courtney, J. & Debus, S.J.S. (2006). Observations on the post-fledging period of the Barn Owl *Tyto alba*. *Australian Field Ornithology* **23**, 159–162.

Cramp, S. (Ed.) (1985). *The Birds of the Western Palearctic, Volume 4: Terns to Woodpeckers*. Oxford University Press, Oxford, UK.

del Hoyo, J., Elliott, A. & Sargatal, J. (Eds) (1999). *Handbook of the Birds of the World, Volume 5: Barn-owls to Hummingbirds*. Lynx Edicions, Barcelona, Spain.

Ducouret, P., Romano, A., Dreiss, A.N., Marmaroli, P., Falourd, X., Bincteux M. & Roulin, A. (2020). Elder Barn Owl nestlings flexibly redistribute parental food according to siblings' need or in return for allopreening. *American Naturalist* **196**, 257–269.

Fisher, K. & Fisher, L. (2014). Barn Owl display. *Boobook* **32**, 49.

Fleay, D.H. (1968). *Nightwatchmen of Bush and Plain.* Jacaranda Press, Brisbane.

Fowler, J. & Cohen, L. (1987). *Statistics for Ornithologists.* British Trust for Ornithology, Hertfordshire, UK.

Higgins, P.J. (Ed.) (1999). *Handbook of Australian, New Zealand & Antarctic Birds, Volume 4: Parrots to Dollarbird*. Oxford University Press, Melbourne.

Hollands, D. (2008). *Owls, Frogmouths and Nightjars of Australia*. Bloomings Books, Melbourne.

Hutton, K. & Brickhill, J. (1985). Exceptional concentrations of Barn Owls *Tyto alba* in the Riverina District of New South Wales. *Australian Birds* **20**, 8–11.

Jackson, P.& Cresswell, W. (2017). Factors determining the frequency and productivity of double brooding of Barn Owls *Tyto alba*. *Bird Study* **64**, 353–361.

Jønsson, K.A., Poulsen, M.K., Haryoko, T., Reeve, A.H. & Fabre, P.-H. (2013). A new species of masked-owl (Aves: Strigiformes: Tytonidae) from Seram, Indonesia. *Zootaxa* **3635**, 51–61.

König, C. & Weick, F. (2008). *Owls of the World*. 2nd edn. Helm, London.

Lenton, G.M. (1984). The feeding and breeding ecology of Barn Owls *Tyto alba* in Peninsular Malaysia. *Ibis* **126**, 551–575.

Mahmood-ul-Hassan, M., Beg, M.A., Mushtaq-ul-Hassan, M., Mirza, H.A. & Siddique M. (2007). Nesting and diet of the Barn Owl (*Tyto alba*) in Pakistan. *Journal of Raptor Research* **41**, 122–129.

Mawson, P.R., Dawson, R. & Saunders, D.A. (2024). Breeding by Barn Owls *Tyto alba* in artificial nest hollows established for an endangered black cockatoo in the northern wheatbelt of Western Australia. *Australian Zoologist* **44**, 26–34.

McLaughlin, J. (1994). Aspects of the Ecology and Behaviour of the Barn Owl *Tyto alba* (Scopoli) in the Mallee Wheat-belt of North-western Victoria, Australia. MSc thesis, La Trobe University, Melbourne.

McLaughlin, J.G. & Debus, S.J.S. (2025). Selection of nest and roost sites by Eastern Barn Owls *Tyto alba delicatula* in north-western Victoria. *Corella* **49**, 44–54.

McLaughlin, J.G. & Debus, S.J.S. (In press). Responses of Eastern Barn Owls (*Tyto alba delicatula*) to changes in prey abundance in north-western Victoria. *Corella* **49**.

Meaney, K.M., Peacock, D.E., Taggart, D. & Smith, J. (2021). Rapid colonization, breeding and successful recruitment of Eastern Barn Owls (*Tyto alba delicatula*) using a customized wooden nest box in remnant mallee cropping areas of southern Yorke Peninsula, South Australia. *Wildlife Research* **48**, 334–344.

Nagarajan, R., Thiyagesan, K., Natarajan, R. & Kanakasabai, R. (2002). Patterns of growth in nestling Indian Barn Owls. *Condor* **104**, 885–890.

Olsen, P.D. & Marples, T.G. (1993). Geographic variation in egg size, clutch size and date of laying of Australian raptors (Falconiformes and Strigiformes). *Emu* **93**, 167–179.

Pande, S. & Dahanukar, N. (2012). Reversed sexual dimorphism and differential prey delivery in Barn Owls (*Tyto alba*). *Journal of Raptor Research* **46**, 184–189.

Purchase, D. (1972). A report on the banding of Barn Owls. *Australian Bird Bander* **10**, 74–75.

Roulin, A. (2020). *Barn Owls: Evolution and Ecology, with Grass Owls, Masked Owls and Sooty Owls*. Cambridge University Press, Cambridge, UK.

Roulin, A., Kölliker, M. & Richner, H. (2000). Barn Owl (*Tyto alba*) siblings vocally negotiate resources. *Proceedings of the Royal Society of London B* **267**, 459–463.

Saunders, G.R. & Giles, J.R. (1977). A relationship between plagues of the House Mouse, *Mus musculus* (Rodentia: Muridae) and prolonged periods of dry weather in south-eastern Australia. *Australian Wildlife Research* **4**, 241–247.

Schodde, R. & Mason, I.J. (1980). *Nocturnal Birds of Australia.* Lansdowne Press, Melbourne.

Siegel, S. (1956). *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill, Tokyo.

Singleton, G.R. & Redhead, T.D. (1989). House Mouse plagues. In: Noble, J.C. & Bradstock, R.A. (Eds). *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management,* pp. 418–433. CSIRO Publishing, Melbourne.

Southern, H.N. (1955). Nocturnal animals. *Scientific American* **193**, 88–98.

Steyn, P. (1982). *Birds of Prey of Southern Africa: Their Identification and Life Histories.* Croom Helm, Beckenham, UK.

Taylor, I. (1994). *Barn Owls: Predator–Prey Relationships and Conservation*. Cambridge University Press, Cambridge, UK.

Uva, V., Päckert, M., Cibois, A., Fumagalli, L. & Roulin, A. (2018). Comprehensive molecular phylogeny of barn owls and relatives (Family: Tytonidae), and their six major Pleistocene radiations. *Molecular Phylogenetics and Evolution* **125**, 127–137.

Wilson, R.T., Wilson, M.P. & Durkin, J.W. (1986). Breeding biology of the Barn Owl *Tyto alba* in central Mali. *Ibis* **128**, 81–90.

Co-author's note. This paper originated as a collaborative effort with John McLaughlin in 2019 on the basis of his long-unpublished MSc thesis, but John was unable to review and revise draft papers arising from those chapters before contracting leukaemia and passing away on 28 January 2025. The data collection, analysis, interpretation and thesis were entirely John's, leaving only post-1994 literature review to insert in an edit of his thesis chapter.

Received 3 February 2025, accepted 18 May 2025, published online 7 August 2025