

THE PYGMY FALCON
POLIHIERAX SEMITORQUATUS

by

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Introduction

Since Sir Andrew Smith first collected the pygmy falcon near Kuruman in 1836 (Smith, 1849) the subspecific variations of this little raptor have been the subject of some debate (Bowen, 1931; Friedmann, 1930; Grant and Mackworth-Praed, 1934; Oberholser, 1904; Sclater, 1924; Swann, 1922). Its myology has been dealt with in considerable detail by Berger (1956). Otherwise, except for a good account of its biology by Hoesch (1935), it has not figured widely in the ornithological literature. This is not altogether surprising when one considers the relative paucity of ornithologists in the Kalahari and other centres of pygmy falcon distribution. Most of the biological notes on this bird have been of a most general nature (e.g. Braine and Braine, 1968; Grossman and Hamlet, 1964; Mackworth-Praed and Grant, 1952, 1962; McLachlan and Liversidge, 1957; Smithers, 1964; Von Erlanger, 1904), so that the present study is intended to fill, in part at least, the gaps in our knowledge of the pygmy falcon.

The study was an incidental one conducted in the Kalahari Gemsbok National Park from late 1964 to early 1966 during a 19-month investigation of the sociable weaver *Philetarius socius*, a species with which the pygmy falcon lives in close association.

Range and Taxonomy

The pygmy falcon *Polihierax semitorquatus* has an interesting, discontinuous distribution in Africa (Fig. 1). The southern population inhabits the dry western parts of the northern Cape, South West Africa and Botswana and is referable to the subspecies *semitorquatus*; another southern subspecies, *homopterus*, was made by Oberholser (1904), but the grounds for his claim are too slender to regard this division as valid. The northern population inhabits East Africa and constitutes the subspecies *castanonotus* (sometimes written *castanotus*); this northern population has been divided into three different subspecies namely: *castanotus*, *deckeni* and *major* (Bowen, 1931), but Friedmann (1930) and Grant and Mackworth-Praed (1934) have shown that only two subspecies are recognizable, *semitorquatus*

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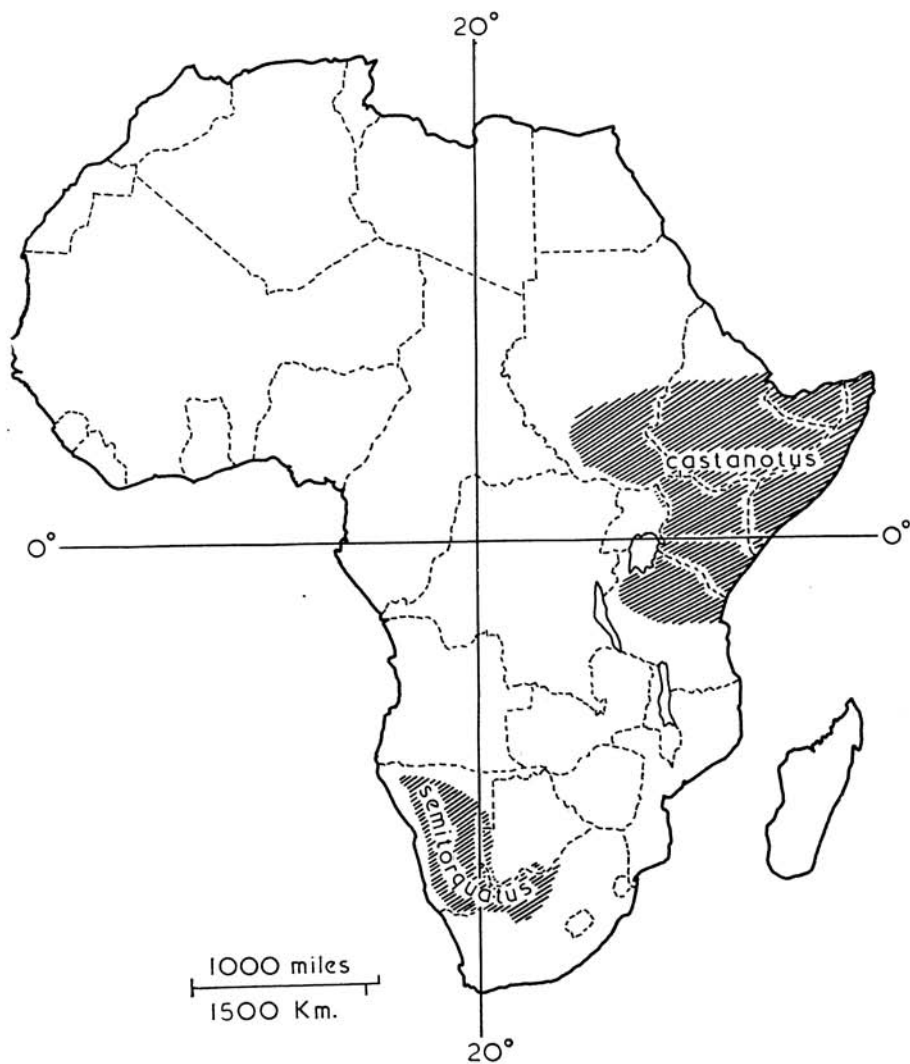


Fig. 1. Map of Africa showing the distribution (cross-hatching) of the two subspecies of pygmy falcon, *Polihierax semitorquatus castanotus* in East Africa and *P. s. semitorquatus* in western South Africa.

in the south and *castanotus* in the north. Most authors today are agreed on this latter subdivision.

The range of *P. s. semitorquatus* corresponds almost exactly with the range of the sociable weaver (Smithers, 1964) and this in turn corresponds roughly to the drier *Acacia* savanna of which *A. giraffae* and, in some places, *A. haematoxylon* are the dominant trees. The habitat of *P. s. castanotus* in East Africa is also *Acacia* savanna (Von Erlanger, 1904) in which various species of so-called "sociable" weavers (Plocepasserinae), buffalo weavers (Bubalornithinae) and true weavers (Ploceinae) are common. In both populations, the falcons are dependent on the weaver nests for roosting and breeding purposes.

The genus *Polihierax* is monotypic and confined to Africa. Another species, *P. insignis*, has been described from India (Baker, 1927), but this bird is now placed in the genus *Neohierax* (Grossman and Hamlet, 1964). Berger (1956) has shown on myological grounds that *Polihierax* is very closely related to *Falco* and does not warrant its own subfamily, although Grossman and Hamlet (1964) still place this genus in the subfamily Polihieracinae along with *Spizapteryx*, *Neohierax* and *Microhierax* (they remove *Gampsonyx* to the subfamily Elaninae in the Aquilidae, although Berger included it with the Polihieracinae).

The purpose of this brief taxonomic outline is merely to indicate the systematic position of *Polihierax* within the Falconidae. The bird with which the rest of this paper is concerned is the southern pygmy falcon *P. s. semitorquatus*.

Nest Associates and Distribution

Of the East African pygmy falcons it is stated that it nests mainly in the nests of "Weavers, Sociable Weavers and Glossy Starlings, sometimes in the middle of a colony" (Mackworth-Praed and Grant, 1952). In southern Africa it is primarily associated with the sociable weaver, but is also known to nest in "Buffalo Weaver and starling nests" (McLachlan and Liversidge, 1957), while I have seen it using the double-entrance nest of a white-browed sparrow-weaver *Plocepasser mahali* for roosting purposes in the Kalahari Gemsbok National Park.

The range of the pygmy falcon is so closely governed by the range of the sociable weaver that it does not occur in what appears to be otherwise suitable country, such as Botswana (Smithers, 1964); the distribution map for the pygmy falcon in McLachlan and Liversidge (1957) is therefore quite inaccurate. Hoesch (1935) also said: "Im Damaraland bewohnt der Zwergfalke—und zwar nach meinen bisherigen Feststellungen ausschliesslich—die Nester des Siedelwebers (*Philetairus socius*)."

The presence of pygmy falcons in a sociable weaver nest mass is always indicated clearly by the white faecal deposit at the entrance to whichever chamber they are occupying (Fig. 2). The number of chambers occupied by a pair of falcons varies from two (one for breeding and one for roosting) to four, but may be as high as ten in exceptional instances. When such a



Fig. 2. The under surface of a sociable weaver nest mass showing the white faecal deposit at the entrance to a chamber occupied by a breeding pair of pygmy falcons. The chamber to the upper left of the falcon nest contained young sociable weavers.

large number of chambers is taken over by the falcons, the sociable weavers may abandon the entire nest mass and move off elsewhere.

In my experience there was never more than a single pair of falcons in one weaver colony, but Braine and Braine (1968) have found at least two and perhaps three breeding pairs in a single nest mass. This must be unusual, since Hoesch (1935) also found only one pair of falcons per nest mass, each pair occupying two chambers.

In the Kalahari Gemsbok National Park study area (Fig. 3) there were ten pairs of pygmy falcons representing slightly less than 25% occupation of the available weaver colonies. These pairs occupied the colonies shown in Table 1, which shows also that the falcons will use nest masses whether or not they are occupied by the weavers. The percentage occupation of weaver colonies by pygmy falcons given by Hoesch (1935) is also nearly 25% (7 out of 30), but in this instance, six out of seven pairs were using occupied nest masses. The percentage of nest masses unoccupied by weavers was not given, so that there may have been relatively fewer than I found in the Kalahari Gemsbok National Park.

Nest masses occupied by pygmy falcons were seldom less than half a mile apart (Fig. 3) indicating a considerable degree of territoriality. This makes the observations of Braine and Braine (1968) all the more intri-

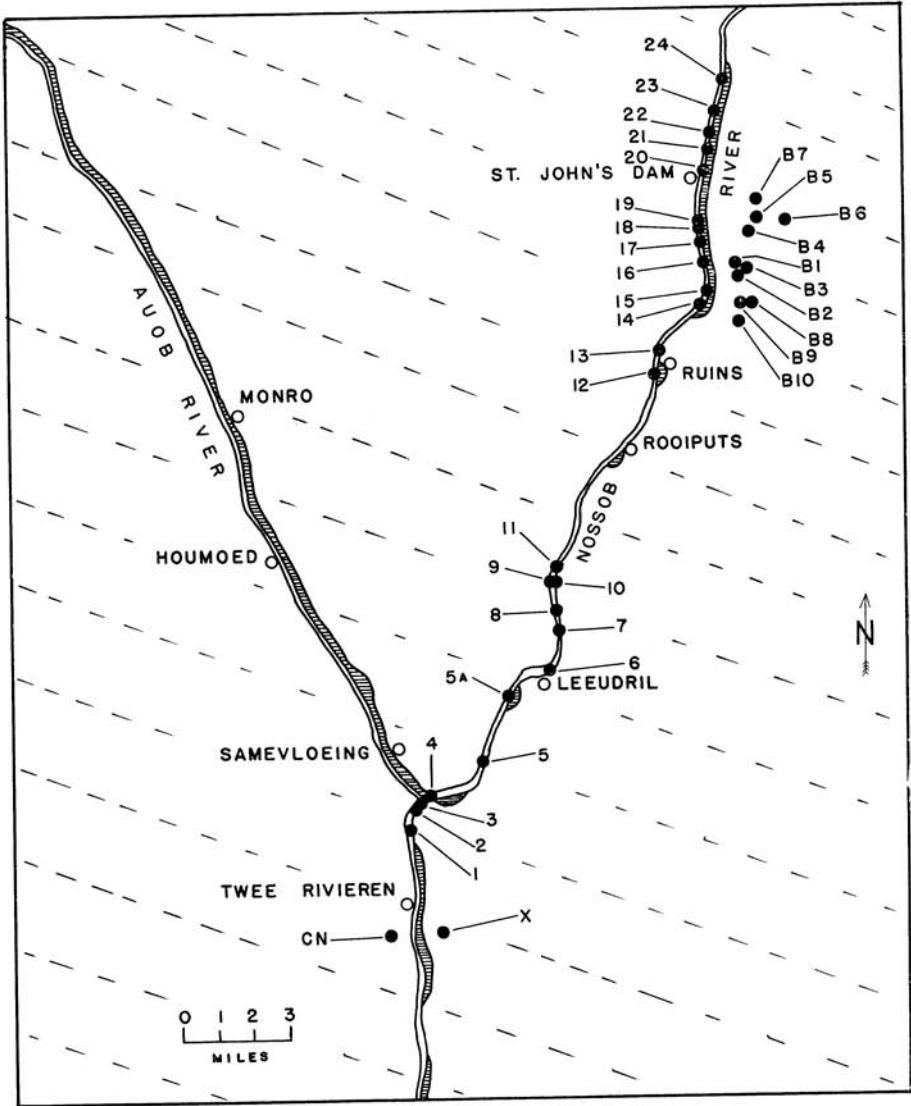


Fig. 3. Map of the study area in the southern Kalahari Gemsbok National Park showing the game wells (open circles) and the sociable weavers nests (solid circles with nest numbers). The broken diagonal lines indicate the extent and direction of the dune country, while the small hatched areas on the east banks of the Auob and Nossob Rivers show the extent of the stony calcrete.

Table 1

Distribution of Pygmy Falcon Pairs showing occupation of Sociable Weaver Colonies in the Kalahari Gemsbok National Park Study Area (Fig. 3)

<i>Pygmy falcon pair number</i>	<i>Sociable weaver colony number</i>	<i>Nest occupied (+) or unoccupied (—) by sociable weavers</i>
1	6 and 7	—
2	8	—
3	11	+
4	12 and 13	—
5	16 and B1	+
6	17	+
7	19	+
8	20 and 21	—
9	22	+
10	24	+

guing. Although I have never observed any actual territorial conflict between adjacent pairs, it must at times occur.

By ringing falcons with coloured plastic rings it was possible to identify certain individuals in the field. Altogether 32 pygmy falcons were ringed in the study area and, although the colours were bright enough to be seen clearly with field glasses, the rings soon became soiled so that re-identification of a bird was often possible only by retrapping and examination in the hand. Of the 32 ringed birds, three were adult males, six were adult females, four were juvenile males, seven were juvenile females and 12 were unsexed chicks. All the chicks and juveniles were ringed while still in the nest; adults were caught either in mist nets or in the nest chambers.

It has been claimed that "the Social Weavers do not seem to resent these little hawks" (McLachlan and Liversidge, 1957) and conversely that the sociable weavers desert their nests during occupation by the pygmy falcon (Roberts, 1940). The truth lies somewhere in between. If weavers are in occupation of a nest mass into which a pair of pygmy falcons move, they will not desert unless the falcons take over too many chambers. Although the weavers will stay on after falcon occupation and will even breed in adjacent nest chambers, they most definitely resent the falcons' intrusion. Whenever a pygmy falcon appears, the weavers immediately utter alarm calls until the falcon is out of sight inside a nest chamber or right away from the nest tree. As long as the falcons are not visible to the weavers, they go about their activities as usual.

It has also been said that the pygmy falcons do not molest the weavers (Grossman and Hamlet, 1964) and by and large this is probably true. However, I have indirect evidence that a falcon will take young sociable

weavers if it encounters them in a nest chamber that it is investigating with a view to using it for breeding purposes. Furthermore 14 out of 333 (4.2%) pygmy falcon pellets contained sociable weaver feathers. It was not possible to say whether the weavers eaten were adults or young. Pygmy falcons may be trapped using live adult sociable weavers as bait, so they may indeed catch adult weavers as part of their natural diet, at least at times. Molestation of the weavers must, however, be minimal.

Hoesch (1935) says that flying young of the sociable weaver are not molested by the pygmy falcons, but that the approach of a falcon is announced by the "erregte Warnrufe" of the adult weavers. He also mentions (and my own observations confirm this) that the falcons take no notice of the weavers.

Food and Feeding

The food of the pygmy falcon was determined by (a) detailed analysis of regurgitated pellets found in and under nests, (b) examination of larger pieces of prey animals dropped below nests and (c) direct field observations on hunting and feeding falcons.

Many hundreds of pellets were collected in the Kalahari Gemsbok National Park, but to date only 333 have been analysed. These pellets measure about 17.9 mm by 8.6 mm (means of 20 randomly selected pellets) and contain the remains of insects, reptiles, mammals and birds in the proportions shown in Table 2. Further analysis of pygmy falcon pellets will appear in a later publication.

Table 2

Analysis of Regurgitated Pygmy Falcon Pellets in the Kalahari Gemsbok National Park Study Area (Fig. 3)

	<i>Insects only</i>	<i>Lizards only</i>	<i>Mixed insects and lizards</i>	<i>Mixed rodent and lizards</i>	<i>Mixed rodent and insects</i>	<i>Mixed bird and insects</i>
No. of pellets	122	38	123	7	29	14
Percentage	36.7	11.4	36.9	2.1	8.7	4.2

The pellets contain only keratinous, chitinous or enamel remains. Bones of vertebrate prey seem to be completely digested as they do not figure in the pellets at all. Insects remains are mainly those of larger carabid beetles and grasshoppers; these remains await a more detailed identification. Insects occur in a total of 288 pellets (86.5%) and comprise the bulk of the diet. Second most important item on the food list are lizards which occur in a total of 168 pellets (50.5%). These remains are

almost exclusively those of the ocellated sand-lizard *Eremias lineo-ocellata*, although I have found dismembered parts of the spiny agama *Agama hispida* and the common striped skink *Mabuya striata* below pygmy falcon roosts, so these lizards are also taken occasionally.

The identification of sociable weavers from the few feathers found in the pellets is still somewhat tentative, even though the feathers do agree in colour and sometimes in pattern with those of sociable weavers. The small numbers of these feathers in each pellet is curious and perhaps indicates that the falcons seldom feed on the weavers. Similarly rodent remains are scattered sparsely through the pellets; there were no pellets consisting entirely of rodent fur or bird feathers.

The pygmy falcon, then, is primarily insectivorous. About half the pellets contained some lizard remains, while the frequency of rodent remains was only 10.8%. The rarity of bird remains indicates that birds form an insignificant part of the pygmy falcon's diet.

The collection of pellets on a systematic chronological basis was not possible in the rather short study period, since the falcons move about to some extent in the winter. It was therefore not possible to determine seasonal variations in the proportions of prey taken. However, the falcons were seen eating lizards far more often in summer than in winter, no doubt because the lizards were more active and therefore available in the warmer weather. It is therefore probable that the proportion of insect food in winter is higher than in summer. That insects are available in the Kalahari during the winter months has already been indicated (Maclean, 1967).

Pygmy falcons hawk their food from a perch like a shrike. They do not hover. When the prey is spotted, the falcon dives from the perch; as it nears the ground it holds the wings stiffly at a high dihedral and dangles the legs. The strike is made and the falcon returns to its perch to consume the food. Prey is carried either in one foot or in the bill while the bird is in flight. The prey is then held in one foot and the falcon begins to feed at the head end.

Calls and Displays

There are six basic calls in the pygmy falcon. At least three of these calls have two main functions, depending upon their intensity and the context in which they are uttered. The interpretation that follows is necessarily tentative in so incomplete a study. The basic calls are:

1. "tsip tsip" or "tsee tsee" (thin and squeaky)
2. "kiki kik" or "twee twee twip" (sharp or mellow with the last syllable accented)
3. "ki kikik" (sharp with the first syllable accented)
4. "ki-ki-ki-ki-ki-ki-ki" (very sharp and ringing)
5. "krrr krrr krrr" (soft and purring)
6. "see see" (squeaky begging call of chicks).

Calls 1, 2 and 3 are arranged in order of increasing intensity. They are

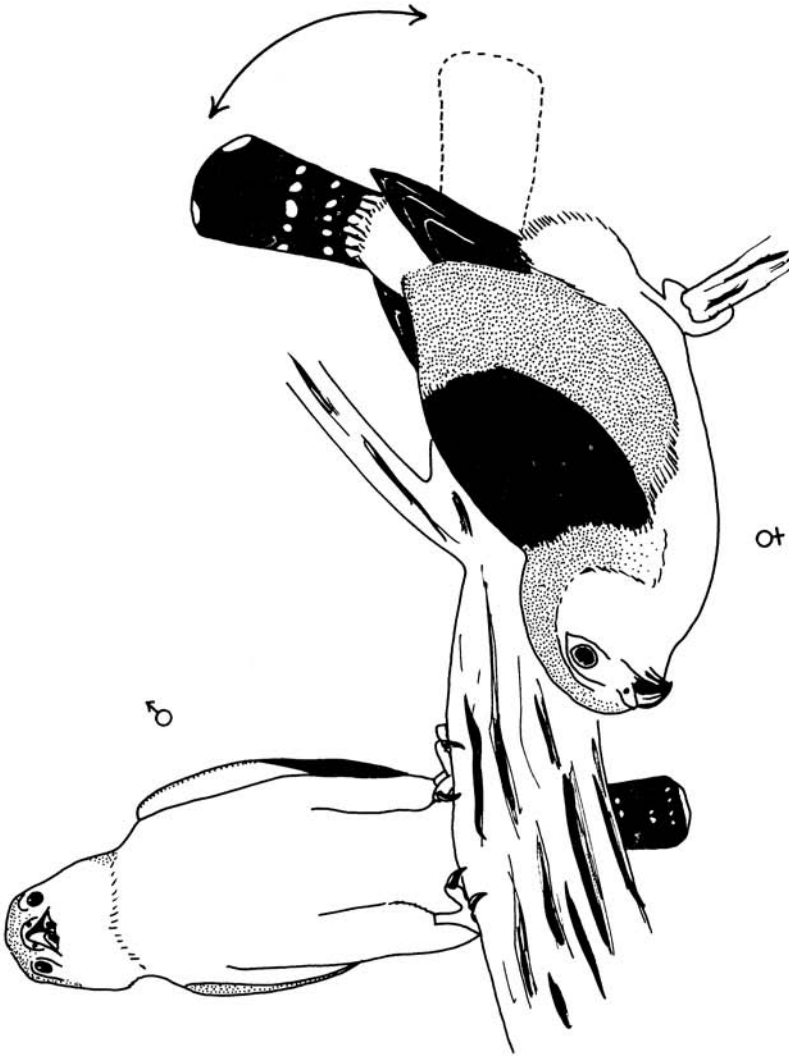


Fig. 4. The greeting display of a female pygmy falcon to her mate; she is in the submissive posture which presents the chestnut back patch to the male. At the same time the tail is wagged up and down as shown by the arrow.

essentially contact calls and may be used as alarm notes, greeting calls or contact calls according to context. Call 1 may precede call 2 in an alarm situation, in which case both are rather harsher and of higher intensity. At lower intensities these two calls accompany a tail-wagging display, usually by the female as she greets the male with a submissive posture (Fig. 4). Call 2 is always used by the male to call an incubating female from the nest chamber in order to be fed. It may also be uttered by the female as she flies to the nest chamber with food for the chicks.

Call 3 uttered loudly is the highest intensity alarm call in adult pygmy falcons, but I have heard a muted version of this call from a nest chamber, which a pair of falcons had just entered to roost; in the latter case it could have constituted a greeting call. Calls 2 and 3 are therefore probably just variations of the same basic theme.

I have heard call 4 only from young, almost fully fledged falcons as they adopt the threat posture (Fig. 5). It is of indefinite duration with each note equally accented. It is interesting that adult pygmy falcons do not usually adopt threat postures or utter threat notes when handled; they usually remain quiescent even when being extracted from a mist net or being held for ringing purposes.

Call 5 is heard only from mated adult pygmy falcons during copulation or in the pre-copulatory and pre-egg-laying phases of the breeding cycle when both members of the pair perform the tail-wagging greeting ceremony to each other. It may have the function of appeasement.

The tail-wagging greeting ceremony is of particular interest. It is most commonly performed by the female towards the male as he lands next to her on a perch, often with a lizard which he offers her as part of the courtship ritual. Feeding, however, is not essential to release greeting in the female. She invariably bows forward during this display and may erect her white rump feathers (Fig. 4). The forward bow serves to display her chestnut dorsal patch to the male which lacks the dorsal coloration and does not bow during the tail-wagging display. Tail-wagging in both sexes effectively accentuates the black-and-white tail pattern.

Exaggerated head-bobbing may accompany the greeting ceremony in the male, but not (apparently) in the female. Head-bobbing also precedes take-off in both sexes, particularly when a bird appears to be judging the flight path to the entrance of a nest chamber from a perch below the nest.

Call 6 is uttered by the chicks in response to the arrival of a parent with food. Since the context here is one of solicitous appeasement, the begging call may be cognate with call 1, which has a similar tonal quality and probably similar functions of appeasement, submission and solicitation.

Breeding Biology

1. *Pre-egg-laying phase*

The breeding season of the pygmy falcon in the Kalahari is an attenuated one, lasting from August to March. It is thus an exclusively



Fig. 5. An almost fully fledged young pygmy falcon male in threat posture.

summer season. The pair bond appears to be maintained throughout the year and the pair always roost together. In winter, however, the pair may move locally to a neighbouring nest mass within the territory, usually not more than a mile from where they bred the previous season. For instance, a male ringed as an adult at nest No. 7 during the breeding season in January 1965 was observed at nest No. 6 in March 1965 after the close of the breeding season. Similarly a pair of falcons moved between nest Nos. 16, B1, B2 and B3 from one season to the next.

Should one member of a mated pair disappear for some reason, the remaining member will immediately pair up with another bird which adopts the original territory as its own, apparently regardless of the sex of the new mate. For example, female No. 7 lost her mate (male No. 8), because the following summer she was paired with male No. 4, which was in fact her own son from the previous breeding season! This shows, too, that pygmy falcons are capable of breeding at the age of one year. This pair remained at nest No. 17 where female No. 7 had nested the previous year, but this may be because her new mate had been reared in this same nest and had not yet left the "home" territory.

In another case, female No. 23 which was caught on the nest at B1 on 18 August when she had just laid the first egg of the 1965 summer season was found dead (apparently killed by a predator) on 7 October. By 11 November the male had taken a new mate, female No. 2, which had been ringed as an adult at nest No. 16 on 24 November 1964, and she had already laid her first egg of the season. Once again, however, the new mate did not come from far away since nest Nos. 16 and B1 cannot be more than half a mile apart. The indications are therefore that pygmy falcons are rather sedentary birds.

At the onset of the breeding season the pair begin to investigate new nest chambers if they move to a new nest mass. (They often breed in the chambers which they have been using as roosting chambers during the winter). It is at this time of the year that the likelihood of predation by the falcons on the sociable weavers is greatest, for if there are any young weavers in the chambers under investigation, they will almost certainly be eaten by the falcons. It is, however, not usual for the weavers to have young at the beginning of summer, since their nesting is entirely dependent upon rainfall, which is rare in winter in the Kalahari.

Once the nesting chamber has been decided upon, it is used by one or both sexes until the first egg is laid, when the male roosts in an adjacent chamber occupied for this purpose.

The sequence of behavioural events involving copulation occurs as follows:

- (a) male sits next to female on perch;
- (b) female greets male with silent tail-wagging submissive display;
- (c) male mounts female and copulation occurs accompanied by call 5;
- (d) male dismounts;

- (e) female remains in submissive posture with tail raised and directed towards male;
- (f) male makes flight-intention movements and flies into nest chamber uttering low-intensity versions of calls 1 and 2;
- (g) female follows male into nest and utters call 1.

The male may then leave the nest chamber, but the female continues to give call 1 for a few minutes following his departure. In one case the female then came out to perch next to the male, but neither bird displayed; after a while they began to preen. I have never observed mutual preening (= allopreening) in the pygmy falcon.

2. *Egg-laying and incubation*

The clutch is completed within three weeks after copulation. In two cases clutches of three eggs each were completed within seven days from the laying of the first egg, with an interval of two to three days between the second and third eggs of the clutch and perhaps a similar interval between the first and second eggs. At any rate there is an interval of well over 24 hours between the laying of successive eggs.

Incubation may begin with the first egg, but sometimes not until the second egg has been laid. Both sexes incubate, although the male seems to do less incubation than the female. Throughout the incubation period the male feeds the female, usually with lizards; he brings a lizard to a perch near the nest, calls the female out as already described and gives the lizard to her. She eats the food before returning to the nest to continue incubation. This feeding is no doubt an extrapolation of courtship feeding and may serve to maintain and strengthen the pair bond.

The exact incubation period is not known, but my data show that it is more than 27 days and less than 31 days. This compares favourably with the incubation period of 30 days in the American kestrel *Falco sparverius* (Willoughby and Cade, 1964).

3. *Clutch size*

Clutch size in the pygmy falcon varies from two to four eggs. The number of eggs laid appears to be governed within these narrow limits by the effects of rainfall (Table 3). The 1964/65 summer was preceded by a dry year, but at the end of the summer (March and April 1965) good rains fell. It was by then the end of the falcon breeding season, but the effect of these late summer rains was to improve conditions for the following summer season (1965/66). The numbers of clutches for the two seasons are too small to be subjected to any kind of adequate statistical analysis, but the indications are that the difference in mean clutch size between the two seasons may be a significant one. The overall mean clutch size for both seasons was 3.1.

Mean measurements of 17 pygmy falcon eggs in the Kalahari Gemsbok National Park are 27.9 mm by 22.3 mm.

Table 3

Clutch Size in the Pygmy Falcon over Two Breeding Seasons in the Kalahari Gemsbok National Park Study Area

Clutch size	Number of clutches	
	1964/65	1965/66
c/2	1	0
c/3	8	7
c/4	0	2
Mean clutch size	2.9	3.2

4. Care and development of the young

When newly hatched the young pygmy falcon has a bright pink skin covered with pure white down; it is blind at first, but the eyes open within a few days. The chicks of a single brood do not hatch synchronously, since incubation begins before the completion of the clutch, so the chicks will be of slightly discrepant sizes.

The first feather quills appear within a week and the young falcon is fully feathered by the age of 21 days, although the tail is still quite short and it may retain traces of natal down around the head. The juvenile plumage is similar to that of the adults, but for a strong chestnut wash which is most intense on the back and upper chest. Even so, the sexes can be easily differentiated at this age, since the female's chestnut dorsal patch is already fully developed.

The age at which young pygmy falcons first leave the nest is difficult to determine because they return to the nest for some time after the initial departure, which is between the ages of 27 and 40 days. The mean nestling period up to the first departure from the nest must be about 30 days.

When still unable to fly, the young falcons exhibit a strong thigmotaxis and photonegativity. When placed in the open, a chick moves backwards until it touches an object or gets into a corner where it settles down. Feathered chicks removed from the nest are able to clamber back up the entrance tunnel to the chamber unaided; once inside, they turn to face the entrance and sit with their backs against the far wall of the chamber. If threatened, larger chicks flip on to their backs and prepare to fight with their feet.

After leaving the nest, but before becoming independent of their parents, the young pygmy falcon usually returns to its original nest chamber, although it may not enter the correct chamber every time. The young may remain with their parents up to two months after they can fly, but by that time they are fending for themselves. The young

may still be tolerated by the parents even after they have begun to care for a second brood.

The usual feeding procedure is that the male parent brings food (usually a lizard), calls the female out of the nest, gives the food to her and she then flies into the nest to feed the chicks. It is possible that the male may also feed the chicks at times, although I have never actually seen one take food into the nest chamber. The female appears to do little hunting herself until the chicks are fully feathered. Once the young have left the nest they are fed by both parents.

5. *Number of broods*

In the 1964/65 summer season I recorded one second brood in the study area; in the 1965/66 season there were two second broods. Most of the pygmy falcon pairs, however, raised but one brood a season and none raised more than two broods. The time interval between the departure of the first brood and the laying of the first egg of the second clutch is quite variable.

In one case the parents were still feeding a newly flown young bird when they had begun to copulate; this was on 14 December and on 5 January the female was incubating a complete clutch of three eggs. In another case the young left the nest at the beginning of November but the next clutch was not laid until the middle of December. In the third case the chicks became independent around 20 October and the first egg of the next clutch was laid on 11 November. These three intervals were about two weeks, six weeks and three weeks respectively. In each of these three cases of second broods, the first and second clutches were the same size (three eggs in every case).

6. *Breeding success*

Out of 64 eggs in both breeding seasons, 34 chicks (53.1 %) hatched and 29 chicks (45.3 %) reached flying age. Thus less than half the eggs laid produced chicks that left the nest. But 85.3 % of the chicks that hatched eventually left the nest, so that the mortality seems to be higher at the egg stage than after hatching. This, however, is a false impression. At least seven eggs (10.9%) were infertile, 14 (21.9 %) were abandoned by the parents as a result of human interference and four (6.3 %) were taken for albumin protein analysis. The fate of the remaining five eggs was not determined. Infertility therefore is the principal natural cause of failure of the eggs to hatch and if the parents had been more used to our nest examination routine (as they later indeed became) the hatching success would have been considerably greater. Predation on eggs and chicks is slight.

The causes of chick losses were not usually determinable. Four of the five chicks that failed to survive disappeared unaccountably within the first week after hatching. The fifth chick was one that hatched a week after the first chick of the same brood and was unable to compete for

food with its stronger and larger siblings for more than 15 days. It steadily grew weaker and finally disappeared; the possibility that it was eaten by its nest mates cannot be ruled out.

7. *Intruder reactions of parents*

When there are eggs in the nest the parents are usually less demonstrative towards human intruders than after the eggs have hatched. An incubating parent will usually just fly out of the nest, perch on a nearby bush or tree and utter alarm calls 2 or 3. These calls serve to summon the mate and both birds may then call together.

If an incubating bird does not leave the nest, it backs up to far wall of the chamber and prepares to fight, either with its feet or by pecking with the bill. Sometimes, however, I have been able to extract an adult pygmy falcon from its nest chamber without its putting up any resistance at all.

Once the eggs have hatched (and sometimes even before this), the behaviour of the parents changes to one of intense aggression, which manifests itself in physical attacks on the head or hand (when this is at the chamber entrance) of the intruder. The birds rake with their hind claws, often drawing blood, but seldom inflicting severe wounds. The attacks are performed in complete silence. A charge may not end in actual contact, since the bird may swerve away at the last moment before striking.

Discussion

The distribution of *Polihierax semitorquatus* shown in Fig. 1 is worth further consideration. *P. s. castanotus* apparently does not occur further south than the "Central Railway Line, Tanganyika Territory" (Mackworth-Praed and Grant, 1952) and Williams (1963) states that the species "does not occur Rhodesias." Since the southern populations of *P. s. semitorquatus* occur only as far east as the western Transvaal at Wolmaransstad (Anon., 1907; Bucknill, 1908) and Barberspan (Farkas, 1962), which is also the eastern limit of the range of the sociable weaver, it is unlikely that it occurs in Moçambique. Although McLachlan and Liversidge (1957) claim that the pygmy falcon occurs as far north as Angola, Traylor (1963) says that he "can find no records."

This is borne out by Roberts (1940) who gave the northern limits of *P. s. semitorquatus* as "Damaraland and Ngamiland", and also by Winterbottom (1964) who found this bird only at Okaukuejo in northern South West Africa, even though this expedition took him as far north as Ondangua. It is even unlikely that it occurs in Ngamiland, since Smithers (1964) says that it occurs in Botswana only in the extreme south-west in the Gemsbok National Park and is "otherwise apparently absent." It is therefore highly improbable that the pygmy falcon occurs in the south-western Congo.

There is therefore a wide belt of Africa from the Congo across Zambia, Rhodesia, Malawi and Moçambique from which the pygmy falcon is

absent. The distribution map for this species shown by Grossman and Hamlet (1964), as well as the statement by Friedmann (1930) that *castanotus* and *semitorquatus* "meet in Kenya Colony", are based on surmise alone and are certainly incorrect. The two subspecies of pygmy falcon are widely separated geographically. For this reason it would be instructive to have comparative behavioural and biological data for the East African birds.

How could the pygmy falcon-sociable weaver association have arisen? Assuming a close relationship between *Polihierax* and the other falconets of the genera *Microhierax*, *Neohierax* and *Spizapteryx*, one can see that they all have in common a hole-nesting habit. At least some members of the falconid genera *Herpetotheres* and *Falco* also nest in holes in trees. Many species of *Falco* also use the nests of other birds for breeding purposes. It is therefore not too great an evolutionary step for a hole-nesting species of bird belonging to a family given to using the nests of other birds to take to living and breeding in the closed nests such as are built by the weavers. Initially the falcons might have used old or deserted nests, but later they could have begun to use occupied nests in colonies of separate weaver nests or compound nest masses like those built by the sociable weaver.

More important is the question of the adaptive significance of the falcon-weaver association, since this association has become almost an obligatory one for the falcons. The fact that pygmy falcons will also use unoccupied sociable weaver nest masses is of small import, since these nest masses tend to disintegrate after a time in the absence of maintenance by the original builders. Selection would therefore favour the use of occupied nest masses. The selective advantages of the association to the pygmy falcon are obvious: the weaver nest provides a place in which to roost and to breed, to escape from the heat of summer and the cold of winter. The nest masses of the sociable weaver are also relatively well protected from all predators except certain species of snakes.

What advantages, if any, do the weavers derive from the association with the falcons? Hoesch (1935) put forward the idea that ". . . es besteht vielleicht sogar eine Art *Symbiose*, gegründet auf die Gewährung einer bequemen Brutstätte einerseits und dem Fernhalten nesträuberischer Reptilien andererseits." He mentions further that no reptiles were ever found in nest masses occupied by pygmy falcons. This has also been my experience, except for the lizard *Mabuya striata*, which occurs regardless of the presence of the falcons.

However, Braine and Braine (1968), whose observations, like those of Hoesch, were made in northern South West Africa, claim that 80% of the sociable weaver nest masses that they examined had a "resident" boomslang *Dispholidus typus*. Whether or not the snakes were really resident is not important. What is important is that they found pygmy falcons, sociable weavers and boomslangs "living in harmony together." I have already shown that there is no "harmony" between the falcons and the weavers and I find it hard to believe that any exists between the birds

and the snakes. No doubt it is a case of "out of sight, out of mind", although the weavers do indeed become habituated to the presence of a snake in the nest mass if it remains there for an hour or more.

The only ophidian predator of sociable weaver nests in the Kalahari is the Cape cobra *Naja nivea* (the boomslang does not occur in the Kalahari Gemsbok National Park), which is not strictly an arboreal snake. There is therefore no question of its being resident in the nests. Like the boomslang, it will coil up in a nest chamber to rest during its examination of a nest, but it always returns to the ground after feeding. This does not necessarily apply to the boomslang, and one would imagine the pickings at a sociable weaver nest to be constantly good for these snakes, since they can feed on adult weavers when the birds are not breeding.

The question of the protective value of the pygmy falcons' presence in a weaver colony in areas where boomslangs occur seems then not to arise. I believe, however, that a systematic analysis of the situation would probably show that the degree of snake (even boomslang) predation on sociable weaver nests is less at those nests where a pair of pygmy falcons is in occupation too. My own unpublished work on the sociable weaver indicates that this is certainly the case in the Gemsbok Park. But as Hoesch (1935) said: "Hier fehlt es noch an zuverlässigen Beobachtungen." Only a very great number of observations will show whether the falcons help to reduce predation on the weavers by snakes or not.

If it is not the case, it is difficult to see what benefits may accrue to the sociable weavers from the falcons' presence. Predation on the weavers by the falcons must surely be very small, since it would not be good adaptive economy on the part of the falcons to reduce too drastically the architects of their exclusive roosting and breeding places.

Although the falcon-weaver association is close, I found no reason at all to support the strange claim by Braine and Braine (1968) that "the Pygmy seems to have adopted some of the weavers' habits and calls, 50 % of the latter appearing to be identical to that of the Sociable Weaver." I can see no good reason why the falcons should do this (unless it be to reduce the amount of alarm on the part of the weavers when a falcon utters its notes) and my own observations show that the calls of the pygmy falcon and sociable weaver are quite distinct, easily distinguishable and highly characteristic. There is of course the possibility of regional dialect differences in the pygmy falcon calls (as happens in other bird species) and the northern birds may have developed some calls, different from those of the more southerly birds, that resemble those of the sociable weaver. Even if this is so, it would seem to be purely fortuitous.

The calls of the pygmy falcon may be homologized with those of other falconids (*cf.* Willoughby and Cade, 1964) and present no unique or particularly remarkable features. Much the same can be said about most of the pygmy falcon's behaviour patterns, such as maintenance activities, which is why I have not dwelt on the general behaviour of these birds.

Only the flight is not similar to that of the genus *Falco*. Pygmy falcons

fly in an undulating manner like a woodpecker, with rapid bursts of wing-beats alternating with a dip in the flight path. This may, however, merely be a function of the birds' small size and the relatively short, rounded wings.

The food of the pygmy falcon appears to fill all the bird's water requirements, as I have never seen it drinking, even after rain. My own observation on the nature of the prey taken confirms those of Andersson (1872) who lists "small birds, mice, lizards and coleopterous insects, the latter being . . . its chief food." Hoesch (1935) recorded insects, lizards and small birds in stomach contents of adult pygmy falcons and actually observed a falcon take a *Prinia* once.

There is little published information on the breeding biology of the pygmy falcon. Hoesch (1935, 1955), McLachlan and Liversidge (1957) and Roberts (1940) record only clutches and broods of three eggs or young. Mackworth-Praed and Grant (1952, 1962) mention that two or three eggs are laid. Nowhere can I find mention of clutches larger than three eggs. It is therefore probable that 4-egg clutches are laid only in exceptionally good seasons, but more data are needed to confirm this. However many eggs comprise the clutch, it is apparent that almost all those that hatch give rise to flying young. Cases of starvation by competition from older siblings in the same brood are rare, at least in an average season. In a poor year, when food becomes scarce, this type of brood-size reduction may occur more frequently, in which case it would tend to ensure the survival of the remaining young.

The high survival rate of nestling pygmy falcons can be regarded as further evidence that snake predators are kept at bay by the parents.

The inequality of parental roles in the two sexes during incubation and early nestling periods raises the question of sexual size differences. Measurements in McLachlan and Liversidge (1957) indicate that there is no sexual size difference, while an anonymous report (1963) in *Animal Kingdom* says that "females are distinguished by being slightly bigger . . ." The matter awaits resolution.

Summary and Conclusions

The pygmy falcon *Polihierax semitorquatus* is a small raptor of discontinuous distribution in Africa, with one subspecies in the drier parts of southern Africa and another widely separated subspecies in the drier parts of East Africa. The range of the southern population coincides with the range of the sociable weaver *Philetairus socius* in whose communal nest masses the pygmy falcons roost throughout the year and breed in summer from August to March.

The food of the pygmy falcon consists largely of insects, but also of lizards, small rodents and small birds in decreasing order of importance. The falcons feed to some extent on the sociable weaver, but this predation is minimal. Hunting is by hawking from a conspicuous perch.

The clutch consists of two to four eggs, usually three. The main cause

of non-hatching of eggs is infertility. Survival of nestlings is high. Predation on eggs and chicks is slight and it is possible that the falcons themselves keep snakes from the weaver nest masses, so that the two bird species are mutually beneficial. Pygmy falcons may be double-brooded in a single season.

Calls and displays are described and interpreted where possible. Other behaviour patterns are fairly typically falconid.

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