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Territorial behaviour of the Hen Harrier in winter

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Abstract

Observations in central Europe suggest that the Hen Harrier *Circus cyaneus*

shows marked territorial behaviour in the wintering grounds. During the day, dominant females occupy the best feeding areas (with high vole densities) and defend them, primarily against conspecifics but to some extent also against other raptors. Subdominant females and all males are attacked by dominant females and evicted from defended territories, and sometimes their prey is stolen. Territorial behaviour is expressed through certain interactive behaviour, specific calls and a distinctive posture termed the 'Kong' display by the author. Males are generally confined to more peripheral or suboptimal areas. The hypothesis that similarity in plumage between young males and adult females could represent a form of mimicry is discussed. Agricultural intensification may have increased the natural winter territorial behaviour of Hen Harriers; loss of habitat diversity seems to have had a negative impact on males in particular. The greater risk of predation for males and young birds, combined with the need to expend more

energy while hunting, may affect overwinter survival rates and in turn have an impact on population dynamics on the breeding grounds, notably the occurrence of polygyny.

Introduction

The Hen Harrier *Circus cyaneus* is able to withstand the often harsh and snowy winters in central Europe. This is partly explained by its ability to locate voles acoustically, even under a low cover of snow, which is a key attribute since voles make up the bulk of the winter food for Hen Harriers in this region (Cramp & Simmons 1980).

The territorial behaviour of Hen Harriers on the breeding grounds is well described (e.g. Cramp & Simmons 1980), whereas in the wintering areas 'nothing is known about territorial behaviour against conspecifics and other birds of prey' (Glutz *et al.* 1971). Cramp & Simmons (1980) also stated that 'winter hunting ranges lack clearly defined boundaries; are not defended as territories'. Accordingly, there is little or no published information on the territorial calls and behaviour of Hen Harriers on their winter hunting grounds.

Studies on the social structure of the Hen Harrier during winter have so far been largely limited to their roosts. Interactions on the winter hunting grounds have probably been largely overlooked because of the difficulties in establishing the age and sex of ringtail harriers, and especially of separating individual birds (Dobler 2020). The primary aim of this study was to document previously unreported behaviour and to derive initial working hypotheses for interpretation. In this context, possible reasons for the

similarity in appearance between juvenile males and adult females will also be discussed. In addition, I suggest a possible reason why the survival rates of female Hen Harriers are generally higher than those of males (cf. Picozzi 1984, Mebs & Schmidt 2014). Ultimately, I wish to encourage birdwatchers to make further observation-based studies to add to the basic picture described in this paper.

Methods

This study is based on field observations made during the winter months over the last 40 years, but especially during 2015–20. In the past six years, observations were carried out mainly in the open landscapes around Memmingen and the Federsee, with some around Ulm and G ppingen (all in southern Germany) and a few in the open habitats of northeastern Burgenland, Austria. These areas are mainly agricultural (and nowadays predominantly arable) countryside, with a patchwork of mixed woodland too. The winter food of Hen Harriers in these areas consists mainly of voles, predominantly Common Voles *Microtus arvalis*, with locally significant proportions of Water Voles *Arvicola terrestris* and Field Voles *M. agrestis*.



71. A typical view of the study area, c. 2.5 km north of the Federsee, in southern Germany, November 2020.

The behaviour of Hen Harriers was studied in their winter hunting habitat, mostly at relatively long range (roughly 150–500 m) to ensure that the birds were undisturbed by the observer. In some cases I used a hide for photography, but most observations were carried out using binoculars and the Zeiss Harpia spotting scope; the latter proved ideal for such a challenging task, enabling the observer to switch quickly between a wide field of view and high magnification. This is the only way to observe complex and sometimes rapid behavioural processes, and then to identify the individuals concerned. Recognising individual birds involves no special skills, just experience and many hours of field observation, which leads to familiarity not only with small differences in plumage and other physical cues, but also with behaviour. In combination, these factors allow recognition of individuals in the same way that familiarisation allows a shepherd to recognise individual sheep in their flock.

Photographic documentation, using a digital camera and a long lens, was obtained mainly during the winter months of 2019 and 2020, and again mostly from long range, as this was a non-intrusive study. I consider this important when so many research projects depend on the capture and handling of the study species, and the attachment of devices such as radio transmitters and wing tags; these may have some effect on the birds' behaviour and their ability to function normally, and thus potentially have some impact on their fitness. Age and sex of ringtail harriers was established

using the criteria set out in Dobler (2020).

Results

Intraspecific territorial behaviour

Hen Harriers show pronounced intraspecific territorial behaviour on their wintering grounds, and sometimes even at key feeding places during migration. Areas with a high density of voles in open country are defended as territories, chiefly by females. These places are typical agricultural landscapes, mainly grassland, but also certain crops (for example sunflowers, winter barley with mustard or oilseed rape) or reedbeds that are not too wet: in short, areas which offer good conditions for small mammals, especially voles, and enable harriers to feed without the expenditure of too much energy.

Owing to their physical superiority, females are dominant over males, and typically establish more or less exclusive access to the most productive feeding areas. The size of a defended feeding territory depends on prey density and accessibility, which affects hunting success rate. Preliminary observations suggest that these territories are generally between about 2 and 100 ha, although larger areas (more than about 30 ha) cannot be consistently defended on all sides. Conversely, smaller territories may be defended beyond their 'borders', so that the smallest 'defended unit' is about 8 ha. Territory holders, defined as a dominant female that successfully defends a feeding place for at least one day, are predominantly adult females, but the proportion of juvenile females among them is not inconsequential; strong juvenile females are quite capable of driving weaker adult females from their territory. Of 73 territories observed between 2018 and 2020, and occupied for

more than one day, 11 (15%) were held by juvenile females.

Territories are found exclusively in open terrain (which allows the owner to recognise approaching competitors, as well as predators, at a distance of up to several hundred metres), although adjacent small copses and scattered rows of trees sometimes form the territory border. Areas with dense vole populations that lie close to the edge of a forest are not defended as territories, probably mainly because of the risk of being attacked and killed by Northern Goshawks *Accipiter gentilis* in those areas. Territory holders normally defend their territories during the daytime, and arrive in the early morning after leaving the roost, which can be up to 20 km away.

Territorial defence typically conforms to the following general pattern: the territory holder watches from the ground, rarely from a slightly elevated position such as a fence post, and scans the surroundings (plate 72). As soon as another Hen Harrier is visible, and flying towards the feeding territory, it is observed intently. As the intruder gets closer, it is made aware of the territorial claim by warning calls from the territory holder. This warning call is a high-frequency, elongated 'wiiii(e)', which drops slightly towards the end, and is quite similar to the begging call of the female during the breeding season (Cramp & Simmons 1980). The warning call is normally repeated 2–3 times in quick succession by a perched bird, but can also be emitted in flight. The distance to the approaching intruder when the warning calls are given is usually between 100 and 500 m. If the intruder does not veer away, the warning call is repeated, occasionally extended to four or even five single calls, or the territory holder takes flight to initiate an attack. Very few territory holders make no calls before initiating a flight attack.



72. This powerful adult female Hen Harrier scans the skies around its feeding territory for intruders; Memmingen, January 2020.

The territory holder does not try to gain height quickly like many raptors, but rather approaches the intruder in fast, low-level flight, generally 0.5–3.0 m above the ground. On most occasions the intruder is ‘escorted’ from the territory (plate 73). The territory holder often flies behind and below the retreating bird (e.g. plate 77), seemingly to prevent the intruder from landing or hunting for prey (and recalling the eviction of intruders at breeding sites in Orkney; Cramp & Simmons 1980). If a territory holder is in flight when it encounters an intruder, it will attack immediately, without calling. In most cases, intruders turn away as soon as a territory holder comes into view.



73. An adult female territory holder chases a juvenile female out of its feeding territory; Memmingen, January 2020. Note the broader wings, the strong neck and massive head of the adult Hen Harrier.

In some cases, however, intruders manage to enter a territory unnoticed, for example while the holder is distracted by another harrier approaching from the opposite direction. In such instances, once the intruder has been detected, territory holders attack either immediately if in flight, or after calling only once or twice before or during take-off if at rest. If the intruder does not leave the territory immediately, it is attacked, typically from below. In such conflicts (plate 74), the harassed victim, both males and females, often emits a characteristic call: a variable low, vibrant 'girrirr(irr)'.



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74. An adult female territory holder attacks a juvenile intruder 20 m above ground in typical manner, approaching from below. The juvenile calls under pressure; Biberach December 2020.

Feeding areas with the highest prey densities are usually occupied by dominant adult females, while surrounding areas are occupied by subdominant adult and juvenile females. Some of the latter manage to establish short-term (a few hours) territories, but the most dominant females try to drive subdominant females and all males out of these more peripheral territories. There are casual fights, mostly between equally strong females (plate 75), and a significant posture is adopted in connection with these: the 'Kong' display is apparently used to claim dominance during these conflicts (plate 76) without the need to fight. (I termed this display posture the 'Kong' display as it reminded me of the movie character King Kong!) In this posture, the wings are stretched out to a variable extent and the head feathers and cheek feathers, including those of the rear edge of the pale collar, are erected

as well as the feathers of the neck down to the back in a striking way. The 'Kong' display, often adopted by both birds, clearly serves to intimidate the opponent. As soon as one of the birds abandons its challenge, its 'Kong' display collapses immediately, whereas the display of the victor usually remains in place for a few seconds longer. Disputes between equally strong females in adjacent territories are sometimes decided vocally. I have observed them sitting on the ground, some 60–100 m apart across a road, having a battle by 'wiii(e)' calls for several minutes, sometimes showing the 'Kong' display to some extent. Under these circumstances the 'wiii(e)' calls are occasionally interspersed by the familiar chattering 'keke(ke)...' warning calls.



75. Territorial fight between two juvenile female Hen Harriers; Riedlingen, December 2019.



76. A juvenile female Hen Harrier demonstrates the 'Kong' display against another juvenile female; Riedlingen, December 2019. Note the erect feathers along the cheeks to the end of the collar and from the nape to the base of the back.

In good feeding areas outside established territories (for example, towards the forest edge) females often try to drive each other out, a process during which the defeated female usually flies above the attacker (plate 77). After the weaker bird is evicted, the stronger female turns away, flies back or continues hunting, but sometimes remains on the ground adopting the 'Kong' display posture, while the weaker female escapes (plate 78).



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77. During the territorial chase, the dominant female often flies below and behind the weaker bird, in this case a juvenile female; Riedlingen, February 2020.



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78. The 'Kong' position adopted on the ground by the dominant juvenile female against an escaping juvenile female; Riedlingen, February 2020.

Attack flights by females against invading adult males are conducted mainly with high levels of aggression, including by juvenile females. Such chases rarely exceed more than 1.5 km and usually end after a few hundred metres. Males also show territorial behaviour among themselves, but normally in a less distinct way, although adult males have been observed chasing other adult males in a broadly similar manner over a distance of about 1 km. Since males, especially adult males, are often seen far from the roost, it is clear that these birds are widely spaced in the wintering landscape, which leads to fewer encounters and fewer opportunities for serious competition among them. Short conflicts between males of all age classes sometimes occur in feeding areas; these are frequently accompanied by the low, vibrant 'girririrr(irr)' calls.

Males generally flee from any attack by a female, whether juvenile or adult; I have never seen a male seriously fighting back. Territorial disputes between females and particularly between males usually involve posturing without any serious injuries, although they sometimes grab each other by the legs and claws. Of about 50 observed close territorial fights, where claw contact between females was ascertained, I have recorded only one that resulted in visible injury. In this case, a passing adult female was chased and attacked by a territory-holding adult female, c. 230 m beyond the territory border; after the fight, the leg of one opponent was left hanging from the body, presumably

indicating a sprained joint. Fights become really serious when a subdominant female or a male takes prey in the vicinity of a dominant female. Dominant females attack prey-carrying subdominant females and males and chase them like skuas, often stealing their prey successfully.

When males or subdominant females catch prey, they usually do not fly off with it immediately, unless a dominant competitor is directly threatening. Nor do they start to feed or cover prey with their wings (mantling); instead, they observe their surroundings attentively and seem to show that they have settled down to rest. If there are no competitors in the area, they begin to feed by tearing the prey apart. I have not observed voles being swallowed whole, even though this might seem intuitive in such pressured situations. Faced with competitors in the vicinity, the bird flies out of the hunting area as directly as possible, with prey drawn up under the belly feathers (plate 79a), where (depending on the prey size) it becomes largely invisible. Smaller males are somewhat disadvantaged, since their prey is more difficult to hide.

In order to feed undisturbed, young males and subdominant females try to escape from heavily frequented hunting areas. If they are discovered by a dominant female on departure, I have noticed that they pull their catch further into their belly plumage with one leg, while the other leg is visibly stretched outwards (79b), perhaps to suggest that it is not carrying prey. However, if the bird is pursued directly, it pulls back the protruding leg and typically flies upwards into the open sky. A dogfight in the sky (79c) can last up to a minute, but is usually shorter. If the pursued bird is no longer able to hold its prey pulled into the belly plumage (79d), then inevitably it becomes visible (79e). Usually, the prey is dropped shortly afterwards and taken in the air by the stronger female (79f).





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79 a A juvenile female tries to sneak out of a

territory with its catch hidden underneath its belly feathers. This female shows unusual parallel and contrasting banding on the secondaries, more typical of juvenile males. **b** After the territory holder has taken off, the escapee stretches one of its legs away from the body. **c** The territory holder has approached and starts a dogfight in the sky. **d** The escapee still holds its catch close to the body under the belly feathers. **e** The victim seems no longer able to hide the catch and it becomes clearly visible. **f** A few seconds later the victim drops its prey while the territory holder grabs it from the air. All photos from the same sequence; Memmingen, November 2019.

On the edge of defended territories and beyond, I have occasionally (so far seven cases) observed juvenile males flying straight into the area, aggressively driving away juvenile females (plate 80), and in one case even a subdominant adult female, for a short period of time, even a minute or two. Although this behaviour is not successful for any length of time, the juvenile male may still have the opportunity to catch a vole and escape with it. In order to feed undisturbed, they sometimes fly close to the forest edge (within 100 m), an area usually shunned by females (and in a few cases they may even escape into the forest to avoid chasing females, which normally do not enter forests). However, carrying prey into forests exposes juvenile males to a

high risk of being killed by Goshawks. Adult males avoid the forest and I have not yet seen an adult male escaping into the forest, even though they sometimes hunt 50–150 m from the forest edge, depending on the height of the trees. They tend to approach closer to forests when the trees are young, but keep farther away from the edge of mature forest.



80. Juvenile male Hen Harriers occasionally manage to push juvenile females away from their current feeding area; Federseeried, January 2020.

Males in their winter quarters cannot sustainably prevail against the stronger females at all, and are regularly harassed by females even when not carrying prey (plate 81). They are either forced to stay on the edge of good feeding areas or territories (and hunt opportunistically, for example while a territory holder is at the far side of a territory or engaged in a separate conflict) or to move to more suboptimal feeding areas. In my study areas, some older males hide in longer vegetation (for example crops of sunflowers, mustard, oilseed rape or barley) and start sporadic hunting flights from there. However, they also hunt on the ground in these fields, which support high densities of voles.



81. In most cases juvenile males are chased away from good feeding areas, even by juvenile females; Memmingen, January 2020.

Some males appear to avoid territorial aggression from females by remaining mobile, roaming greater distances from their traditional roost. In January, I have recorded a moulting juvenile male in areas 20 km apart on consecutive days. Similarly, within one day, a distinctively coloured juvenile male was observed hunting in two places 11 km apart. Individuals that show no commitment to any locality are mostly males, young or old.

In some good feeding areas favoured by females during the day, I saw males (mostly juveniles but sometimes adults) arrive very early in the morning, hunting successfully before the arrival of the females. Prey was eaten on the spot, but when the first females arrived, it was carried to a less favoured area, for example nearer the forest edge, for consumption. Occasionally, prey-carrying males fly over forests, in order to find undisturbed areas to consume the prey. A similar situation arises when territory holders depart for the roost

in the evening, and males exploit a brief window of hunting opportunity.

Some subdominant females will establish themselves at the edge of occupied territories. At the occasional approach of a territory holder, they quickly evade but then in turn push away juvenile but especially adult males from their feeding area. During the resting phases, I have occasionally observed how these subdominant females hide effectively in low vegetation, while still being able to view their surroundings. The bird lies flat on the ground, the head hardly visible, even among the lowest vegetation (plate 82). They remain in this position for up to an hour before heading to the next – risky – hunting flight phase.





82. Three images from the same camera position; Ehingen, March 2020. A subdominant adult female steps into low grass crouching down as it goes and makes itself almost invisible. In such a position, there is a good chance that this bird would have been overlooked during a monitoring scan for harriers in these fields. This individual stayed in position c for about 40 minutes.

In the winter of 2019/20, a juvenile female established its territory in an area containing a Hen Harrier roost occupied by up to 27 birds. This female was able to defend its territory successfully during the day, and in the evening it displayed defensive behaviour against the first harriers arriving at the roost. Its haunting 'wiii(e)' calls were presumably intended to cause the approaching harriers to retreat, but as dusk progressed and more arrived, the calls gradually diminished, and all the birds went to their sleeping places,

including the local territory holder. A similar situation was observed in December 2020 at a different roost, this one composed of 15–19 Hen Harriers in a field of winter barley with some phacelia, 40 cm high. This 3.5-ha field was vigorously defended as feeding territory during the day by an adult territory holder. In the evening, a concert of 'wiiii(e)' calls awaited the first arriving conspecifics; some females that ignored it were attacked, whereas the males stayed away, remaining in the adjacent ploughed fields until the territory holder gave up its defence calls and flights.

The arrangement of territories is liable to change during the winter, as stable conditions rarely prevail. In today's intensively cultivated agricultural landscape, territories that exist for a whole winter season are exceptional, because territories with a high density of voles are often ploughed during the winter. A territory established and maintained for weeks can disappear within hours, with an army of Red Kites *Milvus milvus* and Common Buzzards *Buteo buteo* arriving to feed and scavenge on the dead voles. Similarly, if Goshawks arrive and stay for a while in the area, territories are abandoned immediately; and in one case a falconer with his large Gyr Falcon *Falco rusticolus* hybrids unknowingly destroyed the structure of the local Hen Harrier territories in one of the study areas. Snow cover may also force rearrangement of territories. At worst, a territory might be defended for only a few hours, but exceptionally one might be held for a whole winter season.

In a protected reedbed area close to the Federsee, which is largely unaffected by human disturbance, stable conditions exist, not only in terms of the habitat, but also in relation to the harriers' social system. An old territory holder (recognised by distinctive plumage) was able to successfully defend and occupy her territory there for at least three winters (2017–20). A few times I watched this female remain in her territory in the evening, using the

tall reed and grass vegetation to roost, even though a communal roost was only about 2 km away. Only the core of the territory was defended permanently. Occasional hunting excursions to the periphery were made, which led to immediate evasion by conspecifics there. Two juvenile males, however, remained along the rarely visited boundaries of this territory, probably because they could hide in the slightly higher *Juncus* cover during the day, and from there repeatedly make short hunting excursions to the meadows about 200 m away. Neither male ever consumed prey in these meadows, but always took the prey away to their resting places in the *Juncus*.

In 2018/19, a small wintering group of 4–5 Hen Harriers near Guppinger, in southwestern Germany, showed a less pronounced territorial system. This group consisted of two juvenile females and one adult female, as well as a juvenile male. Seemingly, voles were distributed over a large area (c. 75 ha) with no pronounced concentrations, and one of the juvenile females was dominant. An adult male regularly observed at the adjacent roost was seen rarely within the feeding area, and when it was, it was usually evicted by the dominant female. On the other hand, the juvenile male stayed continuously for at least two months in the wider area of the feeding habitat, as it was attacked only occasionally and far less intensively. Similar behaviour was confirmed in exactly the same area in winter 2020/21 after a period of snowfall, when this area was frequented by an adult female, two juvenile males and one adult male. There was very little territoriality apparent from this group, apart from a clear escape reaction of the adult male as soon as the adult female approached within about 15 m.

Interspecific competition and territoriality

Territory holders regularly attempt to drive Common and Rough-legged Buzzards *B. lagopus* from their territory, and are often able to do so. However, this applies primarily to flying buzzards; ground-hunting birds are less easily intimidated. While conspecifics are often approached in low-level flight, Hen Harriers immediately fly upwards in order to attack flying buzzards from above. During the chase, Hen Harriers occasionally show at least some kind of 'Kong' display in flight, with feathers at the back of the head and the neck erect (plate 83).



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83. A juvenile territory holder chases a juvenile Rough-legged Buzzard *Buteo lagopus* out of its territory. Note the erect feathers on the head and neck of the harrier as it attacks from above; Memmingen, February 2019.

Dominant juvenile females sometimes appear to 'flaunt' their catch in the close presence of buzzards, making the prey clearly visible underneath their

body (plate 84). After a short chase, buzzards realise that an attack on the faster-flying Hen Harrier is generally useless, and abandon the attempt. Nevertheless, buzzards sometimes manage to attack and take prey from feeding Hen Harriers of both sexes by surprise; they are essentially stronger than Hen Harriers and, consequently, buzzards are not normally robbed of their prey by Hen Harriers.



84. A juvenile territory holder carries prey that is clearly visible to the pursuing Common Buzzard *Buteo buteo*; Memmingen, November 2019.

The number of Red Kites spending the winter on the traditional feeding grounds of Hen Harriers in southern Germany has increased in recent years. These are strong opponents, although occasionally they may be evicted from territories by female Hen Harriers. In the winter of 2019/20, certain individual Red Kites in the Federsee area specialised on kleptoparasitising Hen Harriers. They observed the harriers either from isolated trees or while circling in the

sky and began the chase as soon as the harrier made a catch. It is unclear how successful that strategy was, but I watched them taking voles from juvenile male Hen Harriers on three occasions during that winter.

Food competition from Common Kestrels *Falco tinnunculus* is apparent by mutual attacks on the feeding grounds. In open country, Hen Harriers usually prevail and are not driven away for any sustained length of time by Kestrels; but on occasion Kestrels may dominate, meaning that there is always the potential for conflict between these species. From perches on trees, Kestrels may be surprisingly successful in harassing Hen Harriers, as they can make repeated and assertive attacks at regular intervals, often causing harriers to leave the area. Similar behaviour is apparent from Short-eared Owls *Asio flammeus*, although these are not common in my study area. The owls harass Hen Harriers obviously for territorial or defence reasons, while I have noticed adult male Hen Harriers chasing vole-carrying Short-eared Owls on two occasions.

Eurasian Sparrowhawks *Accipiter nisus* and Hen Harriers, especially males, are sometimes brought together in good songbird habitats along hedgerows and in clumps of trees. Their occasional skirmishes do not usually cause injury, but sometimes go on for several minutes.

Hen Harriers are regularly mobbed by Carrion Crows *Corvus corone*. Young male Hen Harriers, which are roughly the same size as Carrion Crows, are the ones mainly affected, and they are more frequently attacked when they are carrying prey. Hen Harriers are faster and more agile so it is quite rare that they lose prey to Carrion Crows, or even Common Ravens *C. corax*, but the effort involved in avoiding them increases the energy expenditure of males in particular (plate 85). Several minutes of bloodless skirmishes caused by

mobbing Carrion Crows can be observed quite regularly, with harriers often fighting back aggressively (plate 86). Fights between Magpies *Pica pica* and (mostly male) Hen Harriers along shrubberies and edges of groves are usually superficial but often cause the harriers to leave.



85. Juvenile male Hen Harriers carrying food are quite often chased by Carrion Crows *Corvus corone* and have to expend additional energy to keep their prey; Riedlingen, February 2020.



86. Mobbing Carrion Crows provoke skirmishes with Hen Harriers in the study area on an almost daily basis; Federseeried, February 2020. Here, a juvenile male performs a counter-strike; note the moulted adult-type tail feather.



87. Most female Hen Harriers, like this juvenile bird, take little notice of crows while

Discussion

This study suggests that intraspecific territorial behaviour of Hen Harriers in the winter quarters is important. The territoriality of female Hen Harriers is particularly conspicuous. The penetrating 'wiiii(e)' call given by female territory holders can be classified as a territorial warning call, uttered to dissuade conspecifics from entering the feeding territory without expending the energy required for a flight attack. Clearly, acoustic communication in Hen Harriers is not confined to the breeding season, but plays a major role in the defence of winter territories. This territorial call is louder and much more striking than the less obtrusive conflict call given during close conflicts and disputes at the roost. The 'kekeke(ke)' warning call is also given quite frequently during the winter season in conflict situations, with conspecifics but in particular with other species, for example both buzzard species, Red Kites and Short-eared Owls, as well as during the harassment of Red Foxes *Vulpes vulpes* and perched Goshawks.

The 'Kong' posture is important in the context of winter territoriality and conflict situations. I have observed this posture mainly in juvenile and occasionally in adult females; I have not seen it in any males so far. Since the display is usually performed only for a few seconds, often for less than a second, it is hardly perceptible to most human observers watching from a distance, and has probably remained undetected as a result. It also occurs, at least in a similar form, in interactions with other food competitors, such as buzzards.

The territorial behaviour of male Hen Harriers during winter is less pronounced than that of females, partly owing to their generally submissive behaviour towards the females. Males can sometimes appear loosely connected, rather like buddies, their behaviour characterised by a high degree of tolerance. This may change under conditions of serious food shortage, which have not yet been encountered during my study. So far, having observed more than 300 close encounters between ringtails of the kind represented in plates 74, 75 and 81 in the feeding areas, I have seen only about ten, insignificant encounters between males (adult and/or juvenile) and not a single dogfight between females (of any age) and adult males. Adult males clearly avoid futile, energy-consuming skirmishes and confrontation. Instead, they prefer to seek out less favoured areas, presumably using their experience to compensate, and cover their energy expenditure in more remote or less productive places.

The strategy of some males of keeping themselves hidden from females in taller vegetation or crops may expose them to a higher risk of being killed by Red Foxes, which now occur in some parts of the study area at extremely high density. Goshawks also take their share of wintering harriers. Kratzer (1994) reported Goshawk attacks on feeding Hen Harriers in a nearby study area; one male harrier was taken within 160 m of the forest edge whereas three attempts at distances of 400–600 m failed. He suggested a critical distance of about 400 m from the forest edge, related to the findings in Glutz *et al.* (1971). During recent years I have witnessed only one incident, which involved a juvenile female Goshawk killing a juvenile male Hen Harrier about 100 m from the forest edge. The Goshawk came straight out of the forest in low-level flight and took the harrier, which had already made about 4 m of an escape flight. About a minute or two after the capture, the Goshawk

carried the harrier back into the forest without any noticeable difficulty.

Another potential factor lowering the winter survival rate of males, especially the less experienced juveniles, is repeated snowfall. Heavier females in good condition are better able to survive for a period in snow-covered feeding areas, being able to catch prey by cutting through crusty snow; and birds in better condition are better equipped to move larger distances to find more accessible prey. The last birds hunting the study area after moderate snowfall are the strong female territory holders (plate 88), while the males have already left the area. Einstein (2000) showed that roost counts at Federsee from 1975 to 1991 revealed a minor and insignificant decrease in the numbers of adult males between autumn and spring migration, whereas there was a significant decline in the numbers of ringtails, consistent with a lower survival rate of juveniles during winter.



88. A powerful adult female Hen Harrier, remaining in its feeding territory despite the conditions, its weight enabling it to cut through a cover of icy snow to catch voles; Riedlingen December 2020.

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In the winter social system described, males – especially juveniles – emerge as the losers. On average, they have to find food farther from the roost, often

in suboptimal habitats, while facing an increased risk of predation, all of which reduces their survival chances. Females and older, more experienced birds are thus more likely to arrive on the breeding grounds in good condition. Within this social structure, limited food availability – as a result of snowfall and other environmental factors – leads to a lower survival rate among males, and hence to a skewed sex ratio when the birds return to their breeding grounds.

The phenotypic similarity between adult females and juvenile males may have evolved partly as a form of mimicry as a result of intraspecific competition for food and the social system prevailing in winter quarters. This hypothesis is supported by the observation that juvenile males have been able to push juvenile females away from certain feeding areas close to the edge of territories for short periods, although this behaviour is by no means common. If young males resemble adult females, this could provide a survival advantage in certain situations, and might help young males avoid kleptoparasitism, mobbing and even predation to some extent. The fact that they are less strongly attacked and expelled by females than the adult males is consistent with this idea.

The observations and interpretations reported here are mostly preliminary and further studies are needed. Nevertheless, the results correlate with the observations of polygyny in various breeding areas, mainly attributed to a skewed sex ratio in favour of females (Balfour & Cadbury 1979; Newton 1979; Picozzi 1984), and with reports of males missing from breeding areas in northern Germany in recent years (Knipping & Stahl 2018, Knipping pers. comm.). Polygyny has been described in Northern Harriers *Circus hudsonius* in North America, and there are indications of similar territorial behaviour of female Northern Harriers during winter (Dunne 2017).

The winter territorial system of the Hen Harrier may have evolved over millennia, as regular snowfall in continental Europe left limited and scattered patches for harriers to hunt. However, that territorial behaviour is perhaps more evident today, following the transformation and simplification of the agricultural landscape in recent decades. In other words, winter territoriality may have increased in modern agricultural landscapes, with the associated loss of permanent pasture, drainage and clearance of open land, the increase of large-scale cereal production, chiefly corn monocultures, and the loss of food-rich side strips, headlands and field margins – all of which gives fewer hunting opportunities for males and subdominant birds. Rough grassland still occurs along forest edges but these are dangerous areas for hunting Hen Harriers because of the close proximity of Goshawks. All of this means that the areas populated by voles are more localised and clustered than in earlier times.

As well as agricultural intensification, climate change is an important factor, in that vole populations benefit from less severe winter weather, remaining relatively high in dry years with limited snowfall (as in recent winters). How the harriers' social system reacts to below-average food supply – in wetter or more snowy winters – remains to be examined further. Male Hen Harriers, as partial bird hunters, are also affected by the drastic decline of songbirds in the winter months. The large flocks of Common Chaffinches *Fringilla coelebs* and Bramblings *F. montifringilla* as well as those containing Linnets *Linaria cannabina*, Greenfinches *Chloris chloris*, Yellowhammers *Emberiza citrinella* and Reed Buntings *E. schoeniclus* have decreased dramatically over the last 20 years or more, not only in my study area but throughout much of western and central Europe.



89. A typical winter scene in the study area in southern Germany, January 2021.

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