

Home range, habitat use and diet of Honey-buzzards during the breeding season

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Abstract Four adult male Honey-buzzards *Pernis apivorus* were fitted with GPS satellite transmitters in northern Germany. The tags were deployed during the nestling period and the birds followed until they started their autumn migration. For one male, data were also collected throughout the following breeding season. The four birds occupied home ranges that varied between 13.5 and 25.8 km². The birds spent most of their time in woodland and apparently found most of their food there: of 35 wasp and two bumblebee nests that were found, 78% were in woodland. In all, 99% of the locations received from the four males were within a radius of 4 km of the nest. The birds roosted at different sites, some of which were close to the nest, but sometimes close to wasp nests that had not been fully exploited. As the young developed, the males visited new areas for foraging, and spent more time farther from the nest. The most frequently recorded food item was the Common Wasp *Vespula vulgaris*. Possible effects of the recent changes in the occurrence patterns of key wasp species, especially the German Wasp *V. germanica*, are discussed.

The generally secretive Honey-buzzard *Pernis apivorus* is a difficult species to monitor effectively in its European breeding areas. In the past decade or so, the European population was estimated at 110,000–160,000 (BirdLife International 2004) or approximately 130,000 breeding pairs (Mebs & Schmidt 2014), although population estimates should be viewed with caution. In Europe as a whole, the population is believed to be stable (BirdLife International 2004), yet an analysis of breeding populations, productivity and survival rates provides clear evidence of population declines in some areas, including parts of its range in northwest Europe (Bijlsma *et al.* 2012).

The factors influencing this decline could operate on the breeding grounds, on migration and/or in the birds' winter quarters, in West and Central Africa, where forest destruction

continues at a rapid rate (Martin 1991; Oates 1999). Continuous tracking of a number of individual birds throughout the year may help to identify problems and determine where they are occurring. Between 2001 and 2011, we fitted solar-powered satellite transmitters (platform transmitter terminals, or PTTs) of various types, weighing 18–22 g, to 12 adult Honey-buzzards in Germany. (For more information on the technique of satellite tracking, see Meyburg & Fuller (2007) and Meyburg & Meyburg (2007, 2009, 2013).) From 2009 onwards, we were able to use transmitters that gave precise GPS fixes, and these provided the bulk of the information reported here, which relates to the breeding season only.

Study area and methods

Our studies were carried out in eastern Schleswig-Holstein (the most northerly

German federal state), an undulating, agricultural landscape with heights between 20 and 80 m asl. Most of the farmland is arable, but there is some grassland, managed by a combination of grazing and silage. The fields, on the mainly sandy/clay soils, are often separated by banked hedgerows (an earth bank, with hedgerow planted along the top) interspersed with numerous patches of woodland. In a rectangular area of 630 km² that encompassed the home ranges of all the Honey-buzzards studied (mid-point 54.22°N 10.43°E), the proportion of woodland was 15% while the total length of banked hedgerows (as an indicator of the density of boundary lines) was 2,945 km, or 4.7 km/km². Most of the woodland is managed for timber and deciduous trees (notably Beech *Fagus sylvatica*) predominate; in the area of 630 km² referred to above, 47% of the woodland is mixed, 40% is deciduous and 13% coniferous.

We fitted seven adult Honey-buzzards (three females and four males) with solar-powered GPS PTTs between 2009 and 2011. All birds were captured close to the nest during the nestling stage. Since the females spend a great deal of time near the nest while brooding small nestlings and in general spend little time in the sun during the breeding cycle, the solar cells did not provide sufficient charge for a usable amount of data

Table 1. Number of fixes per day for the tagged male Honey-buzzards.

	Argos transmitter ID number	fixes/day	
		range	mean
male 1	95770	8–17	12.2
male 2	95771	10–19	15.4
male 3 (2010)	52033	0–9	2.1
male 3 (2011)	52033	0–13	3.8
male 4	68561	0–19	2.9

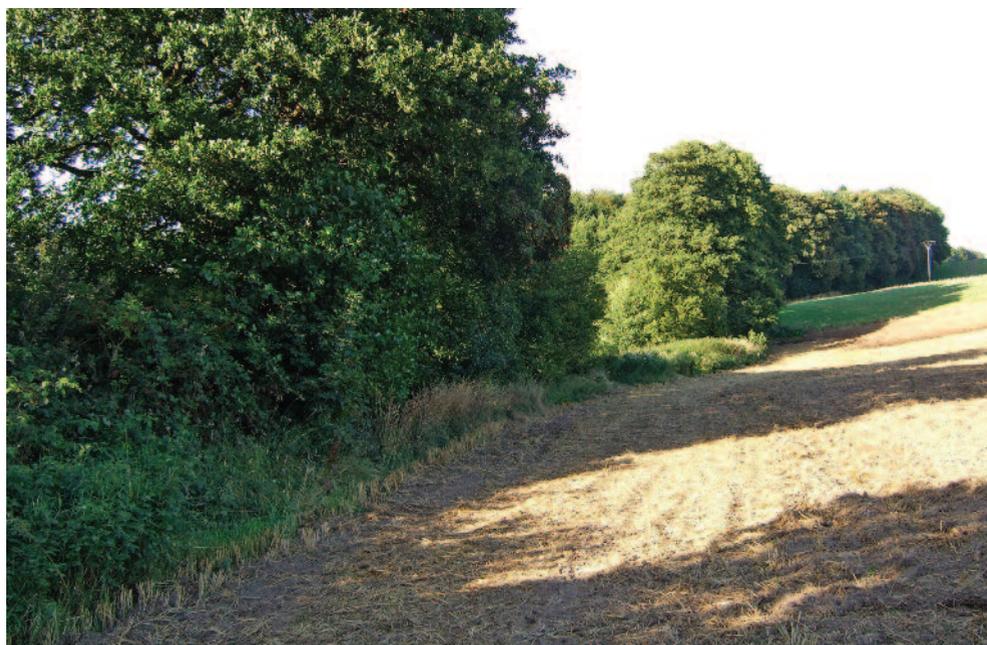
to be collected from females. However, sufficient data were obtained from the four males to measure various attributes of their home range and behaviour. Data were collected from the beginning of the day after the transmitters were fitted until the birds' departure from the breeding area.

The transmitters used in 2009 (birds 1 and 2) broadcast two-dimensional (2D) coordinates. In 2010 and 2011, the three-dimensional (3D) transmitters fitted to birds 3 and 4 also provided information on height above sea level (asl) as well as flight speed and direction. Because 3D transmitters require more power than 2D transmitters, they provided markedly fewer fixes when the bird was not in direct sunlight (table 1). According to the manufacturers, Microwave Telemetry, these tags are accurate to within ± 18 m for longitude and latitude, ± 22 m for height and



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262. A view over the Plön region of Schleswig-Holstein, Germany, in August 2009 – part of the home range of Honey-buzzard *Pernis apivorus* male no. 1 in this study.



262. A typical field boundary in Schleswig-Holstein, comprising a banked hedgerow where a wasp nest has been excavated by a Honey-buzzard; August 2009.

± 1 km/h for speed when this exceeds 40 km/h.

Fixes from the birds' daytime activity phase were plotted to calculate the home range and other parameters. The local times of sunrise and sunset were used to determine the overnight roost sites. If the bird's first morning movement was more than 80 m from the roost, the start of the daily activity phase was assumed. Conversely, the first fix from the overnight roost was taken to represent the end of the daily activity phase.

Data from the nestling period are available for all birds. Male 3 returned the year after it was tagged, again bred successfully at the same nest and was tracked throughout the breeding period in this year.

Various models were tested to provide the most accurate representation of home range. Home ranges can be represented as boundaries of the fix locations (Minimum Convex Polygon, or MCP; Kenward 2001). An MCP is the smallest polygon with outer angles $>180^\circ$, which encloses a defined percentage of all fixes. In order to exclude occasional excursions to distant areas, which would greatly increase the size of the MCP, it is standard practice to include only the closest 95% of fixes in the calculation (MCP 95). Some

authors also calculate the MCP 80, to illustrate the parts of the home range which are used most regularly. MCPs thus comprise a cluster of fixes, but do not tell us how those fixes are distributed within the home range. The most useful model proved to be the Kernel Density Estimation (KDE), which was used to map the utilisation distribution. This contour-based method is often used for mapping home ranges and evaluates utilisation distribution by generating high-density centres based on contour lines (Bowman 1985; Worton 1989). The dots represent the GPS fixes, the lines the kernel isopleths. The kernel isopleth lines mark the probability of occurrence: from 95%, 90%, 80%, 70% and so on down to 10% (and so the outside line encompasses 95% of the probable locations visited). Thus, the highest utilisation density is in the centre, decreasing towards the periphery.

We evaluated the GPS data with the software package GIS ArcView 3.2a. In addition, we used the Google Earth satellite photo program with diverse supplements for analysis. To evaluate the GPS fixes, the home range extension for ArcView© from Rodgers & Carr (1998) and the home range tools for ArcGis© from Rodgers *et al.* (2007) were

used. These programs also calculate MCP. For MCP 95 and MCP 80, the Floating Amean method (proximity to recalculated mean of selected fixes) was used. Thereby the arithmetic mean of all fixes is calculated, then the most distant point determined and deleted, and once again the arithmetic mean of all remaining fixes established. This process is repeated until only 95% or 80% of the fixes remain. Google Earth Pro Version 7.1.2.2041 was used to create the maps, which are published on the basis of Google Order ID 577948 (licence holder B-U. Meyburg).

Here, we present the size of the home ranges as 95% KDE alongside the MCP that contains 80%, 95% or 100% of all fixes, in order to provide easier comparison with the results of other authors.

The extent of woodland within the birds' home ranges was assessed using the countryside information system of the Schleswig-Holstein State Office for Agriculture, Environment and Rural Affairs and maps produced by the Schleswig-Holstein State Survey Agency 2009. Where clusters of fixes indicated excavated wasps' nests, these were searched for, mainly within the following few days.

Table 2. Brood development and nesting phenology of the tagged Honey-buzzards.

	GPS data recorded	chick ringing data		derived phenology	
		date	age of first chick	first-egg date	first chick hatched
male 1	20.07–26.08.2009	22 July 09	19 days	1 June	3 July
male 2	19.07–29.08.2009	22 July 09	20 days	31 May	2 July
male 3 (2010)	08.08–24.08.2010	25 July 10	21 days	2 June	4 July
male 3 (2011)	19.05–13.08.2011	30 July 11	35 days	22 May	25 June
male 4	16.07–18.08.2011	30 July 11	25 days	3 June	5 July

Table 3. Size of home ranges (km²); see text for explanation of different measures used to define home range.

	KDE 95	MCP 80	MCP 95	MCP 100	no. of fixes	date range
male 1	17.3	9.7	12.3	28.7	456	20.07–26.08.2009
male 2	25.8	10.1	17.4	39.8	637	19.07–29.08.2009
male 3 (2010)	–	7.0	14.0	14.3	35	08.08–24.08.2010
male 3 (2011)	13.6	2.8	6.3	13.2	332	19.05–13.08.2011
male 4	13.5	3.1	6.4	9.2	100	16.07–18.08.2011

Table 4. The number of fixes in woodland and in other areas.

	woodland		non-woodland		total no.
	no.	%	no.	%	
male 1	387	85	69		456
male 2	558	88	79		637
male 3 (2010)	24	69	11		35
male 3 (2011)	367	94	25		392
male 4	81	81	19		100

Table 5. Woodland area (km²) and proportion of woodland (%) in the home ranges.

	KDE 95		MCP 80		MCP 95		MCP 100	
	km ²	%						
male 1	2.4	13.9	2.0	20.5	2.4	19.2	3.8	13.4
male 2	5.4	21.1	2.4	23.5	3.9	22.4	7.6	19.2
male 3 (2010)	–		3.0	43.5	3.4	24.3	3.4	23.9
male 3 (2011)	3.0	22.2	2.0	71.2	3.8	60.7	4.7	35.9
male 4	1.8	13.1	0.9	28	1.4	21.2	1.5	16.7

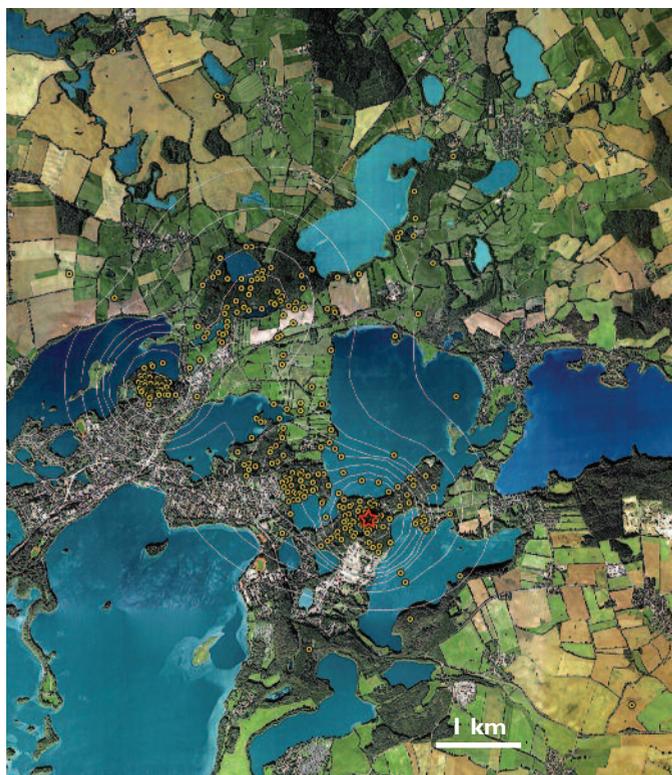


Fig. 1. Home range of Honey-buzzard male 1 (95770), on the city limits of Plön (KDE; the outside line encompasses 95% of the probable locations visited, the inner lines represent 90%, 80% and so on down to 10%; see text for details). Dots: 456 GPS fixes between 20th July and 26th August 2009; red star denotes breeding site.

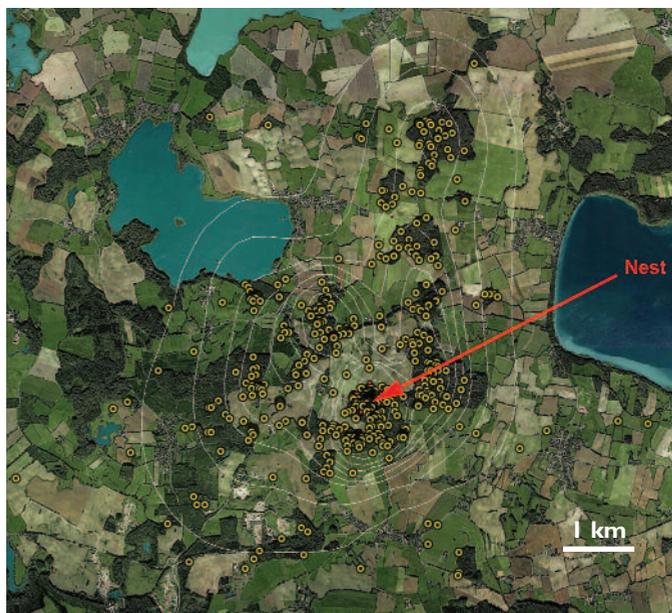


Fig. 2. Home range of Honey-buzzard male 2 (95771), to the west of the Selenter See (KDE). Dots: 637 GPS fixes between 19th July and 29th August 2009.

Results

Breeding data

Basic information on brood development and the period during which the GPS fixes were recorded are shown in table 2. The age of the chicks at the time of ringing was determined using the growth curve in Bijlsma (1997). The calculation of the first-egg date and hatching of the first chick is based on an assumed incubation period of 33 days from laying of the first egg, and a laying interval of two days (van Manen *et al.* 2011).

Home range and habitat selection

The sizes of the different home ranges varied between 13.5 and 25.8 km² (KDE 95%) (table 3, figs. 1–4). By far the greatest number of fixes (69–94%) were from woodland areas (table 4). This is much more than expected based on the proportion of woodland within the home ranges. For male 3, which nested in a woodland of 5 km², 61% of the home range was woodland, but the other three males had only around 20% of woodland within their home ranges (MCP 95; table 5). The male Honey-buzzards clearly preferred to remain in the woods, although they occupied a landscape where the woodland is highly fragmented.

The absolute size of the total area of woodland in the home range of the four Honey-buzzards varied between 1.8 and 5.4 km² (KDE 95%) and 1.4 to 3.9 km² (MCP 95%; table 5).

Diet

A cluster of fixes can suggest that a Honey-buzzard has exploited a food source at a particular location over several hours or even days. However, such food sources can be identified only if visible remains are left behind. The easiest of the regularly exploited food sources to find are the excavated nests

of ground-dwelling wasps. With three exceptions (one bumblebee *Bombus* and two Common Wasp *Vespula vulgaris* nests), all finds were in July and August. Additionally, during fieldwork, ten Common Wasp and two bumblebee nests were found by chance. One bumblebee and one wasp nest had been exploited by Honey-buzzards while two wasp nests showed scratches but remained unharmed.

In total, 29 of 37 (78%) excavated wasp and bumblebee nests were found in woodland, four at the edges of pasture land (e.g. along fences, ditch lines), three in banked hedgerows and one in a harvested rape field, 5 m from a hedgerow (figs. 5–6, table 6).

Temporal and spatial use of home range

In total, 1,609 of the 1,620 fixes (99%) from the four males were within 4 km of the nest, including all overnight roosts. Male 1 flew up to 6.2 km from the nest, the greatest distance recorded. In general, however, the proportion of fixes for all four males decreased with distance from the nest (fig. 7). Birds were most often found in



Fig. 3. Home range of Honey-buzzard male 3 (52033), near Eutin. Dots: 35 GPS fixes between 8th and 24th August 2010 (yellow) and 332 fixes between 19th May and 13th August 2011 (red, plus KDE contours).



Fig. 4. Home range of Honey-buzzard male 4 (68561), near Malente (KDE). Dots: 100 GPS fixes between 16th July and 18th August 2011. Red star denotes breeding site.

Table 6. Wasp and bumblebee nests excavated by tagged Honey-buzzards.

	Common Wasp <i>Vespa vulgaris</i>	German Wasp <i>V. germanica</i>	bumblebee <i>Bombus</i>
male 1	10	1	0
male 2	11	1	0
male 3 (2010)	1	0	0
male 3 (2011)	6	0	1
male 4	5	0	1
Total	33	2	2

the woodland where their nest was located, with other concentrations of fixes in the nearest neighbouring woods.

At night, the distribution of fixes differed among individuals. Whereas male 1 often roosted close to the nest (within 250 m), males 2 and 3 seldom did so, instead roosting at various locations within their hunting area (but most commonly within 1 km of the nest; fig. 8). Occasionally, males 1 and 2 roosted close to wasp nests that had not fully been exploited. Only five night-roost fixes were recorded for male 4, and in 2010 only one night-roost fix for male 3, so that an evaluation of roosting behaviour in these cases was not possible.

For male 3, we were able to study the distances flown from the nest during all stages of the breeding season in 2011. This individual arrived in the breeding area on 19th May that year and on the morning of 20th May it was observed repeatedly chasing one or more rival males and flying with a female (similar to, and presumed to be the same as, its mate from 2010). The laying and incubation period (calculated back from the ringing dates of the young) began on 22nd May and ended on 25th June. The period during which the male had

to brood small chicks, at times when the female was away from the nest, was assumed to be from 26th June to 10th July. Male 3 left the breeding area on 13th August, when the first chick was about 49 days old, and the day after the second chick had been killed by a Northern Goshawk *Accipiter gentilis*.

During the pre-hatching period, almost half of the fixes from male 3 were from the nest and its immediate vicinity (40% within an 80-m radius, 47% within a 250-m radius around the nest). During the period in which the chicks had to be brooded, this proportion hardly changed (42% and 45% respectively). Thereafter, this male was more wide-ranging and active up to 3 km from the nest, so 23% and 28% of fixes were within 80 m and 250 m of the nest respectively (fig. 9).

As the breeding season progressed, the focus of the birds' activity shifted and they spent more time farther away from the nest (fig. 10). The most likely explanation for this pattern is the increased demand for food by growing nestlings, requiring the exploitation of more distant resources. Larger young require less protection from the adults and can be left for longer periods.

The nestling period has been reported as



263. An excavated wasp nest at the edge of a ditch in the study area; August 2009.

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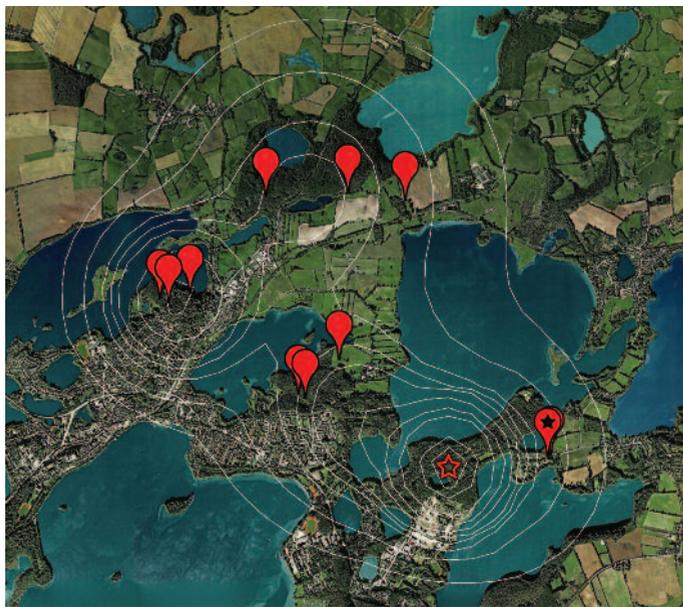


Fig. 5. Wasp nests exploited by Honey-buzzard male 1 (95770): ten Common Wasp and one German Wasp (black star) nests, from 20th July to 26th August 2009. Red star denotes breeding site.



Fig. 6. Wasp nests exploited by Honey-buzzard male 2 (95771): 11 Common Wasp and one German Wasp (black star) nests, from 19th July to 29th August 2009. Red star denotes breeding site.

37–42 days in Honey-buzzards and the post-fledging period (the time between fledging and the young becoming independent) as 5–25 days (Bijlsma 2009). Of the three females and four males tracked by us, the first adult of each pair left the breeding area when the first chick was 44–49 days old, while the remaining adult left when the first chick was 46–58 days old. In two pairs it was the female that departed first. However, in two pairs observed in 1993 and 1995 respectively, one female and one male were the first to leave (Zieseimer 1997).

Diurnal activity patterns

As a rule, adult Honey-buzzards were already active at first light. On a few days they were more than 80 m from their overnight roost more than half an hour before sunrise, e.g. male 1 on six of 16 days and male 2 on four of 29 days. In contrast, male 3 (2011) was still at its overnight roost at sunrise on the 11 days for which data are available. Longer distances were sometimes flown early in the day. For example, on 8th August 2009, male 2 was at the nest 42 minutes before sunrise, after having spent the night 2 km away.

Hourly fixes were too imprecise to record the start and end of diurnal activity accurately. It was noticeable, however, that the birds became active early, often around first

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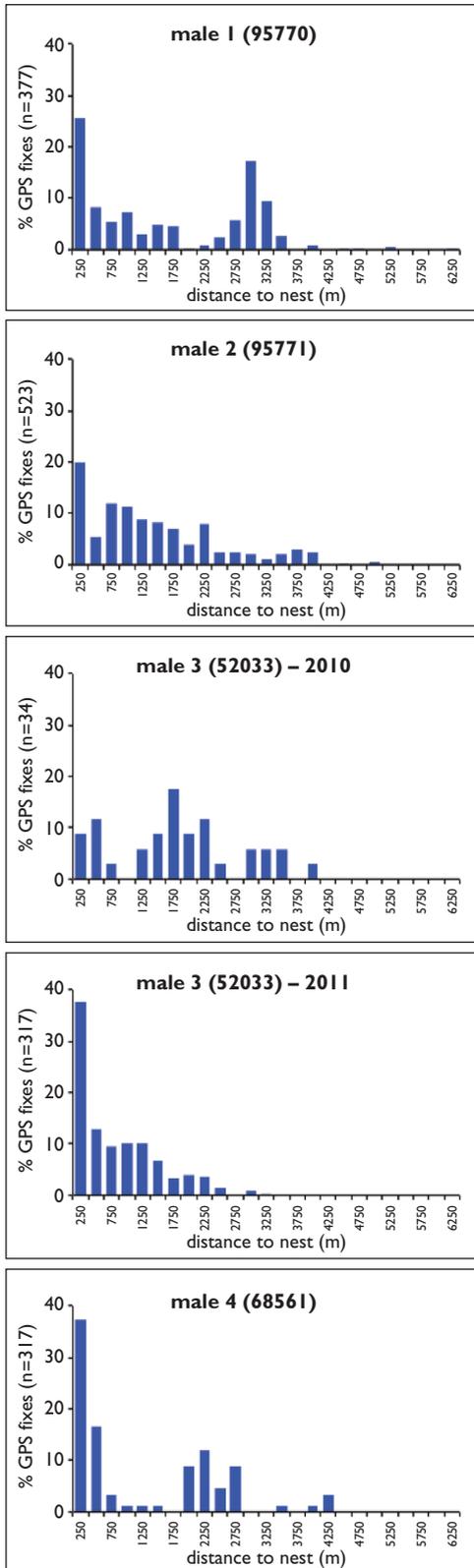


Fig. 7. Distance of daytime fixes from the nest.

light, although not on dark and rainy days. In addition, when a bird brooded overnight into the daylight hours, it left the nest only when relieved by its partner. It was also clear that birds ceased to be active towards sunset. Three males studied in the Netherlands ended their diurnal activity on average 28 minutes before sunset (van Diermen *et al.* 2009).

Honey-buzzards search for the nests of wasps and bumblebees by following their flight movements (Glutz von Blotzheim *et al.* 1971; Högestedt 1976). For example, the Common Wasp starts flying very early in the morning. At first, worker wasps that have spent the night outside the nest return, while soon after others begin to leave the nest. Thus on average, and depending on the time of year, activity can be higher in the early

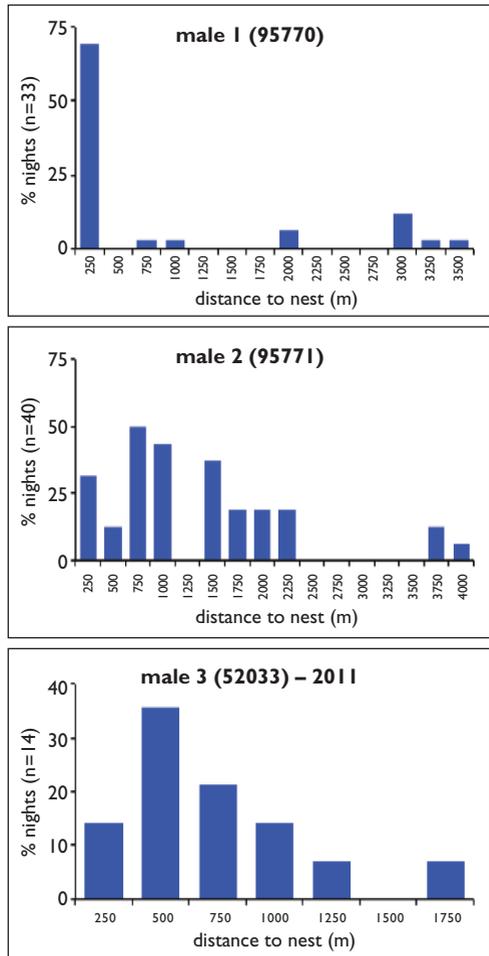


Fig. 8. Distance of overnight fixes from the nest, for males 1, 2 and 3.

morning than later in the day. Thereafter, activity remains more or less constant through the day, but can tail off towards evening; the start and end of activity is determined primarily by whether there is enough light to navigate by. Other wasp species appear to have a similar activity pattern, and hornets are known to be active at night (Spradbery 1973; Matsuura & Yamane 1990; Archer 2005, 2012). It remains unclear why Honey-buzzards tend to curtail their activities earlier in the day than some of their key prey species.

Discussion

Size of the home ranges

The home range (KDE 95%) of three of the four males was within the range 13.5–17.3

km², while male 2 had a markedly larger home range, of 25.8 km². Male 2 foraged in woodlands to the west and north of its nest, which are known to regularly support breeding Honey-buzzards, although we do not know whether these territories were occupied in the study year. Home ranges of

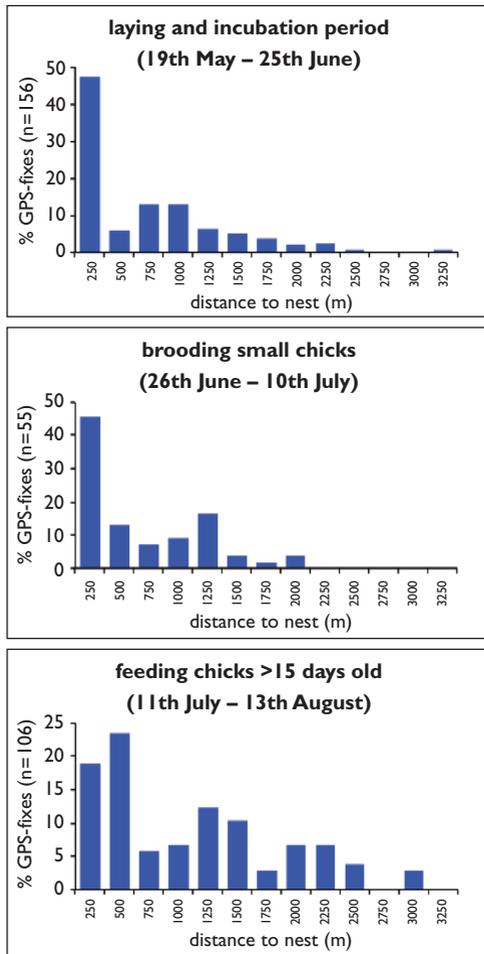


Fig. 9. The spatial distribution of daily fixes of male 3 (52033) in 2011, plotted in relation to the nest site, during three different phases of the breeding cycle.

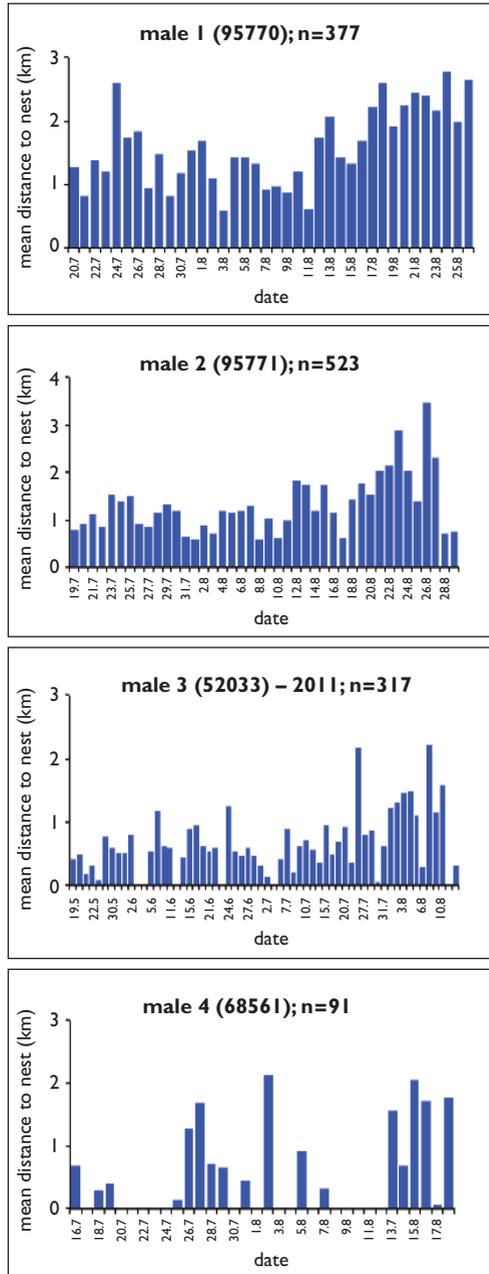


Fig. 10. Mean distance from the nest of fixes during each day as the breeding season progresses (all fixes plotted, from 30 minutes before sunrise to 30 minutes after sunset).

males can overlap (van Manen *et al.* 2011; pers. obs.), but the frequency with which male 2 visited these woods may indicate that neighbouring territories were not occupied in 2009 and that, compared with the other males, this individual was able to make use of a larger area than usual without encountering other breeding birds.

The 15 males studied by van Manen *et al.* (2011) in the Veluwe area of the Netherlands had home ranges (KDE 95%) of 5.7–13.1 km² with a mean of 9.6 km², thus smaller than those in Schleswig-Holstein. The proportion of woodland in the Veluwe area is, at 49%, considerably greater than the 15–20% woodland cover in the Schleswig-Holstein study area. Since wasp nests are found primarily in woodland, it is likely that the Veluwe Honey-buzzards were able to find sufficient food within a smaller area than in Schleswig-Holstein. The density of wasp nests is known to be one of the factors affecting the size of the home range (Gamauf 1999).

A greater proportion of woodland does not automatically result in a smaller home range, however. The home ranges of six male Honey-buzzards in the southern part of the Netherlands, where the study areas had 28–33% woodland cover, were 13.8–45 km² (MCP 95%) during the second half of the nestling period, larger than in Schleswig-Holstein during the equivalent period (6.3–17.4 km²; van Diermen *et al.* 2013). The authors noted a declining attachment to woodland of four of the six males through this period, and found that traps set out in August to determine wasp density caught more wasps outside than within woodland. The large home ranges in this well-wooded study area may reflect the depletion of wasp nests within woodland during the year.

Diet

After their arrival in the breeding area, Honey-buzzards initially feed mainly on amphibians, young birds and (less frequently) reptiles. As colonies of social wasp species develop, Honey-buzzards switch to wasp larvae as their staple diet (Holstein 1944; Itämielä & Mikkola 1972; van Manen *et al.* 2011).

Social wasps (Vespidae) pursue one of two life strategies. In the first, they develop small colonies with a lifespan of 3–4 months, in nests that are free-hanging in vegetation or built close to the surface of the soil, and which benefit from direct warmth from the sun. The Red Wasp *Vespula rufa* and the long-faced wasps *Dolichovespula* spp. pursue this strategy. The alternative strategy, followed by the German Wasp *V. germanica* and the Common Wasp (Archer 2012), is to develop large colonies that can live for 5–6 months in underground nests, where they are insulated against cool weather in autumn. Although all wasp species begin to develop their colonies at about the same time, in mid May, those using the first strategy can complete their colony-building as early as July, weeks before the latter reach their peak development. The timing of the German and Common Wasp colonies fits in better with the food requirements of young Honey-



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264. An excavated wasp nest in deciduous woodland in the study area; July 2011. This shows the characteristic remains of a wasp nest that has been exploited by a Honey-buzzard, with empty but intact comb fragments – Honey-buzzards eat the individual grubs, whereas mammals would chew the comb.



265. Adult male Honey-buzzard *Pernis apivorus* carrying wasp comb; Germany, August 2014.

buzzards. As the colonies of these species also contain more larvae than any of the other species, they tend to dominate the diet of older chicks. Hornets *Vespa crabro* also pursue the second life strategy. However, since their nests are mostly built in tree holes, they are less accessible to Honey-buzzards, unless built in rotting soft wood (van Diermen *et al.* 2013; Harmsen & Bijlsma 2014).

Based on satellite fixes, 33 Common Wasp, two German Wasp and two bumblebee nests were located and recorded as Honey-buzzard prey in this study. In 1993–95, Zieseimer (1997) recorded more varied prey of four male Honey-buzzards, which included 43 Common Wasp, nine German Wasp and 13 nests of four other wasp and bumblebee species. This predominance of the two wasp species with the largest colonies (especially Common Wasp) is probably due not only to the fact that their nests offer more food, but also to the research method used. The probability of observers locating food remains increases with the conspicuousness of the remains left behind. The exploitation of a small hanging wasps' nest in a bush leaves few visible remains, while large wasps' nests excavated from the soil are most likely to be found by human observers. Since, in our study, the Honey-buzzards were not fitted with transmitters until July/August, the

chance of establishing *Dolichovespula* species and *V. rufa* as prey species were reduced. In addition, the timing of transmitter broadcasts (one fix every hour, at best), meant that the likelihood of observers finding a nest was greater if a Honey-buzzard had been occupied with it for a number of hours. With less than one fix per hour, as was often the case, the probability of finding any food remains at all was greatly reduced. Yet although the technology did not permit a representative interpretation of prey choice, it did show that the Honey-buzzards located large wasps' nests, the main source of food for rearing their young, above all in woodland (78%) and in the edge habitats of the agricultural landscape.

It is not clear why the German Wasp is so under-represented as prey compared with the Common Wasp. Both species occur widely in Europe where, according to Gusenleitner (1975), Common prefers cooler regions than German. Both species are generally common in Schleswig-Holstein, though they differ in their habitat requirements. Common occurs both in woodland and elsewhere, whereas the German Wasp tends to avoid woodland (Dvorak 2007). Honey-buzzards will seek and locate wasp nests both within and outside woodland, however, so differences in habitat preferences of the two wasp species are not necessarily the reason for the marked

variation in their occurrence in the prey list. A noticeable decline in the population of German Wasps was reported in England in the period 1970–2000 (Archer 2001), and is also suspected to have occurred in Germany (Witt 2010).

As well as a possible population decline, a change in the seasonal occurrence of the German Wasp is a potential reason for its under-representation in prey. Tryjanowski *et al.* (2010) and Visser & Both (2005) point to the fact that some wasp species, including German Wasp, have markedly advanced their flight times in association with climate warming. Bijlsma (2012a) established that, for several years now, German Wasps had reached the peak of their activity as early as mid July, and that nests could be largely abandoned by the beginning of August. The reduction in availability of such an important prey item, especially at the time of greatest demand for food, could affect Honey-buzzard breeding success and further study would be worthwhile.

The density of all wasps' nests combined – and therefore the Honey-buzzard's main food supply – is subject to strong fluctuation. According to a frequently cited example from England (the Royal Horticultural Society gardens at Wisley, in Surrey, 1921–1949), this can vary by a factor of about 42 (Archer 2012). Bijlsma (2012b) found a similar range of fluctuation (factor of 40) in the Netherlands during the period 1974–2011. To date, however, only wasp availability in extreme years has had a noticeable effect on the breeding success of Honey-buzzards. Seemingly, in years when wasps are scarce, sufficient alternative prey, such as frogs and young birds, was available.

Distance from the nest

It is not possible to determine the fine detail of the tagged birds' movements in

this study because of the interval between fixes (one hour or longer). Although males search for food in all parts of their home range, they tend to actively defend their territory within a radius of 2 km of the nest (Gamauf 1988; Ziesemer 1997). In good weather conditions, they can spend a great deal of time in the air. Flights to more distant locations are primarily foraging trips, and we attributed all fixes within a radius of 80 m of the nest to the immediate care of the brood (nest-building, breeding, feeding, on watch, etc.).

In Honey-buzzards, both sexes contribute to incubation and brooding. There are, however, differences in the division of tasks between the partners (e.g. Holstein 1944, Roberts & Law 2014). The proportion of fixes within 80 m of the nest recorded for male 3 in 2011 was 40% during egg-laying and incubation, 42% when the nestlings were small, but just 23% when the nestlings were large enough to be left unattended. This corresponds fairly well to the values recorded for several males in the Netherlands by van Manen *et al.* (2011): around 40% until the young hatched, 30–40% in the period when small nestlings had to be kept warm and about 10% subsequently.

The distances that males travelled away from the nest were also similar in both studies. In this study, 99% of all fixes were within a radius of 4 km of the nest, whereas the equivalent figure in van Manen's study



266. Male and female Honey-buzzards *Pernis apivorus* at the nest site, with small chick; the male bird (left) has arrived with a piece of wasp comb; Germany, 13th July 2014.

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was 94%. During the course of the breeding season, the Dutch males extended their search for food from 1.5 to 3 km from the nest, on average. This corresponds with flights of increasing distance in Schleswig-Holstein (figs. 9 & 10), although it is not possible to attribute these to particular activities. In the same way, van Manen *et al.* (2011) found that most of the males roosted at night at different locations, on some occasions at wasp nests that had not yet been exploited. Such 'guarding' of exposed wasp nests reflects the fact that they are otherwise easily exploited by other Honey-buzzards (Zieseimer 1997; van Diermen pers. comm.).

In the Netherlands, it was found that females regularly foraged more than 10 km from the nest (van Manen *et al.* 2011), whereas males remained closer to the nest site, as in our study. During these longer flights, females specifically visited individual, food-rich locations. In this way, their home range could be regarded as several, widely separated areas that, taken together (based on KDE 95% for foraging positions), could be even smaller than the home range of the males. Similar flights have also been recorded in Schleswig-Holstein; for example, one female traversed several other Honey-buzzard territories, about 1–2 days before the first chick hatched (Zieseimer 1997). This is unusually early, as in most years females will undertake long foraging flights only once the chicks are old enough to maintain their body temperature unaided (van Diermen pers. comm.). Later, when the chicks are well grown (four weeks or more), females frequently visit distant foraging areas, as far away as 124 km from the nest and for one or several days, before subsequently returning, sometimes to feed their young (van Diermen *et al.* 2013).

Habitat

The fixes of all four males in our study showed a clear preference for woodland, even after taking into account the fact that nests are situated within this habitat. This, we believe, relates to the biology of social wasps and bumblebees, which build their nests underground as well as in trees and bushes. Ground nests, which are frequently built in abandoned mouse holes, can be constructed

only in unbroken soil. Thus arable land, which is tilled annually, is usually avoided, while grassland is suitable only to a limited extent, owing to the trampling of livestock and disturbance of the soil by heavy machinery. Wasp nests in human settlements can be exploited only if there is little human disturbance, for example in the large gardens on the outskirts of small settlements (Zieseimer 1997; van Manen *et al.* 2011). Wasps' nests are therefore predominantly accessible to Honey-buzzards in woodland, as well as around the margins of the agricultural land, particularly in banked hedgerows but also verges and embankments, etc. The significance of woodland was also demonstrated in this study by the fact that 78% of the exploited wasp and bumblebee nests we found were in this habitat.

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