

Title	Courtship behaviour of western hedgehogs (Erinaceus europaeus) in a
Author(s)	Haigh, Amy; Butler, Fidelma; O'Riordan, Ruth M.
Publication date	2012
Original citation	Haigh, A. Butler, F. and O'Riordan, R. M. (2012) Courtship behaviour of western hedgehogs (Erinaceus europaeus) in a rural landscape in Ireland and the first appearance of offspring', Lutra, 55(1), pp. 41-54.
Type of publication	Article (peer-reviewed)
Link to publisher's version	http://www.zoogdierwinkel.nl/content/lutra-551haigh-et-al2012 Access to the full text of the published version may require a subscription.
Rights	© 2012, Zoogdiervereniging.
Item downloaded from	http://hdl.handle.net/10468/2545

Downloaded on 2017-02-12T09:34:20Z



University College Cork, Ireland Coláiste na hOllscoile Corcaigh

Courtship behaviour of western hedgehogs (*Erinaceus europaeus*) in a rural landscape in Ireland and the first appearance of offspring

Amy Haigh, Fidelma Butler & Ruth M. O'Riordan

School of Biological, Environmental and Earth Sciences (BEES), University College Cork, School of BEES, The Cooperage, Distillery Fields, North Mall, Cork, Ireland, e-mail: amyjohaigh@yahoo.com

Abstract: A study was conducted to investigate the timing of the breeding season of western hedgehogs (*Erinaceus europaeus*) in a rural landscape in Ireland, their courtship activity and the first appearance and possible dispersal of juveniles. Between June 2008 and June 2010, 24 hedgehogs (18 $\stackrel{<}{\circ}$ and 6 $\stackrel{\bigcirc}{\circ}$) were caught and monitored by radio tracking and direct following. A preponderance of males was recorded in both adults and juveniles at the study site and the sex ratio deviated significantly from a 1:1 ratio. Courtship behaviour took place between April and July and occurred almost exclusively in a nine ha pasture. An individual female paired with up to seven males in a season. The first appearance of juveniles was recorded in September (2008) and July (2009). The majority (*n*=22) of juvenile sightings, both alive and as road kill, occurred in July but they continued to be recorded up until November (*n*=3). The presence of juveniles at the study site in October 2008 and a pregnant female being found in September 2009 indicated that late litters occur in Ireland.

Keywords: sex biases, multiple pairings, juveniles, second litters, dispersal.

Introduction

The breeding season in the western hedgehog (*Erinaceus europaeus*) has been reported to begin soon after the hedgehog has emerged from hibernation in April until August, with peaks in activity varying depending on latitude (Morris 1961, Morris 1969, Kristiansson 1984, Riber 2006, Jackson 2006). In New Zealand, introduced hedgehogs have a breeding season centred around November-March (equivalent to the April-August breeding season in Europe), but the milder climate in New Zealand permits breeding well outside this core period (Parkes 1975).

Female western hedgehogs are polyoestrus and, in the male, spermatogenesis occurs between early April and mid August peaking between mid April and June in the UK (Deanesly 1934). Courtship behaviour in hedgehogs is characterised by the male circling around the female with one or both sexes snorting loudly (Reeve & Morris 1986). According to Jackson (2006) this ritual may continue for over an hour, with the majority of displays failing to end in a successful mating.

According to Emlen & Oring (1977), in species where one sex is largely freed from parental care, as is the case with the western male hedgehog, individuals of this sex should remain active for the duration of the period during which members of the other sex become sexually receptive, in order to mate with as many females as possible. For a non-territorial animal, like a hedgehog, which remains receptive for the majority of its active period, the possibility to mate with multiple individuals

^{© 2012} Zoogdiervereniging. Lutra articles also on the internet: http://www.zoogdiervereniging.nl

is high. In previous studies individual males made mating attempts with several females, in some cases during the same night (Reeve 1981, Kristiansson 1984, Jackson 2006, Warwick et al. 2006). During the breeding season males' home ranges increase in order to cover the range of as many females as possible (Kristiansson 1984), and multiple paternity has been reported (Moran et al. 2009).

In the UK, following a pregnancy of 31-39 days (Morris 1961), during which females may accumulate a mass of 50-150 g (Jackson 2006); between 2-7 young are born (Morris 1961, Morris 1966, Jackson 2006). The number of offspring in New Zealand, also falls within this range (Parkes 1975). In Sweden, hedgehogs have a single litter, which is larger, with Kristiansson (1981) reporting a mean litter size of 5.2 with numbers ranging up to eleven. Kristiansson (1990) reported an equal sex ratio. However a preponderance of males was found by Morris (1969), Reeve (1981) and Riber (2006) in the UK and Denmark.

Possible late litter (any time after August) as suggested by Barrett-Hamilton & Hinton (1911), has been reported in the UK (Morris 1966, Jackson 2006) and matings can occur in late August and early September (Morris 1961). Courtship or pregnancies may therefore be found during most of the active year i.e. March-October (Reeve 1981). However, as the active period is short, it is unlikely that an individual female could successfully rear two litters and gain the required weight to survive hibernation (Reeve 1994). Jackson (2006) found that at least three females, who reared a second litter, died in an emaciated state soon after the young emerged. Therefore, most late litters are thought to be the result of a failed first litter or produced by females born in the preceding August or September, that might not be ready to breed until nearly a year old (Deanesly 1934). Morris (1961) and Morris (1966) found that mothers deprived of their earlier litter are highly fertile and will readily breed again during the same season. It is not known whether a second or late litter occurs amongst Irish hedgehogs.

Juveniles, in the UK, reach independence at six weeks of age at which time they weigh between 220-235 g (Reeve 1994). Hedgehogs have been recorded to reach sexual maturity between nine months (Allanson 1934) and two years of age (Kristiansson 1990). However, Deansley (1934) felt that they reach sexual maturity once they have reached a required weight. There is little known about the dispersal of young hedgehogs but Doncaster (1993) suggested that hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage. However, Doncaster et al. (2001) observed that although natural dispersals were relatively rare events, hedgehogs were capable of travelling up to 3.8 km from a release point and up to 9.9 km in total.

With no previous data on the ecology of Irish hedgehogs, the breeding season, courtship behaviour and first appearance of juveniles in Ireland is unknown. Therefore the present study aimed to investigate patterns of courtship behaviour of a study group i.e. the number of mates, duration of courtship and the identity of pairings. The study also aimed to investigate the first appearance of juveniles, the timing of litters, the number of offspring and the possible patterns of dispersal by juveniles. It also aimed to test the following hypotheses that:

- Due to the increased home range of males during the breeding season, males would attempt to mate with multiple females.
- A late or second litter occurs amongst Irish hedgehogs and is evident amongst the study group and through the appearance of juvenile road kill
- In line with research in the UK, little dispersal occurs amongst juveniles.

Materials and methods

Site

The study was carried out between June and November 2008 on a site (51° 53' 59.5"N lati-

tude, 8° 29'03.7"W longitude) in SW-Ireland, 36.8 km from Cork city and 5.3 km from the nearest town of Bandon. The site of 97 ha consisted of 23% arable, 64% pasture, 7% residential garden, 1% scrub, 1% marsh, and 4% wood. Crops grown in the arable field consisted of barley and wheat, fungicides were applied once a year in May and the crop was cut in September. Pasture was grazed by horses. Hedgerow was maintained in all of these fields with each having a thick bramble understory. The walls around the various habitats did not appear to act as a boundary to the movement of hedgehogs and they were observed scaling these walls with little difficulty.

Capture and marking

Hedgehogs were captured by hand with the aid of spotlights. The animals were marked using a unique colour combination of 15 heat shrink plastic tubes (RS Components Ltd, Corby, UK) which were attached with glue (Evo-stik, Bostik Ltd, Leicester, UK) to a number of spines in three specific regions on the animal (left of head, centre and right of head). Reflective tape was also applied to one of the middle markers so that the head region could be identified while tracking. The tubes acted as a visual aid and minimised the need to recapture the animal for individual identification. The hedgehogs were also marked using passive integrated transponder (P.I.T.) tags inserted into the upper hind leg (Doncaster et al. 2001, Jackson et al. 2004). This allowed individuals to be re-identified after hibernation. All procedures were carried out in accordance with current regulations, with licenses being obtained from the Department of Environment, Heritage and Local Government.

All hedgehogs caught were classified as adult or juvenile, sexed and hind foot measurements were taken. Individuals were weighed weekly, using digital scales (Harvard Apparatus, Holliston, MA, USA), to assess weight changes associated with pregnancy and monitor juveniles. The hedgehog was considered to be a juvenile if it satisfied all of the following criteria: weight less than 600 g when first caught; hind foot length of less than 3.6 cm; and presence of growing spines all over the pelage.

Direct following

Spotlighting for hedgehogs took place between 26th June 2008 and 28th September 2008. Any hedgehogs caught during spotlighting nights were fitted with a tip light (MK IV, Murray and Co. Ltd, Cork, Ireland) placed on the back and monitored by direct observation using a UV filter placed over a spotlight. Fixes were taken at ten minute intervals using a Garmin GPS 60 (CH Marine, Cork, Ireland). Every ten minutes the behaviour and location of each hedgehog were recorded.

Radio tracking

All hedgehogs caught after 28 September 2008 were equipped with radio tags. Eight individuals were fitted with 173 MHz, R1-2B transmitters (Holohil Systems Ltd, Ontario, Canada) in 2008, 16 in 2009 and six in 2010. These tags were attached to the hedgehog as described in Jackson & Green (2000). The entire tag weighed 10 g. Individuals were than tracked using a SIKA receiver (Biotrack Ltd, Dorset, UK). When the hedgehog was located, its position was documented and a ten minute focal sample was conducted before locating the next tagged individual. In 2008, radio tracking was carried out from dusk until they returned to their nests at dawn. In 2009, Individuals were monitored for either the first six hours of the night after emergence or the six hours before dawn.

Courtship behaviour

Courtship behaviour was identified based on the description by Reeve & Morris (1986), i.e.



Figure 1. The months in which courtship behaviour was observed among the females (*n*=total number of observations of courtship).

"courtship involves the male circling closely around the female, with one or both sexes snorting loudly". When courtship behaviour was observed, the identification of individuals involved was recorded, in addition to their location, the length of time which they spent engaged in courtship behaviour and whether the behaviour concluded in a successful mating.

Road kill

In March 2008, an appeal was sent out on the University College Cork website informing people about the project and appealing for carcasses. The public was also made aware of the project through the distribution of 320 surveys to agricultural colleges, gun clubs and rural areas, requesting records of hedgehog sightings (Haigh et al., in press). Carcasses of road kill were subsequently collected by both the authors and members of the public from all over Ireland. These were sexed, weighed and aged by one of the authors, using the same criteria as described previously. The time of year and the location of the incident were also recorded. Carcasses of females were inspected for signs of lactation and if pregnant the numbers of foetuses were recorded.

Results

Sex ratio

Between June 2008 and June 2010, 24 hedgehogs (18 \bigcirc and 6 \bigcirc) were caught at the site. The sex ratio of those caught was 3 (male) : 1 (female) which deviated significantly from 1:1 (Chi-squared test: χ^2 =6.760, df=1, *P*<0.01) (χ^2 =6.8 following Yates correction). Eight of these hedgehogs were juveniles (6 \bigcirc and 2 \bigcirc) and as was the case with adults their sex ratio was also 3:1.

Courtship behaviour

Courtship behaviour was usually first obvious by the loud hisses of the female. The hedgehogs faced each other, the male attempting to approach the female who would lunge forward, pushing her head underneath his body, while she forcefully pushed him away. The male would again edge forward and attempt to move behind the female, progressing in wide circles, and moving behind large clumps of grass. The female quickly circled around to avoid the male approaching behind her and again the hissing resumed.

Time of occurrence of courtship

In 2008, when 14 hedgehogs were monitored at the site for 375 hours over 81 nights from June to November 2008, there were only two observations of courtship behaviour, both in August (figure 1).

In 2009, 16 hedgehogs were observed for a total period of 624 hours over 104 nights, with twelve of these individuals being observed in courtship behaviour. From emergence in April until July 2009, there were 33 observations of courtship behaviour involving four adult females (figure 1), with no further observations of courtship behaviour after July.

In 2010, six hedgehogs were monitored for 76 hours over 38 nights. Courtship behaviour was first observed in May, and there was one female tagged at this time. Four incidents of courtship behaviour were observed between March and June, all taking place in May and involving this female. This female (524A) was killed on the road in June 2010 and no further courtship behaviour was observed (figure 1). Prior to this all courtship displays in 2010 had involved this female.

Duration of courtship events

Of the 39 observations of courtship behaviour over the entire study period, involving 16 individuals (4 \bigcirc and 12 \eth) no successful copulations were witnessed. Bouts of courtship behaviour had a mean duration of 60 (± 0.05) minutes. However, on one occasion in 2009 a bout lasted for up to 140 minutes. On this occasion, while one pair was involved in courtship behaviour in the pasture, two males approached from two different directions. One remained stationary behind a clump of grass for the duration of the interaction, while the other approached the female and attempted to mate with her.

Courtship always terminated with the male moving away and immediately starting to forage, while the female remained stationary until the male had moved away from the area.

Of the 1132 fixes from twelve (8 d and 4 φ) individuals obtained between April and July 2009, during 292 (26%) of these, hedgehogs were engaged in courtship behaviour. There was no significant variation in the number of fixes where courtship behaviour was observed for either sex (χ^2 =2.381,df=1, *P*>0.05). Out of 458 fixes obtained from females (*n*=4) between April and July 2009, in 139 (30%) of these, courtship behaviour was observed. In the same time period, out of 678 male (*n*=8) fixes, during 153 (23%) of these courtship behaviour was observed.

Identification of pairings

In 2008, there were two observations of courtship behaviour and they involved three of the tagged males and one female (FA56). In 2009, a male was observed paired with this same female on up to six different occasions (mean 2.4 ± 0.38 occasions per female). Males were observed in courtship behaviour with up to three different females during the breeding season (mean 1.6 ± 0.31 occasions per male) (figure 2). For example in 2009, male 8C88 was observed paired with female FA56 on three occasions, female 411D twice and once with female 524A. In 2010, female 524A was the only female observed at the site and all of the tagged males (n=4) were observed attempting to mate with her (figure 2).



Figure 2. The number of times a female was observed paired with a particular male in 2009.

Location of courtship events

During the breeding season, both sexes concentrated their activity in pasture, and moved out of this area when the breeding season terminated. In total, 92.3% of courtship behaviour took place here, with only one observation in the marsh and two in the garden. Courtship behaviour in the garden occurred in August 2008, when breeding had terminated in the following two years. A female (411D) from the periphery of the site (*1 figure 3) moved down to the pasture (* figure 3) where all the courtship took place in Mav 2009. It was as she moved down into this area that a courtship event was observed in the marsh (*2 figure 3) between her and an adult male (8C88). Females occupied three neighbouring areas of pasture during the breeding season and this area was completely encompassed by the adult males. The pasture represented the core area of the females home range at this time in all years, and while their mean annual home range was 16.5 ± 0.49) ha (n=3 adult females), the males occupied 56.0



Figure 3. The home range of adult males and females (100% mcp).



Figure 4. Fixes of an adult female (524A) monitored over three years.

(\pm 0.67) ha (*n*=4 adult males) (Haigh 2011) (figure 3).

The most detailed information, over the three years, is available for adult female (524A). She was first caught in September 2008 in the arable field (1 in figure 4) and tagged until her death in June 2010. In the two consecutive years she moved away from the core area of her home range (2 in figure 4), at the end of May, after being involved in several courtship events (figures 1 and 2). At this time she moved into neighbouring pasture (0.53 km) (3 in figure 4). In September she moved back with the other adults (4 in



Figure 5. Month in which juveniles were either recorded alive (at the study site and by the public) or as road kill during the research period.

figure 4). In May 2009, her weight increased by 112 g in six days. When she was next seen active, and weighed, seven days later, she had lost 198 g, suggesting that she had given birth.

First appearance of juveniles

In 2008, the first juvenile (\bigcirc) was caught at the study site on 19 September. The remaining (*n*=4) juveniles were caught on 17 and 18 October of that year, their weight (244-281 g) indicating that they had just reached independence. In 2009, the first juveniles were caught at the site in July.

Four out of 35 road kill females collected as road kill (7 June, 23 June, 14 July and 6 September 2009), were pregnant when killed. In two of these cases the foetuses were well developed (between 4-7 g and 14-20 g and 2 cm long) with one female pregnant with five foetuses and the other with six. Only the litter of six could be accurately sexed and they showed a sex ratio of 1:1. None of the female carcasses showed obvious signs that they were lactating and none of the female carcasses collected in 2008 and 2010 were pregnant when killed.

Twenty-eight of the road casualties were

juveniles (figure 5) and 88 were adult, the remaining 29 were too damaged to accurately identify. The incidences of juveniles being killed on the road peaked in July, but they were found up until November (figure 5).

Movement of juveniles from natal nest

Juvenile movement in 2008

Juveniles made exploratory movements away from their natal nest, but returned and remained close to the area of their birth. There were 135 fixes obtained from juveniles in October and November 2008. In the first few days after tagging in October 2008, the four late juveniles (3 $\stackrel{\frown}{\circ}$ and 1 $\stackrel{\bigcirc}{\circ}$) confined their activity to a small area of the arable field, and all of them returned to the same nest every morning. This is illustrated by one of these juveniles, a male (56EA) who was radio tagged (figure 6A). After the first week they all were observed foraging further into the field and occupied separate day nests, however they all remained in the arable field, where the adults were also foraging (figure 6B). The greatest distance moved was 0.20 km in October and 0.24 km in November. He remained in the



Figure 6. The movement patterns of a juvenile male (56EA) from first capture in October (A), November (B), March and April 2009 (C).

arable field throughout hibernation and did not leave this habitat until the following year. He emerged on 30 March 2009 and moved 0.06 km within the arable field. In April 2009 (figure 6C) he entered the nine ha area of pasture (0.50 km from first capture, 0.33 km from hibernacula).

Juvenile movement in 2009

The first juvenile of 2009 was again found in the arable field, but in July weighing 299 g. This animal, a male (ACD7) remained in the southern portion of the arable field for the first two months of independence. He gradually dispersed 0.23 km into the arable field, and was recorded on two occasions making exploratory trips into the neighbouring pasture in September (0.43 km) (figure 7). This individual was killed by a dog in the arable field at the end of September 2009.

Two more juveniles (both 3) were found in three ha of pasture, at the site in August and September 2009. They remained in this area throughout the monitoring period. However, in October 2009 one of the juveniles (D89D) entered the arable field and built a hibernaculum there. Both of these hedgehogs were monitored throughout hibernation. One failed to emerge but the other (D89D) emerged in March 2010. This animal remained in the pasture and despite making exploratory trips of 0.64 km (figure 7) into the neighbouring pasture returned to the core area of the pasture, where he was eventually killed by a mowing machine in June 2010.

Discussion

At the study site there was a sex bias in favour of males, for both adults and juveniles 3:1. Similarly, a strong preponderance of males in both juveniles (7:2) and adults (8:5) was noted by Reeve (1982) and Riber (2006), who caught 24 adult males and 7 females. However, Kristiansson (1990) in Sweden found an equal sex ratio. Reeve (1982) suggested that a male bias may be due to transient males, as he did not notice this bias amongst juveniles. This may partly explain the bias in the current study as four of these males were first caught between April and July 2009, at the height of the breeding season. Furthermore all of these individuals were first caught while trying to mate with tagged females. Two of the adult males were not seen again and the other two were known to have moved outside the core $(56.0 \pm 0.7 \text{ ha})$ home range after the breeding season ended in August 2009, with one returning again to attempt to mate in May 2010. It therefore must be considered that the strong male bias was



Figure 7. The greatest recorded distance (km) that a juvenile moved from the location where it was first captured to the furthest fix each month.

a result of the male's larger home range and small study area. It may therefore have not been as apparent if the study site was larger. However, in the present study a bias was also observed amongst juveniles in both years, with a litter of four juveniles in 2008 having just one female. In 2009, all of the three juveniles caught were male. Kristiansson (1990) noting the discrepancy between estimated litter size at birth (6.5) and the recruited number of juveniles per adult (2.79), and suggested a high mortality rate from birth to catchability. Therefore, mortality may be higher amongst female offspring as one of the litter of foetuses recovered from a pregnant female showed a sex ratio of 1:1. Clutton-Brock & Iason (1986) examined mammals increasing their fitness by varying the sex ratio of their progeny, in response to differences in the costs and benefits of producing males and females. They found that in species where males may disperse from their natal area, while females share their mother's home range, the female siblings are likely to compete for resources, so the mothers produce male biased sex ratios. However, as there is little information on whether juvenile hedgehogs disperse, it is unclear whether this could be the case in hedgehogs.

In the present study, a peak in sexual activ-

ity was observed in July which was similar to peaks in the UK (Reeve 1981, Jackson 2006) and Sweden (Kristiansson 1981). The breeding season of hedgehogs is often characterised by an increased movement of males in order to encompass the range of as many females as possible (Kristiansson 1984). The males who were tagged in the present study increased their range during the breeding season with one male covering an area of up to 30 ha, at its peak movement in July before reducing his range to eleven ha in August when breeding behaviour ceased (Haigh 2011).

Jackson (2006) reported that females were promiscuous and were estimated to have sexual encounters, though not necessarily matings, with at least five males. In the present study copulation was never observed, but 39 incidents of courtship behaviour were witnessed. Successful matings appear to be rare with Reeve & Morris (1986) reporting only five successful copulations in 76 courtship displays and Jackson (2006) only observing ten. Jackson (2006) felt that this reflected the brevity of mating (minutes) relative to the time spent courting (up to an hour or more). In shrews (Sorex araneus), as females cannot always distinguish between close kin they may copulate with several different males, thereby reducing the risk that all of their offspring will be sired by a close relative (Stockley et al. 1993). Multiple paternity, which has been reported in shrews and hedgehogs (Moran et al. 2009), may be a useful way for a non territorial animal, like the hedgehog, to reduce inbreeding depression and the need for dispersal.

Surprisingly, 92.3% of courtship events occurred in a core area of pasture. Potential prey was consistently poor in this habitat throughout the year (Haigh 2011), which may have meant that there was less distraction from breeding. Prey abundance was also lower here, than in areas of arable, which hedgehogs began to enter once the breeding season finished (Haigh 2011). Therefore, habitat selection appeared to be the motivated by courtship behaviour at this time. They spent up to 35% of their time engaged in courtship behaviour and 26% of their time foraging (Haigh 2011). Three of the females concentrated their activity in this habitat during the breeding season and the fourth female (411D), moved down here from the periphery of the site. While, the reason for the selection of this pasture for courtship events is undetermined, it would appear that access to multiple mates is advantageous for both sexes. In other polyandrous species such as the marsupial Antechinus agilis, the female benefits through increased growth rates by mating with multiple males (Fisher et al. 2006). In the present study, females were found with up to seven different males and males were observed trying to mate with up to three different females. Over the breeding season an individual male attempted to mate with the same female up to six times. On two occasions the male attempted again to mate with the same female later in the same night. However, it was still unsuccessful. With animals that were tagged for more than one season, the same male attempted to mate with the same female the following year. This is in contrast to data from the UK, where Reeve (1981) and Jackson (2006) both reported that the probability of the male being found with the same partner was low. In Reeve & Morris' (1986) study, ten of the 76 incidents involved partners who had been previously recorded together up to three times, but twelve of the females were courted by at least ten different partners. The high incidence of repeated pairings of the same individuals in the present study may be due to the high male bias and small number of females at the site, with only four adult females recorded in the two and a half year study. The two juvenile females caught in 2008 were not seen again after hibernation.

In all cases courtship behaviour was characterised by the aggressive behaviour of the female, in the same manner previously described by Reeve & Morris (1986) and Jackson (2006). Cox & Le Boeuf (1977) indicated that this behaviour, of rejecting a suitor, allows the female to test the vigour, tenacity and speed (indicators of fitness) of a potential suitor and select a union which results in optimal genetic consequences. Reeve (1994) too suggested that the courtship ritual allows plenty of time for a female to judge her suitor and less vigorous males may be displaced. In the present study a courting pair of hedgehogs was often approached by up to two other males. The males ran to the pair with their heads raised suggesting that they had been alerted to the pair either by the sound of the aggressive female or through her scent. Reeve (1994) suggested that odour plays an important part in hedgehogs' pre-mating behaviour. with males attracted to females in oestrus and certainly in this study this appeared to be the case with a male seen running towards a lone female from the other side of the nine ha pasture in June 2010. Aggressive female behaviour during mating has also been described in e.g. elephant seals (Mirounga angustirostris) that respond to male advances by loud vocalisations and escape movements, this alerts neighbouring males and competition ensues among males of varying ranks, with the result that the highest ranking male is selected (Cox & Le Boeuf 1977, Christenson & Le Boeuf 1978). As in the present study no observations

of courtship behaviour resulted in copulation, it is uncertain whether there was any effect of male dominance in the outcome of a mating attempt. However, in the present study on the two occasions when a male hedgehog, who was known to have been born the previous year, attempted to mate with a female, they were in both cases joined by an older male, who was aggressive towards the younger hedgehog that subsequently retreated.

According to Kristiansson (1990) female hedgehogs do not produce young until their third summer i.e. at about two years old. Jackson (2006) found that only four of 48 sub adults were found paired with a female, and none were definite sub adults. However, earlier estimates of sexual maturity have been reported, with Allanson (1934) suggesting nine months for males and Morris (1969) recording one female reaching an oestrus condition by the end of its first summer at an age of less than six months. Deansley (1934) suggested that hedgehogs reached sexual maturity once they have reached a required weight. The two males in the present study would have been seven months and ten months respectively, when found paired with a female, having both reached weights close to that of the adults at this time. However, as mentioned above, in both incidents of courtship behaviour, they were displaced by an older hedgehog.

In 2008, although spotlighting at the site began in June, juveniles were not seen at the site until September and October, 6-8 weeks after the only courtship displays had been observed in August 2008. On 17 October 2008, four juveniles were found with a mean weight of 259.5 g (± 0.99). In the UK Reeve (1994) reported weights of 200-235 g (about ten times) birth weight, at around 40 days and they are newly independent at about six weeks. Their size and the fact that these animals remained in close proximity to one another and returned to the same nest indicated that these animals were newly independent in October 2008. Although late in the year, second or late litters have been reported

in a number of studies (Barrett-Hamilton & Hinton 1911, Deanesly 1934, Morris 1961, Morris 1966). Jackson (2006) found that 81% of females bred again in the later part of the season and in his study all nine adult females, that had failed early season breeding attempts, attempted to breed again. It is unlikely that all hedgehogs have two litters a year, since some, including parous animals, do not come into their first oestrus until June or even later (Deanesly 1934). Animals born in the preceding August or September might not be ready to breed until nearly a year old, and these may account for some of the pregnancies in the second half of the breeding season (Deanesly 1934). A late litter was also recorded in the present study in a hedgehog collected as road kill. A hedgehog killed on the 6th September 2009, was in the latter stages of pregnancy with six young. In 2009, courtship was observed from April onwards and similarly juveniles were found at the site earlier than in 2008, with the first observed in July, weighing 299 g. This coincided with the month in which there were peaks in newly independent juveniles collected as road kill.

According to Doncaster et al. (2001) hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage. Becher & Griffiths (1998) examined genetic differentiation among local hedgehog populations in the UK, and found significant genetic differentiation, and restricted gene flow, among closely spaced hedgehog populations, indicating that dispersal among hedgehog populations occurs rarely. This therefore raises the question of the amount of genetic variation that exists between local populations and the effects of inbreeding. As a non territorial animal the hedgehog is largely free from the constraints of moving, to form new territories, and so may remain if there is a sufficient food and nest sites available. In the present study the late juveniles caught in 2008 were at first observed all returning to the same nest, but, as the week progressed they

gradually moved further into the 15 ha arable field and began occupying separate nests. One juvenile hedgehog was tagged throughout hibernation and for the first week after emergence in 2009, he remained in the arable field, before moving into the pasture that was occupied by all of the tagged adults. While two transient males were seen at the site in 2009 during the breeding season, all of the tagged hedgehogs remained in the study area for the duration of the study and occupied the same area each year. In the present study, a juvenile caught in 2009 occupied the same area in the first month after hibernation and then gradually made exploratory trips out of the core area. However, despite this he always returned to the central home range occupied by adults, until he was killed in June 2010. It therefore seems probable that although male hedgehogs may disperse during the breeding season, in order to encompass the range of as many females as possible, they will return to the core area of their home range if sufficient resources are available. The home range of males completely overlapped not only with one another, but also all of the adult females allowing the males to locate more females. In contrast females occupied mutually exclusive areas (Haigh 2011). In two consecutive years, the adult female whose range slightly overlapped that of another female, moved away from the core area at the end of May, before moving into the arable field in September with the other adults. In 2009, her weight and condition just prior to this time indicated that she was about to give birth, having put on 112 g. When she was next seen active (and weighed) she had lost 198 g. Jackson (2006) found that a female's mass increased by 50-150 g during pregnancy and dropped suddenly at birth. With respect to the female who was collected as road kill in the latter stages of pregnancy, the four foetuses were found to weigh 164 g in total. In the present study the movement of one of the females from her core home range area at the time she gave birth may have been a mechanism for regulating

numbers in her central home range, thereby reducing resource competition and the possibility of inbreeding. In rodents of the genus *Peromyscus*, home ranges are maintained by mutual avoidance at low densities and pregnant females will frequently abandon their home range and establish a new home range in a nearby habitat, suggesting that females are more instrumental than males in regulating recruitment (Wolff 1989).

Conclusion

This is the first record of courtship behaviour, sex biases and observations of offspring in Irish western hedgehogs. A strong male bias was observed amongst the study group, which could account for the high number of repeat pairings observed in the group, in comparison to studies elsewhere. Similar to research elsewhere in Europe, courtship behaviour was observed between April and July and males attempted to mate with multiple females. The presence of newly independent juveniles in October at the site and as road kill, indicate that, similar to the UK, late litters occur in Ireland. Little dispersal was observed amongst the study group, outside the breeding season and densities of hedgehogs at the site remained high, indicating that resources must be available to support this high density of hedgehogs.

Acknowledgements: The authors would gratefully like to acknowledge the assistance of the following people, Digger Jackson, Pat Morris, Nigel Reeve and Anouschka Hof for their invaluable advice on hedgehog research at the start of this work, Helen Bradley for all of her many hours of assistance with G.I.S. Padraig Whelan and all of the people who collected hedgehog carcasses. The Department of Environment, Heritage and local Government for granting licenses, the Crawford Hayes fund for PhD scholarship and all the staff and students in U.C.C who assisted in this study. We furthermore thank the two anonymous referees for their constructive comments. Finally this would not have been possible without the assistance of the land owners, who co-operated throughout this study.

References

- Allanson, M. 1934. The reproductive processes of certain mammals. VII. Seasonal variation in the reproductive organs of the male hedgehog. Philosophical Transactions of the Royal Society of London Series B, Containing Papers of a Biological Character 223: 277-303.
- Barrett-Hamilton, G.E.H. & Hinton M 1911-1921. A history of British mammals. Volume 2, 748 pp. Gurney & Jackson, London, UK.
- Becher, S.A. & R. Griffiths 1998. Genetic differentiation among local populations of the European hedgehog (*Erinaceus europaeus*) in mosaic habitats. Molecular Ecology 7 (11): 1599-1604.
- Christenson, T. & B. Le Boeuf 1978. Aggression in the female northern elephant seal, *Mirounga angustirostris*. Behaviour 64 (1): 158-172.
- Clutton-Brock, T. & G. Iason 1986. Sex ratio variation in mammals. Quarterly Review of Biology 61 (3): 339-374.
- Cox, C.R. & B.J. Le Boeuf 1977. Female Incitation of male competition: a mechanism in sexual selection. The American Naturalist 111 (978): 317-335.
- Deanesly, R. 1934. The reproductive processes of certain mammals. Part VI. The reproductive cycle of the female hedgehog. Philosophical Transactions of the Royal Society of London Series B, Containing Papers of a Biological Character 223: 239-276.
- Doncaster, C. 1993. The influence of predation threat on foraging pattern: the hedgehog's gambit. Revue d'ecologie (La Terre et la Vie) 48: 207-213.
- Doncaster, C., C. Rondini & P. Johnson 2001. Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. Journal of Animal Ecology 70 (1): 33-46.
- Emlen, S.T. & L.W. Oring 1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. Science 197 (4300): 215-223.
- Fisher, D.O., M.C. Double & B.D. Moore 2006. Number of mates and timing of mating affect offspring growth in the small marsupial *Antechinus agilis*. Animal Behaviour 71 (2): 289-297.

- Haigh, A. 2011. The ecology of the European hedgehog (*Erinaceus europaeus*) in rural Ireland. University College Cork, Cork, Ireland.
- Haigh, A., F. Butler & R. O'Riordan (in press). A review of techniques for detecting hedgehogs (*Erinaceus europaeus*) in a rural landscape. Journal of Negative Results.
- Jackson, D. 2006. Factors affecting the abundance of introduced hedgehogs (*Erinaceus europaeus*) to the Hebridean island of South Uist in the absence of natural predators and implications for nesting birds. Journal of Zoology 271 (2): 210-217.
- Jackson, D.B., R.J. Fuller & S.T. Campbell 2004. Longterm population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to introduced hedgehogs (*Erinaceus europaeus*). Biological Conservation 117 (2): 151-166.
- Jackson, D.B. & R.E. Green 2000. The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. Biological Conservation 93 (3): 333-348.
- Kristiansson, H. 1981. Distribution of the European Hedgehog (*Erinaceus europaeus* L.) in Sweden and Finland. Annales Zoologici Fennici 18 (2): 115-119.
- Kristiansson, H. 1984. Ecology of a hedgehog Erinaceus europaeus population in southern Sweden. University of Lund, Lund, Sweden.
- Kristiansson, H. 1990. Population variables and causes of mortality in a hedgehog (*Erinaceous europaeus*) population in southern Sweden. Journal of Zoology 220 (3): 391-404.
- Moran, S., P.D. Turner & C. O'Reilly 2009. Multiple paternity in the European hedgehog. Journal of Zoology 278 (4): 349-353.
- Morris, B. 1961. Some observations on the breeding season of the hedgehog and the rearing and handling of the young. Proceedings of the Zoological Society London 136 (2): 201-206.
- Morris, B. 1966. Breeding the European hedgehog *Erinaceus europaeus* in captivity. International Zoo Yearbook 6 (1): 141-146.
- Morris, P. 1969. Some Aspects on the ecology of the hedgehog (*Erinaceus europaeus*). University of London, UK.
- Parkes, J. 1975. Some aspects of the biology of the hedgehog (*Erinaceus europaeus* L.) in the Mana-

watu, New Zealand. New Zealand Journal of Zoology 2 (4): 463-472.

- Reeve, N.J. 1981. A field study of the hedgehog (*Erinaceus europaeus*) with particular reference to movements and behaviour. PhD thesis. University of London, London, UK.
- Reeve, N.J. 1982. The home range of the hedgehog as revealed by a radio tracking study. Symposium of the Zoology Society, London 49: 207-230.
- Reeve, N.J. 1994. Hedgehogs. Poyser, London, UK.
- Reeve, N.J. & P.A. Morris 1986. Mating Strategies in the hedgehog (*Erinaceus europaeus*). Journal of Zoology 210: 613-644.
- Riber, A.B. 2006. Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area. Acta Theriologica 51 (4): 363-371.
- Stockley, P., J. Searle, D. Macdonald & C. Jones 1993. Female multiple mating behaviour in the common shrew as a strategy to reduce inbreeding. Proceedings: Biological Sciences 254 (1341): 173-179.
- Warwick, H., P. Morris & D. Walker 2006. Survival and weight changes of hedgehogs (*Erinaceus europaeus*) translocated from the Hebrides to mainland Scotland. Lutra 49 (2): 89-102.
- Wolff, J.O. 1989. Social behavior. In: J.L. Kirkland & J.L. Lane (eds.). Advances in the study of *Peromy-scus* (Rodentia): 271-291. Texas Technical University Press, Lubbock, USA.

Samenvatting

Hofmakerij bij egels (Erinaceus europaeus) in een landelijke omgeving in

lerland en het eerste moment van geboren worden van de jongen

Wij onderzochten het verloop in de tijd van het voortplantingsseizoen van egels in Ierland: het hofmaken, het eerste moment waarop de jongen worden geboren, en het mogelijk zich verplaatsen van de jongen. Tussen juli 2008 en juni 2010 vingen we 24 egels (18 $\stackrel{\frown}{\circ}$ en 6 $\stackrel{\bigcirc}{\circ}$), die we zenderden en volgden. Het laatste deden we ook door de dieren direct achterna te lopen. Mannetjes waren oververtegenwoordigd, zowel bij volwassen als bij jonge dieren, waarbij de geslachtsverhouding bij de adulten significant afweek van 1:1. Het hofmaken vond plaats tussen april en juni en bijna uitsluitend in een negen ha groot weidegebied dat onderdeel uitmaakt van het studiegebied. Eén vrouwtje paarde in een seizoen met zeven mannetjes. De eerste jongen werden in 2008 in september waargenomen en in 2009 in juli. In juli werden de meeste jongen waargenomen (n=22), hetzij als verkeersslachtoffer of als zichtwaarneming; de sterfte onder jongen door het verkeer liep door tot in november (n=3). De aanwezigheid van jongen in het onderzoeksgebied in oktober 2008 en de aanwezigheid van een zwanger vrouwtje in september 2009 toont aan dat in Ierland late worpen voorkomen.

Received: 14 April 2012 Accepted: 26 May 2012