

Surveys of Hedgehogs in The Regent's Park, London 2014-2021

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Working in partnership with



Summary

Spring and autumn night-time spot-lighting hedgehog surveys have been carried out by volunteers in The Regent's Park since 2014. The background to these and other studies carried out on the hedgehogs, and the methods used, have been detailed in a series of previous reports (see References). The surveys have provided data on the number and distribution of hedgehogs within the Park (note: Primrose Hill was surveyed in 2015 but no hedgehogs were found; it has not been included in subsequent surveys). Here we provide an overview of the survey data collected from spring 2014 through to autumn 2021. ZSL Veterinary Services provided veterinary support and the Garden Wildlife Health Project carried out post-mortem examinations on dead hedgehogs found within the Park.

Up to 120 volunteers carried out each survey using standard methods. To carry out the surveys, the Park was divided into six zones. Each zone was surveyed by a group of five volunteers in a systematic way using torches and thermal imaging cameras in two shifts, 21.00-12.00 and 00.30-04.00, on each of two successive Friday nights in each survey. A seventh zone, the grounds of London Zoo, was surveyed by zoo personnel. The survey programme was interrupted in 2020 when no survey was carried out in the spring because of Covid-19 lockdown restrictions. In the autumn of that year, it was possible to carry out the survey but with modifications to the standard protocol. This resulted in the survey effort being slightly different and lower than normal and the data collected should be treated with caution. Each hedgehog captured was uniquely marked with six yellow numbered plastic sleeves attached to the spines on the back of the neck. They were sexed, weighed, and examined for ectoparasites and injuries. Sick or injured hedgehogs were examined by the vets and either released back into the Park after treatment or euthanised if the injuries were severe. An analysis of the small number of hedgehogs that missed being captured in a survey but known to be alive from prior and subsequent capture, has provided encouragement that the survey method adopted has been efficient at sampling the hedgehog population at the times they were carried out.

The population of hedgehogs in the Park over the period 2014 to 2021 has been small averaging 26 individuals known to be alive at the time of each survey. However, numbers fluctuated from year to year and season to season. In all but the last year, 2021, autumn numbers have been higher than spring numbers because of recruitment of young from summer/autumn breeding. There have been two population lows during the study. The first was in spring 2016 when the population dropped to 12 individuals, 10 of which were females; the population recovered by the following season. It should be noted that generally the adult sex ratio was skewed towards females, particularly when numbers were low. The second low point in the population was autumn 2021 when only 11 individuals were captured, six females and five males. It remains to be seen whether some hedgehogs eluded capture at this time. Whether this small population can recover as in 2016 will not be known until the surveys are carried out in 2022.

On average, adult female hedgehogs were slightly heavier than males and autumn adult females and males slightly heavier than spring females and males; in general, the hedgehogs captured appeared to be in good body condition.

Breeding success varied from year to year and was particularly low in 2015 (three juveniles captured) leading to the low spring population the following year. Breeding success was also low in 2021 (four juveniles). In other years recruitment was moderate (range 6-15 juveniles) and unremarkable, except for 2017 when it was relatively high (21 juveniles).

The difference between the loss of hedgehogs during summer (between spring and autumn surveys) and winter (between autumn and spring surveys) was small. For the whole study period, summer loss averaged 10.4 hedgehogs per year and winter loss 12.5 hedgehogs per year. There were differences between years and particularly noticeable were the lower-than-average losses over the summers of

2016-2018, and higher losses over the summers of 2014, 2015, 2019, 2021. There were also high losses over the winter 2014-2015, 2017-18 and 2018-19. An overall pattern was observed in that the higher the total number of individuals in the population at the start of a season, the more individuals were lost.

A similar positive relationship was found between the numbers of male and female hedgehogs that persisted (survived) over winter and the total number present in the autumn. Such relationships were not observed over the summer. There was a difference between the sexes in that persistence was consistently better in females than males. Otherwise, persistence varied between seasons and years without discernible pattern. Net persistence (the difference between the numbers that persists and the numbers than are lost) was positive over some seasons and negative over others such that the numbers of individuals in the population fluctuated from season to season and year to year around a low average level. Average persistence or survivorship was looked at by pooling the data across all years. Seventy per cent of males and 52% of females disappeared within one year, and 91% of males and 81 % of females within two years. No individuals captured in the autumn so far have persisted for four years. Because many hedgehogs captured in the autumn surveys were at least 6 months old or older, a further persistence analysis was carried out on just the juvenile hedgehogs captured in the autumn; these individuals would have been weaned in the summer or autumn. Apparent mortality was high in this cohort of animals with about 80% of females and 83% of males disappearing within the first year. Thereafter, few individuals survived to three years of age. Critically these analyses show that the persistence or survivorship of hedgehogs in The Regent's Park is poor and appear to be much lower than reported in other studies where some individuals may live for 6 or more years.

Between the start of the surveys in 2014 and 2021, zoo or park staff, members of the public and volunteers have found 81 hedgehogs that were dead or so badly injured such that they have been euthanised by the vets. This group of dead animals includes 22% of the 175 individual hedgehogs tagged since 2014. Most dead hedgehogs were found in summer and fewest in autumn. Where the cause of death has been identified, 43% of adults and 95% of juveniles are believed to have been killed or badly injured by predators. The main injuries in these instances were broken or severely damaged hind legs. Foxes are almost certainly the chief culprits although dogs cannot be ruled out. Other deaths include road kills, lung infections, ear infections and drowning. For such a small population, these numbers are high especially since many deaths must go undetected. Also, we are unable to account for deaths of young animals in the nest, before they begin to forage independently.

The distribution of captures within the Park has been patchy and has shifted over the eight years of study. In the beginning, in 2014 and spring 2015, there were many captures to the west, south and north-east, including the Zoo Car Park. Elsewhere, there were low numbers of captures including few on or around the sports pitches in the mid-northern part of the Park. Then the situation changed quite quickly over the summer in 2015. Hedgehog captures dropped dramatically in the south and west and these areas have never recovered; captures between 2016 and 2021 have been few and sporadic. Between 2016 and 2020 there was a modest increase in captures on or around the sports fields as the north-east continued to be a stronghold. However, captures in the Zoo Car Park declined over this period such that no hedgehogs have been found there in the last two years of the study. In 2017, a part of the Zoo Car Park was requisitioned by Thames Water to replace a major water main, and more recently by HS2 as a lorry holding area during the building of the high-speed rail line out of Euston. Although these works may have affected animals in the area, it is unlikely that they are entirely responsible for the loss of hedgehogs. The Royal Parks, ZSL and Nigel Reeve continue to liaise with the ecologists at HS2 on the impacts of their works in the Zoo Car Park and mitigations. A second major shift in the distribution of captures occurred recently, 2020 and 2021. Numbers of captures have dropped markedly in the north-east with relatively more captures in the north of the Park and in the grounds of the Zoo. From 2015, 10 cm holes cut in the boundary fence to the Zoo have facilitated the movement of hedgehogs into and out of the Zoo grounds, which appears to have taken on greater importance recently.

The major shifts in distribution in 2015 and 2021 occurred at times when the population declined and clearly there are links between distribution and abundance. The reasons for these changes are not clearly understood although further analyses are being carried out. Based on area and habitat available, it is not clear why the Park doesn't hold three or four times the number of hedgehogs than it has done in recent years. It is also not known why hedgehogs do not persist or survive for very long or why females fare slightly better than males. In truth, it is likely to be a combination of factors that is preventing growth and limiting distribution in this population.

The population of hedgehogs in The Regent's Park is isolated, small and has been fluctuating around a low level for several years. Quite simply, it is susceptible to extinction by chance at any time. It remains to be seen whether the population can recover from the very small numbers in autumn 2021. The plan is to continue the surveys for a further two years and then take stock, but the precarious state of the current population warrants more urgent discussion as to whether other conservation actions can and should be done.

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1. Background

Research on the hedgehogs in The Regent's Park, the last known breeding population of hedgehogs in central London, started in 2014 with the objective of obtaining data to develop an evidence-based conservation strategy for this important but vulnerable population. So far there have been four reports written summarising this research, in 2015, 2016, 2017, 2021 (see References).

Since the beginning of the studies, a six-monthly volunteer spotlighting survey of the Park has been carried out every year. This report updates the results from these surveys through to 2021. As a result of national Covid-19 restrictions in 2020, only the autumn survey was carried out and with a slightly modified survey method.

The hedgehog studies have involved a productive partnership between The Royal Parks and the Zoological Society of London (ZSL), and other organisations including the Garden Wildlife Health project, People's Trust for Endangered Species Wildlife Trusts, and the Central Royal Parks Wildlife Group. Community engagement has been vital to the success of the studies, which has involved recruiting and training many volunteer fieldworkers.

2. Aims of the surveys

The aims of the surveys reported here were:

- 1. to carry out standardised spotlighting surveys of hedgehogs in both May (spring, pre-breeding) and September (autumn, post-breeding) each year to estimate the distribution and population size of hedgehogs in The Regent's Park (not including Primrose Hill).
- 2. to work with ZSL to investigate and record causes of deaths and injuries of hedgehogs found in the Park.
- 3. to support ZSL and The Royal Parks in negotiating with HS2 to mitigate the impacts of works to the Zoo Car Park area.
- 4. to engage volunteers, the local community and other stakeholders in the work.

3. Project partners

The Regent's Park Hedgehog Research Project is indebted to a generous gift from The Meyer Family which supported the work during the first years of the project. A dedicated hedgehog fund was established in 2017 that ensures funding for the project through to 2024. This project is a partnership between the following organisations and individuals:

The Royal Parks is the charity that cares for London's eight Royal Parks (registered charity 1172042). Former project leads were Clare Bowen, Ledy Leyssen, Marion Buggins, Sara Harrison and Tess Pettinger whilst the current lead is Bryony Cross.

The Zoological Society of London (ZSL), founded in 1826, is an international scientific, conservation and educational charity whose mission is to promote and achieve the worldwide conservation of animals and their habitats. ZSL provide veterinary support during the surveys in May and September each year. The Horticulture Manager, Sven Seiffert, provides guidance, volunteer support and organises the surveys in the Zoo grounds (15 ha). The project team liaises with Dr Chris Carbone and Dr Marcus Rowcliffe, Senior Research Fellows at the Institute of Zoology, concerning camera trapping foxes and hedgehogs within the Park and elsewhere in London.

The Garden Wildlife Health project (GWH), co-ordinated by the Institute of Zoology in partnership with the British Trust for Ornithology, Froglife and the Royal Society for the Protection of Birds, conducts post-mortem examinations and reports on any dead hedgehogs found within the Park.

The Central Royal Parks Wildlife Group of amateur and professional naturalists and ecologists with an interest in the wildlife within the Central Royal Parks originally identified the need for a hedgehog survey in The Regent's Park and have subsequently provided guidance and volunteer support in the field.

The 'Hedgehog Hero' volunteers. Each period of fieldwork was supported by a team of more than 100 fantastic volunteers, many of them were repeat volunteers, consisting of individuals with a wide range of backgrounds but sharing a keen interest in wildlife and conservation. A number of experienced volunteers again acted as Volunteer Supervisors, leading small teams in the field during the fieldwork.

4. Survey organisation

4.1 Survey dates 2021

The survey methods used in 2021 were as in previous years (see previous reports) This involved two all-night sessions of intensive spotlighting in May (spring), after the hedgehogs had emerged from hibernation and become sexually active, and two in September (autumn), after breeding and after the majority of youngsters will have left the maternal nest, and prior to hibernation. Hedgehogs were hand captured, tagged and released.

The dates were:

Spring - 21/5/21 and 28/5/21

Autumn – 3/9/21 and 10/9/21

4.2 Survey zones

For the purposes of the survey, the Park (160 ha), was divided into the seven zones as in previous years. Primrose Hill (Zone 8) was surveyed in 2015 but no hedgehogs were captured. It has not been surveyed since and the 2015 results are not included here. Zone 2 (Cumberland Green, Gloucester Green and Zoo Car Park) was searched in two sections, 2a and 2b (Figure 4.1). Zone 1 was also divided into two sections, 1a and 1b. Areas of the Park not accessed during the surveys include Winfield House, The Holme and St John's Lodge. Access to the Regent's University was granted from 2017. Park Square Gardens (Crown Estates Paving Commission) and the Open Air Theatre (OAT) were surveyed in 2018 and 2019.



Figure 4.1 Aerial view of Regent's Park (160 ha) showing boundaries of the survey zones and walk routes (dashed lines). Areas shaded yellow had limited access or no access. OAT=Open Air Theatre.

4.3 Surveyors

Spotlighting surveys were carried out by volunteers organised by the Royal Parks' team; many of the volunteers were regulars. There were 111 volunteers in May 2021 and 112 in September 2021. The Zoo (Zone 7) was surveyed by zoo personnel as in previous years (see 2017 report). The Royal Parks Volunteer Manager liaised closely with volunteers and managed the scheduling timetable. Volunteer training sessions were held in Regent's Park in the week before each survey period where each volunteer received a comprehensive survey guide including a detailed risk assessment.

4.4 Veterinary support

The Veterinary Services team at ZSL were on standby during all periods of fieldwork. Hedgehogs that appeared unwell or injured were boxed and delivered to the vet team on site at ZSL. If a hedgehog could be treated, it was released back into the Park or placed with an experienced hedgehog carer, Sue Kidger. As well as sick or injured hedgehogs being found during the surveys, zoo or park staff and members of the public report sightings of dead or sick hedgehogs. Where possible, these hedgehogs were retrieved. All dead hedgehogs were submitted to the Garden Wildlife Health (GWH) project

based at ZSL's Institute of Zoology. GWH vets conducted a detailed post-mortem examination on each animal, and where possible, established a cause of death and any significant underlying conditions. A full tissue archive was retained from each case for further studies as required.

5. Survey methods

The survey methods used in 2021 were the same as those established in 2016, which were modified slightly from the methods used in 2014 and 2015 (see 2016 report). No survey took place in spring 2020 and the survey in autumn 2020 was slightly modified because of Covid-19 restrictions.

5.1 Spotlighting, using torches and thermal imaging cameras (TIC)

Survey groups typically consisting of five volunteers carried out systematic nocturnal searches along established routes within each of the survey zones (Figure 4.1). There were two shifts, 21.00-12.00 and 00.30-04.00, on each of two successive Friday nights in each survey. Hedgehogs were detected by sound (rustles in undergrowth or noises made during courtship or fighting) or with the aid of bright LED Lenser torches. Each group (except Zone 7) also used a high specification thermal imaging camera (TIC). The cameras used were FLIR E60s, or similar more recent models, and their set up and operation are described in Bowen *et al.* (2020). The method of searching by the groups is described in previous reports.

In autumn 2020, it was possible to carry out the survey but with modifications to the standard protocol because of Covid-19 restrictions. Essentially, only six volunteers were allowed in the Park at any one time. In consequence, the six zones were divided into three groups of two, and each of two zones were surveyed by three volunteers over three consecutive nights (Friday, Saturday, and Sunday). This procedure was repeated the following weekend. The survey effort therefore was slightly different and lower than normal, and the data collected should be looked at with this in mind.

Hedgehogs that were found were individually marked with 10 mm lengths of yellow plastic spine sleeves with pre-printed numbers as described by Reeve *et al.* (2019). Six sleeves, each with the same ID number, were glued to spines at the back of the neck using superglue; these were topped up to six on recapture if any had been lost. For each hedgehog captured, its GPS location, sex, weight, circumference, ectoparasitic load, general health, and the habitat in which it was found were recorded on a proforma. The location of the hedgehog was also recorded on a map as were incidental fox sightings.

5.2 Data handling

Location records are presented on Google Earth Pro maps and data analysed using Excel, Xlstat, Minitab and Ranges software. Distribution maps are presented for the years 2019-2021, habitats used for 2016-2021 and maps of fox sightings for 2019-2021. In all other respects the analyses of population demography and distribution according to survey zone are presented for the entire study period, 2014-2021. Hedgehogs <=700 g in weight captured in the autumn surveys have been termed juveniles, unless marked in a previous survey. The term persistence has been used rather than survival to describe how long hedgehogs remain in the surveyed population because of a lack of information on whether animals that 'disappeared' have died or simply not been captured. Sample sizes are small and life history measures (e.g. productivity, persistence) reported as proportions should be treated with caution. The number of hedgehogs found dead or euthanised each year are reported. Hedgehogs with severe injuries to their hind limbs, or with obvious bite marks elsewhere have been interpreted as predation. The numbers of hedgehogs in the population at the time of a survey have been presented as the minimum number known to be alive (MNA) based on the number of individuals captured plus the number of marked individuals not captured but were found before and after the survey. No

surveys were carried out in spring 2020 because of Covid-19 restrictions and the surveys carried out in autumn involved slight variations to the normal protocols, and these findings must be treated with caution. Pearson's correlation coefficient has been used as the measure of association between two variables when the variables are normally distributed. However, for all correlations where the sample size is <10, Spearman's correlation coefficient has been used. Lines of best fit have been drawn on correlograms as an aid to visual interpretation and do not imply dependence.

Information collected on methods of detection and detection distances (see Bowen *et al.* 2020), longevity of animal markers (see Reeve *et al.* 2019), time of capture during the survey nights and the nest box survey are not reported here (see previous reports).

6. Results

6.1 Population dynamics

6.1.1 Numbers of individuals

The first survey was carried out in spring 2014. From autumn 2014 onwards a few individuals that were marked prior to a survey were 'not captured' in that survey but captured subsequently, and it was females rather than males that generally fell into this category. Between Autumn 214 and Spring 2021 an average of 1.08 females (SD = 0.862, N = 13) were 'not captured' per survey, and 0.15 males (SD = 0.376, N = 13). Nine individuals missed capture in one survey, two individuals two consecutive surveys and one female (#164) was captured in Spring 2017, Spring 2019, Autumn 2020 and finally Spring 2021 missing capture in four surveys¹. This evidence shows that few marked hedgehogs available to be captured in the population prior to a survey, failed to be captured in that survey and suggests that the survey methods were reasonably efficient at finding marked animals.

Between Spring 2014 and Autumn 2019 the average minimum number of hedgehogs alive (MNA) in each survey was 28. This dropped to 26 if the surveys for 2020 and 2021 are included. More individuals were captured in autumn, as young were recruited into the population, than spring in all years except 2019 (Figure 6.1). In spring 2016, there was a low MNA of 12 individuals. In this instance, numbers subsequently recovered by the autumn. No survey was carried out in spring 2020. Thereafter numbers declined from Autumn 2020 to a low of just 11 individuals captured in Autumn 2021².

Except for autumn 2017, fewer adult males than females were captured in all surveys (Figure 6.2). There was also a positive but non-significant association between the adult sex ratio (M/F) and MNA ($r_{15} = 0.54$, P = 0.37; Figure 6.2). The adult sex ratio for autumn 2021 based on very small numbers is out of line with the other results; if this point is omitted, the association between sex ratio and MNA is strengthened, $r_{14} = 0.72$, P = 0.004.

6.1.2 Recruitment

From the autumn surveys, there is evidence that breeding took place every year. The largest number of juveniles captured, and the largest number of juveniles captured per adult female captured was in autumn 2017 suggesting a good recruitment year. In contrast, the fewest number of juveniles captured and the fewest juveniles per adult female captured was in autumn 2015 prior to the

¹ No survey was carried out in Spring 2020.

² It should be noted that a slightly different survey methodology was used in Autumn 2020 (see Methods).

population low in spring 2016 (Figure 6.3). Apart from 2014 the numbers of juveniles per adult female captured in the autumn in the remaining years were quite low, ranging between 0.55 and 1.00. These are minimum numbers because it is possible that young from some autumn litters were too young to be captured at the time of the autumn surveys. Even so, recruitment seems low in comparison to that in a Swedish study in which the average numbers of independent surviving juveniles in the population each year varied between 1.33 and 4.13 per adult female (Kristiansson, 1990).

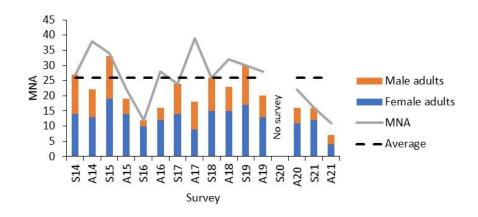


Figure 6.1 Minimum Number of hedgehogs known to be Alive (MNA) at the time of each survey (season-year). The average is the long-term average MNA = 26.

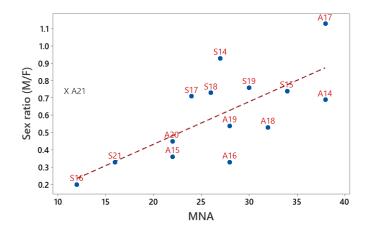


Figure 6.2 The relationship between adult sex ratio and the Minimum Number of Individuals Alive (MNA) at each survey. A = Autumn, S = Spring - followed by year. The dashed line is the line of best fit. Outlier X A21 = Autumn 2021 when 3 adult males and 4 adult females were captured giving a sex ratio of 0.75; the MNA was 11.

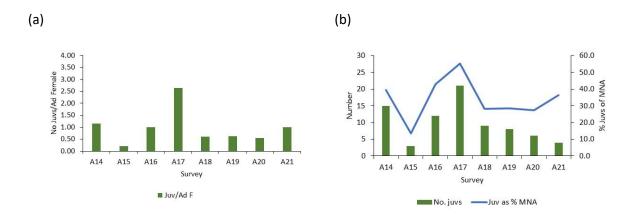


Figure 6.3 (a) Number of juveniles captured per adult female in the autumn surveys, (b) Number of juveniles captures and the per cent of juveniles of MNA in each survey.

6.1.3 Seasonal loss of hedgehogs from the population and persistence

On average each year 10.4 individuals disappeared or were lost from the population over summer between spring and autumn (CV = 65%, N= 7) and 12.5 individuals over winter from autumn to spring (CV = 41%, N = 6). However, numbers lost varied across years and according to season and were positively related to the numbers of animals in the population at the start of the period (Figure 6.5). The data has been broken down into the loss of males and females over summer and winter (see Appendix Figure A2). Here can be seen that there is a positive association between loss of males and MNA over the winter period ($r_7 = 0.96$, P = 0.007).

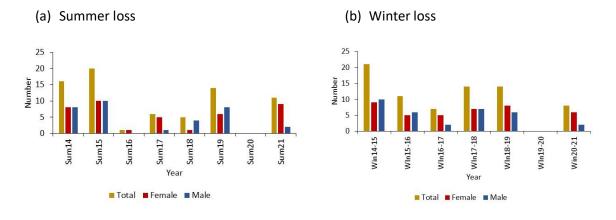


Figure 6.4 Hedgehogs lost from the population during the summer and winter each year. No survey was carried out in spring 2020.

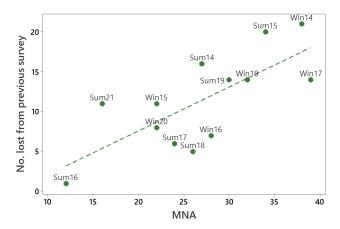


Figure 6.5 The relationship between the total numbers lost over each summer (Sum) and winter (Win) seasons and MNA at the start of the season. The dashed line is a line of best fit. Pearson's correlation coefficient for all seasons, $r_{13} = 0.74$, P = 0.004.

The complement to numbers lost between seasons is persistence. Generally seasonal persistence is slightly higher and more consistent in females than males (females - summer: mean = 7.7, CV = 36%, range = 3-11, winter: mean = 10.0, CV = 20%, range = 7-13, N = 6; males – summer: mean = 4.9, CV = 52%, range = 2-9, N = 7, winter: mean = 6.0, CV = 46%, range = 2-9, N = 6 (Figure 6.6). Few males persisted over the winter period 2015-2016 and summer 2016, and few males and females persisted over the summer of 2021. Generally, there is a positive relationship between summer and winter seasonal persistence for both males and females and the number of hedgehogs known to be alive at the start of each season (Figure 6.7). Correlations are weak and insignificant for summer persistence in males and females but stronger and significant in both sexes over winter (Figure 6.7).

The persistence of cohorts of all males and females captured each autumn, and for all years are shown in Figure 6.8(a) males, and Figure 6.8(b) females. Because of small numbers, no distinction is made between adults and juveniles. Numbers drop quite steeply over the first year and then more slowly over the next one or two years. The variation in persistence among cohorts is small but females appear to have a slightly higher persistence than males. Pooling the data shows that over the course of the study, 30% of males and 51% of females persisted for one year and 9% and 20% for two years respectively. Few hedgehogs persisted for three years (Figure 6.8(c). The longest persisting animal was female #164 mentioned in section 6.1.1. This hedgehog was first captured in spring 2017 and last captured in a spring 2021 and if the spring data are included, it survived for a minimum period of four years.

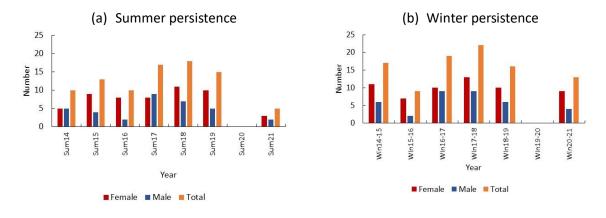


Figure 6.6. The persistence of hedgehogs over the summer and winter each year. No survey was carried out in spring 2020. The y axis scale is the same as Figure 6.4.

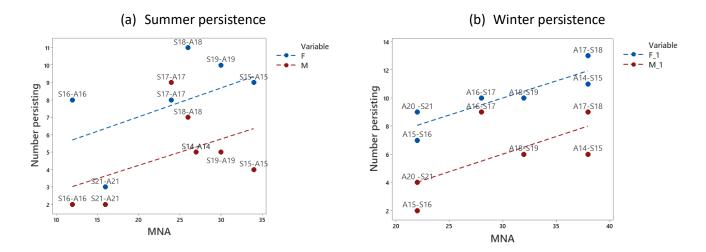
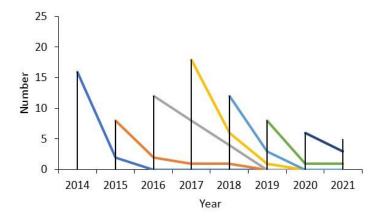
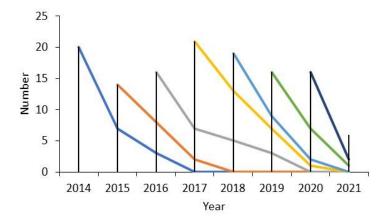


Figure 6.7 The relationship between persistence of each sex over (a) summer and (b) winter seasons and MNA at the start of the season. F = Female, M = males. The dashed lines are lines of best fit. Spearman's correlation coefficients (a) Females r_7 = 0.46, P = 0.304, Males r_7 = 0.46, P = 0.299, (c) Females r_6 = 0.88, P = 0.020, Males r_6 = 0.97, P = 0.001. (d)

(a) Males



(b) Females



(c) Persistence curves

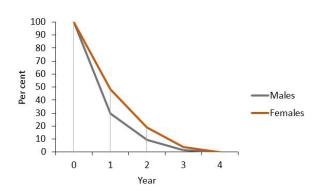


Figure 6.8 Persistence of cohorts of individuals captured each Autumn, irrespective of age. (a) Males, (b) Females, (c) Persistence curves for 2014-2019 combined data.

The curves in Figure 6.8 are not strictly equivalent to traditional survivorship curves. They are based on autumn data, and recaptured individuals will have appeared in the cohorts of previous years. If not marked the hedgehogs may already have survived for six months or more and endured a period of high mortality that occurs in very young age classes. To look more closely at 'survivorship', Figure 6.9 follows the fate of 32 male and 34 female juveniles captured in the autumn, pooled across the study. This is equivalent to a cohort life table (Townsend *et al.* 2003). Females persist slightly better than males, but there is a very steep decline over the first year in both sexes with, as above, few animals persisting for three years. For comparison Figure 6.9 also shows post-weaning survival data from Morris (1969) based on the shrinkage of successive age classes at a specific time: a static life table. Although the data have been obtained in different ways, persistence, or survival of hedgehogs in The Regent's Park is poor and inferior to those in Morris' study across all age classes. A small number of individuals in the latter study survived to 6 years old.

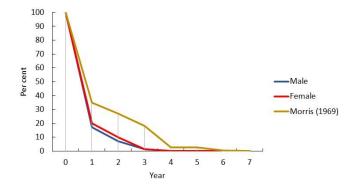


Figure 6.9 Persistence of cohorts of juvenile male and females captured each Autumn for 2014-2019 combined data and post-weaning survivorship curve for a combined sex sample of 244 UK hedgehogs (Morris 1969)

6.1.4. Deaths

Eighty-seven hedgehogs were found dead or injured in the Park during the study. Six injured animals were treated by the vets; two were rehomed with a carer and four released. All the others were found dead or euthanised by the vets if their injuries were severe, for example if they had serious leg injuries. For some deaths, information on sex, age, whether marked and precise location where found are not known. Also, in some cases, the cause of death has not been established but in in the others death has been attributed to roads, predators, leg injuries or a variety of other factors (e.g., disease, drowning) (Figure 6.9). It is believed that most leg injuries result from bites by predators (foxes, maybe

dogs) and in the summaries of the data presented here the results for predation and leg injuries have been combined (Figure 6.9, Table 6.1). Overall, 57% of deaths have been attributed to predators/leg injuries (Figure 6.9), 41% adults (N=40) and 95% juveniles (N=21, Table 6.1). Slightly more deaths have been recorded in summer than spring, with fewest in the autumn (Table 6.1, Figure 6.10). Most adult predation was recorded in the summer, but similar numbers of juveniles were predated in summer and autumn (Table 6.1).

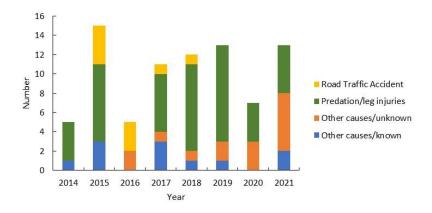


Figure 6.9 Number of known deaths reported in the Park each calendar year.

Table 6.1. A summary of known deaths according to age and season.

Age	Season	C - Other causes/known	O - Other causes/unknown	P - Predation/ Leg injuries	RTA - Road Traffic Accident	Total
Adults	Spring	1	2	0	0	3
	Summer	3	4	12	3	22
	Autumn	4	2	5	4	15
Juveniles	Spring	0	0	0	0	0
	Summer	0	0	11	0	11
	Autumn	1	0	9	0	10
Unknown	Spring	1	2	3	0	6
	Summer	0	4	4	1	9
	Autumn	1	1	2	1	5
Total		11	15	46	9	81

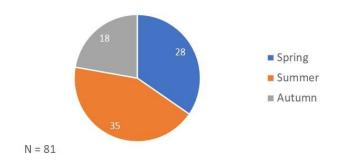


Figure 6.10 Deaths recorded according to season.

Ninety-three per cent of adults and 11% of juveniles were tagged. Over the course of the study, 175 individuals have been tagged and released, of which 22.3% have been found dead. An approximate (minimum) age of the tagged individuals that died has been calculated from time of first capture to death (Appendix Figure A2). The median age at death was 348 days (IQ range = 628, N = 43). The maximum age was 1294 days.

6.1.5 Body weight

Mean body weight of adult hedgehogs varied from year to year and season to season (Figure 6.11). No particularly pattern can be detected in Figure 6.11 except for low mean body weights in males in spring 2016 and to a lesser extent in both males and females in spring 2015. However, some insights can be found by considering body weights of males and females in spring and autumn averaged over the study. There is no significant interaction between sex and season (Figure Appendix A3) or between males and females ($F_{1,282} = 3.23$, P = 0.074) even though females are slightly heavier than males within each season. However, the difference between body weights in spring and autumn is significant ($F_{1,282} = 37.42$, P < 0.001; mean weight of all animals in spring = 843 g, SD = 160.8 g, N = 161, in autumn mean = 958 g, SD = 125.0 g, N = 125) (Figure 6.12).

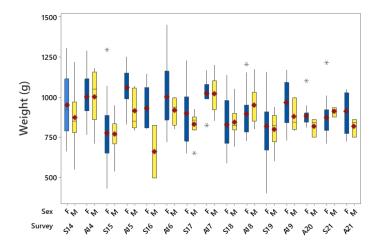
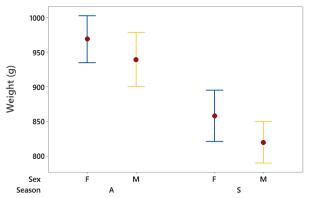


Figure 6.11 Box plots of adult female (blue) and male (yellow) hedgehog body weights. Blue/yellow boxes represent the inter-quartile ranges, whiskers = highest and lowest values, * = outlier, red diamonds = mean values, F = female, M = male Survey = season (S = spring, A = autumn) and year. No survey was carried out in spring 2020.



Individual standard deviations are used to calculate the intervals.

Figure 6.12 Interval plot for adult body weights showing the means and 95% confidence limits for males and females in spring (S) and autumn (A). F = female (blue), M = male (yellow).

6.2 Distribution of captures

6.2.1 Captures 2019-2021

In the spring and autumn of 2019, most captures occurred in the north-east section of the Park, especially in zone 2 (Figure 6.13; see Figure 4.1 for zone map). There were a few captures to the west but none to the south. No survey was carried out in spring 2020. In autumn 2020 the distribution of captures had changed with few captures in zone 2. There was a general scattering of captures across the Park with many on and around the sports pitches and to the south-west of the zoo (zone 7). It is possible that many of the captures outside the boundary to the zoo grounds were of animals that had moved out of the zoo to forage in the Park. It is also noticeable that there were some captures in zone 1 to the south in autumn 2020 representing two animals: a male and a female. No captures occurred in this area in 2019 or 2021.

The location of captures within the Park is not the whole story since most individual hedgehogs will be captured more than once within a survey. The mean number of captures per individual in spring 2019 was 2.7 (SD = 1.58, N = 15) and 2.5 (SD = 1.04, N = 11) in autumn 2021. Minimum convex polygons (MCP) joining the outer points of capture points for each individual are shown in Appendix Figure A4.

6.2.2 Captures within survey zones 2014-2021

Since the beginning of the study in 2014 there has been a considerable shift in the pattern of distribution of captures, and this has been described in some detail in previous reports (Figure 6.14). This can be most easily demonstrated by considering captures within survey zones. In 2014 and spring 2015, Zones 1, 2 and 5 were described as 'hot spots' where most of the hedgehogs were captured (see earlier reports). Between spring and autumn 2015, there was a dramatic loss of captures in zone 1 and to a lesser extent in zone 5. Zone 1 has never recovered and zone 5 has had only few captures since. In contrast, captures in zone 2, increased and remained a "hotspot" until autumn 2020. The Zoo Car Park is within zone 2a and was a "local hotspot" in 2014 and 2015 with 25% of all captures occurring in the Car Park in autumn 2014 and 20% in spring 2015³ (Figure 6.15). No hedgehogs were found in the Car Park in 2000 and 2021. Starting in 2014 there has been considerable disruption to the habitats in the Car Park with major works involved during the replacement of water mains and the construction of a Lorry Holding Park for the HS2 project at nearby Euston Station (see details in 2017 Report).

In other parts of the Park, captures in zone 3 have increased since the start of the study. Numbers of captures in zone 4 have rather fluctuated and captures in zone 6 and the zoo grounds (zone 7) remained low until the autumn of 2020 and spring and autumn 2021 when increased (Figure 6.14).

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³ The Zoo Car Park was not surveyed in spring 2014.



Figure 6.13 Distribution of captures during each survey between 2019 and 2021.

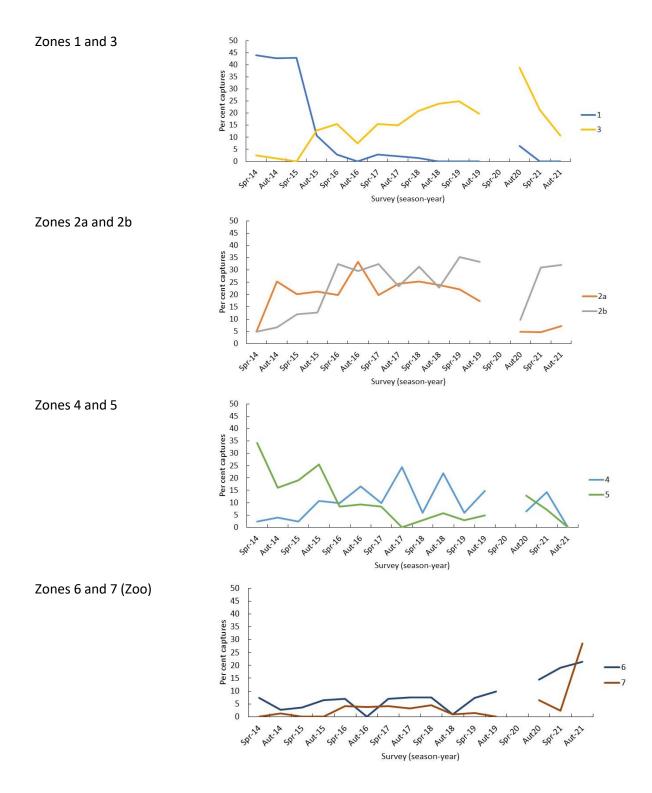


Figure 6.14 Per cent of captures in each zone for spring and autumn surveys, 2014-2021. No survey was carried out in spring 2020. Plotted as lines for illustrative purposes only. The Zoo Car Park in Zone 2 was not surveyed in spring 2014.

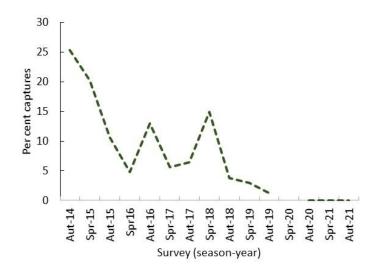
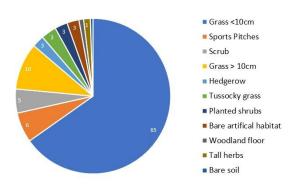


Figure 6.15 Per cent of all captures in the Zoo Car Park

6.3 Habitat

Over the course of the study since 2016, two thirds of captures occurred in short grass (grass < 10 cm high) (Figure 6.16(a). Ten per cent of captures occurred in grass >10 cm high, six per cent on the sports pitches and five per cent in scrub. Captures in the other habitat categories were relatively few. Figure 6.16(b) provides a further breakdown of the top four habitats according to survey. The most noticeable observation is that a change appears to have occurred between autumn 2019 to autumn 2020. An average of 69% of all captures occurred on short grass between 2016 and 2019, but this dropped to 42% in 2020 and 2021. In the latter period there was an increase in captures on the sports pitches (particularly autumn 2020) and taller grass (grass >10 cm high) in spring and autumn 2021.

(a)



(b)

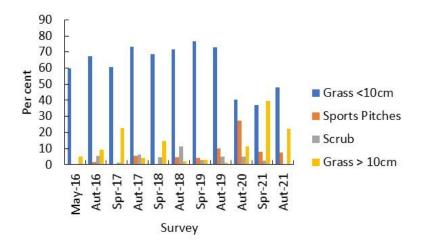


Figure 6.16 (a) Pie chart of the percentage of captures according to habitat for all surveys combined between spring 2016 and autumn 2021. Total number of captures = 719. (b) Per cent captures in the four most used habitat-types from (a) according to survey.

6.4 Foxes

The location of foxes seen by the volunteers are recorded during the night-time surveys. Results from 2019- and 2021 are shown in Figure 6.17. Essentially, foxes are seen throughout the Park although numbers of observations in the east (especially zones 1 and 2) have been more numerous than those in the west (zones 5 and 6).



Figure 6.17 Fox sightings during the surveys in 2019-2022.

7. Discussion

In this report, many of the demographic parameters have been based on the minimum number of hedgehogs known to be alive (MNA) at the time of a survey. This has involved considering individuals captured prior to or after a particular survey but not during that survey, i.e. they missed being captured. In fact, the numbers of individuals that missed being captured were few, were mainly females (mean individuals per survey: female 1.08, male 0.15), and they rarely missed being captured on two or more occasions. These figures provide encouragement that the survey methods used are efficient in catching most of the hedgehogs within the Park at the time the surveys were carried out. Realistically, hedgehogs may 'appear' and 'disappear' between surveys and not be accounted for, such as young born late in the season and not yet foraging outside the maternal nest when the autumn survey takes place in September. The average time between spring and autumn surveys, the summer period, was 111 days (SD = 4.8, N = 7), and autumn and spring surveys, the winter period (253 days, SD = 2.9, N = 6). Winter includes the hibernation period which normally occurs between the months of October and April but can vary in length with activity continuing late into November and awakening occurring as early as March (Reeve 1994). Nothing is known about hibernation or the effects of food availability, weather and climate warming on the hedgehogs in Regent's Park. Unfortunately, the twice a year, standard survey programme was interrupted because of Covid-19 restrictions; no survey was possible in spring 2020 and there were slight changes to the standard methodology in autumn 2020. Regent's Park was open to the public during Covid-19 lockdown and had many visitors, although outdoor venues such as cafes were closed. There is no clear reason why the hedgehog population should be affected by these events. However, even though its likely just a coincidence, numbers have declined since 2020 and there have been some changes in the distribution of individuals and the habitats in which they were found.

7.1 Population dynamics

Studies on the hedgehog population in Regent's Park have been ongoing since spring 2014, a period of eight years. During this time the size of the population has been small, fluctuating around a value of 26 individuals. It dropped to a low of 12 individuals in spring 2016 but recovered within a year. However, numbers have fallen again recently to very low numbers in autumn 2021 and it remains to be seen whether the population can recover this time.

The hedgehog population in the Park is believed to be isolated from other hedgehog populations in London, such as the one at Hampstead Heath to the north (see previous reports). Even so, there does not appear to be any known reason why the population is not larger. According to the area and nature of the habitat available, it is estimated that the Park could hold three or four times the average number. A larger population would be more resilient to environmental and demographic variation and catastrophic events. It is possible that inbreeding depression resulting from the small population may be causing the population to further reduce its size (the so-called extinction vortex) although there is little direct evidence for this. All these points have been discussed in previous reports (see References at end) and will not be reiterated here but it should be noted that simply bringing in hedgehogs from elsewhere to reinforce the population could incur significant risks to both the residents and those translocated into the park (see 8. below).

From the most recent surveys in 2021 it is possible that the population is so small that it will not recover. Demographic uncertainty is a key issue for small populations whereby random variations in reproduction and/or survival during the year could be critical, especially in the face of environmental uncertainty such as changes in food availability or seasonally unfavourable weather. The expectation is that autumn populations will be larger than spring populations because of recruitment from summer/autumn breeding. Excluding 2020 when the surveys were affected by Covid-19 restrictions, this pattern was observed throughout the study up until most recently when the very small numbers in autumn 2021 were lower than spring 2021 numbers.

For the closed population to grow, recruitment must exceed losses. There is evidence that breeding has taken place in each year of the study, including 2021, but at no time has the population exhibited a sustained period of growth over two years or more. Recruitment is affected by the number of adult females that breed, the size of litters and the survival of young through infancy to become independent members of the population. It is noticeable that 10 of the 12 hedgehogs in the population at the time of the low in spring 2016 were females providing a reasonable basis for breeding during the summer and autumn and subsequent population recovery. Of course, this requires the two males to court and mate with many of the females. Generally, hedgehogs are promiscuous, and males tend to expand their home range in the spring and summer looking for mating opportunities. In 2016, the population did recover, and we can assume the males did mate with several females. The spring 2016 the adult sex ratio was very skewed towards females, but in general the adult sex ratio of hedgehogs in Regent's Park has been biased towards females. The sex ratio becomes more skewed towards females as population numbers decline reflecting differences in persistence between males and females; this is considered below. The situation in autumn 2021 is different in that only six females, and five males were captured. It remains to be seen how these individuals overwinter and how many will be alive in spring to breed in 2022.

In last year's report, it was estimated that only about 20% of potential offspring born during the summer in Regent's Park were captured in the autumn survey. This was rather a crude estimate, but for the sake of argument, if a typical hedgehog litter size is between 4 and 5 (see Reeve 1994), then about one individual would survive from each litter. Thus, for the population to grow, and to include males, each female would need to produce more than two individuals to survive and breed in its lifetime. From this we can estimate that each female would need to breed for at least three years⁴. The persistence of individual males and females in the population is considered below.

In this report, considerable attention has been given to losses from the population, known deaths, and persistence (survival) to get a better understanding of the fate of individual animals. Losses between surveys over the winter period (8 months) appears only slightly worse than over summer (a 4-month period); on average, two more Individuals were lost over each winter (12.5) than over each summer (10.4) period, although numbers lost varied from year to year. It is not easy to see patterns in these data; fewer individuals were lost in the summers of 2016-2018 but it depends on how many were present in the population at the beginning of the summer or winter period. In general, the more individuals that were present at the beginning of a season, the more individuals were lost. This was most noticeable for males over winter. It should be remembered that these are small numbers, and the data show a reasonable amount of scatter. The positive relationship between numbers and losses does not imply population regulation by density dependent factors.

Persistence of females appears to have been higher than males although there was considerable variation between seasons and years. Noticeably, few males persisted over the winter 2015-16 contributing to the population low in spring 2016, and therefore few males persisted over the summer in 2016. As with the seasonal loss of individuals, there was a positive relationship between seasonal persistence and the number of individuals in the population at the start of winter or summer. So, the more individuals there are at the start of a season, the more individuals are lost, but also the more individuals persist. Net persistence, the difference between the numbers that persist and the numbers that are lost over summer and winter, is shown in Appendix Figure A5. This shows that the summers from 2016 to 2018 were good in that more animals persisted than were lost. In contrast, summer 2014 through to winter 2015-16, and summer 2021 were poor with losses exceeding persistence.

⁴ Assuming one litter per female per year. Hedgehogs can produce more than one litter a year, although it is not known how many achieve this (Reeve 1994).

The autumn cohort persistence analysis is revealing in that it shows that 70% of males and 52% of females are lost over the first year after initial capture, a clear difference between the sexes. Only one percent of males and four per cent of females survive to their fourth year. The picture is worse if just the juveniles captured in the autumn are considered. These data show a high mortality during their first year after weaning with 80% of females and 83 % of males disappearing, and very few persisting for three years. Overall, the higher death rate of males contrasts with a Swedish study which found no sex difference in age-specific survival (Kristiansson 1990). Moreover, the poor and inferior persistence or survivorship of hedgehogs in The Regent's Park compared with the hedgehogs in Morris' (1969) study points to why the population is on the edge of extinction.

In relation to body weight, adult females were slightly heavier than males and autumn animals heavier than spring animals, but otherwise they were quite variable between surveys and, as discussed in previous reports, offer no insights into rates of persistence.

7.2 Deaths

Over the study, a considerable number of hedgehogs have been found dead or in sufficiently poor condition that they have had to be euthanised, and these known deaths take on greater significance considering the small size of the population. Of course, there must be many other animals that die which go undetected. Even so a consideration of known deaths provides some interesting insights. Most dead hedgehogs were found in summer and least in autumn. Twenty-two per cent of all tagged animals were found dead. Where the cause of death has been identified, 43% of adults and 95% of juveniles have been attributed to predation (most likely foxes, possibly dogs). It would be interesting to know more about losses of nestlings or young hedgehogs to predation since this could be an obstacle to the growth and recovery of the population. Eleven per cent of deaths have been road kills, although none have been reported between 2019 and 2021⁵. Other causes of death include lung infection, ear infection, unspecified internal problems and drowning.

7.3 Population distribution

Changes in the distribution of hedgehogs over the course of the study has been discussed in previous reports. One of the key changes occurred largely over the summer of 2015 with the loss of hedgehogs from the southern part of the Park (zone 1). There also have been relatively fewer captures to the west (zone 5) since that time. Zone 2 (subdivided into 2a in the north and 2b in the south) in the east of the Park was also a favoured area at the beginning of the study and continued to be the dominant zone through to August 2019. Zone 2 includes the Zoo Car Park (about 2.6 ha in area less 0.8 ha of tarmac) which in 2014 and 2015 was described as a local hotspot with over 20% of all captures occurring in this small area. Relative numbers of captures started to decline in zone 2a and the Zoo Car Park from spring 2018 and no individuals have been captured in the Car Park in the last two years. The disturbance, loss and fragmentation of habitat in the Car Park since 2017 when Thames Water established a compound (~ 0.4 ha; Appendix Figure A6) to carry out work on a major water mains diversion (see 2017 Report) may have been a contributing factor in the loss of hedgehogs from this area. However, the works have only affected the eastern end of the Car Park and there has also been a recent reduction in captures across zone 2a. Thus, it is likely that other factors are also involved in the

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⁵ One hedgehog found in November 2021 may have been a RTA but at the time of writing has yet to be autopsied.

loss of animals from this area.⁶ Other trends in the distribution of captures include a relative increase of captures in an around the sports fields since the start of the study and an increase in captures in zone 6 and zone 7 (the Zoo) since August 2020.

7.4. Distribution and abundance

One reason why the Park holds fewer hedgehogs than it might is that all the available space is not being utilised by hedgehogs at the same time, that is the Park is not being used to its full potential. The distribution and abundance of hedgehogs within the Park are clearly related, and a key question is what has caused the changes in their distribution and abundance over the course of the study? There are no definitive answers but some of the possible factors involved (e.g. weather, food availability, predation, habitat management) have been discussed in previous reports and continue to be investigated. Predation seems to be important. If foxes are the main culprits, it seems unlikely that they would be responsible for the shifting patterns in hedgehog distribution; foxes are observed throughout the Park (from sightings during surveys and the independent camera trap studies carried out within the Park by ZSL, Chris Carbone, pers. comm.). However, since there is evidence that foxes predate young animals, it does raise the question as to whether the availability of suitable cover and 'safe' nest and hibernacula sites varies in different areas of the Park and whether this has changed over time. Fifty wooden nest boxes were installed around the park from October 2015 to March 2016. Subsequent checks revealed that, by March 2018, around 37% of these had been used by hedgehogs. This suggests a demand for their use. It is probably coincidental that following the deployment of nest boxes, three good years of recruitment followed. Boxes could be providing breeding nests safe from foxes or dogs. The original boxes have progressively deteriorated and a programme of replacement with rot-proof boxes is underway in 2022. It will be interesting to see what results. Furthermore, volunteer work parties have been creating numerous shelters for hedgehogs made of natural materials in the flower borders and shrubberies.

Radiotracking studies carried out in 2014 and 2015 (see earlier reports) showed that the distance travelled by hedgehogs each night varied between 400 m and 1900 m with reasonably compact overlapping weekly home ranges of between 1.5 ha and 2.2 ha. Although collected in the first part of the study, these data suggest the hedgehogs can find sufficient food within moderately small areas. This also suggests that if numbers in a particular area decline for whatever reason, then recolonisation may be slow and would require a build-up in numbers in the neighbouring areas to encourage individuals to move further afield. It should be noted that some of the wrought iron railing fences within the Park are impermeable to hedgehogs making it more difficult for them to move between areas. To increase permeability, 10 cm holes have been cut in the base of some of these fence lines, including the boundary fence to the zoo grounds. Occasionally hedgehogs have always been seen inside the zoo grounds, but since holes started to be cut in the zoo fences in 2014-15 (Sven Seiffert pers. comm.), and particularly within the last year, there has been an increase in the number of captures around the zoo boundary. This indicates that the holes have enabled hedgehogs to move more easily from within the zoo grounds, where many may nest, to the scrub, mixed and short grassland habitats outside to forage.

Two critical moments have occurred in the studies on the Park hedgehogs since 2014. The first was the drop in population size over the autumn and winter 2015 to a low in spring 2016 and the changes in distribution that occurred over the same period. Population numbers did pick up over the following

⁶ Since 2021 HS2 have taken over the compound as a lorry holding area in support the development of the new rail link out of Euston Station.

⁷ Two individual males in the spring periods travelled further and had larger ranges.

year, but not in the south or west of the Park. The second critical moment was the drop in numbers over the summer of 2021 to the lowest number recorded during the study in autumn 2021. Again, there was a shift in the distribution of captures with fewer to the north and east of the Park, including the Zoo Car Park. The situation in 2021 is slightly different to 2016: it was the autumn rather that the spring, and there were fewer females in the population.

8. The future

The aim is to continue to survey the hedgehogs in Regent's Park each spring and autumn through to 2024 and then to take stock of the status of the population at that time and whether surveys and/or other studies should continue. Habitat improvements for hedgehogs within the Park are ongoing and a range of short-term scientific studies are currently being considered (see 2021 report, e.g. on food availability, movement, nest sites, nest boxes). However, the survey results in autumn 2021 indicate that the population is in a precarious situation and could be heading for extinction. More will be known after the survey in May 2022, but it might be appropriate over the next few months to consider whether further conservation actions are needed.

An important question in this context is whether the dwindling population should be reinforced by introducing new individuals into the Park; such an action should only be carried out as a last resort (Morris 2012). In principle, releasing animals would be quite straightforward and in other situations released hedgehogs do well, especially if released into habitats like those from which they have been removed (Morris 2012). However, there are important prior considerations as detailed in the international guidelines for conservation reintroductions (IUCN, 2013). Of relevance to the hedgehogs in Regent's Park, is the following statement taken from the guidelines:

Any proposed conservation translocation should be justified by first considering past causes of severe population decline or extinction. There should be confidence that these past causes would not again be threats to any prospective translocated populations.⁸

At present, the reasons for the low number of hedgehogs in the Park, why the numbers have fluctuated at a low level, why individual persistence is poor and why the distribution pattern has changed over the eight years of the study are not fully understood. Some things could be important, such as predation, and habitat. However, at present, it is not considered appropriate to control fox numbers, and despite habitat changes being made to the Park with hedgehogs in mind, these have yet to yield the desired outcomes. Furthermore, importing hedgehogs to reinforce the population would require stringent precautions to mitigate disease risks to both the resident and translocated animals. So, with these uncertainties, would releasing hedgehogs have any conservation benefits?

9. Acknowledgements

The Royal Parks is very grateful to:

The Meyer Family for loving hedgehogs, believing in this research and enabling it to happen.

John Gurnell and Nigel Reeve for sharing their wealth of wildlife knowledge with the team throughout the studies and for their incredible patience, leadership, enthusiasm and sheer dedication to the project.

⁸ From: Annexes to Guidelines pp. 8 - Annex 3.2 Assessing extinction causes and threats, Point 1.

The Regent's Park team, especially Mark Rowe and Nick Biddle, and **The Royal Parks Ecology team** for supporting the survey with fieldwork, park management adjustments, keys and car parking permits.

Sven Seiffert and his team at ZSL for co-ordinating access and leading teams of volunteers in London Zoo on the spotlighting nights and working tirelessly on improving the zoo's habitats for hedgehogs.

The veterinary team at ZSL have once again been fantastic at dealing with hedgehog casualties.

The Garden Wildlife Health Project team who carried out post-mortems on hedgehog carcasses.

ZSL for continuing to care about the hedgehogs in the Car Park and the **ZSL press team** for helping to recruit our Hedgehog Heroes!

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This project has only been possible because of the support of our brilliant volunteers...thank you to everyone who has helped.

10. References

Reports:

The following reports on the hedgehog studies in Regent's Park can be found at: https://www.royalparks.org.uk/managing-the-parks/conservation-and-improvement-projects/hedgehogs/hedgehog-research-reports.

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Appendix

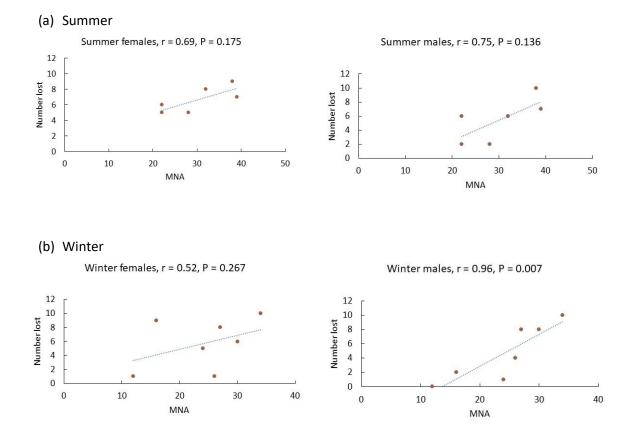


Figure A1 Loss of males and females over (a) summer and (b) winter in relation to minimum population size (MNA = Minimum Number Alive) . Y axes are numbers of individuals lost from the population during the Winter (8 months) or Summer (4 months) period. Correlation coefficients are Spearman's. Dashed lines are lines of best fit. Only the Winter males show a significant positive association.

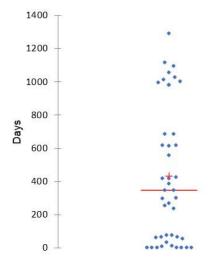


Figure A2 An individual scatterplot of the approximate age of individual tagged hedgehogs that were found dead during the study. The cross is the mean value and the horizonal line is the median.

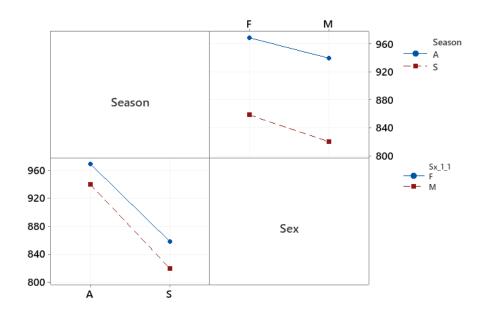


Figure A3 Interaction plot showing means of body weight (g) for sex (F = female, M = male) and season (S = spring, A = autumn). Y-axes are body weight (g). There is no interaction between sex and season ($F_{1,282} = 0.06$, P = 0.809).

Spring 2021



Autumn 2021

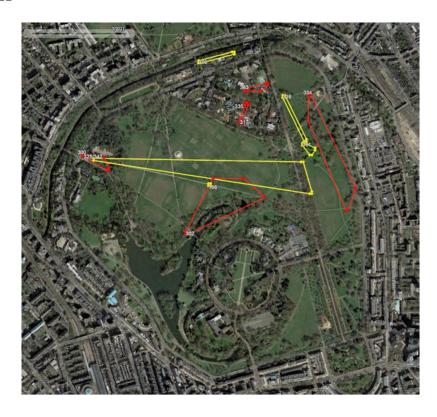


Figure A4 Minimum Convex Polygons for individuals captured in Spring and Autumn 2021. Yellow = female, red = male.

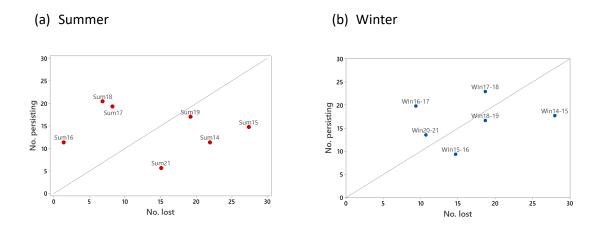


Figure A5 The relationship between the number of individuals that persist and those that are lost over (a) summer and (b) winter. The diagonal line is the line of equal numbers.



Figure A6 Zoo Car Park and the Thames Water compound outlined in red. Google Earth Pro $4^{\rm th}$ November 2020.