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Population viability analysis of hedgehogs in
rural and urban habitats

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SUMMARY

This study used population viability analysis software, Vortex 9.99, parametrised with demographic rates from published field studies, to provide a range of estimates of minimum viable population size (MVP) for UK hedgehog populations. The derived estimates of MVP ranged between 32 and 250, dependant not only on the mortality rate and litter sizes used, but also on the standard deviations around the mortality rates: a measure of interannual variation in survival probabilities which for hedgehogs will be affected by year-on-year changes in predation probability, food abundance, and weather conditions. Which of the estimated values of MVP is most appropriate for a given UK population will therefore depend upon the type and quality of the habitat, which will in turn affect litter sizes, mortality rates and interannual variation in these rates. Locations which are likely to provide high levels of food and shelter, and a low predation risk are likely to be represented by the lower range of MVP size estimates (32 - 60 individuals) whereas areas with higher predation risk, less shelter and food resources, and / or greater variability between years in survival and breeding rates will be more likely to be represented by the larger MVP values of 120 - 250. We argue that "urban" habitats are likely to provide conditions with both lower mortality rates and less interannual variation in these rates, and so are more likely to be represented by values of MVP between 32 and 60 individuals. Conversely "rural" conditions are more likely to foster higher mortality rates, and with greater interannual variation, and so the relevant values of MVP are likely to be between 120 and 250 individuals. The hedgehog densities in these habitat types recorded in the literature permit the further calculation that "urban" populations may require between 0.9 and 2.4 km², with the exception of inner city populations which may require up to 8.2 km², whereas "rural" populations may require between 3.8 and 57 km². It is stressed, however, that these suggested figures are provided with the strong caveat that due to the large range in conditions that are encompassed by the definition of both "rural" and "urban" habitats, the MVP values and corresponding area requirements

should be applied only after first assessing a given locality for its *a priori* suitability for hedgehogs. Our results suggest that 32 individuals should be considered an absolute minimum number of hedgehogs (with a 1:1 sex ratio), and only in the very best habitats, that constitute a viable population.

INTRODUCTION

The aim of this study was to estimate the minimum viable population size (MVP) for UK populations of European hedgehogs, *Erinaceus europaeus*, identifying key habitat and demographic variables. Our approach was to employ pre-existing population viability analysis software, parametrised with demographic rates from published field studies on hedgehogs to derive MVP size estimates for isolated hedgehog populations (i.e. treating the populations as isolated, rather than as constituent parts of a metapopulation, and therefore excluding the possibility of the population being 'rescued' from extinction by dispersal from other subpopulations) under a number of scenarios. We selected VORTEX 9.99 (Lacy, 2000; Lacy et al., 2009) as the most appropriate software package to manage the analysis. Vortex 9.99 is the most appropriate package for bird, mammal and reptile species with low fecundity and long lifespans (relative to, for example, insect species) and with likely population sizes of < 500 individuals, modelled over a number of years and for which the mating system and proportions of each sex breeding are known or able to be estimated (Miller and Lacy, 2005).

Detailed information on Vortex 9.99 is available elsewhere (Miller and Lacy, 2005) but in brief, Vortex models population dynamics as discrete, sequential events (e.g., births, deaths, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modelled as constants or as random variables that follow specified distributions. Since the growth or decline of a simulated population is strongly influenced by these random events, separate model iterations or "runs" using the exact same input parameters will produce different results. Consequently, the model is repeated many times to reveal the distribution of fates that the population might experience under a given set of input conditions.

For the purposes of the present study Vortex 9.99 was used to estimate the population size and carrying capacity - for a given suite of input variables - at which 95% or greater of the modelled populations remained extant over a 100 year period. Models were run for 1000 iterations and the MVP size estimated by setting the initial population size to be equal to the carrying capacity and altering both until the probability of extinction among 1000 runs was 0.05. Setting the initial population size to be equal to the carrying capacity in this way specified model populations which were already at their maximum numbers, and constituted a valid test of whether this maximum would be sufficient to ensure the population's future survival.

Having derived an estimate of MVP for populations under different conditions, this estimate was then compared with published values for population density in a range of UK habitat types to provide an estimate of the area required to support a viable population of hedgehogs.

METHODS: ASSESSING MVP FOR EUROPEAN HEDGEHOGS

Vortex 9.99 requires a series of input parameters to be specified and, as with all such modelling software, the more accurate the estimation of these parameters, the more likely the outputs are to represent a realistic estimation of a given population's likelihood of survival. The input parameters in the present study are necessarily drawn from the wider hedgehog literature, and so a given parameter may have a range of values dependent upon the study: variations in field methods used, the geographical location of the study population, or other external variables (e.g. weather conditions) may all affect the estimation of these parameters. Variability in some parameters, however, is likely to have a larger impact upon the model results than in others. For this reason we adopted an approach of treating some parameters as fixed and others as variable, essentially fixing the majority of input parameters and creating a series of alternate models for those parameters for which contradictory values exist. We then ran sensitivity analyses to ensure that unexamined variations in these parameters would not have substantial impacts on the resulting MVP size estimates. Table 1 presents the list of input parameters, stating the value of each fixed parameter. Parameters marked as "Varied" are those for which

separate models were constructed. The list of these separate models is provided in Table 2, which presents the 12 combinations of values for the input parameters concerning numbers of offspring per female, mortality rates and inbreeding depression. Our analysis therefore comprised running a separate model for each of these 12 combinations of varied parameters (Table 2), while keeping the keeping the fixed parameters (Table 1) constant between models.

Derivation of the fixed model parameters

The fixed model parameters are outlined in Table 1 and were derived as follows:

Environmental variability in carrying capacity was set to 10% of the carrying capacity for all model runs (i.e. in a given year the carrying capacity could be up to 10% higher or lower). No values for this parameter were estimable from the literature but MVP size estimates were relatively robust to alterations in this parameter (see Sensitivity Analyses, below).

Environmental Variability concordance of survival and reproduction was set to "No". This parameter specifies whether a 'good' year for breeding is also a 'good' year for survival (and vice versa). In hedgehogs annual mortality is largely dependent upon winter conditions (Reeve, 1994) whereas breeding success depends mainly upon conditions (and therefore food abundance) during spring to early autumn. The two are not likely to be correlated, because spring conditions are unlikely to determine winter conditions, or vice versa.

Age of first breeding was set to two years (i.e. no model hedgehog bred until its third year). Authors typically divide female hedgehogs into juvenile (< 1 year old and in the season of their birth), subadult (hedgehogs that have overwintered but are < 2 years old) and full adult (having overwintered twice or more) individuals (e.g. Kristiansson, 1990; Jackson, 2007). In some studies of Swedish populations, subadults were not considered part of the breeding population because no captured subadult female had suckled young (Kristiansson, 1990), whereas in some British studies subadults are recorded as having litters (albeit of reduced size) at the end of their second year (Jackson, 2007). This parameter in Vortex 9.99,

however, refers to the age at which the *majority* of individuals begin breeding at their full potential (Miller and Lacy, 2005), and so was set for two years.

Maximum age of reproduction was set to seven years old, because the maximum life expectancy of hedgehogs in the wild is between 6-8 years (studies cited in Reeve, 1994). The number of individuals of this age in the population is not dependent upon this estimate, and instead is modelled by Vortex 9.99 using the mortality rates (specified below). This parameter merely specifies the age at which, were a hedgehog alive, it would attempt to breed. Since all female hedgehogs typically attempt to breed in a season (Jackson, 2006), the maximum age of reproduction is set at the upper limit of survival. However, depending on the mortality rates, there may be no such individuals in a model population (see also Sensitivity Analyses).

Maximum broods per year was set to two, since a number of studies have shown hedgehogs to be capable of two broods per year (Morris, 1969; Reeve, 1994; Jackson, 2006). Although the majority of "second broods" are likely to be replacements for originally lost first broods (Reeve, 1994), Jackson (2006) confirmed the successful rearing - but by a small proportion of females - of two broods in a year.

Maximum progeny per brood was set to seven. A difficulty in setting this parameter is shared with the estimation of the mean number of offspring per litter (see below): that while litter sizes may be large at birth, the number of independent individuals entering the population from a given litter will be lower, due to mortality occurring after birth but before weaning (e.g. Morris, 1977). This becomes a problem because the population mortality rates for juveniles from the literature (specified below) are applied annually and derived from studies in which only individuals which are captured as independent and free ranging in the population contribute to the mortality rates (i.e. annual mortality rates for juveniles in the literature can only be ascertained for individuals that can be captured, and so only after they are weaned and become independent). The available juvenile mortality rates do not take into account mortality of nestlings pre-independence, and so this was accommodated separately by lowering the number of progeny per female. While a number of studies suggest that birth litter sizes may (rarely) be as large as 10 individuals

(e.g. Deanesly, 1934; Morris, 1991; Macdonald and Barrett, 1993), at least 20% of those born would be expected to die before emergence from the nest (Morris, 1977). Seven surviving individuals therefore represents a suitable, conservative, maximum for UK populations (also see Sensitivity Analyses, below).

Sex ratio at birth was set to 50%. Several studies support the presence of a 1:1 sex ratio in hedgehogs (Kristiannson, 1990; Reeve, 1994), including in juveniles (Jackson, 2006).

The distribution of broods among females was calculated from the detailed breeding data presented in Jackson (2006). The calculation was based on the proportions of the adult female population making early (May-June) and late (July-September) breeding attempts (0.96 and 0.81, respectively) and the success rate (i.e. the percentage resulting in the birth of a litter) of those attempts (0.63 and 0.86, respectively) stated in Jackson's (2006) study. Ninety-six percent of females attempted to breed early, resulting in $[96 * 0.63 =]$ 60.5% of females producing a successful early litter. Eighty-one percent of females attempted to breed late, meaning that $[96 - 60.5 =]$ 35.5 % of females attempted to replace a lost early litter and $[81 - 35.5 =]$ 45.5 % of females attempted a true second litter. These attempts resulted in $[35.5 * 0.86 =]$ 30.5% and $[45.5 * 0.86 =]$ 39.1 % of females successfully replacing a lost first litter and having a true second litter, respectively.

The results of the above calculations therefore indicate that 51.9 % of females bred successfully once in a year, with 39.1 % breeding twice and 9.0 % not breeding. These percentages, however, are not an accurate representation of the true number of litters produced in the population per adult female. The reason for this is that Jackson (2006) also noted a substantial proportion of subadult females breeding late in the season. The offspring from these subadult litters cannot be directly incorporated into the Vortex 9.99 simulation, because females are modelled as only breeding when two years old or more (see *age of first breeding*, above), and so the actual figures of litters per extant adult female would be higher than these percentages. To account for this, we adjusted the above figures to incorporate the unacknowledged contribution of litters from subadult females.

From Jackson's (2006) study 64% of subadults attempted a (single, late) litter in a given season with a success rate of 0.62. This equates to $[64 * 0.62 =]$ 39.7% of subadults having successful litters. Subadult litter sizes, however, were 30% smaller than adult litter sizes, and so this figure adjusted into adult litter equivalents is $[39.7 * 0.70 =]$ 27.8%. Since 35% of the female population were subadult and 65% adult in any given year (Jackson, 2006), per 100 adult females we would anticipate $[(100 / 65) * 35=]$ 53.8 subadult females, having $[53.8 * 0.278 =]$ 15.0 additional litters. We divided these additional litters equally between adult females breeding once and twice, yielding the following percentages: 51.9 % of females breeding successfully once in year, 46.6 % breeding twice and 1.5 % not breeding.

The **percentage of adult females breeding** and **environmental variability** in the percentage of breeding females were derived from the above calculations, with the environmental variability simply set at 1.5 to bring the proportion of females breeding to 100% in a "good" year and, conversely, down to 97% in a "bad" year. In practice, however, the quality of the year would be expected to act more upon litter sizes (in particular in the proportion of litters surviving to weaning) and survival rates than upon the percentage of adults attempting to breed , and is therefore incorporated into the litter size and mortality rate data (see below).

Derivation of the varied model parameters (see Table 2)

Models with and without **inbreeding depression** were run separately. The rationale for the inclusion / exclusion of this variable was to demonstrate the long-term fitness consequences (and therefore implications for any MVP) of a population being genetically isolated for substantial periods.

Values from the literature for litter sizes per female per brood are presented in Table 3. The use of these litter sizes for specifying the **number of offspring (and S.D.) per female per brood** was, however, complicated by two factors:

First, stated litter sizes varied between studies, both with locality (country and / or latitude within country) and interannually with external factors, such as weather conditions (e.g. Reeve, 1994; Jackson 2006).

Secondly, litter sizes were not always recorded at the same time post-birth, and may therefore not be directly comparable between studies - because litters recorded relatively early may still suffer additional pre-weaning mortality, whereas litters recorded late and / or as the hoglets become independent are likely to be at their smallest recorded size. For example Morris (1977) recorded a fall in mean litter size from 4.37 at the "early young" stage (less than two weeks old) to 3.72 in young "seen with adult" at about 3-5 weeks old, which indicates mortality (calculated as 19.3%) prior to weaning, although the author acknowledges that some of the apparent decrease may have been due to partial dispersal of young from the litter.

Given the range of values presented in Table 3, we took the approach of using the upper and lower estimates of litter size for UK populations of hedgehogs (see Table 2), aiming to assess the litter at (or just prior to) weaning, so that it was as close as possible to the actual estimate of the number of young per female which join the free ranging population. Using these upper and lower estimates would provide upper and lower estimates for the MVP. We excluded the value of 4.6 for Morris (1961) because uncertainties concerning when the litter was observed mean that further loss of individuals may have been possible prior to weaning. We excluded the estimate from Kristiansson (1990) due to its similarity to that from Jackson (2006); while Kristiansson's estimate is marginally lower, Jackson's (2006) study was of a UK population (as opposed to a Swedish population), and litter sizes may differ between countries (Reeve, 1994; Kristiansson, 1990).

We therefore model two litter sizes, from Morris (1977) and Jackson (2006) (see Table 2; Table 3), as the upper and lower litter sizes, respectively.

Mortality rates were derived from several studies (see Table 4). Vortex 9.99 requires the mortality rate and standard deviation to be input separately for each age class up to adulthood (in this case 0-1, 1-2 and > 2 years of age). However, authors typically have not separated subadult and adult mortality rates (e.g. Reeve, 1994; Kristiansson, 1990) and so in practice we separated mortality rates into juvenile and adult, giving subadults the same rate as adults (Table 2). Several complications arose in the selection of mortality rates to parametrise the models.

Firstly, many of the estimates were from different countries, and so a similar concern exists to that arising in the above estimation of litter sizes; namely that variations in climatic or other conditions may result in substantially different mortality rates in the UK compared with other countries. However the study by Kristiansson (1990) represents the only published eight-season study in existence, and the data from this study are therefore too valuable to discard (Table 2).

Secondly, the value and standard deviation for juvenile mortality provided by Kristiansson (Table 4), is skewed by one atypical year (see Table 1 of Kristiansson, 1990) in which 94% of juveniles died over winter (c.f. a mean value of 26.5% for the seven remaining years; Table 1 of Kristiansson, 1990). To provide a series of realistic options, we used the direct juvenile and adult mortality rates from Kristiansson (1990) for some model runs (Table 2) but also adjusted the mean and standard deviation of the juveniles' rates by removing the data from the abnormal year and recalculating the mortality rate based on the data in Table 1 of Kristiansson (1990). This recalculation, excluding the first, atypical year, provided a juvenile mortality rate of 26.5 with a standard deviation of 8.3 (Table 2).

Thirdly, the estimates provided by Morris, (1988a; 1991), while from UK populations, did not have standard deviations attached to them. Such measurements of error are required by Vortex 9.99 and may represent a source of considerable variation in the outcome of any MVP analysis (see Sensitivity Analyses, below). To accommodate these data we calculated the standard deviation of the two juvenile estimates (60 and 70, giving a standard deviation of 8) and applied this to the adult estimate. While far from perfect, this approach nevertheless permitted mortality rates from a UK study to be included into the model (Table 2). The possible impact on the estimated MVP of this calculated standard deviation being too high or low was modelled in the sensitivity analyses (below).

Fourthly, the rates from southern German studies cited in Reeve (1994), while similar to those from Morris (1988, 1991) (see Table 4), again did not have attached standard deviation values, and were not from studies on British populations. These estimates were excluded from the model runs.

The 12 models run, therefore comprised two levels of inbreeding depression, two litter sizes and three mortality

rates (see Table 2), of which two were derived from studies of Swedish hedgehog populations, and one from UK studies.

METHODS: DERIVATION OF POPULATION DENSITIES

It was desirable to calculate how much area a hedgehog population of a given size would require to accommodate all of its individuals, across a range of habitat types (e.g. urban, suburban, rural etc.). Such a calculation requires known population densities of extant populations of hedgehogs in these habitat types, again derived from literature review. The densities are presented in Table 5. Several difficulties exist with such an approach, however, falling under two broad categories:

The first type of difficulty arises from the terminology used by authors to define an "urban" or a "rural" habitat. Some authors (e.g. Doncaster, 1994) define an urban setting which is effectively a rural setting in which the arable component has been replaced by a mixture of buildings and amenity grassland. Other authors, however, point out that the amount of vegetation in urban city habitats varies between cities and from country to country. For example Huijser and Bergers (2000) distinguish between the Swiss city of Yverdon-les-Bains (from which Berthoud, 1982, derived his density estimates; Table 5) which they consider an "urban centre with little vegetation", and British and Dutch cities which they classify as "urban areas with vegetation". Similarly Hubert et al. (2011) acknowledge that the term "urban" as applied to wildlife in cities is applied broadly, incorporating small towns, neighbourhoods and backyards, cities and/or urban centres (DeStefano and DeGraaf, 2003); such loose use of terminology persists despite evidence that urban mammal population densities may vary along the urban-suburban gradient (Baker and Harris, 2007). Hubert (2011) recommends the use of a more standardised definition of urban areas to improve comparisons between results originating from suburban and urban areas.

For the purposes of the present study "urban" sites were separated into "Inner City" and "Urban general" (Table 5), but even this coarse distinction is made with the caveat that the entry under the "Inner City" category in Table 5 encompassed several London Boroughs which contained relatively large areas

of green space (Plant, 1979). "Amenity grassland" (Table 5) was defined as large, grassy areas set aside for sports or other recreational activities but within reach of urban structures (e.g. villages, suburban habitats); we defined "Rural general" as any area where the predominant land use was agricultural, and so this may include farm buildings and village habitats, provided these were not the dominant landuse.

A second type of difficulty arises, as both Jackson (2007) and Hubert (2011) point out, because the estimation of hedgehog densities stated in the studies of Reeve (1981), Morris, (1988b) and Doncaster (1994) were likely to be overestimates of the actual densities. This overestimation arises because the densities in the aforementioned studies were calculated by dividing the total number of individuals by the area of the site, leading to overestimation because hedgehogs roam widely (Jackson, 2007), and also because the study areas themselves were selected on the basis of being 'good for hedgehogs', and so the densities are averaged over areas which include too few sparsely-populated habitats (Jackson, 2007; Hubert 2011). While neither observation constitutes a criticism of these previous studies - because the densities in these previous studies were mainly used for comparative purposes and the main aim was not to produce representative population densities - this consideration does mean that their use in calculating the area required to support an MVP of hedgehogs is limited. For example, Jackson (2007) states that if he applied the same density calculation method to his own data, the 'density' values in one locality average 81% higher, and those in another 51% higher, than the mean instantaneous values.

Studies that provide 'suitable' densities - which do not overestimate hedgehog densities and so will not lead to an underestimation of the amount of habitat required to support a given population size of hedgehogs - are Jackson (2007), Hubert (2011) and Berthold (1982), as these use similarly appropriate techniques for density estimation (Hubert, 2011). The study of Young et al. (2006) also takes place over sufficiently large, randomly selected areas to avoid being an overestimation. Of these, only the studies of Jackson (2007) and Young (2006) are from the UK (Table 5).

To accommodate the above issues, we produced a reduced set of densities from Table 5, excluding values which are likely to

be overestimates of hedgehog abundance (see Table 6). Table 6 presents this reduced set of densities for the categories Inner City, Urban General and Rural General. While there is no evidence that the study of Plant (1979) is not an overestimation of inner city densities, this figure is sufficiently smaller than those of Urban General to warrant its inclusion in the analyses as being indicative of reduced densities of hedgehogs in Inner City locations.

RESULTS: MODEL OUTPUTS

The minimum viable population sizes (MVP) for each combination of input variables are presented in Table 7. For models without inbreeding depression, MVP ranged from 32 - 250 individuals (with a 1:1 sex ratio). For models incorporating inbreeding depression these values were 52 - 600 individuals. Mean time to first extinction (a measure, for those populations that went extinct in the model run, of the mean number of years taken to go extinct) was larger (range 63.9 - 85.6 years) for models incorporating inbreeding depression than for models without inbreeding depression (range 54.8 - 56.2 years), indicating that inbreeding depression had a delayed effect on extinction probability, such that it increased extinction rates relatively late in the 100 year model period. Table 8 presents the maximum and minimum areas required to accommodate the MVPs derived from Table 7. These values are calculated from the maximum and minimum densities in Table 6.

RESULTS: SENSITIVITY ANALYSES

Sensitivity to variations in mortality rates

The main source of error in estimating MVPs in this study was the differences in recorded mortality rates and their standard deviations (Table 7, 8). The types of field data upon which these estimates and standard deviations are based are difficult to attain and therefore sparse in the literature. This is exemplified by the large alteration to the estimate of juvenile mortality, and its standard deviation, that excluding one outlying observation (in which 94% of the juvenile population died in one year) from Kristiansson's (1990) study made: from 36 (s.d. 26.6) to 26.5 (s.d. 8.3). For this reason

it was desirable to conduct additional sensitivity analyses to examine the likely impacts on the derived MVPs of increasing the standard deviations around the estimates. Table 9 presents the MVPs derived by varying the standard deviations around Morris' (1988) and Kristiansson's (1990) mortality rate estimates (in the latter case excluding the outlying first year juvenile mortality). Table 9 demonstrates that MVPs derived from Kristiansson's (1990) rates are individually robust to increases in standard deviation: increasing the standard deviation around the juvenile estimate from 8 to 15 increased the MVP size estimate by 15 individuals, and increasing the standard deviation for adults by the same amount increased the MVP size estimate by 7 individuals. Covarying the standard deviation for both adults and juveniles, however, more than doubled the MVP size estimate from 38 individuals to 83.

For Morris' (1988) mortality rate estimates, increasing the standard deviation around the juvenile estimate from 8 to 15 individuals resulted in an MVP of 108 (50 individuals greater), whereas the same increase in standard deviation for the adults resulted in an MVP of 78 individuals (20 individuals greater). These findings are reasonable, given that Morris' (1988) mortality rate for adults was lower than that for Kristiansson (1990) - 30 as opposed to 44 - whereas the Morris (1988) juvenile mortality rate was substantially higher (65 as opposed to 26.5). This increased mortality rate, coupled with the higher standard deviation, resulted in substantial population variation and therefore a large MVP. Similarly, covarying Morris' (1988) adult and juvenile standard deviations from 8 to 15 resulted an MVP size estimate of > 700 individuals. This latter finding is cause for concern, because it suggests that comparatively small increases in the variation around mortality estimates acting simultaneously on both adults and juveniles could lead to dramatic increases in the estimate of any MVP.

A partial explanation for the above sensitivity to standard deviation, particularly when mortality estimates are relatively large (e.g. 65%), is demonstrated in Table 10. Table 10 shows that for a mean mortality rate calculated across (for example) 10 years the rate in a given year can be markedly higher or lower than the estimate, depending on the standard deviation. A 10 year mean mortality rate of 30% with a standard deviation of 8, gives a range of mortality rates of

14-40% in any given year. When the standard deviation is increased to 12, this range becomes 0-50%. For mean mortality rates of 65 with a standard deviation of 8, the range is 51-83%, and increasing the standard deviation to 12 results in a range of 37-100% of the population in a given year. In this latter case, the implication for the Vortex 9.99 analysis is that the entire adult or juvenile population may go extinct in any given year simply due to high interannual variation in mortality rates.

Sensitivity to variations in breeding rate parameters

The data in Table 11 suggest that the models were relatively insensitive to variations in the maximum number of progeny per brood. MVPs for two of the mortality rates modelled responded to decreasing the maximum age of reproduction to five years old (from seven years old), but all MVPs were relatively insensitive to decreasing the maximum age of reproduction by one year (to six years old).

Environmental variations in carrying capacity were set at 10% of carrying capacity in all models. Doubling this value to 20% made modest increases in the estimated MVPs (e.g. 60 to 75 individuals; Table 11) and halving it to 5% made modest decreases in estimated MVPs (e.g. 60 to 55 individuals). These results imply that model results are relatively insensitive to alterations in the percentage of environmental variation in carrying capacity specified.

DISCUSSION OF MODEL OUTPUTS AND SENSITIVITIES, AND IMPLICATIONS FOR MANAGEMENT.

The minimum and maximum areas required for a minimum viable population (MVP) of hedgehogs (Table 8) varied principally with the set of mortality rates and standard deviations used in the model, and ranged between 32 - 250 individuals. Given the disparate nature of the estimates for the input parameters from the literature - in particular of mortality rates and litter sizes - it is not possible *a priori* to pick a particular combination as the most representative of UK hedgehogs in any given habitat. An alternative approach to selecting which estimates are likely to be most appropriate is to examine the sensitivity of MVP size estimates to variations

in the model parameters and to then suggest whether variations of the type likely to inflate MVP size estimates will occur in a given habitat.

It is clear that larger standard deviations around the mortality estimates in the models resulted in larger estimates of MVP size (Table 9). In the specific case of the mortality rates derived from Kristiansson's (1990) study, the standard deviation around the juvenile mortality estimate was 26.6. This very large standard deviation originated from a single outlying year in which 94% of the juveniles died over winter. When the effect of the outlying year was removed from the input parameters, the mean juvenile mortality was reduced from 36 (with an s.d. of 26.6) to 26.5 (with an s.d. of 8.3); and the corresponding MVP size estimates were reduced from 250 and 120 (Model 1 and 4, Table 8) to 42 and 32 (Models 2 and 5, Table 8). Kristiansson (1990) provided no explanation for this atypical year and so it is unknown whether this year was unique, and therefore able to be discounted, or whether it represents a type of catastrophe which may be expected to occur with a particular regularity (e.g. once every 5, 10, 20 or 50 etc. years), or, perhaps, merely represents an artefact of limited sampling (the estimate was derived from the fates of 15 juvenile hedgehogs). The impact of this one year does, however, suggest that high interannual variability in mortality rates may require larger populations of hedgehogs to ensure population viability.

In general MVP size estimates, if manipulated separately for juveniles and adults, increased substantially only with standard deviations of > 15 around the mortality rates (relative to the 'base' value of s.d. = 8). Even relatively large standard deviations of 12 surrounding the mortality estimates in Table 9, combined with the smallest estimated litter sizes (a mean of 2.85 per brood), only resulted in MVP size estimates of between 43 and 67 individuals (Table 9). However, when standard deviations around adult and juvenile mortality rates were covaried, relatively small simultaneous increases substantially increased MVP size estimates (Table 9). In situations in which environmental conditions might equally affect both juvenile and adult mortality, therefore, we would predict much larger numbers being required to ensure the population's viability.

Given the above considerations a sensible approach for the use of the MVP size estimates - for any given location - would be to first make a thorough assessment of not only the mortality and breeding rates, but also the degree of interannual variation in mortality rates likely to be experienced by hedgehog populations in the location, and then to apply the relevant MVP. If, for example, it is expected that a given population may suffer irregular catastrophes (e.g. harsh winters, fluctuations in food availability, high predation rates, etc.), then the larger MVPs from Models 1 and 4 (Table 8) are likely to be the most appropriate for use. If the factors affecting mortality rates are likely to remain relatively consistent between years, then the MVP is more likely to fall between 40 and 70 individuals (Models 2, 3, 5 and 6; Table 8).

The above issue of how consistent mortality rates (and therefore environmental variables affecting these rates) would be expected to be between years raises an intriguing potential difference between rural and urban habitats. No field studies to date have provided estimates of mortality and breeding parameters broken down by habitat type, and so it is unknown whether the environmental conditions experienced by urban and rural hedgehogs differ markedly. Several lines of reasoning, however, suggest that urban environments may now provide better (in terms of breeding and survival) conditions for hedgehogs than rural environments. The greater availability of food (mainly pet-food: Hubert 2011) and higher mean temperatures in urban areas may decrease the risk of both summer and winter mortality, and potentially increase the length of the reproductive season (permitting a greater number of second litters). Similarly urban hedgehogs face lower risks from badger predation (Young et al., 2006; Hof et al., 2012). At present few studies have examined these issues in detail, and a number of counter arguments exist. For example, Kristiansson (1981) suggested that female hedgehogs in Sweden - which have shorter reproductive lives and only produce one litter per season, mainly due to climactic conditions - invest in larger litters than those in Britain, and so the impacts of adverse climatic conditions on breeding success may be partially compensated. Similarly, decreases in badger predation in urban areas may be offset by additional mortality due to traffic collisions (Huijster, 2000). Despite these considerations, however, it remains plausible that hedgehogs in urban areas may experience reduced mortality rates and

increased breeding success, both of which would be expected to decrease the necessary population size to ensure viability. Importantly, interannual variation in both litter sizes and mortality rates may be smaller for urban hedgehogs than those in rural areas, because the urban environment is likely to remain more consistent year-on-year - again due to the likely higher mean annual temperatures, more constant food supplies and relative absence of predators. This effect too would be likely to lower the MVP (Table 9), meaning that fewer individuals would be required to constitute a viable population in "urban", than in "rural" habitats.

Due to the lack of habitat-specific data our approach in this study was to model a "generic" British hedgehog population, irrespective of whether the population was in an "urban" or "rural" habitat, and to then apply the densities observed in these habitats to the derived MVPs to create an estimate of the amount of habitat required. However, the above suggestions, while unavoidably speculative, raise the possibility that a contributing factor in the hedgehog's increasing absence from agricultural lands may be the relatively high interannual variability in mortality rates and food abundance in the rural landscape, which could result in a requirement for large populations for which sufficient habitat may be unavailable. It may therefore be more appropriate to use the larger MVP size estimates for "rural" populations, due to the likelihood of rural habitats requiring much larger populations to be viable, and use the smaller estimates for "urban" areas.

Following the above logic, depending on the quality of the arable land and therefore the density of hedgehogs it may be able to support, hedgehogs populations may require between 4 - 57 km² to be viable in "rural" areas (Table 8), whereas in "urban" areas MVP sizes are expected to be lower and densities of hedgehogs higher, putting the likely requirements between 1 - 2.4 km². It must be stressed that all of these figures depend greatly upon the quality of the respective habitats within each habitat type, and so any practical application thereof would have to incorporate careful assessment of habitat quality.

The figures so far discussed are derived from analyses modelled without inbreeding depression (Table 8). Inclusion of inbreeding depression into the models substantially increased

the MVP size estimates in most analyses (Table 7). However, the mean time to first extinction in the inbreeding models ranged from 64 to 86 years, suggesting that the deleterious effect of inbreeding would be unlikely to be significant before ~70 years. In practical terms, if concerns regarding a population's state of inbreeding were identified early (in the first 50 years) it may be relatively simple to avoid increased mortality from inbreeding depression through a program of transferring individuals between isolated populations. For this reason the conclusions of this study are based on models run without inbreeding depression.

A final consideration is that all models in the analyses were conducted without density dependence (a lowering of reproductive rates when populations reach carrying capacity). Data from one study (Kristiansson 1990) suggest that in years of peak density, recruitment rate was considerably lower than in years of lower density. However, Kristiansson (1990) states that the study was of too short a duration to provide conclusive evidence of density dependence operating, and the disconnect (two years) between peak densities and any subsequent fall in reproductive rates leaves substantial room for alternate explanations. For these reasons, and the difficulties associated with estimating an appropriate level of density dependence from so little evidence, the models all excluded density dependence.

CONCLUSIONS AND SUGGESTIONS FOR PRACTICAL USE

This study provides a range of estimates of MVP for hedgehog populations, based upon the figures available in the literature. The values of MVP size estimated by this study varied widely. The smallest value (32 individuals with a 1:1 sex ratio) can be considered the lowest plausible number of hedgehogs that can form a self sustaining population, based on the available parameters from the literature. Similarly the largest value (250 individuals) can be considered the upper limit, in the absence of inbreeding depression. MVP size estimates varied not only with the mortality rate and litter sizes used, but also with the standard deviations around the mortality rates: a measure of interannual variations in survival probabilities which is likely to represent year-on-year changes in predation probability, food abundance, and weather conditions. We argue that "urban" habitats are likely

to provide conditions with both lower mortality rates and less interannual variation in these rates, and so are more likely to be represented by the outputs from Models 2,3,5 and 6 (Table 8). Conversely "rural" conditions are more likely to foster higher mortality rates, and with greater interannual variation, and so the outputs from Models 1 and 4 (Table 8) are more likely to apply. In practice, however, due to the large range in conditions that are encompassed by definition of both "rural" and "urban" habitats, the MVP values and corresponding area requirements should be applied only after first assessing a given area for it's a *priori* suitability for hedgehogs: locations which are likely to provide high levels of food and shelter, and a low predation risk, should receive the lower range of MVP size estimates (32-60 individuals) whereas areas with higher predation risk, less shelter and food resources and / or greater variability between years in survival and breeding rates will be more likely to require the large MVP values of 120 - 250.

In summary, this study provides values for the upper and lower limits of hedgehog population size that are likely to be viable in isolation (i.e. without connection through dispersal to other hedgehog populations), and we suggested that 32 individuals should be considered the absolute minimum number of hedgehogs (with a 1:1 sex ratio), and only in the very best habitats, that constitute a viable population. Our results also highlight the importance of ensuring the stability of hedgehogs' environments over numbers of years to promote the survival of a given population.

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TABLES

Heading	Input Parameter	Setting	
Carrying capacity	Environmental variability	10% of value	
Species description	Inbreeding depression (y/n)?	<i>Varied</i>	
	EV concordance of survival and reproduction (y/n)?	No	
Reproductive system	Age of first breeding (years)	2	
	Maximum age of reproduction (years)	7	
	Maximum broods per year	2	
	Maximum progeny per brood	7	
	sex ratio at birth (% of males)	50	
Reproductive rates	% of adult females breeding	98.5	
	Environmental Variability in % breeding	1.5	
	Distribution of broods (% of females)	One brood	51.9
		Two broods	46.6
		No broods	1.5
Number of offspring (and S.D.) per female per brood	<i>Varied</i>		
Mortality rates	Mortality (and S.D.) from age 0-1 (% of population)	<i>Varied</i>	
	Mortality (and S.D.) from age 1-2 (% of population)	<i>Varied</i>	
	Annual mortality (and S.D.) after age 2 (% of population)	<i>Varied</i>	

Table 1: The input parameters for the Vortex analysis.

Combination	Offspring per female per brood (S.D.)	Mortality rate	
		Adult (S.D.)	Juvenile (S.D.)
Model 1	3.7 (1.0)	44 (10.1)	36 (26.6)
Model 2	3.7 (1.0)	44 (10.1)	26.5 (8.3)
Model 3	3.7 (1.0)	30 (8)	65 (8)
Model 4	2.85 (1.12)	44 (10.1)	36 (26.6)
Model 5	2.85 (1.12)	44 (10.1)	26.5 (8.3)
Model 6	2.85 (1.12)	30 (8)	65 (8)

Table 2: Possible combinations of parameters for number (and S.D.) of offspring per female per brood and mortality rates (adult and juvenile plus S.D. in the rate). Each model was run with and without inbreeding depression to create 12 combinations for model runs.

Author	Morris (1977)	Kristiansson (1981)	Jackson (2006)	Kristiansson (1990)	Morris (1961) (cited in Reeve 1994)
Mean litter size (S.D.)	3.7 (1.0)*	5.2	2.85 (1.12)	2.8 (1.09)	4.6
Age at estimation	At 3-6 weeks (late young / seen with mother)	At 3-6 weeks	At emergence (week 7 onwards)	At weaning	Unknown
Location	UK	Sweden	UK (Scotland)	Sweden	UK

* SD for Morris 1977 calculated from data presented in Figure 2 of Kristiansson 1981.

Table 3: Litter size, location and age at estimation of litters of hedgehogs from studies in Sweden and UK.

Author	Kristiansson (1990)	Morris (1988a; 1991)	Studies cited in Reeve (1994)
Juvenile mortality (s.d.)	34 (26.6)	60-70	70-80
Adult mortality (s.d.)	47 (10.1)	30	20-40
Location	Sweden	UK	Southern Germany

Table 4: Mortality rates recorded in the literature for juvenile and adult hedgehogs.

Source	Inner City	Urban General	Amenity Grassland	Rural General	Woodland
Berthoud (1982) (from Hubert 2011)		25		5	
Bontadina et al. (1999)		50-100			
Doncaster (1994)			178.6	20.8 and 70.3	
Doncaster (1992)				23 and 25	
Hubert (2011)		36.5		4.4	
Jackson (2007)				31.8 and 15.4	
Morris (1988)				22.2	
Morris et al., (1993) (from Harris 1995)					66.7
Plant (1979) (from Harris 1995)	7.3				
Reeve (1981) (from Reeve 1994)			83		
Young (2006)			154	9	
MEAN (s.d.)	7.3	45.5 (26.2)	138.5 (49.6)	22.7 (19.0)	66.7

Table 5: Numbers of European hedgehogs per km² recorded in the literature in different habitat types. All figures are from UK habitats with the exception of the shaded cells, which were from French (Hubert 2011) and Swiss (Berthoud, 1982; Bontadina, 1999) habitats.

Source	Inner city	Urban general	Rural General
Berthoud (1982) (from Hubert 2011)		25	
Hubert (2011)		36.5	4.4
Jackson (2007)			31.8
Jackson (2007)			15.4
Plant (1979) (from Harris 1995)	7.3		
Young (2006)			9.0

Table 6: A reduced set of hedgehog densities produced by excluding likely overestimates from Table 5. Shaded cells represent values from non-UK study sites.

Model	Litter size (s.d.)	Mortality rate		No Inbreeding Depression		With Inbreeding Depression	
		Adult (S.D.)	Juvenile (S.D.)	MVP	Mean time to first extinction (s.d.) in years	MVP	Mean time to first extinction (s.d.) in years
1	3.7 (1.0)	44 (10.1)	36 (26.6)	120	55.67 (3.32)	212	63.91 (3.13)
2	3.7 (1.0)	44 (10.1)	26.5 (8.3)	32	54.8 (4.29)	52	76.04 (2.75)
3	3.7 (1.0)	30 (8)	65 (8)	35	56.15 (3.62)	65	73.37 (3.02)
4	2.85 (1.12)	44 (10.1)	36 (26.6)	250	55.15 (3.29)	600	70.65 (3.10)
5	2.85 (1.12)	44 (10.1)	26.5 (8.3)	42	57.6 (3.56)	81	80.54 (2.76)
6	2.85 (1.12)	30 (8)	65 (8)	58	53.35 (3.36)	126	85.56 (3.38)

Table 7: The estimated minimum viable population size and mean time to first extinction for Vortex 9.99 model runs for each combination of Litter size and Mortality rate. These models were run without inbreeding depression.

Mode 1	Input variables			MVP	Area required (km ²)				
	Litter size (s.d.)	Mortality rate			Inner city	Urban General		Rural General	
		Adult (S.D.)	Juvenile (S.D.)			Max	Min	Max	Min
1	3.7 (1.0)	44 (10.1)	36 (26.6)	120	16.4	4.8	3.3	27.3	3.8
2	3.7 (1.0)	44 (10.1)	26.5 (8.3)	32	4.4	1.3	0.9	7.3	1.0
3	3.7 (1.0)	30 (8)	65 (8)	35	4.8	1.4	1.0	8.0	1.1
4	2.85 (1.12)	44 (10.1)	36 (26.6)	250	34.2	10. 0	6.8	56.8	7.9
5	2.85 (1.12)	44 (10.1)	26.5 (8.3)	42	5.8	1.7	1.2	9.5	1.3
6	2.85 (1.12)	30 (8)	65 (8)	60	8.2	2.4	1.6	13.6	1.9

Table 8: The maximum and minimum areas in km² required to accommodate a viable population of hedgehogs for each combination of input variables and in each habitat type. MVPs shown are modelled without inbreeding depression (see Table 7).

	Adjusted mortality rates from Kristiansson (1990) = 44.0 (adults) and 26.5 (juveniles)			Mortality rates from Morris (1988) = 30.0 (adults) and 65.0 (juveniles)		
Standard Deviation	Adult (Juvenile s.d. fixed at 8)	Juvenile (adult s.d. fixed at 10)	Adult and Juvenile covaried	Adult (Juvenile s.d. fixed at 8)	Juvenile (adult s.d. fixed at 8)	Adult and Juvenile covaried
8	38	42	38	58	58	58
9	40	43	42	62	60	68
10	42	45	45	64	55	74
11	42	46	48	66	60	105
12	43	46	53	67	60	135
13	45	47	63	74	70	230
14	50	48	73	85	75	320
15	53	49	83	108	78	>700
20	120	63	>700	275	125	>>700
25	>700	95	>>700	> 700	350	>>700

Table 9: Sensitivity of MVP size estimates to increasing standard deviation in mortality estimates. Cells contain MVP size estimates for each combination of adult and juvenile standard deviations. For each set of mortality estimates the standard deviations were singly altered for adults (with the juvenile s.d. fixed) and juveniles (with the adult s.d. fixed), and also covaried for both adults and juveniles (i.e. mortality rates for adults and juveniles are given the same s.d.). Shaded cells indicate the MVPs and standard deviations represented by the final models (Table 7). For all models mean litter size was 2.85 (1.12).

Mortality estimate (standard deviation)	30 (8)	30 (10)	30 (12)	65 (8)	65 (10)	65 (12)
Minimum value	14.0	21.9	0.0	50.5	54.2	37.3
Maximum value	39.5	45.4	50.1	83.4	90.4	100.0

Table 10: Maximum and minimum annual mortality values calculated for a theoretical sample of 10 years (assuming a normal distribution) with the given estimated mean and standard deviation.

Mortality rate		Original MVP from models	Maximum age of reproduction (originally 7)		Maximum number of progeny per brood (originally 7)			EV in carrying capacity	
Adult (S.D.)	Juvenile (S.D.)		6	5	8	6	5	20	5
44 (10.1)	36 (26.6)	250	280	425	250	250	300	280	240
44 (10.1)	26.5 (8.3)	42	42	43	39	41	42	50	38
30 (8)	65 (8)	60	64	97	55	60	60	75	55

Table 11: MVPs from model runs with each combination of mortality parameters in which the maximum age of reproduction, maximum number of progeny per brood and Environmental variation in carrying capacity are varied independently. For all models mean litter size was 2.85 (1.12).