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Assessing habitat quality of farm-dwelling house sparrows in different agricultural landscapes

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Abstract

Having historically been abundant throughout Europe, the house sparrow (*Passer domesticus*) has in recent decades suffered severe population declines in many urban and rural areas. The decline in rural environments is believed to be caused by agricultural intensification resulting in landscape simplification. We used giving-up densities (GUDs) of house sparrows feeding in artificial food patches placed in farmlands of southern Sweden to determine habitat quality during the breeding season at two different spatial scales: the landscape and the patch scale. At the landscape scale, GUDs were lower on farms in homogenous landscapes dominated by crop production compared to more heterogeneous landscapes with mixed farming or animal husbandry. At the patch level, feeding patches with a higher predation risk, caused by a wall fitted to the patch to obstruct vigilance, had higher GUDs. In addition, GUDs were positively related to population size, which strongly implies that GUDs reflect habitat quality. However, the increase followed different patterns in homogeneous and heterogeneous landscapes indicating differing population limiting mechanisms in these two environments. We found no effect of the interaction between patch type and landscape type, suggesting that predation risk was similar in both landscape types. Thus, our study suggests that simplified landscapes constitute poorer feeding environment for house sparrows during breeding, and that the population regulating mechanisms in the landscapes differ, but that predation risk is the same across the landscape types.

Keywords: Foraging · Giving-up density · GUD · Predation · Conservation

Introduction

In many areas of NW Europe, farmland bird species have suffered several decades of dwindling population numbers (www.ebcc.info/index.php?ID=457). This can be attributed to agricultural intensification, i.e. a suite of measures that farmers use to increase production per unit area (Donald et al. 2001). Reduced habitat heterogeneity at multiple spatial scales, resulting from this agricultural intensification, has been suggested to be the general cause of the decline of farmland bird populations (Benton et al. 2003).

The house sparrow (*Passer domesticus*) is a farmland bird that once was so numerous in or around human dwellings that it was considered to be a pest (De Laet and Summers-Smith 2007). During the past few decades it has declined severely in numbers in both urban and rural areas in large parts of Western Europe (Engler and Bauer 2002; Newton 2004; Robinson et al. 2005; Klok et al. 2006), including Sweden (Lindström et al. 2011). In the United Kingdom and the Netherlands the house sparrow has even been placed on the Red List as a species of high conservation concern (Klok et al. 2006; Chamberlain et al. 2007). In rural environments, the house sparrow is thought to have been negatively affected by agricultural intensification (Hole et al. 2002). In particular, loss of landscape heterogeneity may lead to spatial and temporal separation of resources in the landscape that could have negative effects on population persistence for sedentary birds (Donald et al. 2001), such as the house sparrow that depend on different resources throughout the year (Hole et al. 2002). The house sparrow depends mainly on seeds and grains, except during the breeding season when it feeds offspring with insects (Summers-Smith 1963; Anderson 2006). In many North European countries the structural rationalization of agriculture, i.e. increasing farming efficiency by specializing production, increasing field size and abandoning unprofitable fields, has resulted in plains dominated by plant production and more forested districts dominated by animal production, with intermediate landscapes still containing mixed farming. If house sparrows need insects promoted by animal husbandry for breeding (Ambrosini et al. 2002; Vincent 2005) and seed resources produced by plant production for winter survival (Hole et al. 2002), it may suffer from agricultural specialisation.

It has also been suggested that predation may contribute to the decline of the house sparrow (Macleod et al. 2006), because the house sparrow is susceptible to predation by sparrow hawks (*Accipiter nisus*) and cats (*Felis catus*) (Götmark and Post 1996; Toms 2003; Woods et al. 2003). Although the decline of farmland birds in general do not coincide with increases in their avian predators (Thomson et al. 1998), a correlative link between house sparrow declines and sparrow hawk recolonization has been shown (Bell et al. 2010). However, this does not on its own explain the declines considering other studies (both experimental and correlative) that have shown significant effects of food availability on demographic patterns (Hole et al. 2002; Vincent et al. 2005; Peach et al. 2008).

The quality of a foraging habitat and the risk of predation for foragers are often difficult to estimate directly. An alternative is therefore to use the animals' own perception of the environment as an indicator of habitat quality (Olsson et al. 1999; Morris and Davidson 2000). However, how animals perceive habitat quality is complicated by the fact that food availability, density of competitors and predation risk may all affect the perception of habitat quality. A useful behavioural tool for ecologists in discerning differences in quality between habitats, which accounts for these complexities, is the measurement of giving-up densities (GUD, Brown 1988; Olsson and Molokwu 2007). The GUD of a food patch is the density of food left in the patch once the animal no longer forages in it (Brown 1988). In most cases, GUD will be proportional to the quitting harvest rate of foraging, i.e. the instantaneous intake rate at which the forager decides to leave the patch (e.g. Kotler and Brown 1990; Olsson et al. 2001). Thus, the GUD is an assay of the foraging animal's decision, and hence its perceptions of environmental quality and immediate circumstances. Foraging theory predicts that a forager should leave a food patch when the energetic gain of foraging equals the sum of the foraging costs, namely the metabolic cost, the cost of predation and the cost of missed opportunities. All these are measured in units of energy. The metabolic cost of foraging may vary between different alternatives, depending on e.g. microclimate. The cost of predation is the energy required to balance the risk associated with a particular foraging option ("hazardous duty pay"; cf. Brown and Kotler 2004). The cost of missed opportunities is the cost of not being at some other place in the environment. It thereby includes all other available foraging options and all activities the animal could engage in instead of foraging (Brown 1988; Olsson and Molokwu 2007). As a food patch is gradually depleted, a forager receives diminishing returns, which should lead it to evaluate which other fitness-influencing factors are becoming relatively more important, and the forager will leave the patch (Brown and Alkon 1990). This will happen sooner in an environment of high quality**,** where the cost of missed opportunities is higher, and the animal's fitness prospects are higher (Olsson and Molokwu 2007), and this will create positive correlations between habitat quality, GUD and fitness. Interestingly, the cost of predation will also be higher in a high quality habitat, even if predation risk does not vary, because of higher fitness prospects and lower marginal value of energy. The driving factor that determines how animals respond to the quality of the environment, thereby influencing GUDs, is often the food availability in the area (Olsson and Molokwu 2007). There are both theoretical predictions and empirical results that show GUDs to be high if alternative food resources are high (Olsson et al. 1999; Olsson and Holmgren 1999; Morris and Davidson 2000; Olsson et al. 2002; Stenberg and Persson 2006; Molokwu et al. 2008). GUD studies can also shed light on how behavioural decisions made in the short term can be linked to important indicators of fitness, such as reproductive success (Olsson et al. 1999; Morris and Davidson 2000) and long-term growth expectations (Stenberg and Persson 2006).

Most studies using GUDs have aimed at determining what risks, in terms of for example predation, that a certain habitat imposes on a forager (for a review, see Brown and Kotler 2004). In such a case, GUDs increase with increasing risk in a microhabitat, linked to the fact that foragers spend more time foraging in a food patch located in a safe microhabitat, thus depleting resources in that patch to a greater extent than those in a risky microhabitat (Brown and Kotler 2004). This makes it possible to estimate non-lethal effects that predators have on their prey (Hochman and Kotler 2007). Indirect predation effects are highly important in regulating prey population densities (Kotler and Holt 1989). For example, responses in foraging behaviour to predation risk is one such critical indirect effect, as it forces the prey individual to forage in a way that reduces their food intake rate, thus affecting the prey population growth and in turn, through trophic cascades and changes in herbivory patterns, shaping the entire ecosystem (c.f. Ripple and Beschta 2004). Within avian communities, different species can have different perceptions of what risks a certain microhabitat imposes on them (Lima 1990), which would consequentially play an important part in shaping the structure of the entire community (Lima and Valone 1991).

The aim of this study was to use giving-up densities to investigate differences in habitat quality for farm-dwelling house sparrows at two different spatial scales. At the larger scale, we investigated differences in habitat quality between landscapes of different agricultural regimes (Fig. 1). The individuals foraging on the different farms and different landscapes are not the same, and the decisions they make will be consistently different due to variations in environmental quality. This means that variation in GUDs between landscape types can primarily be attributed to differences in habitat quality, through its joint effects on the cost of predation and the cost of missed opportunities (Brown 1988; Olsson and Molokwu 2007). On the smaller scale, we made comparisons on each individual farm between adjacent patches that were manipulated to create a variation in predation risk. Between these patches, within farms, only variation in the cost of predation, due to variation in predation risk, should be sufficient to create a variation in GUDs. The cost of missed opportunities does not differ between patches within an environment, and the metabolic cost should only vary negligibly. (Olsson and Molokwu 2007). Also, we investigated if the densities of the investigated populations positively correlated with measured GUD as would be expected if there is a positive correlation between habitat quality, GUD, and fitness.

Materials and methods

The study was conducted in the agricultural landscapes of Scania in southernmost Sweden. Landscape types were defined by overall land cover and main focus of agricultural production (Table 1; Fig. 1a). We identified three agricultural landscape types with differing characteristics; first the open plains landscapes dominated by large fields and crop production (Fig. 1d), second the mixed farming landscapes with on average smaller fields and production focusing on both crops and animal husbandry for meat and dairy (Fig. 1c), and third the forest landscapes where the land to a large extent is comprised of small pastures and leys, and animal husbandry dominates farm production (Fig. 1b). We included 15 farms in the study; five each of the three types of agricultural landscapes. Within each landscape type the landscapes were quite similar. House sparrows rarely move long distances between farms (Summers-Smith 1963) which allowed us to select suitable farms in fairly close proximity to avoid unnecessary transports.

To measure the giving-up density of farm-dwelling house sparrows, we set up feeding stations at the 15 farmsteads. A fixed amount of food was mixed in a substrate, in an area where individuals of sparrows were known to forage. After one day, the feeding stations were inspected and the amount of food left measured, which gave the value of the giving-up density. Each feeding station consisted of two brown, plastic flower pot trays (Ø 280 mm, Hammarplast®), containing 20 mealworms (*Tenebrio molitor*) mixed in coarse gravel, macadam (grain size circa 20 mm; total gravel weight per tray approximately 2.0 kg). The reason for using coarse gravel instead of sand, which is the substrate commonly employed in GUD studies, was that in sand mealworms tend to crawl up to the substrate surface. When mixed in coarse gravel, however, they disperse more evenly in the substrate, placing themselves in spaces between grains or at the bottom of the feeding tray. We left the trays for approximately 24 hours (mean=24.3, s.d. = 3.9, range 14.8 - 32.3). Upon return we counted the number of mealworms left and refilled the trays, so that at the beginning of every session there were 20 fresh worms in each tray. Our route between farms was designed so that farms were visited during different times of day, and emptied after different time intervals, and as a result, there was no difference between farms in these respects.

To create safe and risky foraging patches, we gave one tray in each tray pair a wall of 10 cm height, constructed in the same material as the tray. The wall provides a visual obstruction and thereby modifies the sparrows' time spent vigilant while feeding from the trays, as previously shown by Olsson et al. (2002) though the degree to which vigilance is impaired was not measured directly. Hereafter, the tray with the mounted wall is referred to as a risky foraging patch and the tray without the wall as a safe foraging patch. We switched placements of the trays every day to control for any effects of placement and the immediately surrounding environment.

On top of each experimental set-up we placed a cage with chicken wire to exclude visits from larger birds such as corvids that frequently forage on the farmstead. We also put up a camera trap (ScoutGard™, SG550), on each station to photo document visitors for later identification of the extent to which house sparrows were utilising them, and whether or not there were other bird species foraging at the feeding stations. The photo documentation showed that house sparrows of both sexes were in clear majority amongst the species visiting the trays. Apart from house sparrows also tree sparrows (*Passer montanus*) visited the trays. However, these were in minority (10526 of camera trap images), in relation to the focal house sparrows (19036 images), and therefore not considered a problem in the analysis. Preliminary analysis showed no difference in results if adding the proportion of tree sparrows among the images to the analyzes (no significant change of the main model results, effect of tree sparrows P=0.7). On one single farm a great tit (*Parus major*) was the most frequent visitor and this farm was therefore excluded. On the other farms there were in addition images of three great tits, two starlings (*Sturnus vulgaris*) and 2 rats (*Rattus norvegicus*). Documented house sparrows visiting the patches were apparently provisioning their nestlings, as they picked up a number of mealworms and then left the feeding station.

Data was collected over three weeks in June of 2010 (2nd – 23rd of June). Data collection was preceded by a one week long habituation period, for the birds to discover and become accustomed to using the feeding trays. Population sizes on the farmsteads were estimated through inventories performed during the same time period as the GUD experiments. Inventories were performed between 8.00 and 15.00 and only when weather conditions allowed (wind below 5 on the Beaufort scale and no rain). The inventories were conducted by walking in transects across the farmstead (including stables and storage facilities) for 20-40 minutes depending on the size of the farmstead. During each inventory numbers of pairs (males counted and the figure doubled) were counted twice as an accuracy measurement of the population estimation. Population sizes on the farms varied between 2-102 (average of 31 ± 6 SE individuals).

To simplify the analyses, to avoid pseudo-replication, and to improve the distribution of residuals, we calculated means of GUDs for each farm and food tray. Mean GUDs were then used as the dependent variable in linear mixed effects models, using package lme4 (Bates and Maechler 2010) in R 2.12.1 (R Development Core Team 2010). To represent the experimental design, we used the farm within the landscape as random factor. We ran two different sets of models – one that included population size on the farm as a (fixed) covariate, to control for population size effects on GUD-values, and one without. Both models included landscape type (plains, mixed or forest landscape) and patch type (with or without a wall, i.e. risky or safe) as fixed factors including the interaction term. To test for significant overall effects of the variables we performed likelihood ratio tests on these. Due to insufficient information on abundances of native predators in the three landscape types, such as the Eurasian sparrow hawk (*Accipiter nisus*) and domestic cats (*Felis catus*), they could not be included in the analysis.

Results

The first model that did not include population size effects showed that both landscape (χ^2 = 9.24, df = 2, p = 0.010) and patch type (χ^2 = 12.83, df = 1, p <0.001) had a significant effect on GUDs. The GUDs was the lowest in the open plains, followed by the forest (on average 2.4 more worms left) and the mixed landscape (on average 4.6 more worms left). There was a higher mean GUD in patches associated with a higher predation risk – i.e. feeding trays equipped with a view-obstructing wall (average difference 2.1 worms) compared to the safer patches. The interaction term between landscape and patch was not significant (χ^2 = 0.18, df = 2, p = 0.9).

From the second model, including the logarithm of house sparrow population sizes in addition to the variables included in the previous model, we again found landscape type (χ^2 = 8.59, df = 2, p = 0.014; Fig. 2) and patch (χ^2 = 12.83, df = 1, p <0.001; Fig. 2) to have significant effect on GUDs. Mean GUD was lowest in the open plains farms where they were lower (on average 3.1 worms less) than those in mixed farmlands and the forest farms (which were both very similar). Again patches associated with a higher predation risk had higher mean GUDs than did patches of lower predation risk (average difference 2.1 worms). From this model we also found that GUDs were significantly positively related with population size such that on farms with larger populations GUDs were higher (with an increase of 1.12 worms for every doubling of population size; $\chi^2 = 6.78$, df = 1, $p = 0.009$; Fig. 2).

Neither of the two potential two-way interactions was significant ($p > 0.1$), but the three way interaction was significant. However, the model including all interaction terms did not fit data better and was much less parsimonious than the simple model without interaction terms ($\Delta AIC_c > 6$). Hence, we chose to base our conclusions on the simple model.

Discussion

We found that giving-up densities for rural house sparrows in Scania varied at both spatial scales investigated: the landscape and the patch level. We also found GUDs to increase with population density, but differently depending on landscape.

At the landscape level, GUDs in the open plains were significantly lower than those in the mixed and the forest regions, indicating that this landscape type provides summer foraging conditions of lower quality for house sparrows than the other two landscape types. When GUDs differ between different environments theory suggests that the most likely cause is differences in food availability (Olsson and Molokwu 2007; Whelan and Jedlicka 2007). However, there was no significant difference detected in GUDs between the forest region and mixed farmland when controlling for population density, indicating that these landscape types offer roughly similar alternative foraging opportunities for house sparrows during the summer. The relatively higher food availability in these regions can most likely be related to the high number of livestock that were kept on these farms (Ambrosini et al. 2002). Spilled livestock feed is an important food source for adult house sparrows and the presence of large, insect-rich dung heaps and buildings with livestock provide foraging sparrows with an abundance of food for their nestlings (Shrubb 2003; Anderson 2006).

There is a clear gradient in farming intensity as well as landscape complexity (Benton et al. 2003; Roschewitz et al. 2005) between the three landscape types (Fig. 1, Persson et al. 2010 and table 1). Farming is most intense, with high production yield and the landscape is least structually complex in the open plains. The forest landscape has the least intense farming, and overall most complex landscape, with a fair amount of forest and tree and shrub rich pastures. The farming as such is more varied in the mixed region, where there is a rather even mix between crops, ley and pasture. A low GUD, related to low availability of alternative foods, in the plains is not surprising. It corroborates the findings of several previous studies (Wilson et al. 1999; Siriwardena et al. 2001; Granbom and Smith 2006; Henderson et al. 2009) suggesting that food availability for farmland birds is lower in intensively managed areas.

Our study is not able to separate positive effects on food availability resulting from animal husbandry from effects of a more complex landscape structure, respectively. This is because most of our farms kept livestock (10 out of 14), and those that did not were mainly located in the open plains (3 out of 4). However, the loss of animal husbandry is a major reason for the simplification of the open plains, because of the concomitant loss of grazed grasslands. Previous studies within this system have shown that house sparrow occurrence is significantly lower in open plains landscapes but also more specifically that both occurrence and density is positively affected by presence of animal husbandry (von Post, M. et al. in prep).

At the patch level, GUDs were higher in feeding trays with an edge than in those without, indicating a preference among sparrows to feed in patches where there is no visual obstruction that hampers their predator-scanning abilities (Olsson et al. 2002; Brown and Kotler 2004). Recent research suggests that house sparrows have a visual field constructed in a way that allows predator-scanning even while the animal is engaged in head-down foraging (Fernández-Juricic et al. 2008), something which goes against the classic general perception that foraging and predator-scanning are two separate activities. House sparrows should therefore prefer a foraging micro-environment that allows them to scan their surroundings and forage simultaneously, which was what we found.

We also found GUDs to be positively related with population size. This most likely reflects a higher habitat quality in environments that have dense populations. Although we technically use population size as a predictor, we do not think that a higher GUD is caused by a higher population size. Rather, we believe that high quality environments, with e.g. high food availability, have both higher population densities and higher GUDs. This result, in itself, thus clearly demonstrates that GUD is not merely a passive reflection of how many individuals are foraging in an area; in such a case, GUDs would be negatively related to population size. Interestingly, it also shows that the population of house sparrows is not freely (as in ideal free) distributed. If it were, then there would be no correlation between GUDs and population size, as density of birds would be perfectly matched with resources.

In addition, the fitted curve on GUDs against population density differed between the open plains landscape and the mixed and forest landscapes. This result indicates that population densities in mixed and forest landscapes are below carrying capacity, or that population density in the open plains landscape is overpopulated. This would imply that there are different population limiting mechanisms operating in the open plains compared to the mixed and forest landscapes. Exciting as this result is, at this stage we can only speculate about the possible regulating differences. One likely mechanism could be that populations in the different landscapes are limited at different parts of the year, such that populations in mixed and forest regions are most strongly limited during winter through low over winter survival due to lack of resources (seed) while populations in the open plains are limited by available resources during breeding (insects). Another possible explanation could be that populations in the open plains receive a high immigration rate during the breeding season, resulting in overpopulation. There could also be a difference in predation risks between these environments but due to the fact that we could not see any significant interaction between landscape types and patch type we find that to be rather unlikely (se section below). Further studies on GUDs during non-breeding season would be of high relevance to clarify the speculations above.

GUDs were not affected by any significant interaction between landscape types and patch type, which could be expected as a consequence of variation in habitat quality. That is, in an area with higher food availability the survivor's fitness should be higher and the marginal value of energy lower, which should result in a greater difference in use of safe and risky patches (Olsson et al. 2002). The absence of such an effect can either be a lack of power, or be an effect of higher predation risk in the more heterogeneous landscapes, which could counter the effect of food availability in this regard. Thus, although increased predation has been suggested as a cause for widespread house sparrow declines (Bell et al. 2010), the landscape differences in house sparrow occurrence (von Post et al., in prep) are not associated with differences in predation risk as perceived by house sparrows during breeding.

Behavioural tools can be an effective way to obtain detailed information about how animals perceive their environment, and gain insights into potential factors important for population processes (Olsson et al. 1999; Bradbury et al. 2001; Stenberg and Persson 2006; Whelan and Jedlicka 2007; van Gils et al. 2009). Measuring resource availability for a species can often prove difficult and GUD studies provide a simple method for doing just that. Shedding further light on spatial and temporal resource separation for farmland birds of conservation concern, such as the house sparrow, is important for the planning, evaluation and success of current and future conservation efforts.

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Figure legends

Figure 1. Map of the study area in Scania, southernmost Sweden. In a) the three study regions are shown in different shades, and the study farms are shown as circles. In b), c), and d) an example landscape is shown for each of the three regions. Three coarse land use types are shown in different shades. White areas are either forest, farmyards and houses or fields islets.

Figure 2. Giving-up densities (number of meal worms left) in experimental trays in the three different study regions, in relation to population size.

Table 1. Characteristics of the three landscapes, as defined by circles of 1 km radius around each farm. Farmland is the average percentage of total farmland in the circles, pasture, leys and crops are land uses expressed as percentages of total farmland. Field size is the average field size in hectares.

	Farmland	Pasture	Leys	Crops	Field size
Plains	89	1.5	5.2	91	20.2
Mixed	87	2.8	23	72	6.8
Forest	67	28	44	27	3.2

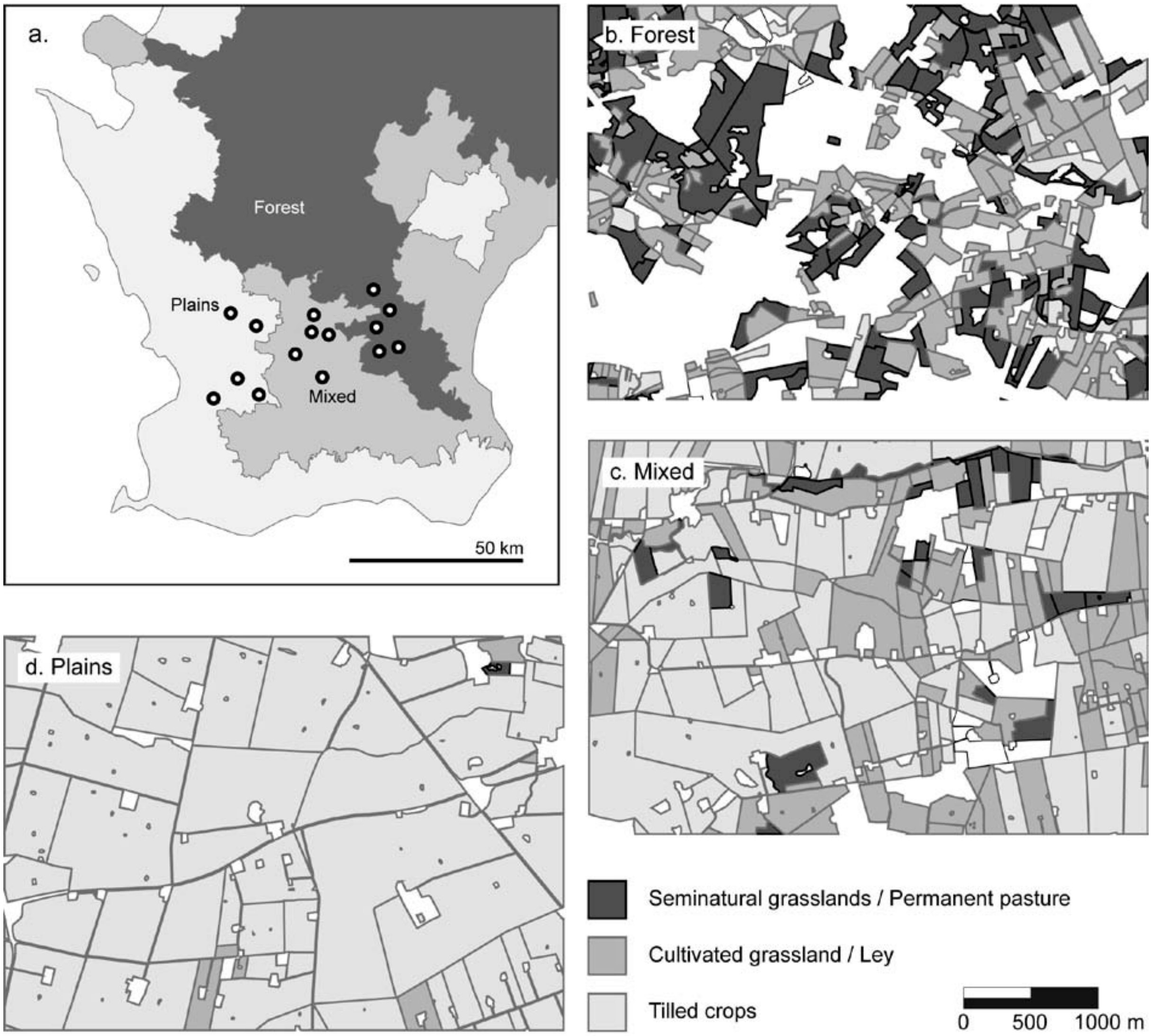

Figure 1. von Post et al.

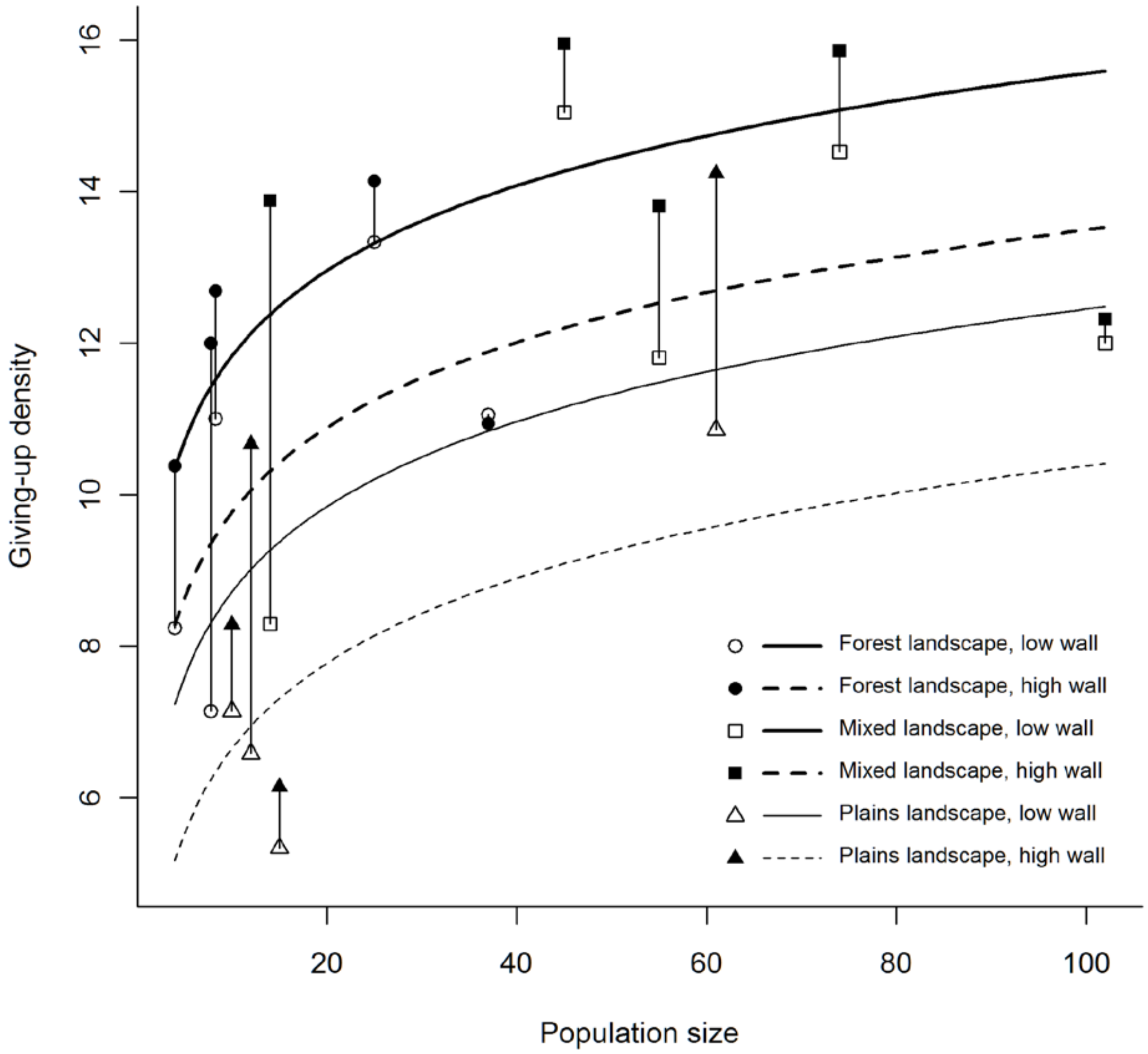

Figure 2. von Post et al.