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Published in:
Oecologia

DOI:
[10.1007/s00442-011-2169-8](https://doi.org/10.1007/s00442-011-2169-8)

2012

[Link to publication](#)

Citation for published version (APA):

Post, M. V., Borgström, P., Smith, H., & Olsson, O. (2012). Assessing habitat quality of farm-dwelling house sparrows in different agricultural landscapes. *Oecologia*, 168(4), 959-966. <https://doi.org/10.1007/s00442-011-2169-8>

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4

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

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16 Author Contributions: OO originally formulated the idea, MvP, PB, HGS and OO designed the
17 experiments and MvP and OO performed the fieldwork. OO and MvP analyzed the data. OO
18 produced the figures. MvP, PB, HGS and OO wrote the manuscript.

20 **Abstract**

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

39

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

41

42 **Introduction**

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

49
50 The house sparrow (*Passer domesticus*) is a farmland bird that once was so numerous in or
51 around human dwellings that it was considered to be a pest (De Laet and Summers-Smith 2007).
52 During the past few decades it has declined severely in numbers in both urban and rural areas in
53 large parts of Western Europe (Engler and Bauer 2002; Newton 2004; Robinson et al. 2005; Klok
54 et al. 2006), including Sweden (Lindström et al. 2011). In the United Kingdom and the
55 Netherlands the house sparrow has even been placed on the Red List as a species of high
56 conservation concern (Klok et al. 2006; Chamberlain et al. 2007). In rural environments, the
57 house sparrow is thought to have been negatively affected by agricultural intensification (Hole et
58 al. 2002). In particular, loss of landscape heterogeneity may lead to spatial and temporal
59 separation of resources in the landscape that could have negative effects on population
60 persistence for sedentary birds (Donald et al. 2001), such as the house sparrow that depend on
61 different resources throughout the year (Hole et al. 2002). The house sparrow depends mainly on
62 seeds and grains, except during the breeding season when it feeds offspring with insects
63 (Summers-Smith 1963; Anderson 2006). In many North European countries the structural

64 rationalization of agriculture, i.e. increasing farming efficiency by specializing production,
65 increasing field size and abandoning unprofitable fields, has resulted in plains dominated by plant
66 production and more forested districts dominated by animal production, with intermediate
67 landscapes still containing mixed farming. If house sparrows need insects promoted by animal
68 husbandry for breeding (Ambrosini et al. 2002; Vincent 2005) and seed resources produced by
69 plant production for winter survival (Hole et al. 2002), it may suffer from agricultural
70 specialisation.

71
72 It has also been suggested that predation may contribute to the decline of the house sparrow
73 (Macleod et al. 2006), because the house sparrow is susceptible to predation by sparrow hawks
74 (*Accipiter nisus*) and cats (*Felis catus*) (Götmark and Post 1996; Toms 2003; Woods et al. 2003).
75 Although the decline of farmland birds in general do not coincide with increases in their avian
76 predators (Thomson et al. 1998), a correlative link between house sparrow declines and sparrow
77 hawk recolonization has been shown (Bell et al. 2010). However, this does not on its own explain
78 the declines considering other studies (both experimental and correlative) that have shown
79 significant effects of food availability on demographic patterns (Hole et al. 2002; Vincent et al.
80 2005; Peach et al. 2008).

81
82 The quality of a foraging habitat and the risk of predation for foragers are often difficult to
83 estimate directly. An alternative is therefore to use the animals' own perception of the
84 environment as an indicator of habitat quality (Olsson et al. 1999; Morris and Davidson 2000).
85 However, how animals perceive habitat quality is complicated by the fact that food availability,
86 density of competitors and predation risk may all affect the perception of habitat quality. A useful

87 behavioural tool for ecologists in discerning differences in quality between habitats, which
88 accounts for these complexities, is the measurement of giving-up densities (GUD, Brown 1988;
89 Olsson and Molokwu 2007). The GUD of a food patch is the density of food left in the patch
90 once the animal no longer forages in it (Brown 1988). In most cases, GUD will be proportional to
91 the quitting harvest rate of foraging, i.e. the instantaneous intake rate at which the forager decides
92 to leave the patch (e.g. Kotler and Brown 1990; Olsson et al. 2001). Thus, the GUD is an assay of
93 the foraging animal's decision, and hence its perceptions of environmental quality and immediate
94 circumstances. Foraging theory predicts that a forager should leave a food patch when the
95 energetic gain of foraging equals the sum of the foraging costs, namely the metabolic cost, the
96 cost of predation and the cost of missed opportunities. All these are measured in units of energy.
97 The metabolic cost of foraging may vary between different alternatives, depending on e.g.
98 microclimate. The cost of predation is the energy required to balance the risk associated with a
99 particular foraging option ("hazardous duty pay"; cf. Brown and Kotler 2004). The cost of missed
100 opportunities is the cost of not being at some other place in the environment. It thereby includes
101 all other available foraging options and all activities the animal could engage in instead of
102 foraging (Brown 1988; Olsson and Molokwu 2007). As a food patch is gradually depleted, a
103 forager receives diminishing returns, which should lead it to evaluate which other fitness-
104 influencing factors are becoming relatively more important, and the forager will leave the patch
105 (Brown and Alkon 1990). This will happen sooner in an environment of high quality, where the
106 cost of missed opportunities is higher, and the animal's fitness prospects are higher (Olsson and
107 Molokwu 2007), and this will create positive correlations between habitat quality, GUD and
108 fitness. Interestingly, the cost of predation will also be higher in a high quality habitat, even if
109 predation risk does not vary, because of higher fitness prospects and lower marginal value of

110 energy. The driving factor that determines how animals respond to the quality of the
111 environment, thereby influencing GUDs, is often the food availability in the area (Olsson and
112 Molokwu 2007). There are both theoretical predictions and empirical results that show GUDs to
113 be high if alternative food resources are high (Olsson et al. 1999; Olsson and Holmgren 1999;
114 Morris and Davidson 2000; Olsson et al. 2002; Stenberg and Persson 2006; Molokwu et al.
115 2008). GUD studies can also shed light on how behavioural decisions made in the short term can
116 be linked to important indicators of fitness, such as reproductive success (Olsson et al. 1999;
117 Morris and Davidson 2000) and long-term growth expectations (Stenberg and Persson 2006).

118
119 Most studies using GUDs have aimed at determining what risks, in terms of for example
120 predation, that a certain habitat imposes on a forager (for a review, see Brown and Kotler 2004).
121 In such a case, GUDs increase with increasing risk in a microhabitat, linked to the fact that
122 foragers spend more time foraging in a food patch located in a safe microhabitat, thus depleting
123 resources in that patch to a greater extent than those in a risky microhabitat (Brown and Kotler
124 2004). This makes it possible to estimate non-lethal effects that predators have on their prey
125 (Hochman and Kotler 2007). Indirect predation effects are highly important in regulating prey
126 population densities (Kotler and Holt 1989). For example, responses in foraging behaviour to
127 predation risk is one such critical indirect effect, as it forces the prey individual to forage in a way
128 that reduces their food intake rate, thus affecting the prey population growth and in turn, through
129 trophic cascades and changes in herbivory patterns, shaping the entire ecosystem (c.f. Ripple and
130 Beschta 2004). Within avian communities, different species can have different perceptions of
131 what risks a certain microhabitat imposes on them (Lima 1990), which would consequentially
132 play an important part in shaping the structure of the entire community (Lima and Valone 1991).

133
134 The aim of this study was to use giving-up densities to investigate differences in habitat quality
135 for farm-dwelling house sparrows at two different spatial scales. At the larger scale, we
136 investigated differences in habitat quality between landscapes of different agricultural regimes
137 (Fig. 1). The individuals foraging on the different farms and different landscapes are not the
138 same, and the decisions they make will be consistently different due to variations in
139 environmental quality. This means that variation in GUDs between landscape types can primarily
140 be attributed to differences in habitat quality, through its joint effects on the cost of predation and
141 the cost of missed opportunities (Brown 1988; Olsson and Molokwu 2007). On the smaller scale,
142 we made comparisons on each individual farm between adjacent patches that were manipulated
143 to create a variation in predation risk. Between these patches, within farms, only variation in the
144 cost of predation, due to variation in predation risk, should be sufficient to create a variation in
145 GUDs. The cost of missed opportunities does not differ between patches within an environment,
146 and the metabolic cost should only vary negligibly. (Olsson and Molokwu 2007). Also, we
147 investigated if the densities of the investigated populations positively correlated with measured
148 GUD as would be expected if there is a positive correlation between habitat quality, GUD, and
149 fitness.

150 **Materials and methods**

151 The study was conducted in the agricultural landscapes of Scania in southernmost Sweden.
152 Landscape types were defined by overall land cover and main focus of agricultural production
153 (Table 1; Fig. 1a). We identified three agricultural landscape types with differing characteristics;
154 first the open plains landscapes dominated by large fields and crop production (Fig. 1d), second

155 the mixed farming landscapes with on average smaller fields and production focusing on both
156 crops and animal husbandry for meat and dairy (Fig. 1c), and third the forest landscapes where
157 the land to a large extent is comprised of small pastures and leys, and animal husbandry
158 dominates farm production (Fig. 1b). We included 15 farms in the study; five each of the three
159 types of agricultural landscapes. Within each landscape type the landscapes were quite similar.
160 House sparrows rarely move long distances between farms (Summers-Smith 1963) which
161 allowed us to select suitable farms in fairly close proximity to avoid unnecessary transports.

162
163 To measure the giving-up density of farm-dwelling house sparrows, we set up feeding stations at
164 the 15 farmsteads. A fixed amount of food was mixed in a substrate, in an area where individuals
165 of sparrows were known to forage. After one day, the feeding stations were inspected and the
166 amount of food left measured, which gave the value of the giving-up density. Each feeding
167 station consisted of two brown, plastic flower pot trays (Ø 280 mm, Hammarplast®), containing
168 20 mealworms (*Tenebrio molitor*) mixed in coarse gravel, macadam (grain size circa 20 mm;
169 total gravel weight per tray approximately 2.0 kg). The reason for using coarse gravel instead of
170 sand, which is the substrate commonly employed in GUD studies, was that in sand mealworms
171 tend to crawl up to the substrate surface. When mixed in coarse gravel, however, they disperse
172 more evenly in the substrate, placing themselves in spaces between grains or at the bottom of the
173 feeding tray. We left the trays for approximately 24 hours (mean=24.3, s.d. = 3.9, range 14.8 -
174 32.3). Upon return we counted the number of mealworms left and refilled the trays, so that at the
175 beginning of every session there were 20 fresh worms in each tray. Our route between farms was
176 designed so that farms were visited during different times of day, and emptied after different time
177 intervals, and as a result, there was no difference between farms in these respects.

178
179 To create safe and risky foraging patches, we gave one tray in each tray pair a wall of 10 cm
180 height, constructed in the same material as the tray. The wall provides a visual obstruction and
181 thereby modifies the sparrows' time spent vigilant while feeding from the trays, as previously
182 shown by Olsson et al. (2002) though the degree to which vigilance is impaired was not measured
183 directly. Hereafter, the tray with the mounted wall is referred to as a risky foraging patch and the
184 tray without the wall as a safe foraging patch. We switched placements of the trays every day to
185 control for any effects of placement and the immediately surrounding environment.

186
187 On top of each experimental set-up we placed a cage with chicken wire to exclude visits from
188 larger birds such as corvids that frequently forage on the farmstead. We also put up a camera trap
189 (ScoutGard™, SG550), on each station to photo document visitors for later identification of the
190 extent to which house sparrows were utilising them, and whether or not there were other bird
191 species foraging at the feeding stations. The photo documentation showed that house sparrows of
192 both sexes were in clear majority amongst the species visiting the trays. Apart from house
193 sparrows also tree sparrows (*Passer montanus*) visited the trays. However, these were in minority
194 (10526 of camera trap images), in relation to the focal house sparrows (19036 images), and
195 therefore not considered a problem in the analysis. Preliminary analysis showed no difference in
196 results if adding the proportion of tree sparrows among the images to the analyzes (no significant
197 change of the main model results, effect of tree sparrows $P=0.7$). On one single farm a great tit
198 (*Parus major*) was the most frequent visitor and this farm was therefore excluded. On the other
199 farms there were in addition images of three great tits, two starlings (*Sturnus vulgaris*) and 2 rats
200 (*Rattus norvegicus*). Documented house sparrows visiting the patches were apparently

201 provisioning their nestlings, as they picked up a number of mealworms and then left the feeding
202 station.

203
204 Data was collected over three weeks in June of 2010 (2nd – 23rd of June). Data collection was
205 preceded by a one week long habituation period, for the birds to discover and become
206 accustomed to using the feeding trays. Population sizes on the farmsteads were estimated through
207 inventories performed during the same time period as the GUD experiments. Inventories were
208 performed between 8.00 and 15.00 and only when weather conditions allowed (wind below 5 on
209 the Beaufort scale and no rain). The inventories were conducted by walking in transects across
210 the farmstead (including stables and storage facilities) for 20-40 minutes depending on the size of
211 the farmstead. During each inventory numbers of pairs (males counted and the figure doubled)
212 were counted twice as an accuracy measurement of the population estimation. Population sizes
213 on the farms varied between 2-102 (average of 31 ± 6 SE individuals).

214
215 To simplify the analyses, to avoid pseudo-replication, and to improve the distribution of
216 residuals, we calculated means of GUDs for each farm and food tray. Mean GUDs were then
217 used as the dependent variable in linear mixed effects models, using package lme4 (Bates and
218 Maechler 2010) in R 2.12.1 (R Development Core Team 2010). To represent the experimental
219 design, we used the farm within the landscape as random factor. We ran two different sets of
220 models – one that included population size on the farm as a (fixed) covariate, to control for
221 population size effects on GUD-values, and one without. Both models included landscape type
222 (plains, mixed or forest landscape) and patch type (with or without a wall, i.e. risky or safe) as
223 fixed factors including the interaction term. To test for significant overall effects of the variables

224 we performed likelihood ratio tests on these. Due to insufficient information on abundances of
225 native predators in the three landscape types, such as the Eurasian sparrow hawk (*Accipiter nisus*)
226 and domestic cats (*Felis catus*), they could not be included in the analysis.

227

228 **Results**

229 The first model that did not include population size effects showed that both landscape ($\chi^2 =$
230 9.24, df = 2, p = 0.010) and patch type ($\chi^2 = 12.83$, df = 1, p <0.001) had a significant effect on
231 GUDs. The GUDs was the lowest in the open plains, followed by the forest (on average 2.4 more
232 worms left) and the mixed landscape (on average 4.6 more worms left). There was a higher mean
233 GUD in patches associated with a higher predation risk – i.e. feeding trays equipped with a view-
234 obstructing wall (average difference 2.1 worms) compared to the safer patches. The interaction
235 term between landscape and patch was not significant ($\chi^2 = 0.18$, df = 2, p = 0.9).

236

237 From the second model, including the logarithm of house sparrow population sizes in addition to
238 the variables included in the previous model, we again found landscape type ($\chi^2 = 8.59$, df = 2, p
239 = 0.014; Fig. 2) and patch ($\chi^2 = 12.83$, df = 1, p <0.001; Fig. 2) to have significant effect on
240 GUDs. Mean GUD was lowest in the open plains farms where they were lower (on average 3.1
241 worms less) than those in mixed farmlands and the forest farms (which were both very similar).
242 Again patches associated with a higher predation risk had higher mean GUDs than did patches of
243 lower predation risk (average difference 2.1 worms). From this model we also found that GUDs
244 were significantly positively related with population size such that on farms with larger

245 populations GUDs were higher (with an increase of 1.12 worms for every doubling of population
246 size; $\chi^2 = 6.78$, $df = 1$, $p = 0.009$; Fig. 2).

247
248 Neither of the two potential two-way interactions was significant ($p > 0.1$), but the three way
249 interaction was significant. However, the model including all interaction terms did not fit data
250 better and was much less parsimonious than the simple model without interaction terms ($\Delta AIC_c >$
251 6). Hence, we chose to base our conclusions on the simple model.

252

253 **Discussion**

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

257

258 At the landscape level, GUDs in the open plains were significantly lower than those in the mixed
259 and the forest regions, indicating that this landscape type provides summer foraging conditions of
260 lower quality for house sparrows than the other two landscape types. When GUDs differ between
261 different environments theory suggests that the most likely cause is differences in food
262 availability (Olsson and Molokwu 2007; Whelan and Jedlicka 2007). However, there was no
263 significant difference detected in GUDs between the forest region and mixed farmland when
264 controlling for population density, indicating that these landscape types offer roughly similar
265 alternative foraging opportunities for house sparrows during the summer. The relatively higher
266 food availability in these regions can most likely be related to the high number of livestock that

267 were kept on these farms (Ambrosini et al. 2002). Spilled livestock feed is an important food
268 source for adult house sparrows and the presence of large, insect-rich dung heaps and buildings
269 with livestock provide foraging sparrows with an abundance of food for their nestlings (Shrubb
270 2003; Anderson 2006).

271
272 There is a clear gradient in farming intensity as well as landscape complexity (Benton et al. 2003;
273 Roschewitz et al. 2005) between the three landscape types (Fig. 1, Persson et al. 2010 and table
274 1). Farming is most intense, with high production yield and the landscape is least structurally
275 complex in the open plains. The forest landscape has the least intense farming, and overall most
276 complex landscape, with a fair amount of forest and tree and shrub rich pastures. The farming as
277 such is more varied in the mixed region, where there is a rather even mix between crops, ley and
278 pasture. A low GUD, related to low availability of alternative foods, in the plains is not
279 surprising. It corroborates the findings of several previous studies (Wilson et al. 1999;
280 Siriwardena et al. 2001; Granbom and Smith 2006; Henderson et al. 2009) suggesting that food
281 availability for farmland birds is lower in intensively managed areas.

282
283 Our study is not able to separate positive effects on food availability resulting from animal
284 husbandry from effects of a more complex landscape structure, respectively. This is because most
285 of our farms kept livestock (10 out of 14), and those that did not were mainly located in the open
286 plains (3 out of 4). However, the loss of animal husbandry is a major reason for the simplification
287 of the open plains, because of the concomitant loss of grazed grasslands. Previous studies within
288 this system have shown that house sparrow occurrence is significantly lower in open plains

289 landscapes but also more specifically that both occurrence and density is positively affected by
290 presence of animal husbandry (von Post, M. et al. in prep).

291
292 At the patch level, GUDs were higher in feeding trays with an edge than in those without,
293 indicating a preference among sparrows to feed in patches where there is no visual obstruction
294 that hampers their predator-scanning abilities (Olsson et al. 2002; Brown and Kotler 2004).
295 Recent research suggests that house sparrows have a visual field constructed in a way that allows
296 predator-scanning even while the animal is engaged in head-down foraging (Fernández-Juricic et
297 al. 2008), something which goes against the classic general perception that foraging and predator-
298 scanning are two separate activities. House sparrows should therefore prefer a foraging micro-
299 environment that allows them to scan their surroundings and forage simultaneously, which was
300 what we found.

301
302 We also found GUDs to be positively related with population size. This most likely reflects a
303 higher habitat quality in environments that have dense populations. Although we technically use
304 population size as a predictor, we do not think that a higher GUD is caused by a higher
305 population size. Rather, we believe that high quality environments, with e.g. high food
306 availability, have both higher population densities and higher GUDs. This result, in itself, thus
307 clearly demonstrates that GUD is not merely a passive reflection of how many individuals are
308 foraging in an area; in such a case, GUDs would be negatively related to population size.
309 Interestingly, it also shows that the population of house sparrows is not freely (as in ideal free)
310 distributed. If it were, then there would be no correlation between GUDs and population size, as
311 density of birds would be perfectly matched with resources.

312
313 In addition, the fitted curve on GUDs against population density differed between the open plains
314 landscape and the mixed and forest landscapes. This result indicates that population densities in
315 mixed and forest landscapes are below carrying capacity, or that population density in the open
316 plains landscape is overpopulated. This would imply that there are different population limiting
317 mechanisms operating in the open plains compared to the mixed and forest landscapes. Exciting
318 as this result is, at this stage we can only speculate about the possible regulating differences. One
319 likely mechanism could be that populations in the different landscapes are limited at different
320 parts of the year, such that populations in mixed and forest regions are most strongly limited
321 during winter through low over winter survival due to lack of resources (seed) while populations
322 in the open plains are limited by available resources during breeding (insects). Another possible
323 explanation could be that populations in the open plains receive a high immigration rate during
324 the breeding season, resulting in overpopulation. There could also be a difference in predation
325 risks between these environments but due to the fact that we could not see any significant
326 interaction between landscape types and patch type we find that to be rather unlikely (see section
327 below). Further studies on GUDs during non-breeding season would be of high relevance to
328 clarify the speculations above.

329
330 GUDs were not affected by any significant interaction between landscape types and patch type,
331 which could be expected as a consequence of variation in habitat quality. That is, in an area with
332 higher food availability the survivor's fitness should be higher and the marginal value of energy
333 lower, which should result in a greater difference in use of safe and risky patches (Olsson et al.
334 2002). The absence of such an effect can either be a lack of power, or be an effect of higher

335 predation risk in the more heterogeneous landscapes, which could counter the effect of food
336 availability in this regard. Thus, although increased predation has been suggested as a cause for
337 widespread house sparrow declines (Bell et al. 2010), the landscape differences in house sparrow
338 occurrence (von Post et al., in prep) are not associated with differences in predation risk as
339 perceived by house sparrows during breeding.

340
341 Behavioural tools can be an effective way to obtain detailed information about how animals
342 perceive their environment, and gain insights into potential factors important for population
343 processes (Olsson et al. 1999; Bradbury et al. 2001; Stenberg and Persson 2006; Whelan and
344 Jedlicka 2007; van Gils et al. 2009). Measuring resource availability for a species can often prove
345 difficult and GUD studies provide a simple method for doing just that. Shedding further light on
346 spatial and temporal resource separation for farmland birds of conservation concern, such as the
347 house sparrow, is important for the planning, evaluation and success of current and future
348 conservation efforts.

349

350 **Acknowledgments**

351 We are grateful to Lisa Berndtsson for assistance in the field, to the farmers that let us work on
352 their land, to Martin Stjernman for development of image analysis and statistical expertise, to the
353 research council Formas, the foundation Oscar och Lili Lamms Stiftelse, Kungliga Fysiografiska
354 Sällskapet i Lund, Lunds Djurskyddsfond for funding, and to SYSAV Natur- och Viltvård for
355 assistance with field equipment.

356

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475 **Figure legends**

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

480

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

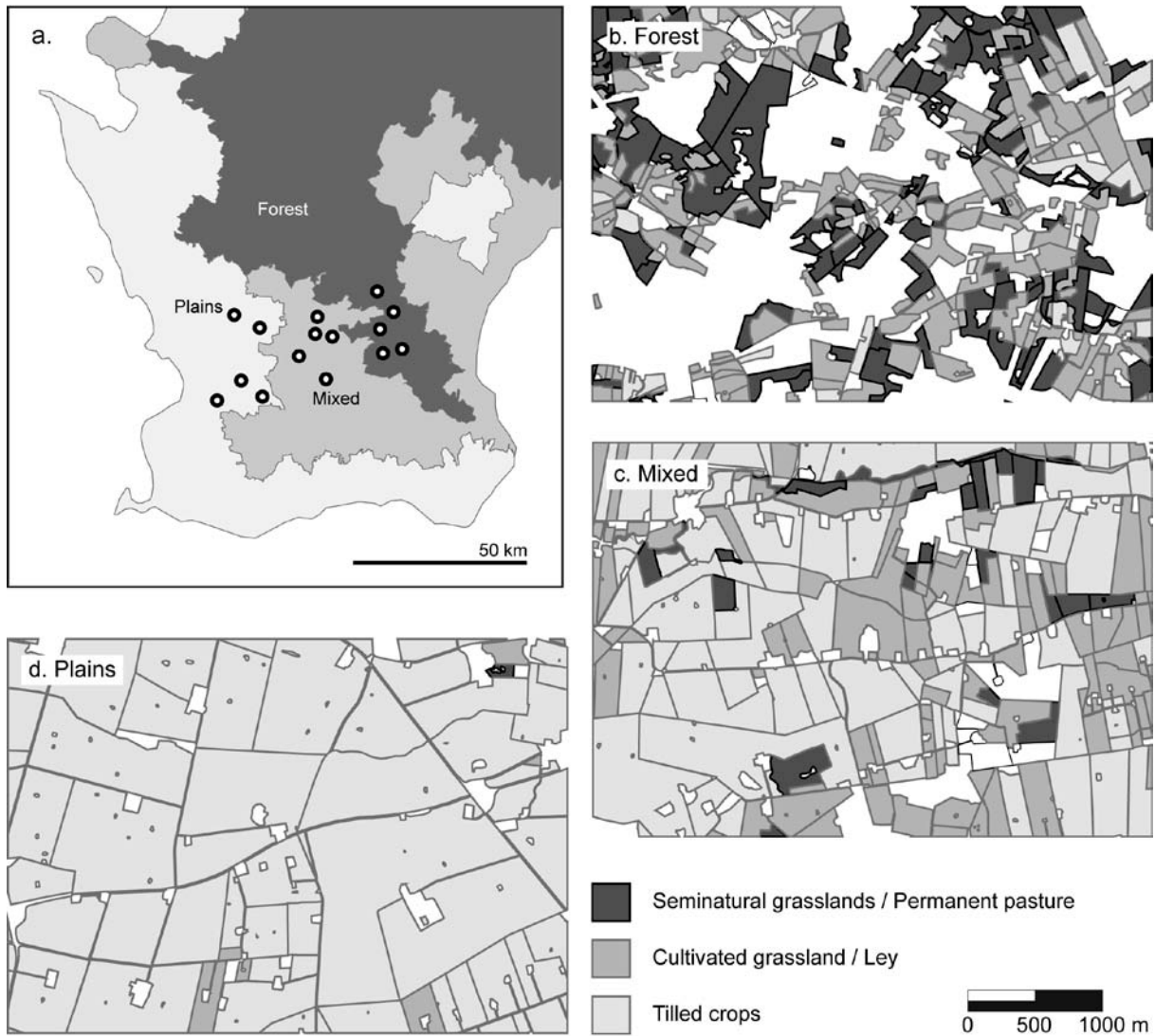


Figure 1. von Post et al.

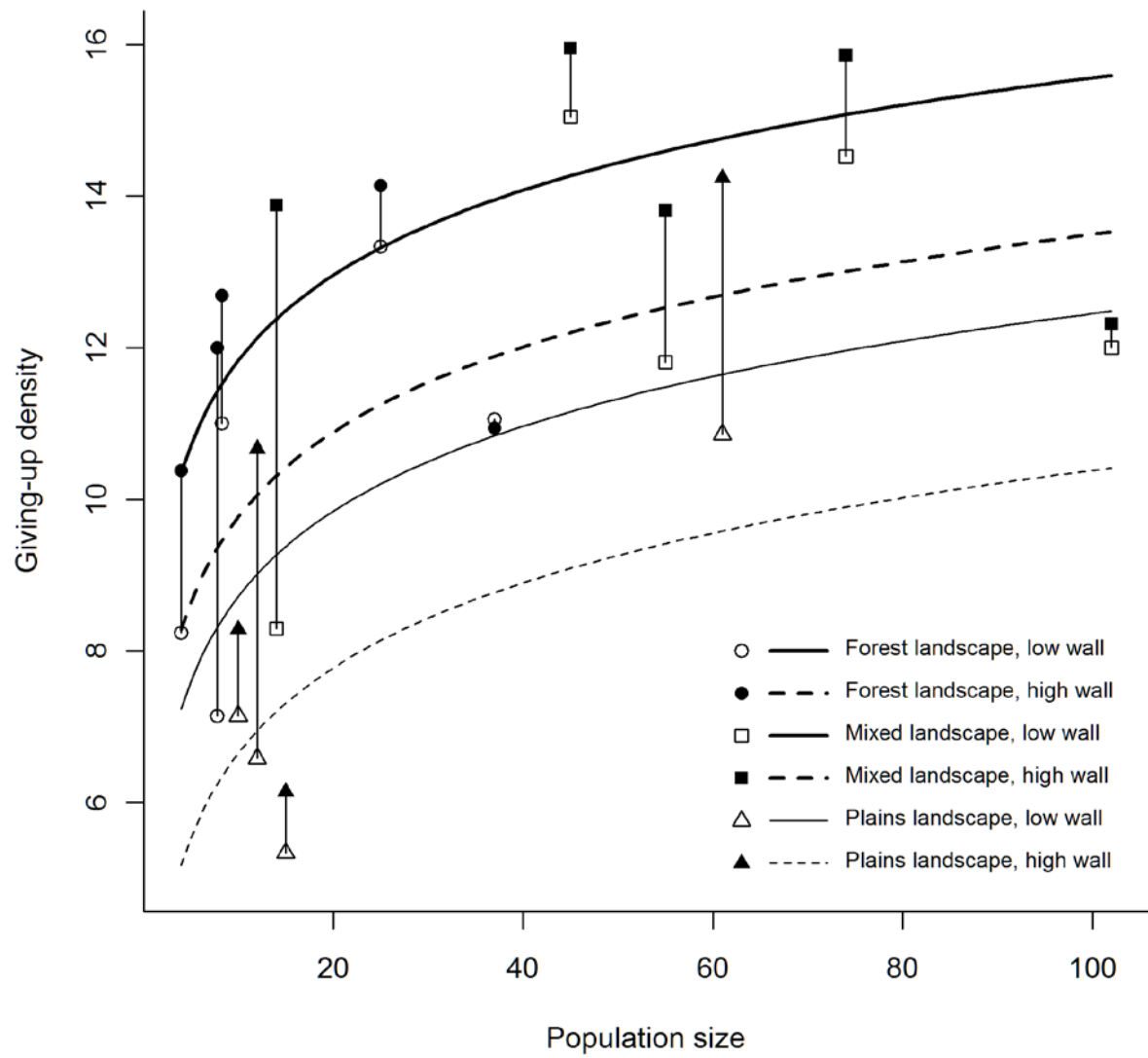


Figure 2. von Post et al.